Discovery of a Flatidae planthopper (Hemiptera: Fulgoromorpha) in the Paleocene of Northern Tibet and its taxonomic and biogeographic significance

Jacek SZWEDO
Adam STROIŃSKI
Department of Palaeozoology, Museum and Institute of Zoology,
Polish Academy of Sciences, 64, Wilcza Street,
PL-00-679 Warszawa (Poland)
szwedo@miiz.waw.pl
adam@miiz.waw.pl

Qi-Bin LIN
State Key Laboratory of Palaeobiology and Stratigraphy,
Nanjing Institute of Geology and Palaeontology,
Chinese Academy of Sciences, Nanjing 210008 (PR China)

Szwedo J., Stroiński A. & Lin Q.-B. 2013. — Discovery of a Flatidae planthopper (Hemiptera: Fulgoromorpha) in the Paleocene of Northern Tibet and its taxonomic and biogeographic significance. *Geodiversitas* 35 (4): 767-776. http://dx.doi.org/10.5252/g2013n4a2

ABSTRACT

A new genus and species of Flatidae planthoppers, *Priscoflata subvexa* n. gen., n. sp., is described here on the basis of tegmen from the Paleocene of Northern Tibet. The tegminal features of this fossil and its importance for classification and phylogenetic studies within Flatidae are given. The comparison of this fossil and other extant and extinct flatids, its systematic position, its biogeographic and evolutionary significance are discussed. "*Ormenis*" *devincta* Cockerell, 1926 from the Eocene of Argentina is placed in Fulgoroidea *incertae sedis*.

KEY WORDS
Flatidae,
Paleocene,
Tibet,
phylogeny,
biogeography,
taxonomy,
new species.

RÉSUMÉ

Découverte d'un Flatidae (Hemiptera: Fulgoromorpha) dans le Paléocène du nord du Tibet et ses importances taxonomique et biogéographique.

Un nouveau genre et une nouvelle espèce de Flatidae, *Priscoflata subvexa* n. gen., n. sp., sont décrits ici, sur la base d'un tegmen du Paléocene du Nord du Tibet. Les caractéristiques de la nervation tegminale de ce fossile, son importance pour la classification et l'étude phylogénétique des Flatidae sont données. La comparaison de ce fossile avec d'autres Flatidae fossiles et actuels, sa position systématique, sa biogéographie et son importance évolutive sont discutées. « *Ormenis* » *devincta* Cockerell, 1926 de l'Éocène de l'Argentine est placé dans les Fulgoroidea en position incertaine.

MOTS CLÉS
Flatidae,
Paléocène,
Tibet,
phylogenie,
biogéographie,
taxonomie,
espèce nouvelle.

INTRODUCTION

Flatidae Spinola, 1839 is one of the largest families within planthoppers (Fulgoromorpha, Hemiptera) with 1447 described species in 298 genera; it is divided into two subfamilies Flatinae Spinola, 1839, with 12 tribes worldwide, and Flatoidinae Melichar, 1901 (Bourgoin 2013). These phytophagous insects (highly diverse in terms of their colour and size) are found on all continents, but especially common and abundant in the tropics (O'Brien 2002). About 20 species of Flatidae are regarded as serious pests of economically important crops such as coffee, tea, cacao, mango, citrus, apple and cherry (O'Brien & Wilson 1985).

Divisio Nephesaria was firstly established by Distant (1906) for a few genera from Indian and Ceylon. However, most of them were afterward transferred to the other Flatidae units. The tribal status Nephesini was given by Melichar (1923), with subdivision into three subtribes: Pseudoflatina Melichar, 1923, Phaedolina Melichar, 1923, and Cryptoflatina Melichar, 1923 (containing also the nominative genus *Nephesa* Amyot & Serville, 1843 [sic!]). Metcalf (1957) subdivided the Nephesini into Pseudoflatina, Phaedolina, Cryptoflatina and Nephesina subtribes. Medler (2001) stated that the Ormenisini deserves a new status as a separate tribe, however he didn't gave the content of this unit. Recently, the content of the tribe Nephesini is narrowed to the members of the former subtribe Nephesina. Zhang *et al.* (2011) stated that the tribe is mainly distributed in the Australasian (with 31 genera) and Oriental (11 genera) Regions, with some genera also in the Afrotropical and Neotropical Regions, but with only single genus in the Palaearctic and Nearctic Regions, respectively. The clear and concise classification for the Flatinae is still far from its final resolution. Medler (1985), in his preliminary analysis, stated that Nephesini do not have natural grouping of genera. Therefore much more attention is necessary while studying Flatidae. Further investigations, new sets of data and interpretations of morphological disparity of the group are highly needed. Below we propose some new features and interpretations of venational features which could help enlighten the mysteries of Flatinae classification.

MATERIAL AND METHODS

The large number of fossils was collected in Dazhuoma area by the geological team of the Jianghan Institution of Petroleum and Gas explored the Qiangtang Basin of the Northern Tibet, China. The material includes about fifty fossil insects, sent to the senior author (QBL) for identification, and a preliminary list of the insect fossils, with the inferred geological age, was given to the Institution. For now, only a single species of Prophalangopsidae (Insecta: Orthoptera) was described (Lin & Huang 2006) from this material. The insect fossils occur mainly in the lower part of the second member of the Niubao Formation (beds 179-249). The fossil insects' assemblage is diversified and abundant. Entomofauna is estimated as Paleocene to Early Eocene in age (Cai & Fu 2003). At least 19 insect species attributed to 17 genera and 11 families are recorded from the Dazhuoma Entomofauna from primary studies, indicating a rather distinct diversity and local characters (Lin & Huang 2006).

The venation nomenclature follows the interpretations proposed by Szwedo & Żyła (2009) and Nel *et al.* (2012). Some additional explanations are given below, referring to the Flatidae tegmen structure.

Abbreviations and terms used

Sc+R	stem of subcosta + radius;
RA	radius anterior;
RP	radius posterior; in fact it is fused RP and MA, but for the reasons explained in Szwedo & Żyła (2009) and Nel *et al.* (2012), such an interpretation is followed here;
M	media; in fact is MP – media posterior, but for the reasons explained in Szwedo & Żyła (2009) and Nel *et al.* (2012), such an interpretation is followed here;
CuA	cubitus anterior;
CuP	cubitus posterior; sometimes termed as claval vein or claval suture, but the claval suture is different structure from the vein CuP. These structures were often misinterpreted as they are place very close each other, in line and sometimes hardly discriminated;
bulla	distinct convexity at basal portion of the Flatidae tegmen, near basal cell;
tornus	postclaval margin of tegmen, from apex of clavus to claval angle.

SYSTEMATICS

Order HEMIPTERA Linnaeus, 1758
Suborder FULGOROMORPHA Evans, 1946
Superfamily FULGOROIDEA Latreille, 1807
Family FLATIDAE Spinola, 1839
Subfamily FLATINAE Spinola, 1839
Tribe NEPHESINI Distant, 1906

Priscoflata n. gen.

TYPE SPECIES. — *Priscoflata subvexa* n. sp. by present designation.

ETYMOLOGY. — Generic name is derived from the Latin "priscus" meaning "ancient" combined with generic name "Flata". Gender: feminine.

DIAGNOSIS. — Tegmen with costal area present, as wide as costal cell; costal area tapering apicad; apical margin arcuate; postclaval margin (tornus) absent; stems Sc+R, M and CuA leaving basal cell separately; stem Sc+R single to the apex of costal area; stem CuA straight and parallel to the claval suture (CuP); bulla present; lack of veinlets between CuA and CuP; single apical line of transverse veinlets present; distal portion of intermedial space between branches M_{1b} and M_{2a} with irregular veinlets, M_{2b} and M_{3a} fused for a distance.

DISTRIBUTION. — Qingtao-Tibet Plateau, Qiangtang Basin, China.

REMARKS

The new genus bears tegminal features found in the representatives of the tribe Nephesini, as recently recognized: e.g., presence of bulla, stem CuA parallel to, but shifted from claval suture. With the genus *Nivalios* Zhang, Peng & Wang, 2011 it shares single line of apical veinlets; stems Sc+R and M leaving basal cell from the same point; stem Sc+RA single to the apex of costal area. *Priscoflata* n. gen. differs from *Nivalios* also by the costal area and costal cell of similar width (costal cell distinctly narrower than costal area in the latter) and by a few veinlets dissecting costal cell (single, oblique vein in the genus *Nivalios*). However, the genus *Priscoflata* n. gen. presents also a number of unique features, i.e. very long clavus, reaching to the apical angle (feature not found among other Nephesini); lack of postclaval area (tornus) (tornus always present in the Nephesini); common portion of branches M_{2b} and M_{3a} (feature not found in remaining Nephesini) and distal portion of intermedial space between branches M_{1b} and M_{2a} with irregular veinlets.

Priscoflata subvexa n. sp.
(Figs 1A-C; 2)

TYPE MATERIAL. — Holotype. Imprint of tegmen with clavus missing, clavus broken along the claval (CuP) vein. Specimen NIGP 135803 deposited in the collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

LOCALITY AND HORIZON. — Gangni Village, Anduo County, Dazhuoma area of the Qiangtang Basin in northern Tibet; Niubao Formation, Paleocene.

DIAGNOSIS. — Stem Sc+R forked distinctly more basal than stem M; branch M_{1+2} forked slightly basad of branch M_{3+4}; stem CuA forked slightly apicad of stem M_{3+4} forking. Cell C1 twice as long as cell C3; cell C3 about 1.8 times as long as cell C5. Apical cells distinctly longer than wide, about 3.5 times as long as wide, longer in median portion.

ETYMOLOGY. — Specific epithet is derived from Latin *subvexus* meaning sloping up.

DESCRIPTION

Total length of tegmen 10.9 mm, maximum width about 5.48 mm (clavus missing, therefore the figure is estimated). Tegmen with costal margin arcuate, distinctly curved at base; anteroapical angle widely rounded; posteroapical angle rounded, apical margin mildly rounded. Apex of clavus exceeding ¾ of tegmen length, postclaval margin (tornus) absent. Bulla present, at the level of stem Sc+R forking. Costal margin distinctly thickened. Costal area present, tapering apicad; costal area as wide as costal cell, with dense veinlets; apex of costal area distinctly basad of claval apex. Costal cell with few transverse veinlets. Basal cell about twice as long as wide. Stems Sc+R, M and CuA leaving basal cell separately, stems Sc+R and M leaving basal cell very close each other. Stem Sc+R short, stem Sc+RA forked at level of costal area apex, reaching the margin with 4 terminals; branch RP distinctly curved mediad at base, forked apicad of stem M_{1+2} forking and basad of stem M_{3+4} and stem CuA forkings; branch RP forked slightly apicad of costal area apex, reaching margin with 6 terminals.

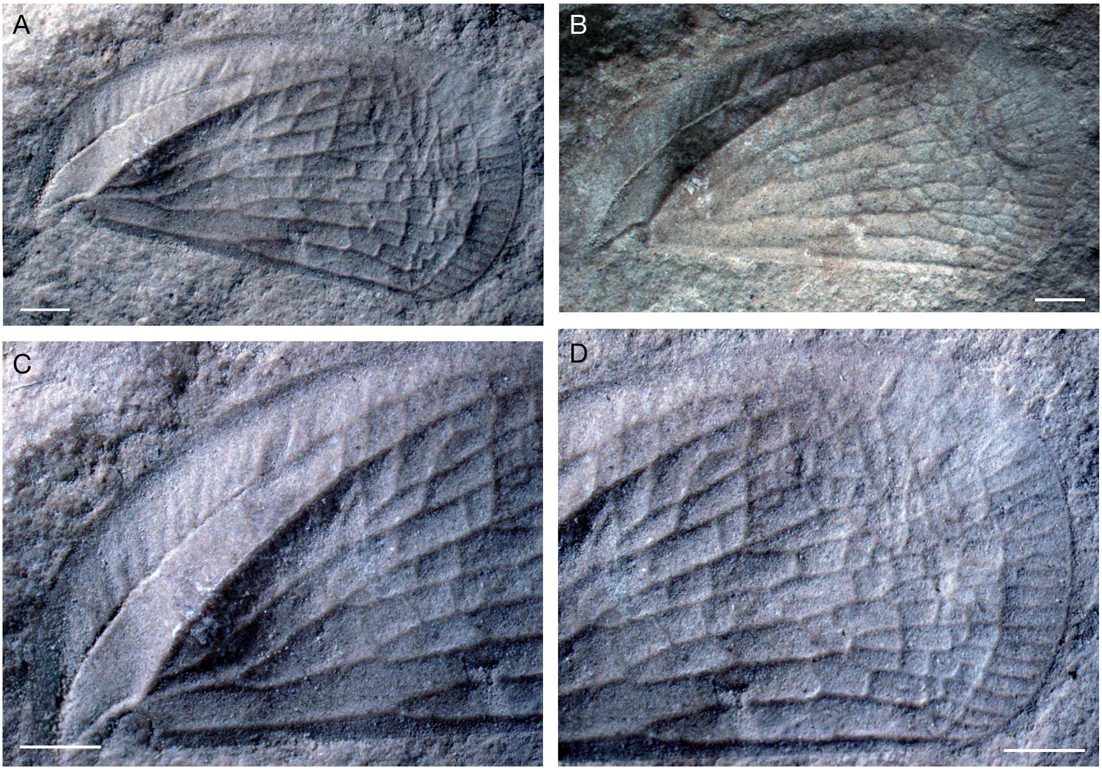

FIG. 1. — *Priscoflata subvexa* n. gen., n. sp.: **A**, **B**, tegmen in various light conditions; **C**, basal portion of tegmen with area of bulla indicated; **D**, apical half of tegmen with common portion of veins M_{2b} and M_{3a} indicated. Holotype, specimen No. NIGP 135803. Scale bars: 1 mm.

Stem M about 3 times as long as stem Sc+R, shorter than half of stem CuA. Branch M_{1+2} forked slightly basad of branch M_{3+4}; branch M_1 forked again, basad of branch M_2 forking; branch M_{2b} with a short common portion with branch M_{3a}; branch M_{3+4} forked slightly basad of stem CuA forking; branch M_3 forked slightly basad of common portion with branch M_{2b}; branch M_4 forked slightly apicad of branch M_3 forking; Stem M reaching apical margin with 19 terminals; some branches of M forked apicad of apical line of veinlets. Stem CuA straight and parallel to the claval suture (CuP); stem CuA the longest, forked apicad of branches RP, M_{1+2} and M_{3+4} forkings; branch CuA_1 forked again basad of apical line of transverse veinlets; branch CuA_2 single. Cell C1 the longest, about twice as long as cell C3; Cell C3 delimited posteriorly by a transverse veinlet of the first corial row; cell C5 shorter than cell C3, anterocubital cell with a few transverse veinlets. First corial row of veinlets (*r-m*, *im* and *m-cua*) at level branchs M_{1+2}, M_{3+4} and CuA forkings. Distal portion of intermedial space between branches M_{1b} and M_{2a} with a few less regular veinlets forming a net. No veinlets between CuA and CuP and between branch CuA_2 and postclaval margin (tornus). Apical cells distinctly longer than wide, about 3.5 times as long as wide, longer in median portion.

DISCUSSION

The new genus described above is to date the oldest record of the family Flatidae. Numerous fossils ascribed formerly to the Flatidae, were recently moved to another families, mainly Nogodinidae (Szwedo *et al.* 2004; Shcherbakov 2006). In addition, we

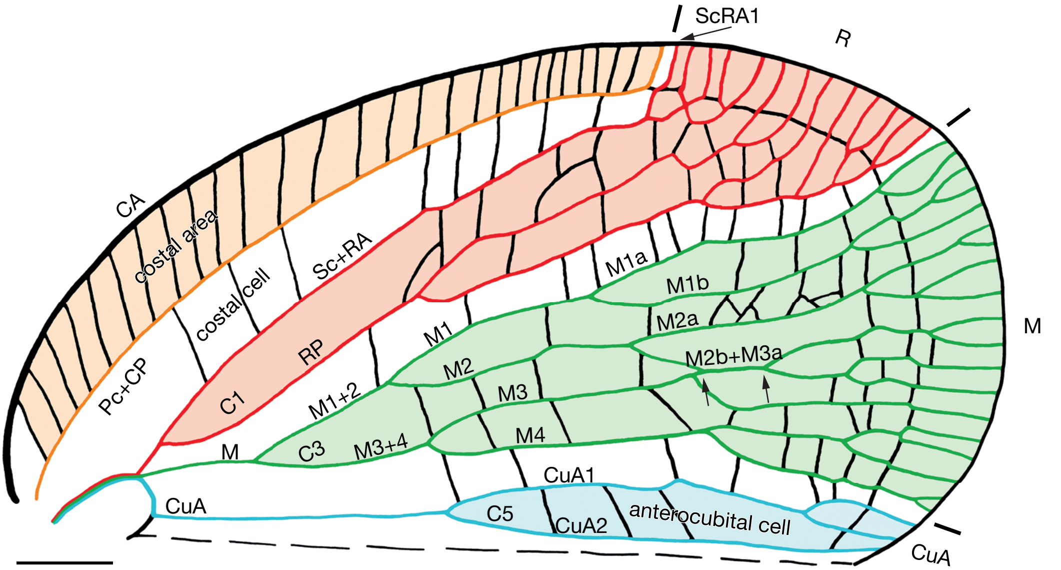

Fig. 2. — *Priscoflata subvexa* n. gen., n. sp.: tegmen venation with veins, cells and areas nomenclature explained; costal area, radial area, medial area and cubital areas shaded. Abbreviations: see Material and methods. Scale bar: 1 mm.

propose to remove from Flatidae the fossil "*Ormenis*" *devincta* Cockerell, 1926 from the Paleocene of Argentina and place it in Fulgoroidea *incertae sedis*. Petrulevičius & Martins-Neto (2000: 137) placed this species under the formal generic name "*Ormenis*". Metcalf & Wade (1966: 131) listed this species in the genus *Ormenis* Stål, 1862 of Flatidae, as *Ormenis devincta* (generic name *Ormenis* is feminine in grammatical gender). Carpenter (1992: 240) referring to Cockerell (1926) paper, listed this taxon in Flatidae. Szwedo *et al.* (2004: 51) listed this species in the genus *Ormenis*. The original description and drawing are too unclear to make the final decision of the placement for this species. It could rather be placed in any of the families Flatidae, Ricaniidae Amyot & Serville, 1843 or Nogodinidae Melichar, 1898. To solve this problem the type specimen must be found and re-examined for details. Unfortunately, Cockerell (1926) did not mention the place of preservation of this material he described from Argentina. Originally, Cockerell (1926) dated this specimen as Tertiary, Sunchal, Jujuy Province, Argentina. This age was subsequently given by Metcalf & Wade (1966) and Carpenter (1992). Petrulevičius & Martins-Neto (2000) give more details stating that this species comes from Maíz Gordo Formation, dated Late Paleocene. Szwedo *et al.* (2004) suggested possible Eocene age for this fossil. Paleocene/Eocene age of locality is suggested by Ponomarenko & Kirejtshuk (2013). According to Clapham & Karr (2011) in the Paleobiology Database the correct name of the formation should be Margas Verdes Formation, and Station 3 of Cockerell (1926) is ascribed there. Lara *et al.* (2012) dated Maíz Gordo Fm. as latest Paleocene-earliest Eocene.

Another taxon – "*Ormenis*" *furcata* Henriksen, 1922 comes from the Paleocene of Denmark (Fur Formation). It was listed by Metcalf & Wade (1966) and Szwedo *et al.* (2004) in the Flatidae. Later, it was proposed by Shcherbakov (2006: 320) to be placed in the genus *Eoricania* Henriksen, 1922 and transferred to the family Nogodinidae.

After these actions, the only remaining fossil flatids are: a nymph mentioned from the Miocene Mexican amber by Fennah (1963) and Flatidae nymph parasitized by a Dryinidae wasp, from the Miocene Dominican amber (El Valle mine) figured by Olmi (1995, fig. V). Therefore, *Priscoflata subvexa* n. gen., n. sp. represents the oldest fossil record of the family.

Venational features of *Priscoflata* n. gen.

Flatidae belong to the informal group of the Fulgoromorpha named "higher Fulgoroidea". These are characterized by relatively wide tegmina, with distinct costal area and rich pattern of longitudinal and transverse veins. One of the striking features of Flatidae is presence of pustules or at least distinct granulation on the claval area of the tegmen.

The features of great importance for the studies of Flatidae is the relative length of costal area in respect to apex of clavus. In the *Priscoflata* n. gen. costal area is not reaching apex of clavus. This feature seems to be associated with lack of postclaval area (tornus) in the *Priscoflata* n. gen. Postclaval area presents extremely high variability among recent Flatidae, but this feature and its mutual relation with costal area length, need much more attention and further research. Another feature of importance is presence of bulla and the implications for shifting and interpretations of forking models of the stems Sc+R and M. In numerous descriptions of the taxa in which bulla is present, the forking patterns of stems Sc+R and M are misinterpreted. Forking of Sc+R, basal portion of branch RP, could be placed basad of bulla, on bulla, rarely in the posterior portion of bulla. These branches are often obsolete at base and shifted towards base of stem M, making an illusion of early forking of stem M, very close to the basal cell, if not thoroughly examined. Next set of features calling for much more attention is the pattern and variability of cells C1, C3 and C5. These are complex characters, but seems to be very useful not only for diagnostic purposed but also for phylogenetic approach (Bourgoin 1997; Bourgoin & Szwedo 2008; Lin *et al.* 2010). In the *Priscoflata* n. gen. cell C3 is lenticulate, due to fusion of branches M_{2b} and M_{3a} for a distance, which is a unique feature of this genus. It seems that also distal portion of intermedial space between branches M_{1b} and M_{2a} with irregular veinlets is a feature of importance of *Priscoflata* n. gen. Cell C5 is very short, due to presence of a few transverse cells of anteriocubital cell. The genus *Priscoflata* n. gen. is also characteristic of a single apical line of veinlets, subparallel to posterior margin of tegmen, and almost continuous to costal area apex.

Biogeographic significance

Recent planthoppers of the family Flatidae are distributed universally, mainly in the tropical and subtropical zones (O'Brien & Wilson 1985; O'Brien 2002). The discovery of a fossil representative of the Flatidae in the Late Paleocene of Qinagtang Basin is very important. At the time of its deposition, Indian subcontinent was still far from Qiangtang Block (Ali & Aitchison 2008), and the area was not so highly elevated as it is in recent times. The fossil comes from the period of global warming, i.e. Paleocene-Eocene Thermal Maximum (Zachos *et al.* 2008; McInerney & Wing 2011). At these times the locality was placed in the Eastern Province of the Boreotropical floristic Region (Meyen 1987; Maslin *et al.* 2005). This area and this particular period is very crucial for understanding of the evolution and dispersal patterns of the so-called "higher Fulgoroidea". Shcherbakov (2006) suggested that the earliest "higer Fulgoroidea" appeared in the earliest Paleocene, just above the Cretaceous/Palaeogene boundary, but the earliest record of Flatidae is later than Eocene. Soulier-Perkins (2000) analysing the family Lophopidae Stål, 1866 postulated the origin of this unit at about 65 million years in the area of the recent South-Eastern Asia. The discovery of fossil Lophopidae in the mid Paleocene Menat Formation of France (Stroiński & Szwedo 2012), lowermost Eocene Oise amber of France (Szwedo 2011), Late Paleocene Fur Formation of Denmark (Szwedo & Soulier-Perkins 2010), Early Eocene of Laguna del Hunco, Argentina (Petrulevičius *et al.* 2010), mid Eocene Messel maar in Germany (Szwedo & Wappler 2006), and mid Eocene Green River Formation of Colorado, U.S.A. (Cockerell 1920) gave new clues to reconstruction of evolutionary and biogeographic scenarios of this family. Another family of "higher Fulgoroidea" – Ricaniidae was found in the lowermost Eocene Oise amber of France (Stroiński & Szwedo 2011). These data altogether with the present finding of Flatidae challenge Shcherbakov's (2006) statement. The question if South-Eastern Asia before the collision with Indian plate was the place of origin of "higher Fulgoroidea" remains open. The recent finding of a new family Weiwoboidae Lin, Szwedo, Huang & Stroiński, 2010 (Lin *et al.* 2010) in the

Eocene deposits of Yunnan makes the answer more difficult. This group presents singular features, absent among fossil and recent representatives of "higher Fulgoroidea", e.g., monotonic furcation of CuA branches, with branches covering half of the tegmen's membrane width; 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. In contrary, the genus *Priscoflata* n. gen., as well as known fossil Lophopidae and Ricaniidae do not present any exceptional features exceeding the known disparity of "higher Fulgoroidea". To solve this problem more focus must be put on taxonomic diversity and morphological disparity of recent and fossil planthoppers.

Acknowledgements
This paper is a contribution to the research project of Ministry of Science and Higher Education of Poland N N303 297 37 "Extinct genus and extant genus in the record of recent insect families" awarded to JS for the years 2009-2012. It also 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" awarded to JS.

REFERENCES

ALI J. R. & AITCHISON J. C. 2008. — Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166-35 Ma). *Earth-Sciences Review* 88: 145-166. http://dx.doi.org/10.1016/j.earscirev.2008.01.007

AMYOT C. J. B. & SERVILLE J. G. 1843. — Deuxième partie. Homoptères. Homoptera Latr. *Histoire naturelle des Insectes. Hemiptères* 1843: 1-676.

BOURGOIN TH. 1997. — The Meenoplidae (Hemiptera, Fulgoromorpha) of New Caledonia, with a revision of the genus *Eponisia* Matsumura, 1914, and new morphological data on forewing venation and wax plate areas, *in* MATILE L., NAJT J. & TILLIER S. (eds), *Zoologia Neocaledonica 3. Mémoires du Muséum national d'Histoire Naturelle, Zoologie* 157: 197-250.

BOURGOIN TH. 2013. — FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8, updated 2013-02-18. http://hemiptera-databases.org/flow/

BOURGOIN TH. & SZWEDO J. 2008. — The 'cixiid-like' fossil planthopper families. *Bulletin of Insectology* 61 (1): 107, 108.

CAI X. & FU J. 2003. — Paleocene and Eocene Palaeobiocoenotic feature in the Dazhuoma section at Gangni village of Qiangtang Basin. *Journal of Northwest University* (Natural Science Edition) 33 (4): 443-446.

CARPENTER F. M. 1992. — Superclass Hexapoda. *Treatise on Invertebrate Paleontology*. Volumes 3 & 4, part R, Arthropoda 4. Geological Society of America and University of Kansas Press, Boulder and Lawrence, 655 p.

CLAPHAM M. & KARR J. 2011. — Paleobiology Database. Station 3, Sunchal (Paleocene of Argentina). http://paleodb.org/cgi-bin/bridge.pl?action=basicCollectionSearch&collection_no=110536

COCKERELL T. D. A. 1920. — Eocene Insects from the Rocky Mountains. *Proceedings of the United States National Museum* 57: 233-260.

COCKERELL T. D. A. 1926. — Tertiary Insects from Argentina. *Proceedings of the United States National Museum* 68 (1): 1-6.

DISTANT W. L. 1906. — *The Fauna of British India, Including Ceylon and Burma*. 3. Lt. Col. C. T., Birgham, 503 p.

EVANS J. W. 1946. — A natural classification of leafhoppers (Jassoidea, Homoptera). Part 1. External morphology and systematic position. *Transactions of the Royal Entomological Society of London* 96 (3): 47-60.

FENNAH R. G. 1963. — New fossil fulgoroid Homoptera from the amber of Chiapas, Mexico, *in* PETRUNKEVITCH A., CAMPBELL J. M., FENNAH R. G., TURK E. & WITTMER W. (eds), Studies of fossiliferous amber arthropods of Chiapas, Mexico. *University of California, Berkeley Publications in Entomology* 31: 43-48.

HENRIKSEN K. L. 1922. — Eocene insects from Denmark. *Danmarks Geologisske Undersoegelse* 32 (2): 1-36.

LARA M. B., GALLEGO O. F. & TASSI L. V. 2012. — Mesozoic Coleopteran Faunas from Argentina: Geological Context, Diversity, Taphonomic Observations, and Comparison with Other Fossil Insect Records. *Psyche*, Article ID 242563, 1-14. http://dx.doi.org/10.1155/2012/242563

LATREILLE P. A. 1807. — *Genera Crustaceorum et Insectorum, secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata.* Parisiis et Argentorati, apud Amand Koenig, bibliopolam. 3. 258 p.

LIN Q.-B. & HUANG D.-Y. 2006. — Discovery of Paleocene Prophalangopsidae (Insecta, Orthoptera) in the Jiangtang Basin, Northern Tibet, China. *Alcheringa* 30: 97-102.

LIN Q.-B., SZWEDO J., HUANG D.-Y. & STROIŃSKI A. 2010. — Weiwoboidae fam. nov. of 'higher' Fulgoroidea (Hemiptera: Fulgoromorpha) from the Eocene deposits of Yunnan, China. *Acta Geologica Sinica* 84 (4): 751-755.

LINNAEUS C. 1758. — *Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata.* 1. Impensis Direct. Laurentii Salvii, Holmiae, 824 p.

MASLIN M., MAHLI Y., PHILLIPS O. & COWLING S. 2005. — New views on an old forest: assessing the longevity, resilience and future of the Amazon rainforest. *Transactions of the Institute of British Geographers* N.S. 30: 477-499.

MCINERNEY F. A. & WING S. L. 2011. — The Paleocene-Eocene Thermal Maximum: a Perturbation of Carbon Cycle, Climate, and Biosphere with Implications for the Future. *Annual Review of Earth and Planetary Sciences* 39: 489-516.

MEDLER J. T. 1985. — New concepts in classification of Flatidae. *Bulletin de la Société d'Entomologie Suisse* 57 (4): 433-434.

MEDLER J. T. 2001. — Review of Flatidae in Southern Africa, with keys and descriptions of new species (Homoptera: Fulgoroidea). *Contributions on Entomology International* 4: 323-375.

MELICHAR L. 1898. — Monographie der Ricaniiden (Homoptera). Annalen des k.k Naturhistorischen Hofmuseums 13: 197-359.

MELICHAR L. 1901. — Monographie der Acanaloniiden und Flatiden (Homoptera). Annalen des k.k Naturhistorischen Hofmuseums 16: 178-258.

MELICHAR L. 1923. — Homoptera. Fam. Acanaloniidae, Flatidae et Ricaniidae. *Genera Insectorum* 182: 1-185.

METCALF Z. P. 1957. — Flatidae and Hypochthonellidae. Part 13. *General Catalogue of the Homoptera. Fascicule IV*. North Carolina State College, Raleigh, 565 p.

METCALF Z. P. & WADE V. 1966. — *A Catalogue of the Fossil Homoptera (Homoptera: Auchenorrhyncha)*. General Catalogue of the Homoptera. A Supplement to Fascicle I. Membracidae of the General Catalogue of the Hemiptera. Contribution from the Entomology Department, North Carolina Agricultural Experiment Station. Paper Nr. 2049, Raleigh, N.C. USA (North Carolina State University at Raleigh), 250 p.

MEYEN S. V. 1987. — *Osnovy paleobotaniki*. Nedra, Moskva, 402 p. Published in English as: MEYEN S. V. 1987. — *Fundamentals of Palaeobotany*. Chapmann and Hall, London, XXI+432 p.

NEL A., PROKOP J., NEL P., GRANDCOLAS P., HUANG D-Y., ROQUES P., GUILBERT E., DOSTÁL O. & SZWEDO J. 2012. — Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of Morphology* 273: 480-506. http://dx.doi.org/10.1002/jmor.11036

O'BRIEN L. B. 2002. — The wild wonderful world of Fulgoromorpha. *Denisia* 4: 83-102.

O'BRIEN L. B. & WILSON S. W. 1985. — Planthopper systematics and external morphology, *in* NAULT L. R. & RODRIGUEZ J. G. (eds), *The leafhoppers and Planthoppers*. J. Wiley & Sons, New York: 61-102.

OLMI M. 1995. — Dryinids and Embolemids in amber (Dryinidae: Embolemidae). *Redia* 68 (2): 253-271.

PETRULEVIČIUS J. F. & MARTINS-NETO R. G. 2000. — Checklist of South American Cenozoic Insects. *Acta Geologica Hispanica* 35 (1-2): 135-147.

PETRULEVIČIUS J. F., RUST J., WAPPLER T., SOLÓRZANO KRAEMER M., SOULIER-PERKINS A. 2010. — Vicariant high latitude genus in the Lower Eocene, the case of tropical planthoppers (Fulgoromorpha: Lophopidae) in northern Denmark and Patagonia, Argentina. *Program and Abstract of the Fossils X3 – the 5th International Conference on Fossil Insects, the 4th World Congress on Amber and its Inclusions, the 4th International Meeting on Continental Palaeoarthropodology, August 20-25, 2010, Beijing.* Capital Normal University, Beijing: 162.

PONOMARENKO A. G. & KIREJTSHUK A. G. 2013. — List of locations of fossil beetles – supplement to catalogue. http://www.zin.ru/Animalia/Coleoptera/eng/paleoloc.htm (last updated July 2013, last accessed 21st November 2013).

SHCHERBAKOV D. E. 2006. — The earliest find of Tropiduchidae (Homoptera: Auchenorrhyncha), representing a new tribe, from the Eocene of Green River, USA, with notes on the fossil record of higher Fulgoroidea. *Russian Entomological Journal* 15 (3): 315-322.

SOULIER-PERKINS A. 2000. — A phylogenetic and geotectonic scenario to explain the biogeography of the Lophopidae. *Palaeogeography Palaeoclimatology Palaeoecology* 160: 239-254.

SPINOLA M. 1839. — Essai sur les Fulgorelles, sous-tribu de la tribu des Cicadaires, ordre des Rhyngotes. *Annales de la Société Entomologique de France* 8: 133-337.

STÅL C. 1862 — Bidrag till Rio de Janeiro-tratkens Hemipterfauna.II. Handlingar. *Kongliga Svenska Vetenskaps Akademien* 3 (6): 1-75.

STÅL C. 1866. — Hemiptera Homoptera Latr. *Hemiptera Africana* 4: 1-276.

STROIŃSKI A. & SZWEDO J. 2011. — *Abraracourcix* gen. nov. of Ricaniidae from the Lowermost Eocene Oise amber. *Annales de la Société entomologique de France* 47 (3-4): 480-486.

STROIŃSKI A. & SZWEDO J. 2012. — The oldest known Lophopidae planthopper (Hemiptera: Fulgoromorpha) from the European Paleocene. *Geobios* 45, 413-420. http://dx.doi.org/10.1016/j.geobios.2011.10.007

SZWEDO J. 2011. — *Ordralfabetix sirophatanis* gen. et sp. n. – the first Lophopidae from the Lowermost Eocene Oise amber, Paris Basin, France (Hemiptera: Fulgoromorpha). *Zootaxa* 2822: 52-60.

SZWEDO J. & WAPPLER T. 2006. — New planthoppers (Insecta: Hemiptera: Fulgoromorpha) from the Middle Eocene Messel Maar. *Annales Zoologici* 56 (3): 555-566.

SZWEDO J. & ŻYŁA D. 2009. — New Fulgoridiidae genus from the Upper Jurassic Karabastau deposits, Kazakhstan (Hemiptera: Fulgoromorpha: Fulgoroidea). *Zootaxa* 2281: 40-52.

SZWEDO J. & SOULIER-PERKINS A. 2010. — Hopping in Palaeo-World – new proposal for migration routes of Lophopidae (Hemiptera: Fulgoromorpha). *13th International Auchenorrhyncha Congress, 7th International Workshop on Leafhoppers and Planthoppers of Economic Significance, 28th of June-2nd of July 2010, Vaison-la-Romaine, France*. Muséum national d'Histoire naturelle, Paris, Département de Vaucluse: 28, 29.

SZWEDO J., BOURGOIN TH. & LEFEBVRE F. 2004. — *Fossil Planthoppers (Hemiptera: Fulgoromorpha) of the World. An Annotated Catalogue with Notes on Hemiptera Classification*. Studio 1, Warszawa, 199 p. + 8 pls.

ZACHOS J. C., DICKENS G. R. & ZEEBE R. E. 2008. — An Early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451: 279-283. http://dx.doi.org/10.1038/nature06588

ZHANG YA-LIN, PENG LING-FEI & WANG YING-LUN. 2011. — *Nivalios* gen. nov. (Hemiptera: Fulgoromorpha: Flatidae), first record of the tribe Nephesini from China. *Zootaxa* 2882: 19-26.

Submitted on 3rd September 2012;
accepted on 26 February 2013;
published on 27 December 2013.