

NEW PLANTHOPPERS (INSECTA: HEMIPTERA: FULGOROMORPHA) FROM THE MIDDLE EOCENE MESSEL MAAR

JACEK SZWEDO¹ and TORSTEN WAPPLER²

¹*Department of Systematics and Zoogeography, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland;
e-mail: szwedo@miiz.waw.pl*

²*Institut für Paläontologie, Universität Bonn, Nussallee 8, D-53115 Bonn, Germany;
e-mail: twappler@uni-bonn.de*

Abstract.— Three new genera of extinct Dictyopharidae, Lophopidae and Eurybrachyidae respectively are described. *Wedelphus* **gen. nov.** with *Wedelphus dichopteroides* **sp. nov.** placed in Dictyopharidae, *Baninus* **gen. nov.** with *Baninus thuringiorum* **sp. nov.** of the family Lophopidae and *Amalaberga* **gen. nov.** with *Amalaberga ostrogothiorum* **sp. nov.** placed in Eurybrachyidae (first fossil record of the family) are described, all from deposits of the Grube Messel Lagerstätte in Germany. A representative of an unrecognised family, possibly related to *Henriksenopterix* Petrulevičius, 2005 is reported. The oil shales of the Messel maar in Hessen are well known for their extremely rich fossil flora and fauna. They are of Lower Middle Eocene age (about 48 million years) and contain a highly diverse insect fauna.



Key words.— Hemiptera, Fulgoromorpha, Dictyopharidae, Lophopidae, Eurybrachyidae, Nogodinidae, Ricaniidae, *Wedelphus*, *Wedelphus dichopteroides*, *Baninus*, *Baninus thuringiorum*, *Amalaberga*, *Amalaberga ostrogothiorum*, new genera, new species, Palaeogene, Lower Middle Eocene, Messel maar, insect fossils.

INTRODUCTION

The Messel maar is located close to the small village of Messel, about 9 km NE of Darmstadt (Hessian State, South Germany). It is an ancient open-cast mine in which oil shales were quarried until the end of 1971. These oil shales originated from sludge deposits at the bottom of a freshwater lake that existed *circa* 48 million years ago. The locality was inscribed into the World Heritage List of UNESCO in 1995, mainly because of its mammalian fossils, which became world famous because they are frequently completely articulated and exhibit excellent soft-tissue preservation. There is also an important record of fossil insects which comprises a highly diverse fauna of primarily

terrestrial insects (e.g., Lutz 1990, 1991, Hörnschemeyer 1994, Hörnschemeyer and Wedmann 1994, Richter and Wedmann 2005, Wedmann and Hörnschemeyer 1994, Tröster 1991, 1992a, 1993a, b, c, 1994a, b, 1999, Wedmann 1994, Wappler and Engel 2003).

A small number of hemipteran insects have so far been reported from the Messel maar: Fulgoromorpha: Dictyopharidae (Wappler 2004), Gerromorpha (Wappler and Andersen 2004), Cimicomorpha (Wappler 2003, 2006) and Pentatomorpha (Kinzelbach 1970).

The present paper reports on four specimens of Fulgoromorpha: Dictyopharidae, Lophopidae, Eurybrachyidae and an unrecognised family from the lower Middle Eocene oil shales from Messel.

MATERIAL AND METHODS

The fossil specimens discussed herein are housed in the collections of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF) and Hessian State Museum, Darmstadt (HLMD). The specimens were studied by immersing the slab in glycerine, which is also used to prevent oxidation. All measurements were made by using an ocular micrometer; structures were measured as preserved. The insects of the Messel Formation were embedded in soft, finely laminated organic rich clays that have been compressed strongly during diagenesis (oil-shale). Therefore, they are preserved as compression fossils with only minor relief (e.g., Lutz 1990, Schaal and Ziegler 1992). Biostratigraphically, Messel represents the European Mammal Reference Level MP11 (Franzen 2005). Recently, $^{40}\text{Ar}/^{39}\text{Ar}$ dating of basalt fragments from the diatreme breccia underlying the lake sediments revealed an age of approximately 47.8 Ma (Mertz *et al.* 2004, Mertz and Renne 2005). The stratigraphy of the Messel maar has been briefly summarized in Wappler and Engel (2003).

SYSTEMATIC PALAEOLOGY

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1947

Superfamily Fulgoroidea Kirkaldy, 1907

Family Dictyopharidae Spinola, 1838

Wedelphus gen. nov.

Type species. *Wedelphus dichopteroides* sp. nov. here designated.

Diagnosis. Similar to *Dichoptera* Spinola, 1838 in general appearance but differs in details of tegmen venation. It differs by the rounded apical margin of the frons (acute in *Dichoptera*), distinctly longer clavus, exceeding $\frac{2}{3}$ of tegmen length (about half of tegmen length in *Dichoptera*), longer branch RA, reaching nearly to anterior angle of tegmen (last terminal of RA well basad of anterior angle of tegmen in *Dichoptera*), claval veins fused distinctly apicad of half of clavus length (veins Pcu and A_1 fused at half of clavus length in *Dichoptera*), nodal line arcuate (nearly straight in *Dichoptera*).

Description. Head elongate, narrower than pronotum. Frons flattened, about two times as long in mid line as wide at frontoclypeal suture, arcuate at upper margin, widest slightly below the level of antennae, with lateral carinae distinct, sublateral and median carinae distinct; postclypeus slightly shorter than

frons, with distinct median carina; anteclypeus about half as long as postclypeus with median carina; rostrum exceeding mid coxae. Tegmen semicoriaceous, widest on membrane apicad of apex of clavus. Costal margin thickened, and slightly curved at base, then mildly curved. Costal margin with vein Pc+CP merely separated from CA since the base then joined at claval region. Veins Sc+R and M leaving basal cell with short common stem, Vein ScRA₁ forked slightly apicad of *ir* veinlet of nodal line, RA with 9 terminals reaching nearly to anterior angle of tegmen. Vein RP forked at same level as CuA, then branching on membrane, distinctly apicad of nodal line, with 5 terminals. Vein M first forking distinctly basad of Sc+R and CuA forking, then mediad branch forked again before the nodal line, all three prenodal branches forked at nodal line. Vein CuA forked at level of claval veins junction, posterior branch single anterior branch forked at nodal line then on membrane, with 5 terminals. Clavus long, exceeding $\frac{2}{3}$ of tegmen length; claval vein Pcu and A_1 fused at $\frac{2}{3}$ apicad of clavus length; claval veinlet *cup-pcu* present, at level of branching of mediad branch of vein M. Nodal line of veinlets distinct, arcuate; subapical line of veinlets present.

Etymology. *Wedelphus* – name of the king of Thuringian tribe in the 4th century. Gender: masculine.

Wedelphus dichopteroides sp. nov.

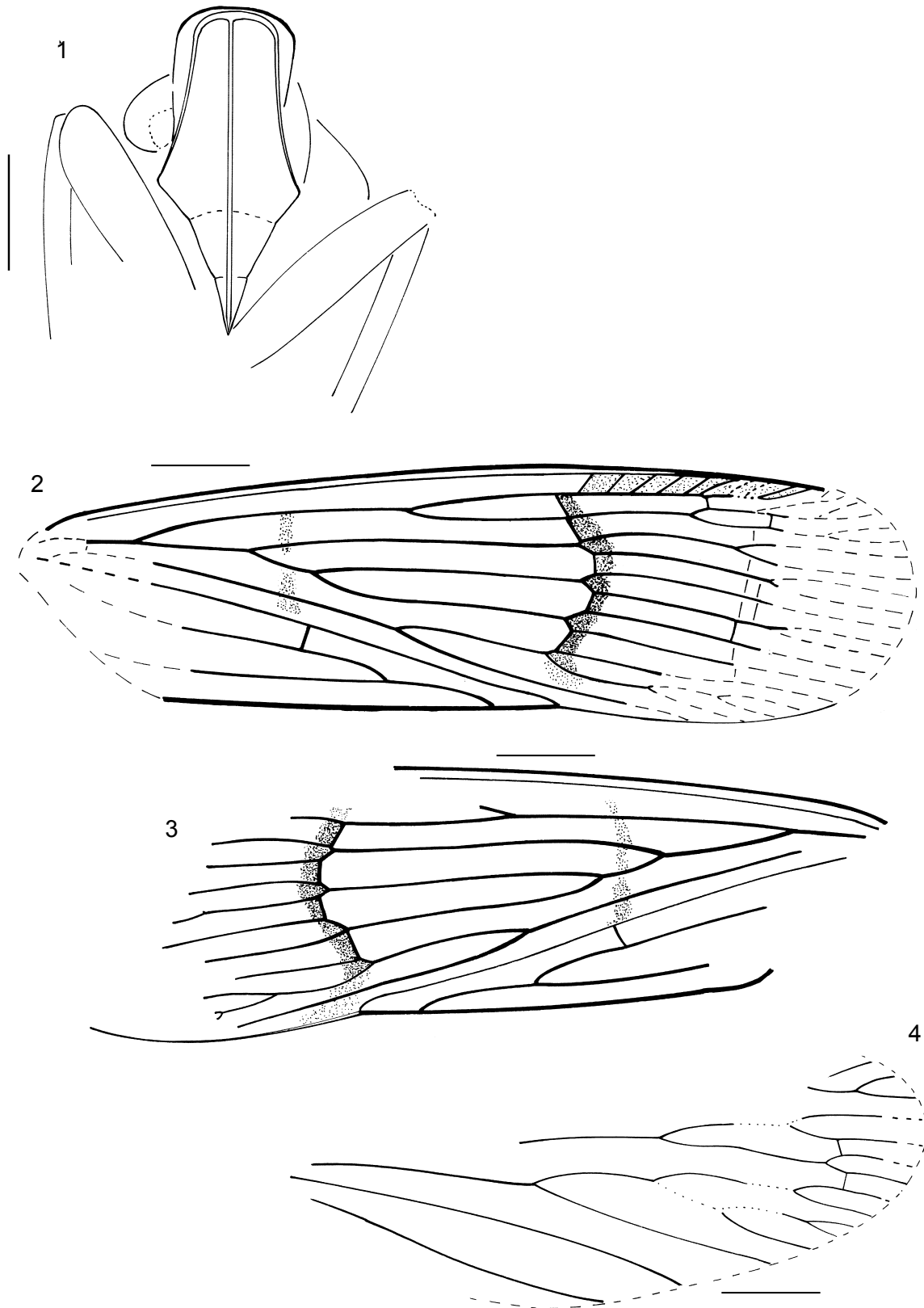
(Figs 1–4, 18)

Diagnosis. Two darker transverse bands on tegmina, first slightly apicad of first forking of vein M, at about $\frac{1}{3}$ of tegmen length, second, darker and wider at level of nodal line, sinuate, at $\frac{2}{3}$ of tegmen length. Hind wing in apical portion hyaline. Vein M on membrane not polymerised, single row of subapical veinlets.

Description. Total length of preserved fragment about 21.1 mm, about 23.5 mm as whole. Frons at widest point between antennae about 1.5 times as wide at upper margin, about 3.6 mm long in mid line. Length of tegmen about 18.7 mm, about 3.5 times as long as wide. Vein ScRA₁ forked slightly apicad of nodal line, vein RA with 9 terminals, vein RP with 5 (?) terminals, vein M with about 10 terminals, vein CuA with 5 terminals. Hind wing with vein RP with 3 visible terminals, vein M with 4 visible terminals, vein CuA with 6 terminals, veins CuP and Pcu single.

Etymology. Specific epithet refers to its similarity to species of the genus *Dichoptera* Spinola, 1838 (Dictyopharidae).

Type material. Holotype: SMF Mel 1512, figured in Lutz (1988: Fig. 103), Tröster (1992b: Plate 1, Fig. 8) and Wappler (2004: Figs 1–3), deposited in Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main. Nearly complete specimen, tarsomeres of



Figures 1–4. *Wedelphus dichopteroides* gen. and sp. nov. (1) Anterior part of the body; (2) left tegmen; (3) right tegmen; (4) left wing. Scale bar 2 mm.

fore and mid legs missing, hind legs missing. Tegmina hyaline with a distinct colour pattern, apical portion not preserved.

Type locality. Grube Messel near Darmstadt (Hessian State, South Germany). Messel Formation.

Stratigraphic distribution. Lower Middle Eocene (Lower Lutetian, ELMA Geiseltalian, MP11, 47.8 Ma).

Remarks. *Wedelphus* gen. nov. is also similar to some representatives of Lophopidae regarding head capsule structure. Costal complex (Dworakowska 1988) with vein Pc+CP merely separated from vein CA and without veinlets between is a feature present in genus *Hesticus* Walker, 1862 removed from Lophopidae and unplaced (Soulier-Perkins 1998). This genus was originally described in Dictyopharidae (Walker 1862, Melichar 1912) but moved to Lophopidae by Muir (1931). The similarity of the specimen described above to the genus *Dichoptera* was raised by Shcherbakov and Popov (2002: 156). It was also described and discussed as "Dictyopharidae gen. et sp. indet." by Wappler (2004).

Family Lophopidae Stål, 1866

Baninus gen. nov.

Type species. *Baninus thuringiorum* sp. nov.

Diagnosis. In general appearance similar to genera *Aluma* Distant, 1909 and *Pseudocorethrura* Melichar, 1915. Differs from *Pseudocorethrura* by vertex shorter in mid line than wide at base (vertex in mid line longer than wide at base in *Pseudocorethrura*); distinct median carina of pronotum (weak in *Pseudocorethrura*); concave posterior margin of pronotum (straight in *Pseudocorethrura*). Differs from *Aluma* by head with compound eyes distinctly narrower than pronotum, about $\frac{1}{2}$ of its width (head with compound eyes about $\frac{3}{4}$ of pronotum width in *Aluma*), and longitudinal veins with short setae. Differs from both genera by shorter clavus, slightly exceeding half of tegmen length (reaching $\frac{2}{3}$ of tegmen length in *Aluma* and *Pseudocorethrura*), only single veinlet connecting CuP and Pcu on clavus (number of veinlets in *Aluma* and *Pseudocorethrura*).

Baninus differs from both genera in coloration, with prevailing portion of tegmen transparent (tegmen coloured in *Aluma* and *Pseudocorethrura*), and by absence of colour eye-spots.

Etymology. *Baninus* – name of the king of the Thuringian tribe during the Early Medieval times. Gender: masculine.

Description. Head with compound eyes narrower than pronotum, about $\frac{1}{2}$ of pronotum width. Vertex in mid line shorter than wide at base. Sublateral carinae

of frons present. Clypeus tricarinate. Median carina of pronotum single, posterior margin of pronotum shallowly concave. Tegmina with short setae along longitudinal veins, with clavus slightly exceeding half of tegmen length. Tegmen with costal margin curved at base, then almost straight, apical portion acutely rounded. Costal field narrow, with transverse veinlets, reaching to the level of clavus apex. Veins Sc+R and M leaving basal cell at same point; vein Sc+R forked at level of CuA forking; vein M forked distinctly anteriorly of claval veins junction, at level of veinlet between veins CuP and Pcu; vein CuA forked slightly posteriorly of claval veins junction, with posterior branch single. Claval veins Pcu and A₁ fused at $\frac{2}{3}$ of length of clavus from base, single veinlet uniting CuP and Pcu present slightly anteriorly of half of clavus length. Hind wing elongate and narrow, about 2.5 times as long as wide. Fore legs with slightly flattened femur. Hind tibia with three lateral spines apically of half of its length and 7 apical teeth; hind basitarsomere elongate with number of apical teeth, probably forming a triangular zone, midtarsomere without apical teeth.

Remark. The genus described above is a member of the *Bisma*+ group of genera (Soulier-Perkins 1998, 2000). This group is recently represented by 17 genera (Soulier-Perkins 1998, 2000), from south-east Asia, New Guinea and Australia.

Baninus thuringiorum sp. nov.

(Figs 5–9, 19, 20)

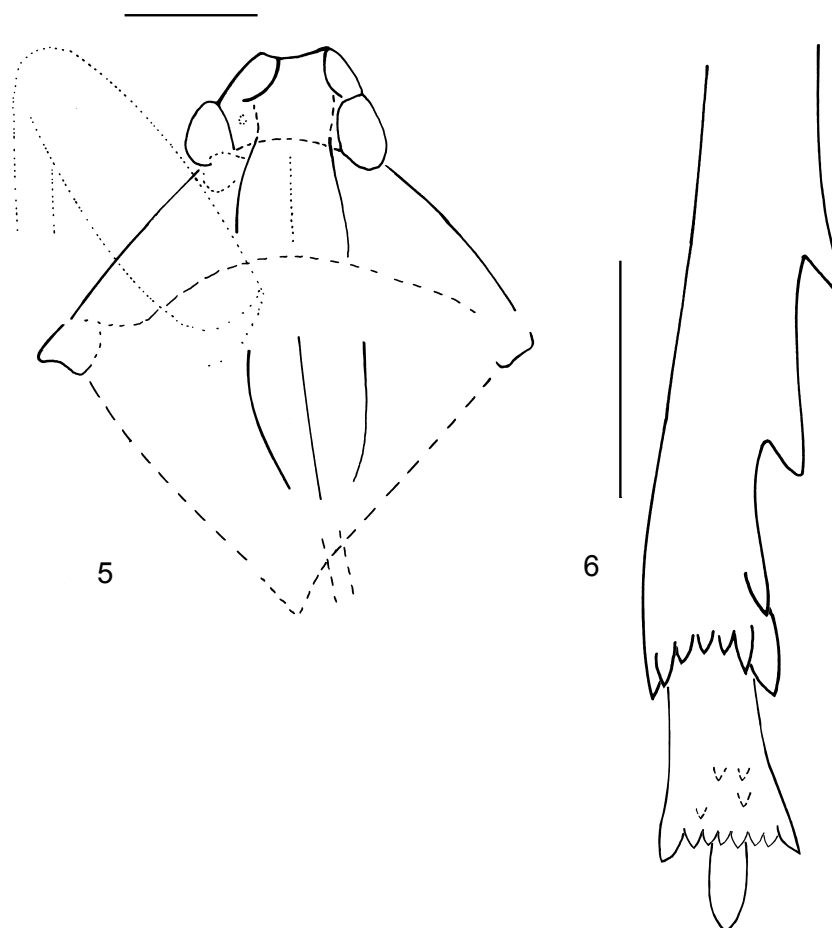
Diagnosis. Tegmina transparent, with darker colour pattern; a transverse narrow band at $\frac{1}{3}$ of its length, second transverse band at half of its length, and darkened apical portion. Tegmen with vein RA with 6 terminals, vein M with 18 terminals, vein CuA with 6–7 terminals. Hind wing with RP with 4 terminals, M with 5 terminals CuA with 6 terminals.

Description. Total length about 13 mm. Length of body about 10.3 mm.

Head with compound eyes about 1.1 mm. Vertex in mid line about 0.5 mm, about 0.7 mm wide at base. Frons with sublateral carinae, about twice as long in mid line as clypeus; clypeus tricarinate; rostrum reaching coxae of mid legs.

Pronotum about 3 mm wide, about 0.8 mm wide in mid line, with median carina, posterior margin slightly convex. Mesonotum about 2.5 mm long in mid line, tricarinate.

Tegmen about 10.5 mm long, about 4 mm wide. Costal margin curved at base, then almost straight, apical portion acutely rounded; clavus slightly exceeding half of tegmen length. Longitudinal veins covered with short setae. Costal field narrow, with transverse veinlets, reaching to the level of clavus apex; costal cell



Figures 5–6. *Baninus thuringiorum* gen. and sp. nov. (5) Anterior part of body; (6) tip of left hind leg. Scale bar 1 mm.

nearly twice as wide as costal field. Veins Sc+R and M leaving basal cell at same point. Vein Sc+R forked at level of CuA forking, branch ScRA₁ forked at level of apex of clavus, RA with 6 terminals; vein RP with 6 terminals on left tegmen, 7 terminals on right tegmen. Vein M forked distinctly anterior of claval veins junction, at level of veinlet between veins CuP and Pcu; anterior branch forked at level of nodal line, posterior branch forked distinctly basad, slightly basad of claval vein junction, vein M with 18 terminals. Vein CuA forked slightly posteriad of claval vein junction, with anterior branch with 5 terminals on left tegmen, 6 terminals on right tegmen, and single posterior branch, i.e. vein CuA with 6–7 terminals. Claval veins Pcu and A₁ fused at $\frac{2}{3}$ of length of clavus from base, single veinlet uniting CuP and Pcu present slightly anterior of half of clavus length. Subapical row of veinlets not regular, not forming a line, not distinct.

Hind wing about 8.5 mm long, elongate and narrow, about 2.5 times as long as wide. Basal cell distinct, veins Sc+R and M leaving basal cell separately. Vein Sc+R forked slightly basad of vein M forking RA with 2 terminals, RP with 4 terminals. Vein M forked at level

of first forking of anterior branch of CuA, with 5 terminals, vein CuA forked basad of Sc+R and M forkings, with 6 terminals. Vein CuP single. Subapical veinlets *r-m*, *m-cu* and *cua-cup* present, apical veinlets *im*, *m-cu* and *icu* present.

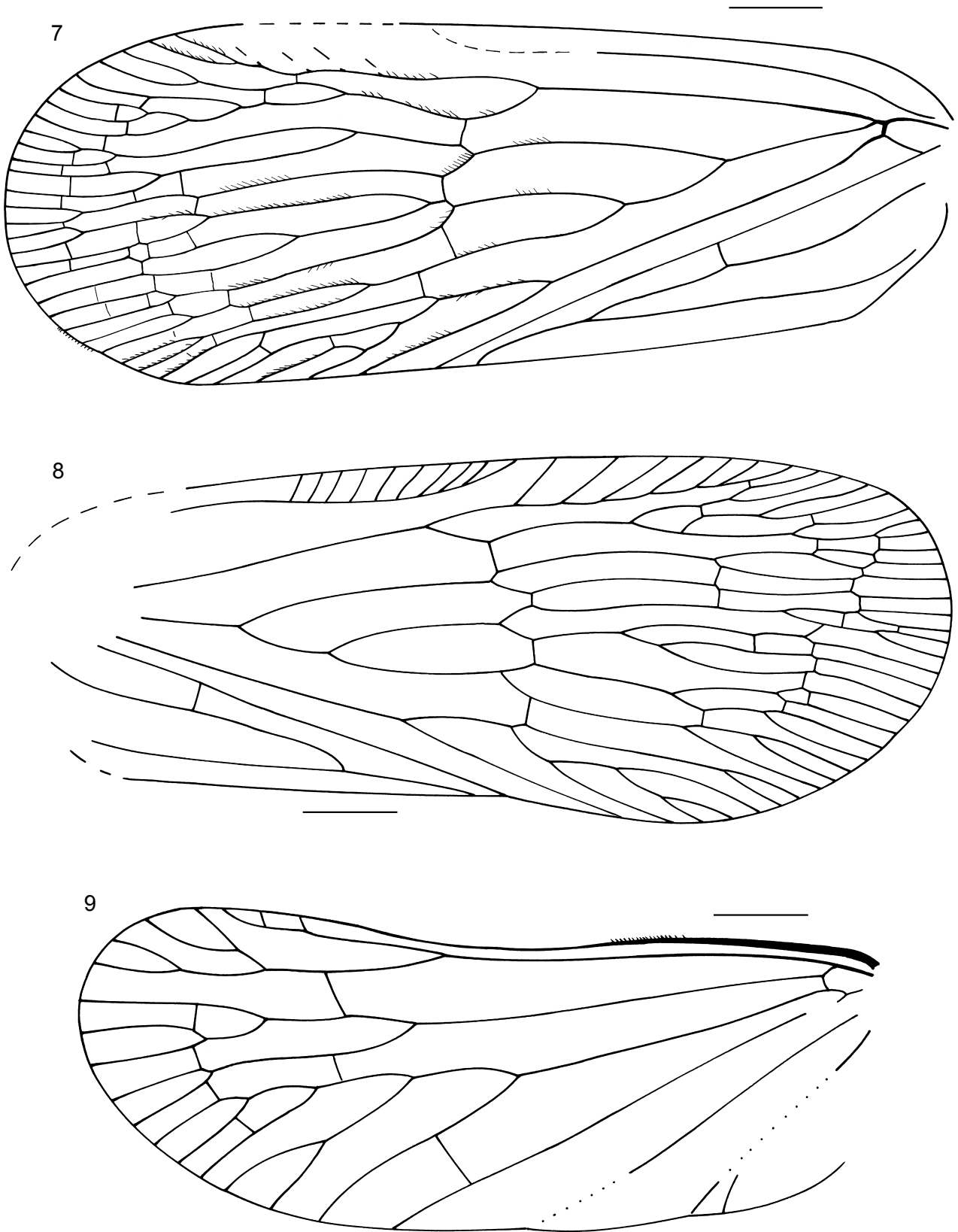
Forelegs with femur slightly widened. Hind tibia with three distinct lateral spines, posteriad of half of its length and 7 apical teeth; tarsus with apical tarsomere missing, basitarsomere elongate, about 0.9 mm long, with number of apical teeth, probably forming triangular zone, 8 apical teeth visible at apex; midtarsomere about 0.4 mm long, without row of apical teeth.

Etymology. The specific epithet is given after the Germanic tribe Thuringii inhabiting area during the Early Medieval times.

Type material. Holotype: male, HLMD-Me-13162, a nearly complete individual, dorsoventrally compressed.

Type locality. Grube Messel near Darmstadt (Hessian State, South Germany). Messel Formation.

Stratigraphic distribution. Lower Middle Eocene (Lower Lutetian, ELMA Geiseltalian, MP11, 47.8 Ma).



Figures 7–9. *Baninus thuringiorum* gen. and sp. nov. (7) Right tegmen; (8) left tegmen; (9) right wing. Scale bar 1 mm.

Remark. The supposed fossil Lophopidae *Scoparidea nebulosa* Cockerell, 1920 was described from Green River Formation, Roan Mountain in Colorado, dated Middle Eocene (Cockerell 1920, Rasnitsyn and Zherikihin 2002, Szweo *et al.* 2004). This fossil presents some characteristics of Lophopidae and suggests the lophopids were present in North America (Soulier-Perkins 2000). It is awaiting redescription, but seems to have nothing in common with *Baninus thuringiorum* gen. and sp. nov. At present Lophopidae are not found in the North America; the genus *Carriona* Muir, 1931 is present in South America – North Peru, Ecuador and Panama (Soulier-Perkins 2000).

Family Eurybrachidae Stål, 1862

Amalaberga gen. nov.

Type species. *Amalaberga ostrogothiorum* sp. nov.

Diagnosis. *Amalaberga* gen. nov. differs from all other Eurybrachidae by the strongly laterally compressed and elongate female genitalia, particularly gonapophysis IX. Tegmen about 2.7 times as long as wide. Wing with vein RP with single terminal. Hind tibia with 3 lateral spines, hind basitarsomere distinctly longer than midtarsomeres, with two rows of apical teeth.

Description. Vertex short, head with compound eyes about as wide as pronotum. Tegmen about 2.7 times as long as wide, anterior portion distinctly curved, costal margin merely concave, apical portion angulately rounded; venation not preserved. Hind wing hyaline, with distinct venation. Vein RP separated from Sc+RA at level of CuA first branching; RA with two terminals, vein RP single; vein M forked apicad of Sc+R and CuA forking, with 4 terminals; vein CuA with 7 terminals; vein CuP single. Hind tibia with three lateral spines and row of 10 apical teeth. Hind basitarsomere with two rows of teeth in apical portion. Gonapophysis IX and gonoplac elongate.

Etymology. *Amalaberga* – name of a niece of Ostrogoth king Theodoric I. Gender: feminine.

Amalaberga ostrogothiorum sp. nov. (Figs 10–16, 21–24)

Diagnosis. Hind wing with RA with two terminal, M with 4 terminals and CuA with 7 terminals. Hind tibia with 3 distinct lateral spines and 10 apical teeth. Basitarsomere with two rows of 6 subapical and 8 apical teeth respectively. Gonapophysis IX elongate with acutely rounded apical portion.

Description. Total length of body 13.1 mm. Head capsule not preserved completely, vertex short, head with compound eyes about as wide as pronotum. Length of tegmen about 12.48 mm. Hind wing hyaline, with veins brownish. Vein RP separated from Sc+RA at level of CuA first branching; RA with two terminals, RP single; vein M forked apicad of Sc+R and CuA forking, with 4 terminals; vein CuA with 7 terminals, differs in forking pattern on left and right wing; the most anterior branch single on right wing, but bifurcate on left wing, median branches bifurcate, the most posterior branch bifurcate at level of *m-cu* veinlet on right wing, and more basad, at level of vein M forking on left wing. CuP single; anal portion of wing not visible. Hind tibia about 6.35 mm long, with three distinct lateral spines and 10 elongate apical spines. Hind basitarsomere about 1.45 mm long, with two rows of teeth in apical portion, 6 subapical teeth and 8 apical teeth; midtarsomere short, about 0.25 mm without teeth, apical tarsomere not preserved. Apical tarsomere of mid leg (?) preserved at side of specimen, about 0.6 mm long, tarsal claws distinct. Pygofer about twice as wide as long. Ovipositor laterally compressed, elongate; gonapophysis IX about 2.1 mm long, with acutely rounded apex. Gonoplac (?) elongate about as long as gonapophysis IX.

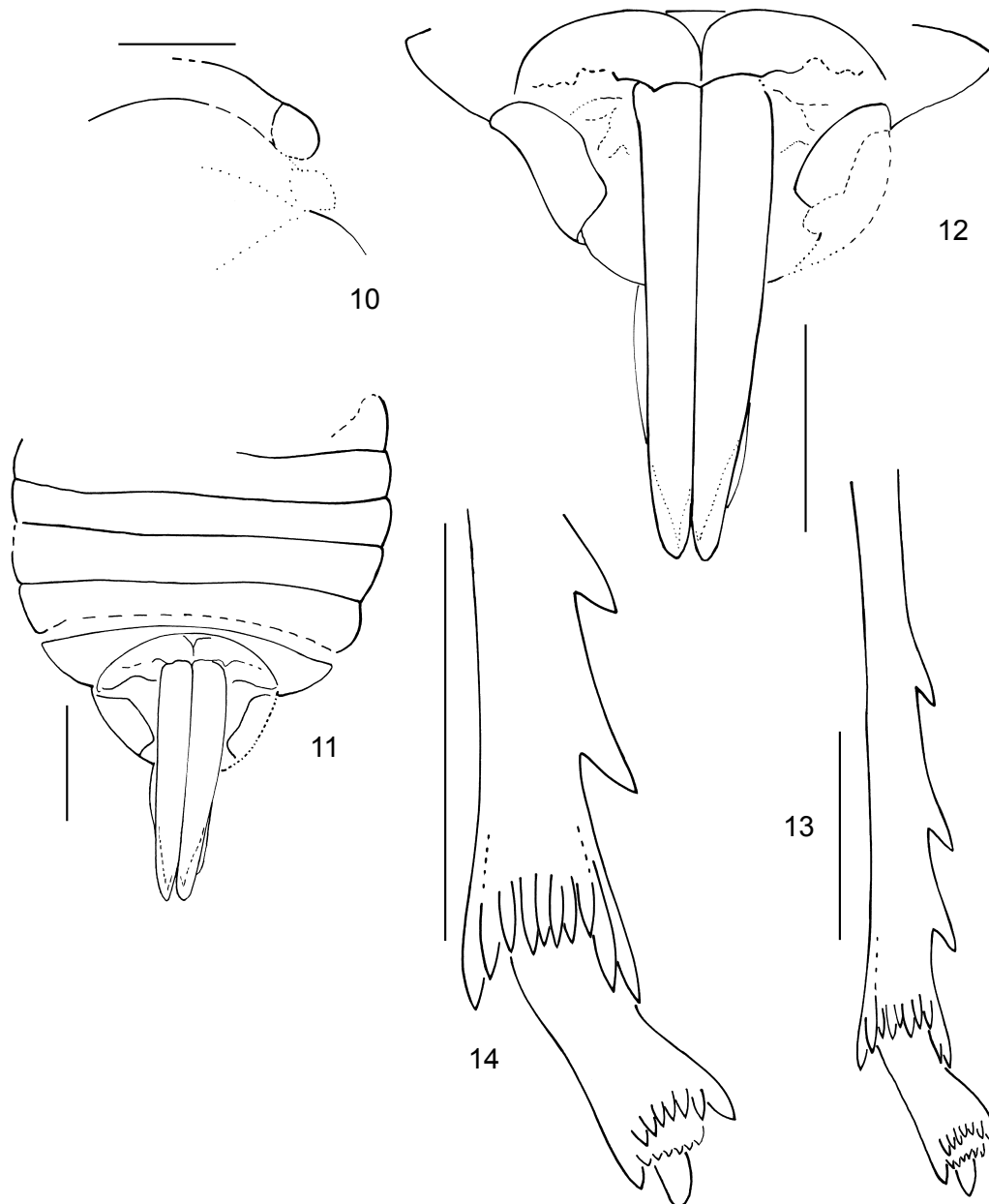
Type material. Holotype: female, HLMD-Me-13193, a nearly complete individual, dorsoventrally compressed.

Type locality. Grube Messel near Darmstadt (Hessian State, South Germany). Messel Formation.

Stratigraphic distribution. Lower Middle Eocene (Lower Lutetian, ELMA Geiseltalian, MP11, 47.8 Ma).

Etymology. The specific epithet is given after the Germanic tribe Ostrogothii inhabiting area during Early medieval times.

Remark. This specimen is a mystery and only tentatively placed in Eurybrachidae on the basis of head capsule, hind leg and wing features. It could be related to Eurybrachidae, but gonapophysis IX is elongate, and visible portions of gonoplac (?) probably also elongate, which is very exceptional among this family. In most Eurybrachidae gonapophysis IX is strongly reduced or absent. An exception is genus *Aspidonitys* Karsch, 1859, with elongate gonapophysis (Soulier-Perkins 2001). In Lophopidae, regarded as relatives of Eurybrachidae, it is reduced, but in Ricaniidae, also believed to be close relatives of Eurybrachidae, it is present, however slightly reduced. Similar conditions is observed in *Hesticus* Walker, 1862 and *Silvanana* Metcalf, 1947, placed once in Lophopidae, but excluded from the family by Soulier-Perkins (1998, 2000, 2001). Regarding the condition of the gonoplac, *Hesticus* and *Silvanana* are characteristic of multilobed gonoplac, while it is bilobed in *Aspidonitys* and Lophopidae, and unilobed in Ricaniidae and Eurybrachidae. Extant



Figures 10–14. *Amalaberga ostrogothiorum* gen. and sp. nov. (10) Anterior part of the body; (11) abdomen in ventral view; (12) ovipositor; (13) right hind tibia; (14) right hind tarsus. Scale bar 1 mm.

Eurybrachidae lay eggs directly on the bark or leaves (Constant, personal communication), so the elongation of the gonoplac and gonapophysis IX could reflect not only phylogenetic relationships but be an adaptative feature. The visible portion of the hind tibia and tarsus also is much more similar to the pattern found in Eurybrachidae. If *Amalaberga ostrogothiorum* gen. and sp. nov. represents Eurybrachidae it is the first fossil record of the family. Global revision of the extant Eurybrachidae is needed in order to fully understand the phylogeny and zoogeography of the family. Recently, Eurybrachidae are known from Afrotropical, Oriental

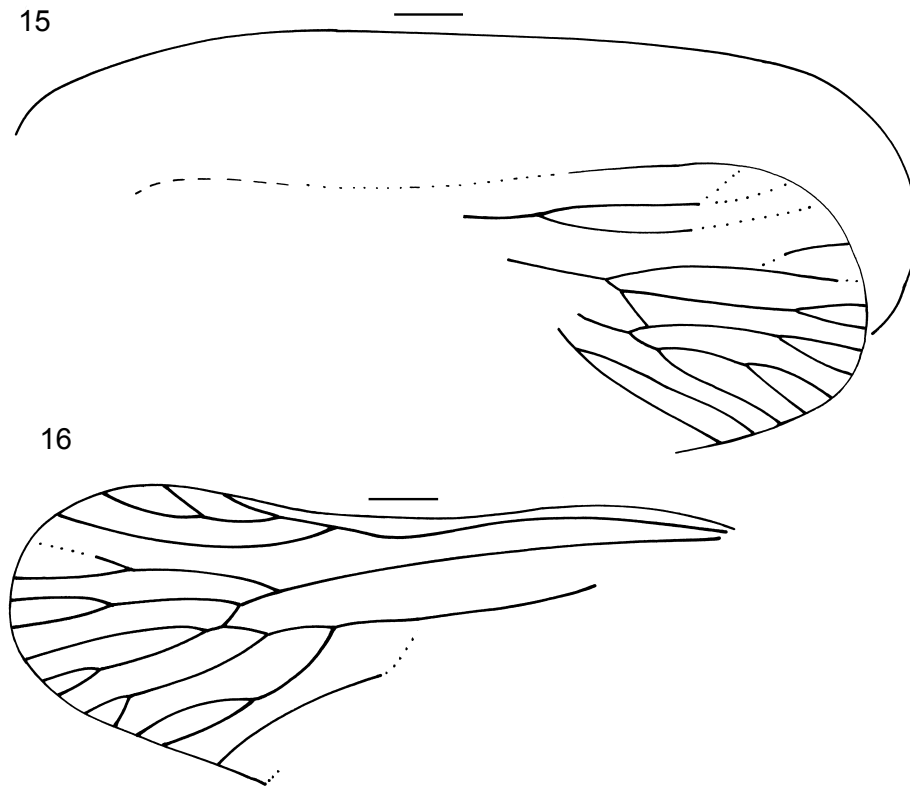
an Australian regions and the present fauna is subject of revisionary studies (Constant 2004, 2005a, b, c, 2006, In press).

Familia indet.

Genus and species indet.

Figs 17, 25

Description. Tegmen about 6.7 mm long, about 2.8 mm wide, elongate, with long clavus. Basal portion of



Figures 15–16. *Amalaberga ostrogothiorum* gen. and sp. nov. (15) Outline of right tegmen and visible portion of wing; (16) visible portion of wing. Scale bar 1 mm.

costal margin distinctly curved, costal margin convex, apical portion elongately rounded; apical line of veinlets present, nodal line present but not distinct. Costal area about twice as wide as costal cell with transverse veinlets. Veins Sc+R and M leaving basal cell at same point. Common stem of Sc+R short. Vein Sc+RA forked at level of CuA forking, RA with 6 terminals; vein RP forked at level and apicad of nodal line, with 11 terminals. Vein M forked basad of RP and CuA forkings, with 11 terminals. Vein CuA forked at level of ScRA forking, with 4 terminals. First veinlet *r-m* present, short, slightly oblique.

Material examined. Isolated forewing (with clavus missing), HLMD-Me-13412.

Type locality. Grube Messel near Darmstadt (Hessian State, South Germany). Messel Formation.

Stratigraphic distribution. Lower Middle Eocene (Lower Lutetian, ELMA Geiseltalian, MP11, 47.8 Ma).

Remarks. The familial and generic assignment of this specimen is still of doubt. It could be tentatively placed in Ricaniidae or Nogodinidae, maybe related to the genus *Henriksenopterix* Petrulevičius, 2005 described from the Uppermost Palaeocene deposits of

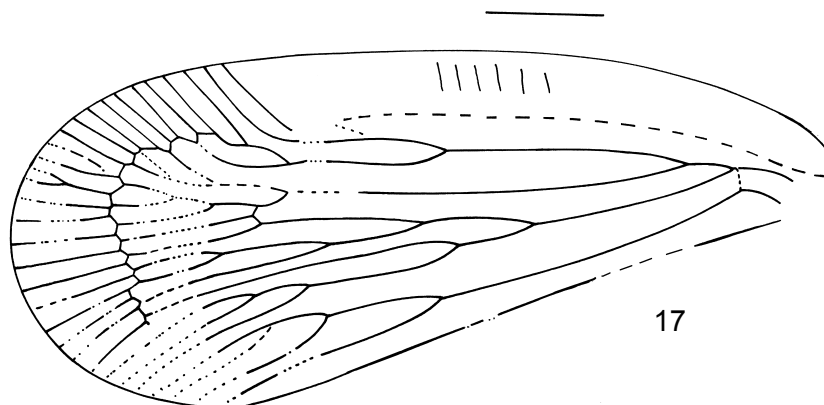
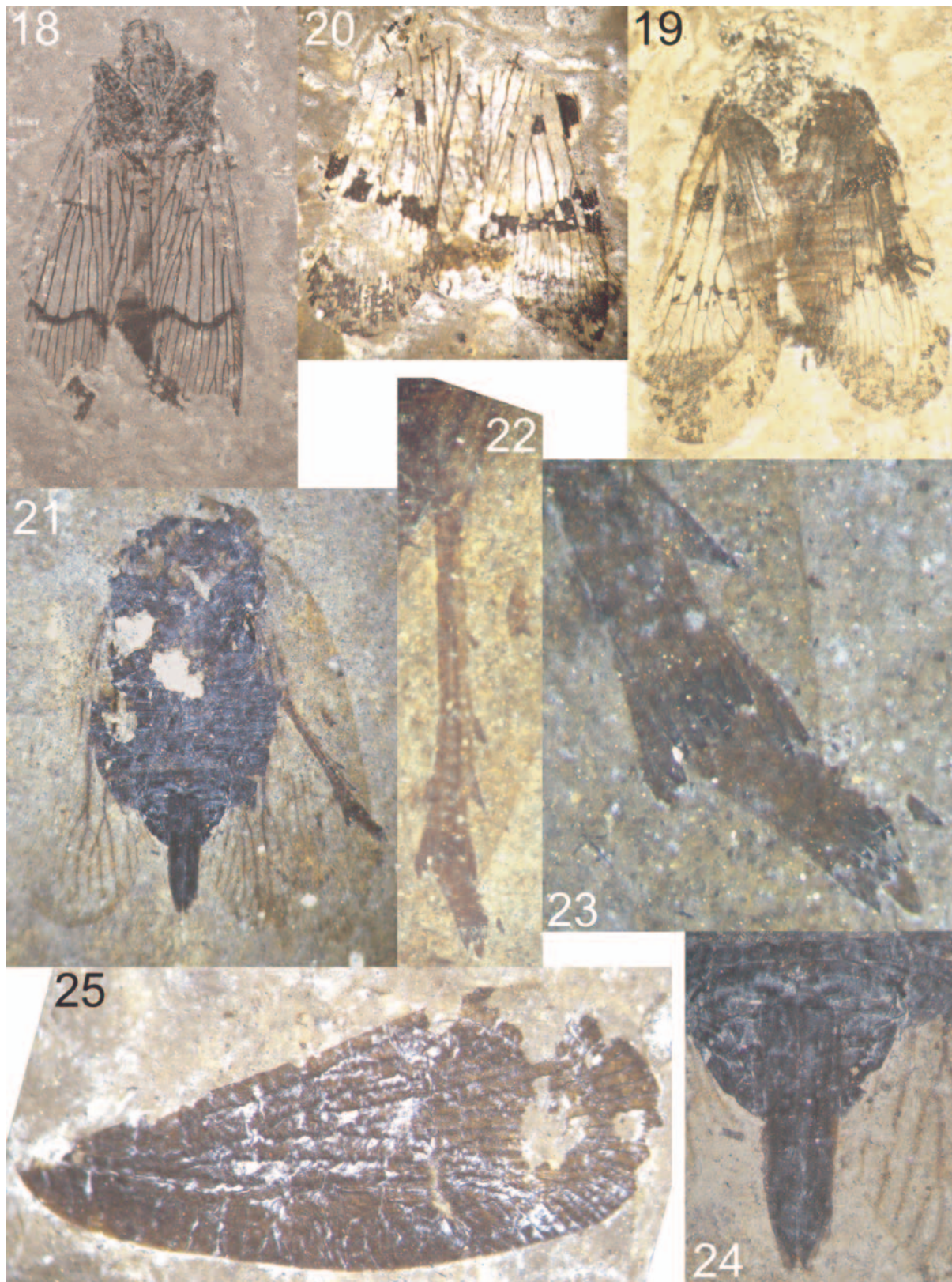


Figure 17. Specimen HLMD-Me-13412; tegmen. Scale bar 1 mm.



Figures 18–25. (18) *Wedelphus dichopterooides* gen. and sp. nov. Holotype SMF Mel 1512; (19) *Baninus thuringiorum* gen. and sp. nov. Holotype HLMD-Me-13162; general view, part (20) counterpart; (21) *Amalaberga ostrogothiorum* gen. and sp. nov. Holotype HLMD-Me-13193, general view; (22) right hind tibia and tarsus; (23) right hind tarsus; (24) ovipositor; (25) specimen HLMD-Me-13412, tegmen.

Jutland in Denmark (Henriksen 1922). *Henriksenopterix paucistriata* (Henriksen, 1922) was placed by Petrulėvičius (2005) in Nogodinidae, based on tegmen shape and venation features, but it calls for re-examination and redescription, and its familial placement is not certain. The specimen HLMD-Me-13412 lacks salient features and due to its fragmentary condition cannot be placed with certainty in Nogodinidae or Ricanidae. Representatives of these two families can be separated based on hind leg and ovipositor features (Emeljanov 1999, Wilson 2005) and tegminal shape and venation characters seem not to be applicable for this purpose (Stroiński, personal communication).

ACKNOWLEDGEMENTS

We thank Dr. N. Micklich, Dr. G. Gruber (both Darmstadt) and Dr. S. Schaal (Frankfurt) for permitting us to study the material described herein. We are grateful to Małgorzata Banaszekiewicz (MIZ PAN, Warszawa), Jérôme Constant (IRScNB/KBIN, Brussels), Lois B. O'Brien (Green Valley, Arizona) for carefully checking the manuscript.

REFERENCES

- Cockerell, T. D. A. 1920. Eocene Insects from the Rocky Mountains. *Proceedings of the U.S. National Museum*, 57(2313): 233–260.
- Constant, J. 2004. Révision des Eurybrachidae (I). Le genre *Amychodes* Karsch, 1895 (Homoptera: Fulgoromorpha: Eurybrachidae). *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 74: 11–28.
- Constant, J. 2005a. Revision of the Eurybrachidae (II). Description of the new genus *Usambrachys*, review of the genera *Harmosma* Fennah, 1964 and *Neoplatybrachys* Lallemand, 1950 and key to the Afrotropical genera (Hemiptera: Fulgoromorpha: Eurybrachidae). *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 75: 29–39.
- Constant, J. 2005b. Revision of the Eurybrachidae (III). The Afrotropical genus *Metoponitys* Karsch, 1890 (Hemiptera: Fulgoromorpha: Eurybrachidae). *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 75: 41–56.
- Constant, J. 2005c. Revision of the Eurybrachidae (IV). The Australian genus *Gelastopsis* Kirkaldy, 1906 (Hemiptera: Fulgoromorpha: Eurybrachidae). *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 75: 57–69.
- Constant, J. 2006. Revision of the Eurybrachidae (VI). The Australian genus *Nirus* Jacobi, 1928 (Hemiptera: Fulgoromorpha: Eurybrachidae). *Annales Zoologici*, 56(2): 305–309.
- Constant, J. (In press). Revision of the Eurybrachidae (V). Description of the new Australian genus *Kirkaldybrachys* Constant (Hemiptera: Fulgoromorpha: Eurybrachidae). *Bulletin de la Société Royale Belge d'Entomologie*.
- Dworakowska, I. 1988. Main veins of the wings of Auchenorrhyncha (Insecta, Rhynchota: Hemelytrata). *Entomologische Abhandlungen Staatliches Museum für Tierkunde Dresden*, 52: 63–108.
- Emeljanov, A. F. 1999. Notes on the delimitation of families of the Issidae group with description of a new species of Caliscelidae belonging to a new genus and tribe (Homoptera, Fulgoroidea). *Zoosystematica Rossica*, 8(1): 61–72.
- Franzen, J. L. 2005. The implications of the numerical dating of the Messel fossil deposit (Eocene, Germany) for mammalian biochronology. *Annales de Paléontologie*, 91: 329–335.
- Henriksen, K. L. 1922. Eocene insects of Denmark. *Denmarks Geologiske Undersøgelse*, 2(37): 1–36.
- Hörschemeyer, T. 1994. Ein fossiler Tenebrionidae *Ceropria? messelense* n. sp. (Coleoptera: Tenebrionidae: Diaperinae) aus dem Mitteleozän der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg*, 170: 75–83.
- Hörschemeyer, T. and S. Wedmann. 1994. Fossile Prachtkäfer (Coleoptera: Buprestidae: Buprestinae) aus dem Mitteleozän der Grube Messel bei Darmstadt, Teil 1. *Courier Forschungsinstitut Senckenberg*, 170: 85–136.
- Kinzelbach, R. 1970. Wanzen aus dem eozänen Ölschiefer von Messel (Insecta: Heteroptera). *Notizblatt des Hessischen Landesamtes für Bodenforschung*, 98: 9–18.
- Lutz, H. 1988. Riesenameisen und andere Raritäten – Die Insektenfauna. *In*: Schaal, S. and W. Ziegler (eds). *Messel – Ein Schaufenster in der Geschichte der Erde und des Lebens*. Senckenbergische Naturforschende Gesellschaft: 55–67.
- Lutz, H. 1990. Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg*, 124: 1–165.
- Lutz, H. 1991. Autochthone aquatische Arthropoda aus dem Mittel-Eozän der Fundstätte Messel (Insecta: Heteroptera; Coleoptera; cf. Diptera-Nematocera; Crustacea; Cladocera). *Courier Forschungsinstitut Senckenberg*, 139: 119–125.
- Melichar, L. 1912. *Monographie der Dictyophorinen*. *Abhandlungen der K.K. Zoologisch-botanischen Gesellschaft in Wien*, 7(1): 1–221.
- Mertz, D. F. and P. R. Renne. 2005. A numerical age fort he Messel deposit (UNESCO World Heritage Site) derived from $^{40}\text{Ar}/^{39}\text{Ar}$ dating on a basaltic rock fragment. *Courier Forschungsinstitut Senckenberg*, 255: 67–75.
- Mertz, D. F., Harms, F.-J., Gabriel, G. and M. Felder. 2004. Arbeitstreffen in der Forschungsstation Grube Messel mit neuen Ergebnissen aus der Messel-Forschung. *Natur und Museum*, 134: 289–290.
- Muir, F. 1931. New and little-known Fulgoroidea from South America. *Proceedings of the Hawaiian Entomological Society*, 7: 469–480.
- Petrulėvičius, J. F. 2005. A plant hopper (Nogodinidae) from the Upper Palaeocene of Argentina: systematics and taphonomy. *Palaeontology*, 48: 299–308.
- Rasnitsyn, A. P. and V. V. Zherikhin. 2002. Appendix: Alphabetic List of Selected Insect Fossil Sites 4.1. Impression Fossils. 437–444. *In*: Rasnitsyn A. P. and D. L. J. Quicke

- (eds.). History of Insects. Kluwer Academic Publishers. Dordrecht/Boston/London, i–xii, 1–517.
- Richter, G. and S. Wedmann. 2005. Ecology of the Eocene Lake Messel revealed by analysis of small fish coprolites and sediments from a drilling core. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 223: 147–161.
- Schaal, S. and W. Ziegler (eds.). 1992. Messel – An Insight into the history of life and of the earth. Clarendon Press, Oxford, 322 pp.
- Shcherbakov, D. E. and Yu. A. Popov. 2002. *In*: Rasnitsyn A. P. and D. L. J. Quicke (eds.). History of Insects. Kluwer Academic Publishers. Dordrecht/Boston/London, i–xii, 1–517. Superorder Cimicidea Laicharting, 1781 Order Hemiptera Linné, 1758. The Bugs, Cicadas, Plantlice, Scale Insects, etc. (= Cimicida Laicharting, 1781, = Homoptera Leach, 1815 + Heteroptera Latreille, 1810): 143–157.
- Soulier-Perkins, A. 1998. The Lophopidae (Hemiptera: Fulgoromorpha): Description of three new genera and key to the genera of the family. *European Journal of Entomology*, 95(4): 599–618.
- Soulier-Perkins, A. 2000. A phylogenetic and geotectonic scenario to explain the biogeography of the Lophopidae (Hemiptera, Fulgoromorpha). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 160: 239–254.
- Soulier-Perkins, A. 2001. The Phylogeny of the lophopidae and the impact of Sexual Selection and Coevolutionary Sexual Conflict. *Cladistics*, 17: 58–78.
- Szwedo, J., Bourgoïn, Th. and F. Lefebvre. 2004. Fossil Planthoppers (Hemiptera: Fulgoromorpha) of the World. An annotated catalogue with notes on Hemiptera classification. Studio 1, Warszawa. 1–208.
- Tröster, G. 1991. Eine neue Gattung der Elateridae (Insecta: Coleoptera) *Macropunctum* gen. n. aus der Messel-Formation des unteren Mittel-Eozän der Fundstelle Messel. *Courier Forschungsinstitut Senckenberg*, 139: 99–117.
- Tröster, G. 1992a. Zur Kenntnis der Gattung *Macropunctum* (Elateridae, Pyrophorinae, Agrypnini) aus der mitteleozänen Fossilagerstätte "Eckfelder Maar" (Eifel) mit der Beschreibung einer neuen Art *Macropunctum eckfeldi* n. sp. *Mainzer Naturwissenschaftliches Archiv*, 30: 111–118.
- Tröster, G. 1992b. Fossile Insekten aus den mitteleozänen Tonsteinen der Grube Messel bei Darmstadt. *Mitteilungen des Internationalen Entomologischen Vereins*, 17(4): 191–208.
- Tröster, G. 1993a. Fossile Schnellkäfer der Gattung *Lanelater* Arnett 1952 (Coleoptera, Pyrophorinae, Agrypnini) aus dem Eozän der Grube Messel bei Darmstadt. *Senckenbergiana lethaea*, 73: 49–60.
- Tröster, G. 1993b. Wasserkäfer und andere Raritäten – Neue Coleoptera-Funde aus dem mitteleozänen Tonsteinen der Grube Messel bei Darmstadt. *Kaupia. Darmstädter Beiträge zur Naturgeschichte*, 2: 145–154.
- Tröster, G. 1993c. Zwei neue mitteleuropäische Arten der Gattung *Tenomerga* Neboiss 1984 aus dem Mitteleozän der Grube Messel und des Eckfelder Maars (Coleoptera: Archostemmata: Cupedidae). *Mainzer Naturwissenschaftliches Archiv*, 31: 169–176.
- Tröster, G. 1994a. Fossile Elateridae (Insecta: Coleoptera) aus dem Unteren Mitteleozän (Lutetium) der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg*, 170: 11–64.
- Tröster, G. 1994b. Neue Arten der Gattung *Macropunctum* (Insecta, Coleoptera, Elateridae) aus der Ölschieferfazies der mitteleozänen Messelformation der Grube Messel bei Darmstadt. *Paläontologische Zeitschrift*, 68: 145–162.
- Tröster, G. 1999. An unusual new fossil click-beetle (Coleoptera: Elateridae) from the Middle Eocene of the Grube Messel (Germany). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1999: 11–20.
- Walker, F. 1862. Characters of undescribed species of Homoptera in the collection of F. P. Pascoe, F.L.S. *Journal of Entomology*, 1: 303–319.
- Wappler, T. 2003. New fossil lace bugs (Heteroptera: Tingidae) from the Middle Eocene of the Grube Messel (Germany), with a catalog of fossil lace bugs. *Zootaxa*, 374: 1–26.
- Wappler, T. 2004. Notes on a plant-hopper (Hemiptera: Fulgoromorpha: Dictyopharidae) from the Middle Eocene Messel maar, Germany. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2004: 694–704.
- Wappler, T. 2006. *Lutetiacader*, a puzzling new genus of cantacaderid lace bugs (Heteroptera: Tingidae) from the Middle Eocene Messel maar, Germany. *Palaeontology*, 49(2): 435–444.
- Wappler, T. and M. S. Engel. 2003. The Middle Eocene bee faunas of the Eckfeld Maar and Messel, Germany (Hymenoptera: Apoidea). *Journal of Paleontology*, 77: 908–921.
- Wappler, T. and N. M. Andersen. 2004. Fossil water striders from the Middle Eocene fossil sites Eckfeld and Messel, Germany (Hemiptera, Gerromorpha). *Paläontologische Zeitschrift*, 78: 41–52.
- Wedmann, S. 1994. Fossile Vertreter der Eucnemidae und Throscidae (Insecta: Coleoptera) aus der mitteleozänen Messel-Formation. *Courier Forschungsinstitut Senckenberg*, 170: 65–73.
- Wedmann, S. and T. Hörnschemeyer. 1994. Fossile Prachtkäfer (Coleoptera: Buprestidae: Buprestinae und Agrilinae) aus dem Mitteleozän der Grube Messel bei Darmstadt, Teil 2. *Courier Forschungsinstitut Senckenberg*, 170: 137–187.
- Wilson, S. W. 2005. Keys to the families of Fulgoromorpha with emphasis on planthoppers of potential economic importance in the southeastern United States (Hemiptera: Auchenorrhyncha). *Florida Entomologist*, 88(4): 464–481.

Received: May 15, 2006

Accepted: August 18, 2006