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.

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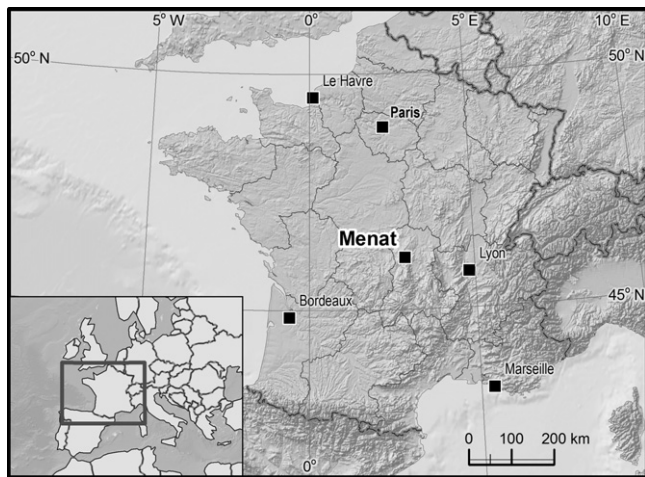
Fig. 1. Map showing the location of Menat fossil site.

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 micro-scope 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 exam-inations 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

wide across the base; anterior margin of vertex straight. Frons with continuous lateral margin, lateral carinae not swollen, connected to median carina below upper margin of frons. Postclypeus tricarinate. Ocelli present. Pronotum tricarinate, with disc protruded; anteriad with margin rounded; anterior margin of pronotal disc reaching anterior margin of compound eye. Mesonotum tricarinate; carinae connected at base. Costal area present, with transverse veinlets along, strongly widened in apical portion. Costal cell with transverse veinlets. Clavus with transverse veinlets. Nodal line absent, membrane with irregular net of veinlets not forming subapical or apical lines. Short common portion of branches M_4 and CuA_1 just basad of half of tegmen length. CuA_2 straight, parallel to CuP, single.

Fore and mid legs not flattened, foliaceous, or very slender. Hind tibia with two lateral spines placed in apical half.

Cintux menatensis nov. gen., nov. sp.
Figs. 2–5
Etymology: Specific epithet refers to the Menat locality.
Type material: Holotype, part and counterpart, type number *MNHN.F.A45773, obverse and reverse compression; specimen labeled '8 MENAT' (dorsal aspect, obverse, and ventral aspect,

reverse), deposited in the collections of the Muséum national d'Histoire naturelle, Paris, France.

Type locality: Menat, département Puy-de-Dôme, France (Fig. 1). The place of find is around the small lake very close to the village of Menat (46° 06′ N; 2° 54′ E), in historical area from which the specimens described by Piton (1936, 1940) come from.

Stratigraphic position: Middle Palaeocene (Selandian), about 60-61 Ma, equivalent to the early Tiffanian Ti-1/Ti-2 land-mammal biozonation sensu Secord et al. (2006), volcano-sedimentary, spongo-diatomite maar (Wappler et al., 2009).

Diagnosis: As for genus as it is the only included species.

Description: Total length about 8.7 mm. Length of tegmen about 6.85 mm, width of tegmen about 3.51 mm, length of clavus about 4.85 mm; Frons in midline about 1.26 mm long, about 0.38 mm wide at upper margin; length of vertex about 0.48 mm, width of vertex about 0.64 mm. Pronotum in midline about 0.54 mm long, mesonotum in midline about 1.52 mm long and about 2.16 mm wide. Hind leg basitarsomere about 0.44 mm long.

Head capsule: angle between the clypeal tangent and the disc of vertex strongly acute. Vertex with anterior and lateral margins carinate; anterior margin straight, lateral margins diverging posteriad, not elevated; posterior margin distinctly excavated;
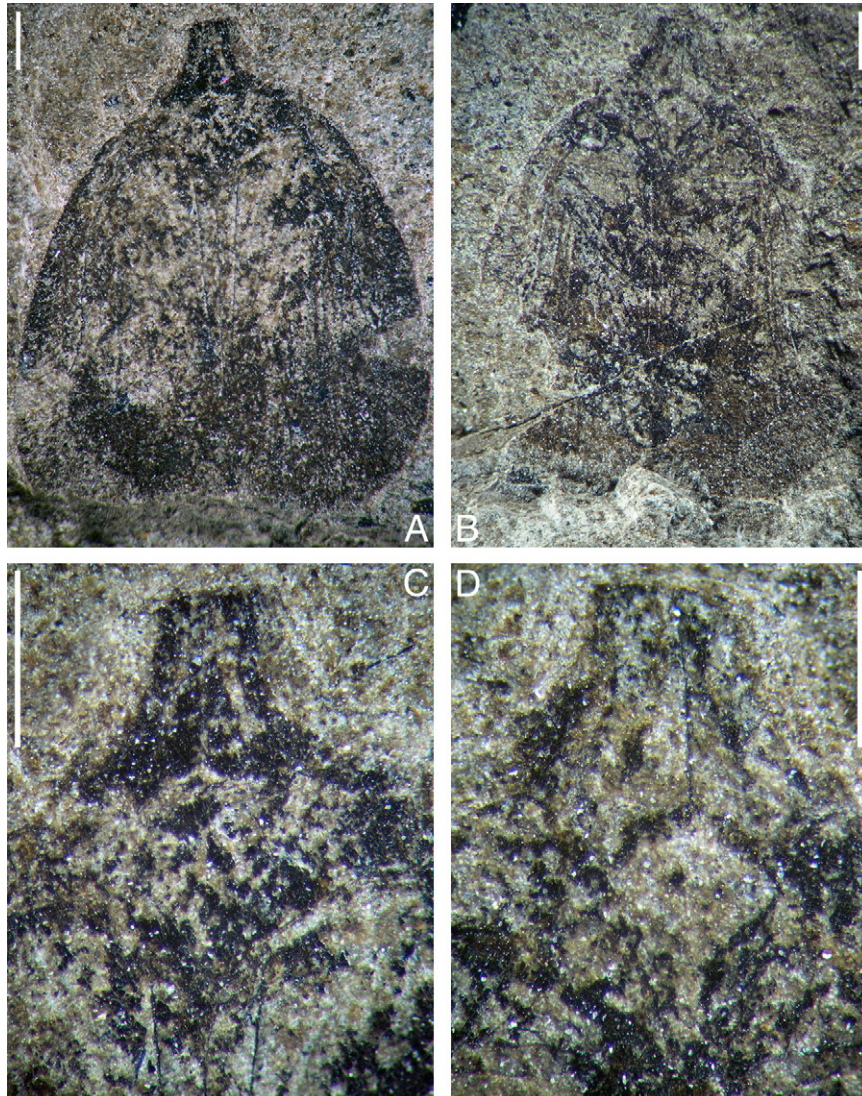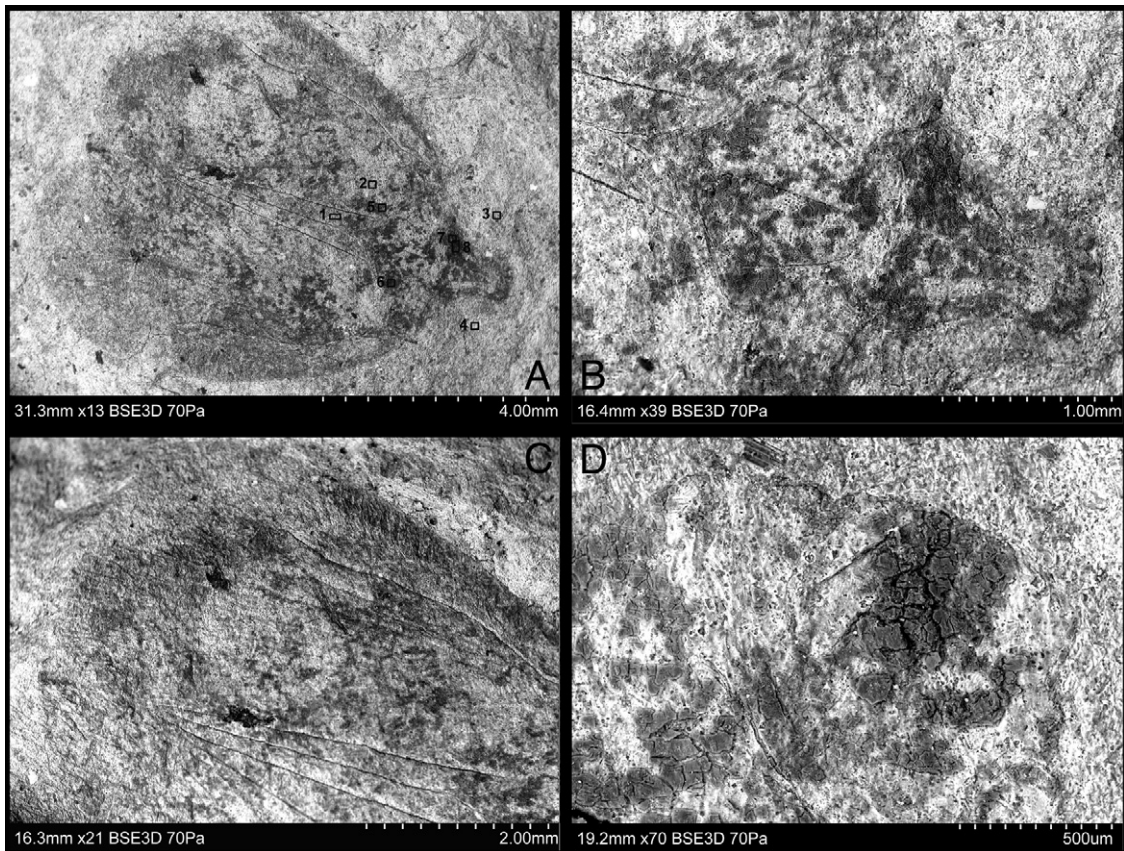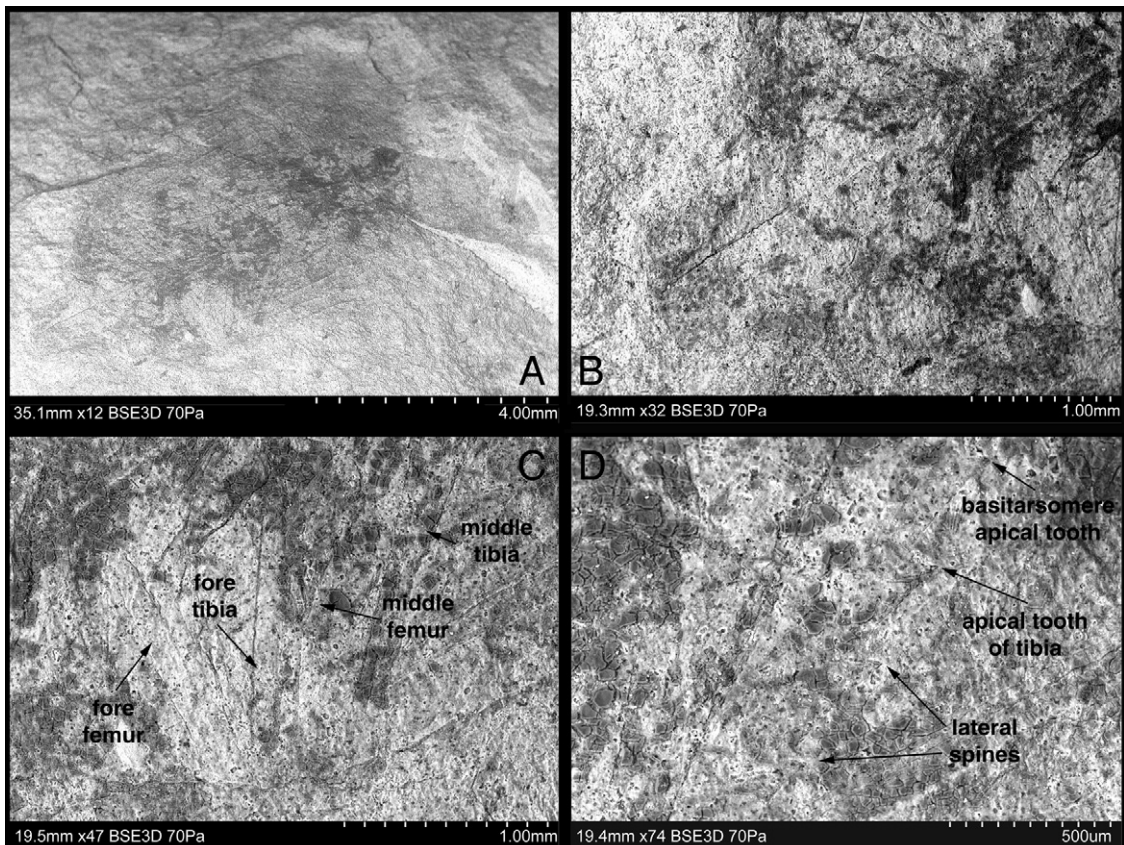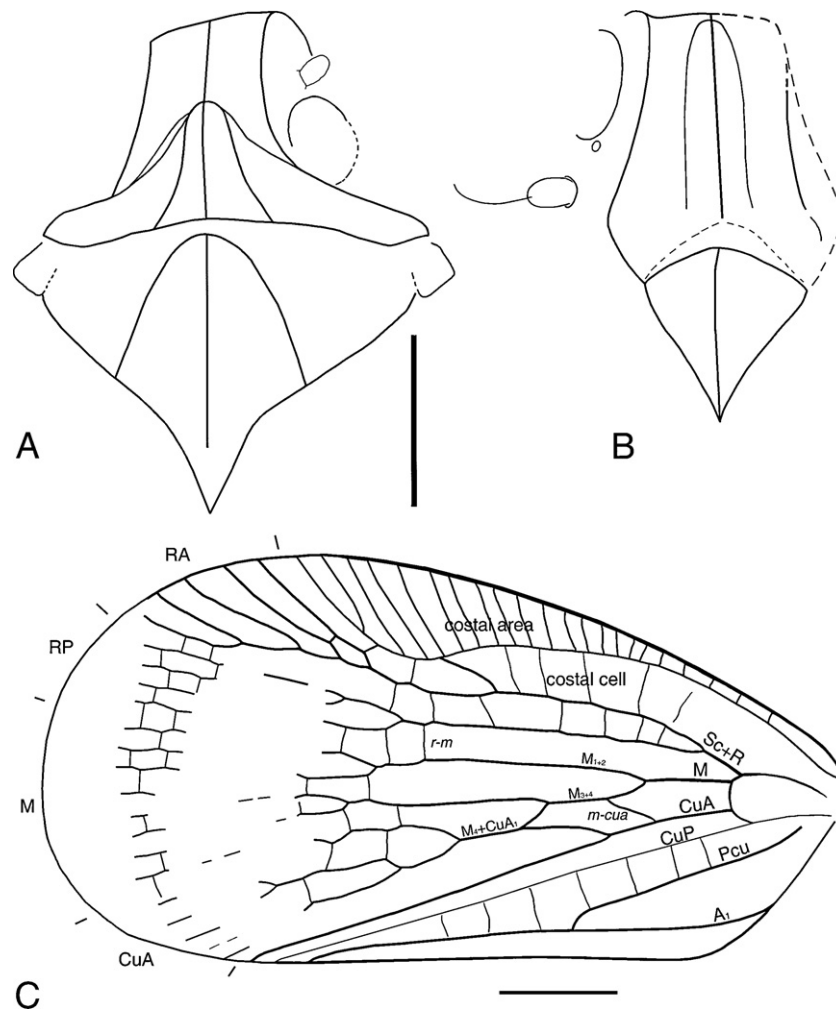

Fig. 2. *Cintux menatensis* nov. gen., nov. sp., light stereomicroscope images. **A.** Specimen, dorsal view. **B.** Specimen, ventral view. **C.** Anterior part of body, dorsal view. **D.** Frons, ventral view. Scale bars: 1 mm.

Fig. 3. *Cintux menatensis* nov. gen., nov. sp., SEM images. **A.** Specimen, dorsal view, with denoted areas selected for EDS analysis. **B.** Anterior part of body, dorsal view. **C.** Tegmina, dorsal view. **D.** Abdomen, ventral view.

Fig. 4. *Cintux menatensis* nov. gen., nov., sp. SEM images, ventral view. **A.** Specimen. **B.** Anterior part of body. **C.** Legs. **D.** Hind tibia and basitarsomere.

Fig. 5. *Cintux menatensis* nov. gen., nov. sp. **A.** Anterior portion of body, dorsal view. **B.** Frons, ventral view. **C.** Tegmen (partly reconstructed), with venation nomenclature. Scale bars: 1 mm.

median carina of vertex distinct, reaching anterior margin of disc; disc of vertex flat. Frons higher than wide, upper margin straight, disc of frons flat, lateral margins carinate, subparallel in upper portion then strongly diverging, angulately rounded in lower ¼ and then distinctly converging; median carina distinctly elevated, almost reaching to frontoclypeal suture; lateral carinae weakly visible, arcuately converging mediad, connected to median carina merely below upper margin of frons, then almost parallel not reaching frontoclypeal suture and ending at about level of median carina apex. Area above frontoclypeal suture delimited by transverse tumosity, then slightly excavated; frontoclypeal suture arcuate, distinct. Compound eyes slightly bulging. Antenna with pedicel longer than its diameter.

Thorax: Pronotum with anterior margin distinctly protruded, posterior margin shallowly concave, disc of pronotum elevated, delimited by weak lateral carinae; median carina of pronotum distinct, median and lateral carinae reaching posterior margin. Mesonotum transverse, wider than long in midline, subtriangular, with elongated scutellum, lateral angles placed closely to posterior margin of pronotum; median carina distinct, reaching to scutellum, lateral carinae connected at base with median carina, arcuately diverging posteriad, reaching to posterior margin of mesonotum.

Legs: Fore and mid femur massive, with carinate margins, subquadrate in cross-section. Fore tibia about as long as fore femur, with carinate margins, subquadrate in cross-section. Mid tibia

slightly longer than mid femur. Hind femur slightly longer than fore and mid femora, more robust. Hind tibia longer than hind femur, with two closely placed lateral spines in apical portion, apex lateral teeth strong. Basitarsus with apical lateral teeth huge, elongate, about 1.9 times as long as cumulative length of mid and apical tarsomeres; mid and apical tarsomeres of similar length, mid tarsomere devoid of lateral teeth, shallowly excavated at apex.

Wings: Tegmen about twice as long as wide, costal margin thickened, weakly curved to apical angle; apical angle wide, posterior margin arcuate, with apex of tegmen at middle, claval angle widely rounded, tornus (postclaval margin) straight, short; apex of clavus exceeding ⅔ of tegmen length. Costal area present, very narrow at basal ⅓ of tegmen length, then widening, strongly widened at apex, with transverse veinlets along the margin; apex of costal area exceeding ⅔ of tegmen length, reaching level of claval apex. Costal cell with transverse veinlets. Basal cell about twice as long as wide. Stem Sc + R leaving basal cell as single, thick stalk; first forking basad of stem M forking, branch ScRA thick, terminal $ScRA_1$ thick, oblique, reaching curvature of veins Pc + CP (costal area); vein RA reaching apical angle, with 6 terminals; branch RP forked basad of claval apex, then forking on membrane, probably with 5 terminals. Stem M forked slightly apicad of stem Sc + R forking, branch M_{1+2} forked distinctly apicad of branch M_{3+4} forking; vein M reaching margin probably with 6 terminals. Stem CuA forked slightly apicad of stem M forking, basad of claval veins junction; branch CuA_1 forked again on corium and membrane,

branch CuA_2 single. Cell C1 with transverse veinlets; Cell C3 without transverse veinlets in basal half of tegmen. Oblique transverse veinlet m_{3+4}-cua present, slightly apicad of stem M forking and basad of stem CuA forking. Nodal line absent, irregular transverse veinlets at level of nodal line present. Membrane with irregular transverse veinlets not forming subapical or apical lines. Short common part of branches M_4 and CuA_1 on corium, just basad of half of tegmen length. Clavus long, exceeding ⅔ of tegmen length, with transverse veinlets between CuP and Pcu and Pcu + A_1; claval veins Pcu and A_1 jointed slightly basad of half of clavus length. Hind wing about ¾ as long as tegmen.

Genital structures: Male, anal tube twice as long as wide. Other structures carbonized, difficult to interpret.

5. Discussion

Cintux nov. gen. cannot be placed in the generic groups proposed and defined by Soulier-Perkins (1998, 2000), which are defined by characters of legs and internal genital structures. The specimen described above preserves only a few leg characters, not sufficient for placement in the generic groups, and no details of genital structures are available for taxonomic placement of this fossil. However, *Cintux* nov. gen. shares some relevant features with various recent genera of Lophopidae. All of them are present as independent characters in the generic groups: Cariona, Makota[+], Sarebasa[+] and Bisma[+] (Soulier-Perkins, 1998, 2000, 2001). A distinctive character of *Cintux* nov. gen. is the connection of the lateral carinae of the mesonotum, present only in *Silvanana*, recently transferred to Ricaniidae (Gnezdilov, 2009).

The taxonomic diversity of the Lophopidae comprises 43 genera and over 140 recent and extinct species. The first fossil representative of Lophopidae found in Europe was *Baninus thuringiorum* Szwedo and Wappler, 2006, from the Messel Maar Lagerstätte, aged Lower Lutetian (Eocene, about 48 Ma), and placed in the Bisma[+] group of genera (Szwedo and Wappler, 2006). Two more fossils of Lophopidae were recently reported by Petrulevičius et al. (2010). One, from the Upper Palaeocene Fur and Ølst Formations in Denmark (aged about 55 Ma), was placed formerly by Rust (1999: 147–149) in the Fulgoridae genus *Lycorma* Stål, 1863. The second specimen is reported from the Lower Eocene (Ypresian, dated 51.6 Ma) Laguna del Hunco, Patagonia, Argentina. The taxonomic position of these fossils is uncertain, as they were assigned to the Bisma[+] group (Petrulevičius et al., 2010), but they also bear the salient features of the Sarebasa[+] group. Recently, another genus was added to the list of European fossil Lophopidae–*Ordralfabetix sirophatanis* Szwedo, 2011 from the Lowermost Eocene Oise amber, aged 53 Ma (Szwedo, 2011). This fossil was also suggested to be placed in the Sarebasa[+] group, but requires testing with a cladistic analysis of fossil and recent Lophopidae and their venational characters. The characters of *Cintux* nov. gen. do not allow its ready assignment to recently recognized generic groups within Lophopidae as most of them are based on leg and genital features (Soulier-Perkins, 1998, 2000, 2001).

Cintux menatensis nov. gen., nov. sp. is the oldest representative of Lophopidae. The occurrences of Lophopidae in the Palaeocene deposits of Europe: mid Palaeocene Menat Formation, France (ca. 61-60 Ma), Late Palaeocene Fur Formation, Denmark (55-54 Ma), Lowermost Eocene Oise amber, France (53 Ma) and Mid Eocene Messel Maar, Germany (49-47.5 Ma) provide a basis for reviewing the previously proposed evolutionary and biogeographic scenario (Soulier-Perkins, 2000). The presented paradigm was that Lophopidae originated ca. 65 million years ago somewhere in southeast Asia (Soulier-Perkins, 2000; Szwedo and Soulier-Perkins, 2010). This opinion is supported by Shcherbakov's (2006) statement that the earliest 'higher' Fulgoroidea are recorded just above the Cretaceous/Palaeogene boundary, in the Early Palaeocene. On the other hand, recent findings of the highly derived family Weiwoboidae in the Palaeocene/Eocene deposits of China (Lin et al., 2010), and the highly diverse fauna of 'higher' planthoppers in the Palaeogene of Europe (Szwedo et al., 2004; Szwedo and Wappler, 2006; Szwedo and Stroiński, 2010; Stroiński and Szwedo, 2011) suggest an earlier (Upper Cretaceous?) diversification of these lineages. It could be assumed that Lophopidae separated from the 'higher' Fulgoroidea stem-group in the mid- to Upper Cretaceous, together with other groups, in response to the mid-Cretaceous re-organisation of the biosphere, ca. 100 Mya (Rasnitsyn, 1988; Szwedo, 2008; Szwedo and Soulier-Perkins, 2010).

Evolutionary patterns in the biogeography and host plant association of Lophopidae were discussed by Soulier-Perkins et al. (2007). New findings of fossil Lophopidae in the European deposits challenged the biogeographic scenario proposed by Soulier-Perkins (2000), and a new hypothesis was recently discussed (Szwedo and Soulier-Perkins, 2010). Rapid Asia-Europe-North America geographic dispersal during the Palaeocene-Eocene Thermal Maximum (PETM) is postulated for Lophopidae. This could be substantiated by the patterns observed in other groups of plants and animals (Sanmartín et al., 2001; Smith et al., 2006a; Cuenca et al., 2008). The ancestor of the family was postulated as feeding on palms, Arecaceae (Arecales), with two later changes of evolutionary lineages to Poaceae (Poales) and to Musaceae (Zingiberales). Australasian origins of Arecaceae (Harley, 2006) is in congruence with this hypothesis of the biogeographical origin of Lophopidae (Soulier-Perkins, 2000; Soulier-Perkins et al., 2007).

6. Preservation properties of the fossil

X-ray EDS spectrometric analysis of the specimen (part and counterpart, obverse and reverse compressions) revealed differences in the elemental composition of the 'light' and 'dark' areas (Fig. 3(A)). The light portion contains distinctly less amount of carbon (weight %). Silicon shows the converse, while a less distinct difference is observable in oxygen and iron ratios, and the other elements found are less regularly distributed (Table 1).

The chemical differences of darker fragments (more rich in carbon) and lighter (more rich in silicon), under SEM examination,

Table 1
Weight percentage (calculated weight concentration expressed as percentage for an element in the sample) of elements recorded in 'light' (pt 1-4) and 'dark' (pt 5-8) areas of specimen (Fig. 3(A)) under Low Vacuum SEM conditions.

	C	O	Mg	Al	Si	S	K	Ca	Ti	Fe
Menat Loph obverse_pt1	32.83	46.19	–	0.65	19.33	0.68	0.05	–	–	0.27
Menat Loph obverse_pt2	30.47	46.56	–	0.78	21.27	0.56	–	–	0.14	0.21
Menat Loph obverse_pt3	26.54	49.95	–	0.96	21.65	0.31	0.09	0.11	0.16	0.23
Menat Loph obverse_pt4	27.54	49.17	0.07	0.81	21.62	0.37	–	0.05	0.16	0.23
Menat Loph obverse_pt5	52.21	34.36	–	0.72	10.94	0.92	0.07	0.10	0.15	0.53
Menat Loph obverse_pt6	55.56	32.91	–	0.63	9.11	1.10	–	–	0.16	0.53
Menat Loph obverse_pt7	52.36	36.15	–	0.70	9.00	0.99	–	0.05	0.23	0.52
Menat Loph obverse_pt8	52.89	35.91	–	0.60	9.10	0.87	–	0.08	0.15	0.41

could be explained by the formation of biofilms (O'Brien et al., 2002, 2008), i.e., diatom mucus mats, during the process of fossilization. These biofilms originated during intervals of rapid diatom growth in the lacustrine environment. Siliceous volanic ash from the nearby areas was weathering to smectite clay and washed into the maar. This resulted in enrichment of dissolved silicon in the water, promoting diatom growth and culminating in a "bloom". Diatom blooming was triggered by chemical change and resulted in the production of a biofilm consisting of a mucus mat with embedded remains of organisms. Insects accumulating on the lake surface were entrapped on these mats, and sank to the maar bottom. The mechanisms and detailed analyses of such a mode of preservation were discussed several times, in respect to fossils from various sites (e.g., Harding and Chant, 2000; O'Brien et al., 2002, 2008; Toporski et al., 2002; Gupta et al., 2007; Allison et al., 2008; McNamara et al., 2010). Notwithstanding, our understanding of the taphonomy of planthoppers from Menat is still far from complete.

Better knowledge of the fossil record is improving our understanding of insect evolution, diversity patterns, and palaeoenvironments (Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005; Zherikhin, 2008). However, we have begun only recently to understand preservational biases that may influence some of the apparent patterns within the record. Attempts to understand preservation bias in the insect fossil record have focused on insect ecology, the chemical components of decomposition, and the influence of the depositional environment. A few experimental studies have been conducted to investigate modes of burial (e.g., Martínez-Delclòs et al., 2004; Smith and Moe-Hoffman, 2007; Smith et al., 2006b; Zherikhin, 2002, 2008; Archibald et al., 2010 and references cited herein). Taphonomic studies are important for evaluating what factors influence insect accumulation and preservation, and for using data on fossil insects more effectively in palaeobiological analyses. The understanding of preservational biases is of great importance for determining the limitations of insect fossil data, and for distinguishing between true patterns of the fossil record and its preservational artifacts.

Acknowledgements

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