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Weiwoboidae fam. nov. of 'Higher' Fulgoroidea (Hemiptera: Fulgoromorpha) from the Eocene Deposits of Yunnan, China

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Abstract: A new family of so-called 'higher' planthoppers, Weiwoboidae fam. nov., from the Lower Eocene of Yunnan is described. A new monotypic genus, *Weiwoboa* gen. nov., with *Weiwoboa meridiana* sp. nov. is also described and illustrated. The characters of tegmen venation of the new family, its evolution, and supposed relationships are briefly discussed.

Key words: Weiwoboidae fam. nov., *Weiwoboa* gen. nov., *Weiwoboa meridiana* sp. nov., new family, higher Fulgoroidea, evolution, Eocene, Yunnan,

1 Introduction

Although Eocene planthoppers (Hemiptera: Fulgoromorpha) are believed to be well recognized in the fossil record, the reality is different. There are a number of taxa described or reported from fossil resins of Europe, as well as rock imprints from Europe and North America (Szwedo, 2004, 2006a,b, 2008; Szwedo and Stroiński, 2010; Szwedo and Wappler, 2006; Szwedo et al., 2004, 2006; Shcherbakov, 2006). The record of Eocene fossil Fulgoromorpha in Asia is scarce; only some unidentified specimens of "Auchenorrhyncha" (could also be Fulgoroidea) have been mentioned from the Lower Eocene Gujarat amber (Solórzano Kraemer and Rust, 2008a,b). There are almost no reports of fossil Fulgoromorpha from the Paleogene of China, but a few taxa were found in younger Miocene deposits of Shanwang, Shandong province (Szwedo et al., 2004; Wang et al., 2006).

The specimen described below is the first representative of the hemipteran suborder Fulgoromorpha, superfamily Fulgoroidea, and represents a new family.

The Fulgoroidea consists of 26 families, and the extinct ones are Jurassic Fulgoridiidae Handlirsch, 1906, which seems to be paraphyletic, but is believed to be ancestral to the other families of the superfamily, and Cretaceous families Lalacidae Hamilton, 1990, Neazoniidae Szwedo, 2007, Perforissidae Shcherbakov, 2007, and Mimarachnidae Shcherbakov, 2007 (Hamilton, 1990; Szwedo, 2007a, 2009; Shcherbakov, 2007a,b). The recognized extant family groups include Achilidae Stål, 1866+Achilixiidae Muir, 1923 (but see Liang, 2001), Caliscelidae Amyot et Serville, 1843, Cixiidae Spinola, 1838, Delphacidae Leach, 1815, Derbidae Spinola, 1839, Dictyopharidae Spinola, 1838, Eurybrachidae Stål, 1862+Gengidae Fennah, 1949, Flatidae Spinola, 1838+Hypochtonellidae China et Fennah, 1952, Fulgoridae Latreille, 1807, Issidae Spinola, 1838+Acanaloniidae Amyot et Serville, 1843, Kinnaridae Muir, 1925+Meenoplidae Fieber, 1872, Lophopidae Stål, 1866, Nogodinidae Melichar, 1898, Ricaniidae Amyot et Serville, 1843, Tettigometridae Germar, 1821, and Tropiduchidae Stål, 1866. The fossil described earlier represents the so-called "higher" Fulgoroidea group of families (i.e. Acanaloniidae, Caliscelidae, Eurybrachidae, Flatidae, Gengidae, Hypochthonellidae, Issidae, Lophopidae, Nogodinidae, Ricaniidae, and Tropiduchidae). This group comprises highly-variable taxa, very often with costal area widened, and well-developed and reticulate venation with polymerized longitudinal veins. The other characteristic feature of this group is a raking–kneading ovipositor (Bourgoin, 1993; Emeljanov, 1999; Bourgoin and Campbell, 2002; O'Brien, 2002).

The fossil described below represents a new family, with the venation pattern of tegmen superficially resembling this found among representatives of so-called "higher" Fulgoroidea.

2 Materials and methods

The specimen was examined using a Nikon SMZ1000 stereomicroscope (Nikon Corporation, Tokyo, Japan), and drawings were made with the aid of a camera lucida. The photographs were prepared using a digital camera (DXM1200; Nikon Corporation, Tokyo, Japan) connected to the above stereomicroscope, and the line drawings were re-adjusted on photographs using image-editing software Combine ZP (Alan Hadley, http://www.hadleyweb.pwp.blueyonder.co.uk/, United Kingdom) and Adobe Photoshop CS (Adobe Systems Incorporated, San Jose, California, U.S.A.). The specimen (Nanjing Institute of Geology and Palaeontology [NIGP] 151834) is deposited at the NIGP, Chinese Academy of Sciences

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in Nanjing. We follow the wing venation nomenclature according to Szwedo and Żyła (2009).

3 Systematics

Order Hemiptera Linnaeus, 1758
Suborder Fulgoromorpha Evans, 1946
Superfamily Fulgoroidea Latreille, 1806.

Weiwoboidae fam. nov. Lin, Szwedo, Huang et Stroiński

Type genus: *Weiwoboa* gen. nov., here designated.

Diagnosis: Superficially resembling some so-called "higher" Fulgoroidea, for example, some Tropiduchidae: Gaetulini, but present venation pattern of veins M and CuA unique among Fulgoroidea. Tegmen fully developed, membranous, with unique venation among known Fulgoroidea. Basal cell wide; costal area well developed, with apex surpassing half tegmen length; costal cell with a few, straight transverse veinlets; terminals of branch Sc+RA reaching margin basad of anteroapical angle of tegmen; stem M forked basad of half tegmen length; stem CuA forked slightly basad of half tegmen length, with both branches forked monotonic to the apex; median field of membrane narrow, cubital field of tegmen's membrane covers half its area. Clavus closed. No transverse veinlets in basal half of tegmen between longitudinal veins Sc+R, M, and CuA.

***Weiwoboa* gen. nov. Lin, Szwedo, Huang et Stroiński**

Type species: *Weiwoboa meridiana* sp. nov., here designated.

Diagnosis: Costal area exceeding half tegmen length, with apical portion not reaching level of claval apex, wider than costal cell, apical portion of costal area not sclerified at stigmal area. Anteroapical and claval angles broadly rounded. Apex of clavus reaching three-quarters of total tegmen length. Stems Sc+R, M, and CuA leaving basal cell with single stalks. Stalks of Sc+R and M subequal in length; stalk CuA more than twice as long as stalks of Sc+R and M. Stem Sc+R forked a little basad of stem M forking. Stem M_{1+2} not forked basad of level of nodal line, stem M_{3+4} forked distinctly basad of stem CuA forking. Stem CuA forked basad of half tegmen length, branch CuA_1 forked a little basad of branch CuA_2 forking. Nodal line of veinlets not developed, apical line of veinlets present. Clavus with a few straight transverse veinlets between CuP and Pcu and Pcu+A_1.

Etymology: Genus name is derived from Weiwobo, goddess of immortality, owner of the Heavenly Peach Garden, and Queen Mother of Paradise West. Gender: feminine.

***Weiwoboa meridiana* sp. nov. Lin, Szwedo, Huang et Stroiński (Fig. 1)**

Diagnosis: Tegmen with branch Sc+R with six terminals, branch RP with four terminals; stem M with eight terminals, branch CuA with 13 terminals; cell C1a long, L-shaped, with single veinlet at the middle; apical cellule, apicad of C1a, ampulliform; apical cells distinctly longer than wide.

Description: Length of tegmen approximately 7.24 mm, width of tegmen approximately 4.32 mm. Tegmen approximately 1.66 times as long as wide. Tegmen membranous, with venation distinct, not convex; elongate, with wider apical portion. Costal margin curved at base, then almost straight; anteroapical and claval angles broadly rounded; apical margin arcuate.

Costal area surpassing half tegmen length, reaching level of claval apex; narrow at base, then widened, tapering toward apex, twice as wide as costal cell at widest point in median portion, with simple, dense transverse veinlets. Costal cell narrower than costal area, with a few (4–5) simple, scarce transverse veinlets. Basal cell huge, rounded, slightly longer than wide. Longitudinal veins not wavy or distinctly curved. Stems Sc+R, M, and CuA leaving basal cell single. Stem Sc+R with stem approximately as long as stem M, branch ScRA forked basad of half tegmen length, branch ScRA forked slightly apicad of stem CuA forking; anterior branch with terminals forming ampulliform cell, four terminals reaching anterior margin, basad of anteroapical angle; posterior branch of RA with two terminals. Branch RP with four terminals, with the last one (RP_4) reaching margin a little anteriad of tegmen's anteroapical angle. Stem M forked a little apicad of stem Sc+R forking, distinctly basad of stem CuA forking; branch M_{1+2} simple, forked in apical portion, with three terminals; branch M_{3+4} forked slightly apicad of stem M forking, branch M_3 forked at the level of nodal line, with four terminals, branch M_4 single to the tegmen's apical margin; vein M with

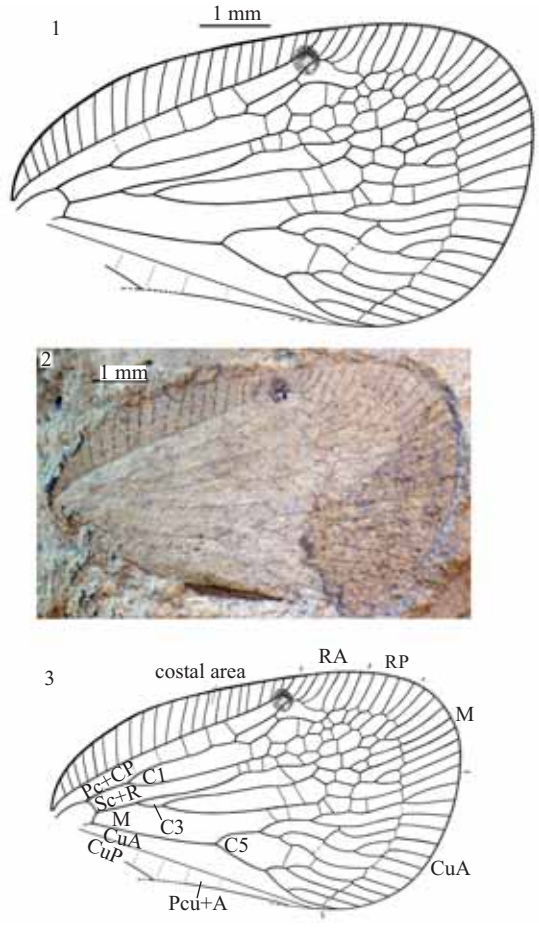

Fig. 1. (1)*Weiowoboa meridiana* gen. sp. nov. Tegmen. (2) *Weiowoboa meridiana* gen. sp. nov. Holotype. NIGP 151834. Imprint of right tegmen with missing lower claval portion. (3) *Weiowoboa meridiana* gen. sp. nov. Tegmen venation pattern and vein nomenclature.

eight terminals at apex. Stem CuA long, forked basad of branch ScRA forking; branch CuA_1 forked more basad than branch CuA_2 forking, with six subsequent forkings, that is, with eight terminals reaching apex; branch CuA_2 forked at level between forkings CuA_1 and CuA_{1b}, branch CuA_{2a} forked more basad than branch CuA_{2b} forking, branch CuA_2 reaching apex with five terminals; vein CuA reaching apical margin with 13 terminals, cubital area occupying a little more than half apical margin of tegmen.

Corium of tegmen without transverse veinlets, nodal line not developed, apical line of veinlets present. The area is limited by apical portions of veins RA_2 and M_3, with a net of transverse veinlets delimiting polygonal cells. The area delimited by apical portions of branches M_3 and CuA_1, with scarce and irregularly-distributed veinlets closing a few cells. Cell C1 long, L-shaped, with single veinlet at the middle. Cell C3 very long, without veinlets basad of nodal line level. Cell C5 twice as long as wide. Apical cells approximately 2–3 times as long as wide. Clavus long, with apex exceeding two-thirds of tegmen length, reaching almost to claval angle of tegmen. A few simple transverse veinlets between CuP and $Pcu+A_1$.

Etymology: Specific epithet is derived from Latin "*meridianus*", meaning "southern" and refers to the geographical position of the locality.

Age and occurrence: Shangyong village, Mengla County, Yunnan Province, southwestern China; ?Lower Eocene (Ypresian), Mengyejing Formation near Shangyong.

Remarks: The specimen described was collected during 1977 from a locality near the Shangyong village, Mengla County, Yunnan Province, southwestern China, close to the border with Laos. The geological setting of this area is poorly known. The original label noted that the specimens came from the Mengyejing Formation, associated with fossil insects, conchostracans, ostracods, spores, and pollens (see Nanjing Institute of Geology and Palaeontology et al., 1975). Fossil insects are diverse and frequent, and are represented by mostly isolated fragments, such as beetle elytra, but have been poorly studied (Lin et al., 2010). The true Mengyejing Formation is an early Late Cretaceous stratum. However, the Mengyejing Formation near Shangyong village, where the present fossil was discovered, could belong to an undefined stratum. Analyses of spore–pollen assemblages suggest an Early Paleogene age, but this does not exclude the possibility of a Late Cretaceous age (Nanjing Institute of Geology and Palaeontology et al., 1975). An early Eocene age (Ypresian) is suggested on the basis of the study of conchostracan *Paraleptestheria menglaensis* (Chen & Shen, 1980; Shen et al., 2006).

Type material: Holotype; field number H3044, cat No. NIGP 151834. Imprint of right tegmen with missing lower claval portion. Deposited at NIGP, Chinese Academy of Sciences, Nanjing, China.

3 Discussion

The specimen described is of great importance, as it originates from very particular locality and times, and presents unique characters.

Shcherbakov (1981) presented a list of characters for the recognition of Fulgoroidea families based on their forewings. However, this list is far from complete, because of enormous variability in the venation of Fulgoroidea, and a poor understanding of evolutionary patterns of wing venation in these insects (Dworakowska, 1988).

The newly-described family Weiwoboidae presents a puzzle of characters regarded as primitive (basal) and modern ones (advanced); these features were not found among recent representatives of Fulgoroidea.

The main feature of Weiwoboidae is the model of longitudinal vein organization. The most striking character of Weiwoboidae venation pattern is the monotonic furcation of CuA branches, with branches covering half of the tegmen's membrane width. In the recent taxa of Fulgoroidea, vein CuA is basically bibranched terminally, but with exceptions where CuA is single or multibranched (Dworakowska, 1988).

Shcherbakov (2006), discussing the venation pattern of extinct tribe Emilianini Shcherbakov, 2006 (Tropiduchidae; Eocene of Florissant, Colorado, USA), presented two possible interpretations. The one with subbasal M+CuA anastomosis seems to be more probable in his opinion, as the other, with extremely multibranched CuA occupying the area as large as R and M put together, is "a condition never found in fulgoroids" (sic) (Shcherbakov, 2006: 316). Weiwoboidae present pattern with multibranched CuA occupying half of the tegmen's membrane area and no subbasal coalescence of stems. Additional bifurcations of CuA branches are present among various taxa of Fulgoroidea, and should be considered at least as diagnostic characters, if even not regarded as a possible apomorphic condition. Often, one of the branches of CuA is more forked, pectinate, or furcate. In Weiwoboidae, both branches CuA_1 and CuA_2 are subsequently monotonically forked, with the domination of CuA_1 terminals reaching the margin of the tegmen. In addition, the basal cell is wide, with stems Sc+R, M and CuA leaving it with distinct, well-separated, and independent stalks.

A well-developed costal area is characteristic for a number of representatives of "higher" Fulgoroidea. It could be relatively narrow, narrower than the costal cell, subequal to it in width, or distinctly wider; this feature is characteristic for a group of genera within particular families, but is not useful for familial level separation. The form and number of transverse veinlets of the costal area is also variable; the veinlets could be relatively scarce or dense, straight, oblique, single, or forked. However, it seems that the length of costal area is an important character; the placement of its tip, distinctly basad of level of the nodal line, slightly basad or apicad of the nodal line level, could be helpful in suprageneric group recognition.

The characteristic feature of Weiwoboidae is the absence of transverse veinlets in the basal half the tegmen, with more numerous veinlets forming polygonal, irregular cells in the apical portion of the radial area; a few veinlets basad of the apical line in the median area, and a distinct apical line of veinlets.

The pattern of vein M in Weiwoboidae is also unique among

Fulgoroidea. Branch M_{1+2} forks in the apical part, slightly basad of the apical line, while branch M_{3+4} forks distinctly basally, at a level one-quarter of the tegmen length. Branch M_3 again forks on the membrane, while branch M_4 reaches the margin as a single terminal.

The new family Weiwoboidae described here presents unique characters, clearly separating it from other Fulgoroidea reported from the Palaeogene deposits. Most fossil taxa from this period originate from localities in the Northern Hemisphere, for example, Paleocene deposits of France, Germany, and Denmark; Eocene and Oligocene deposits of North America, Eocene Oise, and Baltic amber etc. (Eskov, 2002; Szwedo et al, 2004; Rasnitsyn, 2008). The Palaeogene fossil localities of China brought almost no Fulgoroidea representatives (Wang et al., 2006), and only a few are known from the Miocene deposits (Szwedo et al., 2004; Wang et al., 2006). Scarce data on Jurassic and Cretaceous representatives of Fulgoroidea from a few localities have been reported (Szwedo et al., 2004; Wang et al., 2006).

The Gondwanan Fulgoroidea are not well known (Szwedo et al., 2004). Undescribed Jurassic fossils are known from Western Australia (Martin, 2008). The rich and diversified fauna of Fulgoroidea, dominated by Lalacidae, is known from the Lower Cretaceous Crato Formation of Brazil (Szwedo et al., 2004; Szwedo, 2007b), and single Nogodinidae are reported from the Paleocene of Argentina (Petrulevičius, 2005). The known fossil Fulgoroidea from the Paleogene represent the recent families, both recent and extinct tribes, presenting venation patterns as found among recent representatives of these groups. It could be hypothesized that Weiwoboidae represents the poorly-known "Gondwanan" offshoot of Fulgoroidea, as no forms presenting related characters are known from the Northern Hemisphere localities. Although the recent paleogeographical model confirms the traditional view that India became progressively more isolated from the major landmasses during the Cretaceous and Paleocene, it is likely that at various times, minor physiographical features (principally ocean islands) provided causeways and/or stepping stone trails along which land animals could have migrated to/from the subcontinent (Ali and Aitchison, 2008). Assumptions of possible Gondwanan relationships of Weiwoboidae could be supported by the tectonic history of the area in which the locality is placed. The Shangyong locality is placed in an area of great geological activity and environmental changes during the Lowermost Eocene, at the time of the Eocene Thermal Maximum and the subsequent Early Eocene Climatic Optimum (Zachos et al., 2008), periods of global warming. These "hothouse" conditions very probably affected the distributional pattern of insects, enabling them to migrate to the north. During this time, the Indian plate collided with the Asian continent approximately 52 Ma and continued penetrating it (Sato et al., 2001). The 2500 km northward penetration of India gave rise to tectonic deformation in the Asian continent. However, the geological events, plate tectonics, as well as biogeographical scenarios for the area are still under discussion and controversy (Metcalfe, 2006; Aitchison et al., 2007; Ali and Aitchison, 2008).

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