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Original article

The oldest known Lophopidae planthopper (Hemiptera: Fulgoromorpha) from the European Palaeocene☆

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A B S T R A C T

Cintux menatensis nov. gen., nov. sp., the oldest representative of the planthopper family Lophopidae, is described based on the specimen from the Palaeocene of Menat (Auvergne, France). The formerly proposed evolutionary relationship of the family is reviewed in the light of the record of lophopids in European deposits. The biogeographic pattern and host plant relationships of these insects are briefly discussed. The taphonomic features of the fossil specimen are examined under Low Vacuum SEM and the results of X-Ray EDS analysis are presented.

1. Introduction

The planthopper family Lophopidae Stål, 1866 is one of the less diverse, with 43 genera and over 140 species recognized, both recent and extinct. It belongs to the group of so-called 'higher' Fulgoroidea. This group comprises highly diversified taxa, separated in the families Acanaloniidae, Caliscelidae, Eurybrachidae, Flatidae, Genegidae, Hypochthonellidae, Issidae, Lophopidae, Nogodnidae, Ricaniidae, Tropiduchidae and Weiwoboidae. The group is morphologically identified by tegmina very often with a widened costal area, and well developed and reticulate venation, with polymerized longitudinal veins, and a raking-kneading type of ovipositor (Bourgoin, 1993; Emeljanov, 1999; Bourgoin and Campbell, 2002; O'Brien, 2002; Lin et al., 2010). The family Lophopidae is characterized by a narrow head and second hind tarsomere without lateral spines (O'Brien and Wilson, 1985; O'Brien, 2002; Wilson, 2005). This tropical Old World family (except *Carriona* Muir, 1931 from Peru, Ecuador and Panama) is the first to have been subjected to a modern generic level phylogenetic analysis, with biogeographic scenarios proposed and host plants relationships discussed (Soulier-Perkins, 1998, 2000, 2001; Soulier-Perkins et al., 2007; Szwedo and Soulier-Perkins, 2010).

The known fossils assigned to Lophopidae are: *Baninus thuringiorum* Szwedo and Wappler, 2006 from the Eocene of Messel in Germany, and *Ordralfabetix sirophatanis* Szwedo, 2011 from the Lowermost Eocene Oise amber of France (Szwedo and Wappler, 2006; Szwedo, 2011). Two additional fossils of Lophopidae were recently reported by Petrulevičius et al. (2010): one from the Upper Palaeocene Fur and Ølst Formations in Denmark, and another from the Lower Eocene Laguna del Hunco, Argentina. The taxonomic placement of the only supposed fossil lophopid from North America, *Scoparidea nebulosa* Cockerell, 1920 from the Eocene Green River Formation (Roan Mountain, Colorado, U.S.A.; Cockerell, 1920) remains uncertain (Shcherbakov, 2006; Szwedo, 2011), but it presents some salient features of the family.

2. Geological setting and locality information

The Menat Pit fossil site is located approximately 57 km north-northwest of Clermont-Ferrand, near the town of Gannat in the northwestern part of the Massif Central (Chaîne des Puys), within the department of Puy-de-Dôme, France (Fig. 1). It occurs within a N-S-trending chain of basaltic and trachytic cinder cones, basaltic maars, and trachytic lava domes, that was active from the Palaeocene to the Holocene. The origin of the Menat fossil site has been controversial for decades, but it is now considered to represent a deep maar lake that originated from an explosive volcanic eruption (Vincent et al., 1977; Kedves and Russell, 1982; Wappler et al., 2009). The oldest recorded

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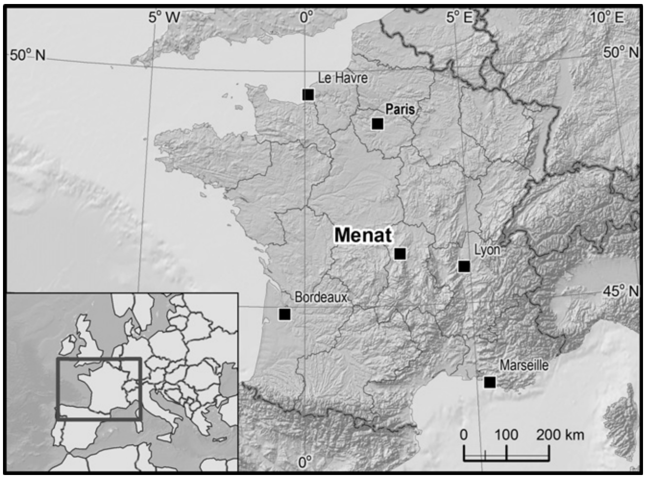

Fig. 1. Map showing the location of Menat fossil site.

volcanism (Palaeocene-Eocene) occurs on the periphery of the massif in the Bourgogne, Causses, Menat, Forez and Bas-Languedoc regions (Vincent et al., 1977). In detail, however, there is no correlation between geographic locality and the age of the volcanism (Vincent et al., 1977; Nel, 2008; Wappler et al., 2009). The sediments are laminated, bituminous shales (spongo-diatomite). The deposit is extraordinarily fossiliferous, with a rich insect, fish, bird and mammal fauna, and macroflora, including leaves, flowers, fruits, seeds and wood, as well as pollen (Fritel, 1903; Laurent, 1912, 1919; Piton, 1940; Kedves and Russell, 1982; Wappler et al., 2009). The insects from Menat comprise a diverse fauna (Piton, 1940; Nel, 2008). The Menat fossil site has currently yielded approximately 5000 fossil insect specimens that are deposited mainly in the collections of the Muséum national d'Histoire naturelle, Paris and the Association Rhinopolis at Gannat (Nel, 2008).

The estimated age of the Menat site was previously dated by pollen analysis, mammal stratigraphy, and radiometric K/Ar analysis as late Palaeocene, approximately 56 Ma (Kedves and Russell, 1982; Nel, 2008; Wappler et al., 2009). However, Wappler et al. (2009), based on macroflora and several lines of more recent evidence, postulated a possible middle Palaeocene (Selandian) age of about 60-61 Ma. There is no recent stratigraphy of the site (the works are in progress, and results are not yet published; A. Nel, pers. comm).

3. Methods

The specimen was observed using a stereoscopic light microscope Olympus SZH10 in normal reflected and transmitted light, and in polarized light. Drawings were made using attached drawing tubes. Photos were taken using an Olympus W5060 digital camera attached to an Olympus SZH10 microscope. SEM examinations were conducted in the Laboratory of Scanning Microscopy of the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, using an Hitachi S-3400 N Scanning Electron Microscope in low vacuum mode, equipped with X-ray EDS spectrometer (Thermo Noran Company) suitable for local chemical analyses. Light microscope and low vacuum SEM photographs taken were readjusted with Adobe® Photoshop Elements 6.0 software. Vein nomenclature follows that of Szwedo and Żyła (2009).

X-ray EDS spectrometric analysis of the specimen (part and counterpart, obverse and reverse compressions) have been conducted. It is the first time such data are obtained for the fossil insects from Menat. The distribution of elements must reflect the processes involved in fossil formation and preservation (Orr et al., 1998). Insects preserved at the Menat fossil site are quite often carbonized. It is believed that insects entombed in the Menat palaeolake became entangled in diatom mucus mats (formed by aggregates of diatoms under stress). Insects were incorporated into layers of sediments and volcanic ash at the bottom of the Menat maar lake. Many of these insects and leaves decomposed leaving imprints. As the sediments compacted and hardened into shale the imprints became impression fossils. Some organisms only partially decayed, retaining a dark colored carbon residue to become compression fossils (carbonization). Many insects known from Menat have their wings preserved as impressions and sometimes their bodies as dark compressions. Compressions are often flattened, having a two-dimensional appearance. However, the preservation in diatom layers allows some organisms to retain their three-dimensional character by covering with biofilms of extracellular polymeric substances (EPS) secreted by diatoms (O'Brien et al., 2008). Entangling of an organism in the diatom aggregates coated with the EPS biofilm could arrest decomposition during sedimentation and burial by the protective nature of the mucus covering it, the properties of which limited the actions of bacteria and grazers and may have enhanced fossilization (O'Brien et al., 2008). Some insects are found with organs and appendages. Such specimens were formed by compression (Vincent et al., 1977; Nel, 2008; Wappler et al., 2009). The organic matter making up the body of the insect has been altered during the insect decay, then during the rock formation from the sediments (Briggs, 1999; Briggs et al., 2000). The decomposition of an insect carcass, degradation by bacteria, by chemical action, by pressure and heat, distillation of volatile compounds and alteration of the proteins, polysaccharides and lipids of tissues chemically transform the organic structures and leave a thin film (Briggs, 1999). The thin, dark film is made of stable, polymerized hydrocarbon molecules that remain after more volatile and unstable compounds are degraded or incorporated (Martínez-Delclòs et al., 2004; Zherikhin, 2008). Preservation of details of fossil morphology suggest that conditions in the maar lake may have slowed down the decomposition before and during burial.

4. Systematics

Class INSECTA Linnaeus, 1758
Order HEMIPTERA Linnaeus, 1758
Suborder FULGOROMORPHA Evans, 1946
Superfamily FULGOROIDEA Latreille, 1807
Family LOPHOPIDAE Stål, 1866
Genus **Cintux** nov. gen.

Etymology: Generic name is derived from the Gallic word for ordinal numeral "cintux" meaning "the first"; third declension: cintux, cintucis. Gender: masculine.

Type species: *Cintux menatensis* nov. gen., nov. sp. by present designation and monotypy.

Composition: Only type species is known so far.

Diagnosis: *Cintux* differs from other genera of Lophopidae by the following combination of characters: median and lateral carinae of the frons present; lateral margins of the frons present and continuous to fronto-clypeal suture; frons in midline higher than wide; clypeus tricarinate; mesonotum tricarinate, with lateral carinae connected to median carina anteriorly; tegmen with costal area present, with transverse veinlets; costal area narrow at base and distinctly widened apically; costal cell with transverse veinlets; common portion of M_{3+4} and CuA_1 present. Clavus with transverse veinlets.

Description: Head with compound eyes distinctly narrower than pronotum. Vertex in midline shorter than width of head with compound eyes with median carina; vertex in midline shorter than