At the roots of Fulgoroidea – Jurassic and Cretaceous planthoppers (Hemiptera: Fulgoromorpha)

Szwedo J.

Museum and Institute of Zoology, Polish Academy of Sciences, 64, Wilcza Street, PL00-679 Warsaw, Poland; e-mail: szwedo@miiz.waw.pl

The Fulgoromorpha (Insecta: Hemiptera) is an ancient suborder of the hemipterans. It comprises three superfamilies: Coleoscytoidea with Coleoscytidae Martynov, 1935 (Permian) and Surijokocixioidea with Surijokocixiidae Shcherbakov, 2000 (Permian - Triassic). These widespread plant-sucking hoppers comprise 21 extant and 7 extinct families. Descending from Surojokocixiidae ancestors Fulgoroidea lead to prolonged prosperity since the Jurassic. Extinct families of Fulgoroidea Latreille, 1807 are: Jurassic 'Fulgoridiidae' Handlirsch, 1939 and Cretaceous ones – Lalacidae Hamilton, 1990, Neazoniidae Szwedo, 2007, Perforissidae Shcherbakov, 2007 and Mimarachnidae Shcherbakov, 2007 (Hamilton 1990; Szwedo 2007, 2008, 2009; Shcherbakov 2007a, b). The monophyly, relationships, range and content of several families (both extant and extinct) is under discussion.

The extinct family Fulgoridiidae Handlirsch, 1939 needs a full revision as numerous taxa described by Geinitz (1880), Handlirsch (1906, 1939), Bode (1907, 1953), Martynov (1927, 1939) and Becker-Migdisova (1962), as well as more recently described by Lin (1986) and Zhang et al. (2004) must be re-analyzed and the characters of genera and species redefined. It has to be seen now as a paraphyletic assemblage (Bourgoin & Szwedo 2008). There are a number of genera and over 150 species placed in 'Fulgoridiidae' and vast majority of them need to be revised (Szwedo et al. 2004, Szwedo & Żyła 2009). Most of the species reported are based on the tegmen imprints, the hind wings or body structures are rarely preserved and available for examination. Despite taxonomic uncertainties and problems 'Fulgoridiidae' comprises ancestral forms to the fossil and recent families of Fulgoroidea (Bourgoin & Szwedo 2008). 'Fulgoridiidae' had body structure resembling the recent representatives of Cixiidae; this general pattern is also retained in most of the extinct families. However, the venation pattern of 'Fulgoridiidae' is variable, but some tendencies observed also in other extinct and recent units are to be found. Two main trends observed is reduc-tion/development of basicostal area. In most 'Fulgoridiidae' this area is narrow, provided with a few transverse veinlets. In some others this part is reduced and veins Pc+CP and CA are fused at least at base. In comparison veins of costal complex are completely fused in vast majority of recent 'basal' or cixiidae-like planthoppers, while in numerous so-called 'higher' Fulgoroidea basicostal area is enlarged, well devel-oped and provided with numerous transverse veinlets. In the Cretaceous Lalacidae the costal margin is thickened, while in another family known from the Lower Cretaceous of northern China the costal margin is weakened at stigmal area, similarly as in some recent Kinnaridae. In most Cixiidae the extravenal pterostigma is developed in various degree (absent in 'Fulgoridiidae'), other modifications in stigmal area are known in fossil and recent cixiidae-like planthoppers. Also basal cell is modified in various degree (in most cases narrowed) in the descendants of 'Fulgoridiidae'. The patterns of forking of stems Sc+R, M and CuA present enormous variability. The most clear evolutionary tendency to be observed is the reduction of number of branches of CuA; Usually there are four main branches of CuA in 'Fulgoridiidae', the condition retained in Lalacidae, but in most descending forms there are two main branches of CuA (sometimes one secondarily polymerized). Also clavus could be modified – in 'Fulgoridiidae' clavus is usually of closed type. In the descending families Achilidae+Achilixiidae+Derbidae, believed to be one of the most ancient lineages of Fulgoroidea, known since the Lower Cretaceous, the clavus is open; open clavus is known also in the Lower Cretaceous families, highly derivative Perforissidae, and Mimarachnidae.

Another Jurassic family distinct from 'Fulgoridiidae' is found in the Lower Jurassic deposits of Southern China. It superficially resembles so-called 'higher' Fulgoroidea in tegmen shape and venation, however differs from 'Fulgoridiidae' by combination of characters. e.g. stigmal area not developed; longitudinal veins with small tubercles; distinct

sigmoid oblique veinlets *m-cua* and *icua* in well basad half of tegmen; apical portion of tegmen with supranumerary irregular veinlets and secondary veinlets forming polygonal cells and false longitudinal 'veins'; postclaval portion slightly widened; the part of apical margin occupied by terminals of M distinctly smaller than part occupied by terminals of CuA. Weakly known planthoppers are also reported from the Lower Jurassic of Western Australia (Martin 2008), probably represent another family, particularly interesting as poorly known 'Gondwanan' fossils.

The Lower Cretaceous seems to be the period of diversification and various 'cixiidae-like' groups are present there. The Lower Cretaceous Jordanian amber bears a form similar in venation pattern to 'Fulgoridiidae', but characteristic of narrow basicostal area with veinlets in apical portion, elongated C1, multibranched stem R and stem CuA_2 forked basad of nodal line. Lebanese amber *Karebodopoides aptianus* (Fennah, 1987) and related forms resemble strongly 'true Cixiidae' but differ in structure of the stigmal area, lacking pterostigma and reinforcement of the costal margin at this level, cell C5 distinctly longer than cell C1, branches RA and M_{3+4} not forked apicad of nodal line. Other inclusions found in Burmese amber are characteristic of high basal cell, stems Sc+R, M and CuA leving basal cell separately, early branching of stems Sc+R and CuA (= long cells C1 and C5), narrow, elongately triangular widening of margin at level of stigmal area, distinctly curved branch $ScRA_1$ at apex of stigmal area, sclerotised membrane of the tegmen basad of branches $ScRA_1$ and RA_2 and three terminals of RA apicad of nodal line.

Also Eocene fossil sites present forms deserving familial status. There are forms from the Lowermost Eocene Oise amber characteristic of strongly reinforced costal margin of tegmen, very short common stem Sc+R, a basally straight RP, long cell C1 and distinctly shorter cell C5, and supernumerary terminals for RA, RP, M and CuA, elongate veinlets *r-m* and *m-cu* present at the level of nodal line and distal transverse veins associated in a curved post-nodal line. An extraordinary form, related to so-called 'higher' fulgoroids was found in the Lower Eocene Deposits of Yunnan, China. It is very peculiar, with multibranched CuA occupying the area as large as R and M together is a condition never found in fulgoroids. The monophyly of recent Cixiidae is also challenged and some evidences from the fossil record could support these opinions.

Exploring the early evolution of the Fulgoroidea is quite challenging. The most crucial for this is the analysis of some morphological features in both extinct and extant representatives of the group. As already pointed out (Bourgoin & Szwedo 2008) for such a comparative approach the best set of characters shared by both extinct and extant families are the tegminal characters which used to be the best preserved and often the only trace we have of these fossil taxa.

Key words: planthoppers; fossil; evolution; classification;

References

Becker-Migdisova E.E. 1962. Nekotorye novye poluzhestokrylye i senoedy. [Some new Hemiptera and Psocoptera.]. *Palontologicheskiĭ Zhurnal*, 1: 89–104. (in Russian)

Bode A. 1907. *Orthoptera und Neuroptera aus dem Lias von Braunschweig*: 218–245.

Bode, A. 1953. Die Insektenfauna des Ostniedersächsischen oberen Lias. *Palaeontographica* (Abt. A), 103: 1–375.

Bourgoin T., Szwedo J. 2008. The "cixiid-like" fossil planthopper families. *Bulletin of Insectology*, 61: 107–108.

Geinitz F.E. 1880. Der Jura von Dobbertin in Mecklenburg und seine Versteinerungen. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 32: 510–535.

Hamilton K.G.A. 1990. Chapter 6. Homoptera. In: Grimaldi, D.A. (ed.), Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History*, 195: 82–122.

Handlirsch A. 1906–1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen*. Engelmann. Leipzig. ix+1640pp.+ 36 pls.
Handlirsch A. 1939. Neue Untersuchungen über die fossilen Insekten, Teil 2. *Annalen des Naturhis-torischen Museums in Wien*, 49: 1–240.
Lin Q.-B. 1986 . [Early Mesozoic fossil insects from South China.] *Paleontologica Sinica*, B, 170 (21): 1–112. (in Chinese, English summary)
Martin S.K. 2008. Hill River rediscovered: Early Jurassic insects of the Perth Basin, Western Australia. *Alavesia*, 2: 7–14.
Martynov A.V. 1927(1926). Jurassic fossil insects from Turkestan. 6. Homoptera and Psocoptera. *Izvestya Akademii Nauk SSSR*, 20: 1349–1366.
Martynov A.V. 1939(1937). Liassovye nasekomye Shuraba i Kizil Kii [Liassic insects from Shurab and Kisyl Kiya]. *Trudy Paleontologischeskogo Instituta Akademii Nauk SSSR*, 7 (1): 1–232. (in Russian)
Shcherbakov D.E. 2007a. An extraordinary new family of Cretaceous planthoppers (Homoptera: Fulgoroidea). *Russian Entomological Journal*, 16 (2): 138–154.
Shcherbakov D.E. 2007b. Mesozoic spider mimics – Cretaceous Mimarachnidae fam. n. (Homoptera: Fulgoroidea). *Russian Entomological Journal*, 16 (3): 259–264.
Szwedo J. 2007. Nymphs of a new family Neazoniidae fam. n. (Hemiptera: Fulgoromorpha: Ful-goroidea) from the Lower Cretaceous Lebanese amber. *African Invertebrates*, 48 (1): 127–143.
Szwedo J. 2008. Distributional and palaeoecological pattern of Lower Cretaceous Mimarachnidae (Hemiptera: Fulgoromorpha). *Entomologia Generalis*, 31 (3): 231–242.
Szwedo J. 2009. First discovery of Neazoniidae (Hemiptera: Fulgoromorpha) in the Early Creta-ceous Archingeay amber of South-West France. *Geodiversitas*, 30 (1): 105–116.
Szwedo J., Żyła D. 2009. New Fulgoridiidae genus from the Upper Jurassic Karatau deposits, Kazakhstan (Hemiptera: Fulgoromorpha: Fulgoroidea). *Zootaxa*, 2281: 40−52.
Szwedo J., Bourgoin T., Lefebvre F. 2004. *Fossil Planthoppers (Hemiptera: Fulgoromorpha) of the World. An annotated catalogue with notes on Hemiptera classification*. Studio 1, Warszawa, 199 pp.+8 pls.
Zhang H.-C., Wang Q.-F., Zhang J.-F. 2004(2003). Some Jurassic homopteran insects from the Junggar basin, Xinjiang, China. *Acta Palaeontologica Sinica*, 42 (4), 548–551.

Acknowledgements

The presentation partly results from the scientific exchange project of Chinese Academy of Sciences and Polish Academy of Sciences “Palaeobiodiversity of Fulgoromorpha and Cicadomorpha (Insecta: Hemiptera) of Daohugou Biota”, and the Chinese-Polish Scientific and Technological Cooperation project “Fulgoromorpha and Cicadomorpha (Insecta: Hemiptera) of the Daohugou Biota: morphology, classification, evolution”.