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Fossil water striders from the Middle Eocene fossil sites of Eckfeld and Messel, Germany (Hemiptera, Gerromorpha)

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with 5 figures and 1 table

Kurzfassung: Wasserläufer (Hemiptera, Gerromorpha) sind eine hochspezialisierte Gruppe von Wasserwanzen, die vorzüglich an das Leben auf der Wasseroberfläche angepasst sind. In der vorliegenden Arbeit werden zwei neue Gattungen und Arten der Gerridae, *Lutetiabates eckfeldensis* n. gen. et n. sp. und *Cylindrobates messelensis* n. gen. et n. sp., aus dem Mittel-Eozän des Eckfelder Maares und der Grube Messel beschrieben. Zudem handelt es sich bei zwei Funden mit einiger Sicherheit um Jugendstadien eines Angehörigen der Gattung *Gerris*. Der Nachweis zwei neuer paläogener Angehöriger der Gerriden und die bislang bekannten Gerromorpha aus fossilen Baumharzen belegen eine eindeutig höhere Diversität von Wasserwanzen im Paläogen Europas als heute. Zudem werden Aspekte der Fossilgeschichte, der Paläobiologie und Paläobiogeografie der Gerridae kurz diskutiert.

Schlüsselwörter: Heteroptera, Gerridae, Mittel-Eozän, Eckfeld, Messel, *Lutetiabates eckfeldensis* n. gen. et n. sp., *Cylindrobates messelensis* n. gen. et n. sp., Paläoökologie.

Abstract: Water striders (Hemiptera, Gerromorpha) are a very distinct ecological group specially adapted for life on the water surface. The present paper reports on four species of Gerromorpha from the Middle Eocene fossil sites of Eckfeld and Messel describing *Lutetiabates eckfeldensis* n. gen. et n. sp., *Cylindrobates messelensis* n. gen. et n. sp. (both Gerridae), and two nymphs most probably of the genus *Gerris*. The record of two new members of Gerridae from the Paleogene as well as the hitherto known Gerromorpha from fossiliferous resins document a distinctly higher diversity of water striders within die European Paleogene than today. Lastly, comments are made on the fossil history as well as on the palaeobiological and palaeobiogeographical significance of the faunas.

Keywords: Heteroptera, Gerridae, Middle Eocene, Eckfeld, Messel, *Lutetiabates eckfeldensis* n. gen. et n. sp., *Cylindrobates messelensis* n. gen. et n. sp., palaeoecology.

Introduction

Gerromorpha comprise about 1.800 extant species classified in eight families (ANDERSEN 1982), commonly called semiaquatic bugs and including the familiar water strider or pondskaters (Gerridae), as well as some less familiar forms. Most of them live on the surface film of freshwater or in the near surroundings of other aquatic and humid terrestrial habitats (ANDERSEN 1982). The phylogenetic relationships between the gerromorph families were analysed and discussed by ANDERSEN (1982, 1998). So far, 38 fossil species belonging to six families of Gerromorpha have been described, spanning more than 120 Ma of geological history (ANDERSEN 1998, 2000, 2001; ANDERSEN & GRIMALDI 2001; PEREZ GOODWYN 2002). Most fossils are of Cenozoic age and only four unequivocal Mesozoic fossils have been recognised (Tab. 1).

The present paper reports on four taxa of Gerromorpha from the Middle Eocene fossil sites of Eckfeld and Messel: two new genera and species of Gerridae and two gerrid nymphs. Although not quite as diverse as the gerromorph palaeofauna in fossiliferous resin, the material from Eckfeld and Messel represents an interesting community of water striders, with evidence of at least two different gerromorph genera, which increase significantly our understanding of Middle Eocene palaeoecology in Europe.

The sediments of both fossil sites consist mainly of "oil-shale", a laminated bituminous clay-stone. This kind of sediment is the result of sedimentation in meromictic lakes under specific morphological conditions (see "Geological setting"). Fossil insects found in the clay-stone deposits from both fossil lagerstaetten belong primarily to terrestrial forms; in particular dominated by beetles which make up over 80 % of all finds at both localities (e.g., LUTZ 1990, 1993). Unfortunately, autochthonous aquatic organisms that could be used as bioindicators are quite rare. This is mainly a result of the chemistry of the monimolimnion which mainly influenced the aquatic flora and fauna. In particular, subaquatic slumpings episodically caused a partial mixing of the mixo- and monimolinion resulting in some degree of poisoning in the upper water body (mixolimnion).

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Tab. 1. Gerromorpha in Mesozoic and Tertiary deposits.

Locality	**Deposit**	**Age**	**Reference**
Mesozoic localities			
Grimmen (northern Germany)	marine	Lower Jurassic (Toarcian)	Popov & Wootton (1977)
Koonwarra bed (Australia)	lacustrine	Lower Cretaceous (Aptian)	Jell & Duncan (1986)
Santana Formation (NE-Brazil)	lacustrine	Lower Cretaceous (Aptian)	Nel & Popov (2000); Perez Goodwyn (2002)
Burmese amber (Myanmar)	amber	Upper Cretaceous (?Cenomanian)	Andersen & Grimaldi (2001); Grimaldi et al. (2002)
Cenozoic localities			
Fur and Ølst formations (Denmark)	marine	Paleocene – Eocene transition	Andersen (1982, 1998)
Havighorst (northern Germany)	marine	Lower Eocene	Illies (1941)
British Columbia (Canada)	lacustrine	Middle Eocene	Wilson (1977, 1978, 1996)
Green River Formation (Wyoming, USA)	lacustrine	Middle Eocene	Scudder (1890); Wilson (1978)
Monte Bolca (northern Italy)	marine	Middle Eocene	Andersen et al. (1994)
Grube Messel (Germany)	lacustrine	Middle Eocene (Lutetian)	Lutz (1990, 1991); **this study**
Eckfelder Maar (Germany)	lacustrine	Middle Eocene (Lutetian)	**this study**
Florissant (Colorado, USA)	lacustrine	Upper Eocene	Scudder (1890); Wilson (1978)
Baltic amber	amber	Eocene (re-deposited in Pleistocene sediments)	Germar & Berendt (1856); Larsson (1978); Schlee (1990); Poinar (1992); Popov (1996); Andersen (2000)
Bitterfeld amber (Germany)	amber	?Eocene (re-deposited in Miocene sediments)	Poinar (1992)
Kleinkemps at Mulhouse (France)	lacustrine	Lower Oligocene	Nel & Paicheler (1993)
Rott am Siebengebirge (Germany)	lacustrine	Upper Oligocene	Statz (1950); Nel & Paicheler (1993)
Enspel (Germany)	lacustrine	Upper Oligocene	Wedmann (2000)
Aix-en-Provence (southern France)	lacustrine	Upper Oligocene	Nel & Paicheler (1993)
Dominican amber (Hispaniola)	amber	Oligocene / Miocene	Andersen & Poinar (1992); Andersen (2001)
Mexican amber (Chiapas)	amber	Oligocene / Miocene	Hurd et al. (1962); Poinar (1992); Grimaldi (1996)
Karagan Formation (northern Caucasus, Russia)	?lacustrine	Miocene	Rasnitsyn & Quicke (2002)
Lunpola Basin (China)	lacustrine	Miocene	Lin (1981)

Geological setting

Eckfeld

The crater of the Eckfeld Maar near Manderscheid, Eifel, Germany, originally had a diameter of 900 m and a depth of about 170 m. The depth of the maar lake initially exceeded 110 m and might have reached 150 m (Pirrung 1992, 1998; Fischer 1999; Pirrung et al. 2001) (Fig. 1). Consequently, its water body was thermally and chemically stratified (meromictic). Anoxic, alkaline conditions and a raised content of electrolytes within the monimolimnion explain the perfect preservation of both the lamination of the oilshale (no bioturbation) and of the fossils (Wilde et al. 1993; Mingram 1998). Up till now more than 30.000 macrofossils have been excavated, all of which document a highly diverse terrestrial flora and fauna (e.g., Neuffer et al. 1996; Lutz et al. 1998; Lutz & Neuffer 2001; Wappler 2002, 2003a; Wappler & Engel 2003; Wilde & Frankenhäuser 1998). These fossils, accurately recovered with their precise stratigraphic position, permit for the first time a correlation between facies and the composition of the insect communities. Nevertheless, it must be mentioned that approximately 84 % of all recovered insects are beetles (Coleoptera).

Biostratigraphically, Eckfeld represents the Middle Eocene mammal reference level MP (Mammal Paleogene) 13 of the European Land Mammal Age (ELMA) Geiseltalian (i. e., Middle Lutetian) (Franzen 1993). Mertz et al. (2000) determined an age of 44.3 ± 0.4 Ma by ^{40}Ar/^{39}Ar dating of basalt from the diatreme breccia underlying the lake sediments. So far, this is the first numerical calibration mark for the terrestrial Eocene in Europe.

Messel

Messel is located on the eastern shoulder of the northern Rhine rift valley. Today, the Messel Pit has a diameter of 700–1000 m (Fig. 1). Despite the fact that Messel's perfectly preserved fossils have been studied for nearly a century (e.g., LUTZ 1990, 1991; HÖRNSCHEMEYER 1994; HÖRNSCHEMEYER & WEDMANN 1994; WEDMANN & HÖRNSCHEMEYER 1994; TRÖSTER 1991, 1992, 1993a, b, 1994a, b, 1999; WAPPLER 2003b), its formation was a matter of considerable debate until only recently (SCHAAL & ZIEGLER 1992; PIRRUNG 1998; LIEBIG & GRUBER 2000; LIEBIG 2002). New geophysical data and evidence from a core drilled in 2001 (HARMS 2002) demonstrate that the Messel locality was a maar like Eckfeld and some other well known European fossil sites (LUTZ et al. 2000, 2001; PIRRUNG et al. 2001), as had previously been proposed by PIRRUNG (1998). However, with an initial diameter of about 1500 m the Messel Maar was considerably larger than the Eckfeld Maar.

Biostratigraphically, Messel represents the European Mammal Reference Level MP 11, thus marking the beginning of the Geiseltalian (i.e., lowermost Lutetian, approximately 49 Ma).

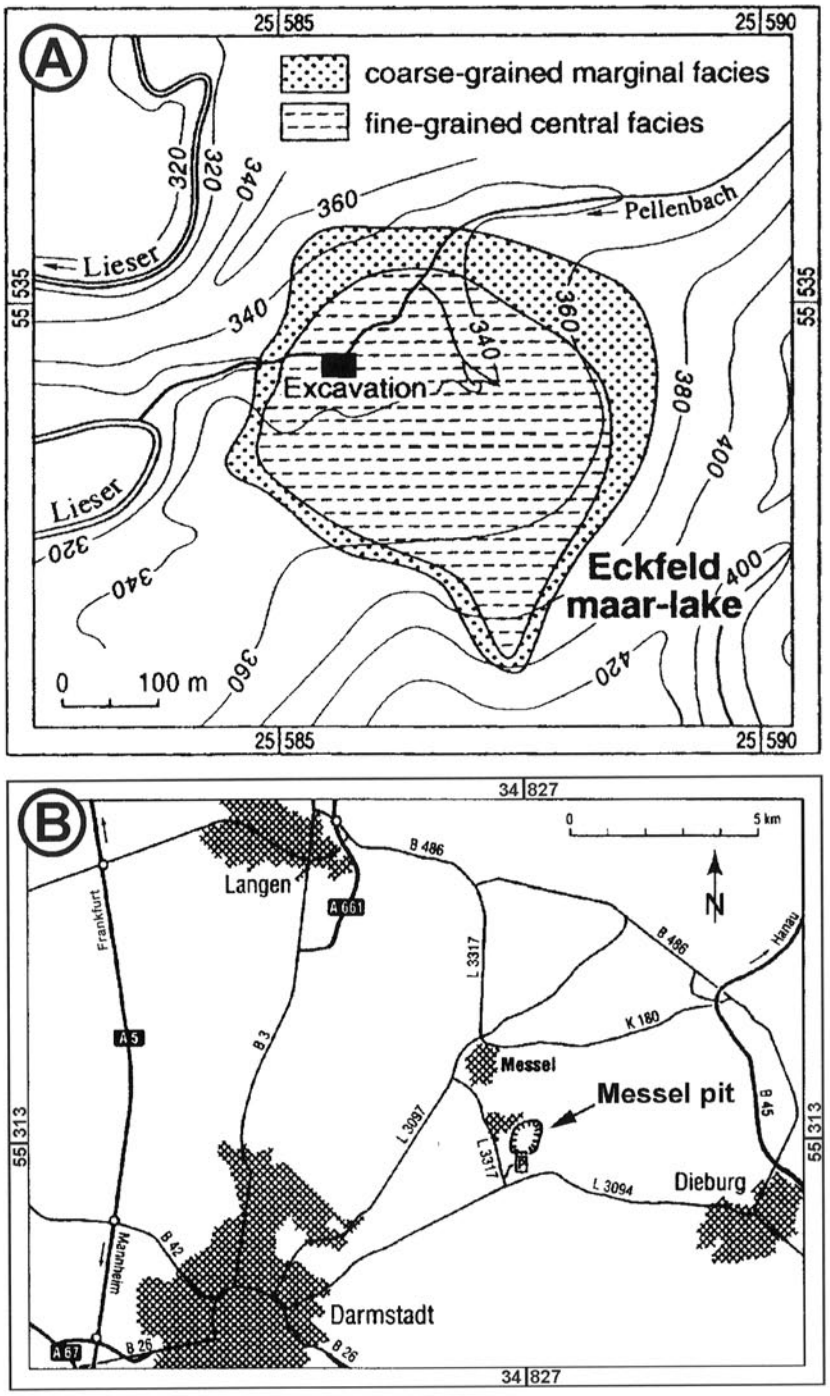

Fig. 1. Location maps. – **A**: Simplified geological map of the Eckfeld Maar (after PIRRUNG 1998). – **B**: Site plan of the "Messel pit".

Material and Methods

The fossils examined in the present work were gathered from the collections of the Naturhistorisches Museum Mainz, Landessammlung für Naturkunde Rheinland-Pfalz (NHMM) and the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF). Specimens were studied by immersing the slabs in glycerine to prevent oxidation. All measurements were made using an ocular micrometer and are given in millimeters; structures were measured as preserved. Total body length was measured from the tip of the head to the apex of the abdomen. Morphological terminology used in the descriptions follows that employed by ANDERSEN (1998).

Systematic Palaeontology

Infraorder Gerromorpha POPOV, 1971
Family Gerridae LEACH, 1815
Subfamily incertae sedis

Lutetiabates n. gen.

Derivatio nominis: The new genus-group name is a combination of "Lutetian" (a stage of the Middle Eocene time period) and "bates" (meaning gliding). The gender is masculine.
Type species: *Lutetiabates eckfeldensis* n. sp., by monotypy.

Diagnosis: Small to medium-sized, apterous gerrids. Body elongate oval. Head relatively short, eyes large, globular, located close to the anterior margin of prothorax. Antennae long, segment 1 about twice as long as head. Rostrum slender and moderately elongated. Pronotum very short, shorter than head, with sides and posterior margin rounded. Mesonotum prolonged; metanotum very short. Forelegs short and robust. Middle and hind legs long and slender. Abdomen relatively short; mediotergites subequal in length; laterotergites (connexiva) very broad. Genital segments (female?) relatively large; proctiger probably button-like, protruding.

Comments: The general structure and in particular the prolonged mesothorax, relatively short forelegs, and very long middle and hind legs which are inserted laterally on the thorax, unequivocally place the fossil species in the gerromorphan family Gerridae. The current classification of this family contains eight extant subfamilies (ANDERSEN 1982) and one extinct subfamily (ANDERSEN & POINAR 1992; ANDERSEN 1998). The fossils from Eckfeld do not reveal many of the characters which are used to identify gerrids to subfamily level (MATSUDA 1960; ANDERSEN 1982), e.g., number of cephalic trichobothria, presence/absence of pretarsal arolia, and presence and structure of a metathoracic scent apparatus. The relatively broad body shape and shortened abdomen of the fossil species suggest affinity with one of the extant subfamilies Charmatometrinae, Eotrechinae, Gerrinae (at least in part), Halobatinae, and Trepobatinae, and also with the extinct subfamily Electrobatinae (see below).

The distinctly shortened pronotum of the apterous form is shared with members of the above mentioned subfamilies, except the Charmatometrinae and most Gerrinae. Some species of the latter subfamily, however, show this character, including the extinct genus *Electrogerris* ANDERSEN described from Baltic amber (ANDERSEN 2000). The Eckfeld species differs from this genus in the following characters (characters of *Electrogerris* in parentheses.

1. Antennae longer, about 0.75x total length (0.4x total length).
2. Antennal segment 4 subequal in length to segments 2–3 (longer than segments 2–3).
3. Rostrum longer, about 0.3x total length (less than 0.2x total length).
4. Segment 1 of fore tarsus very short, less than 0.25x segment 2 (more than 0.25x segment 2).
5. Middle femur longer, 0.8–0.9x total length (about 0.6x total length).
6. Middle tibia subequal in length to middle femur (shorter than middle femur).

Thus, despite of a superficial similarity in size and general body shape, we cannot justify a taxonomic decision that places the fossils in the genus *Electrogerris* (or in the subfamily Gerrinae).

The extinct subfamily Electrobatinae was described by ANDERSEN & POINAR (1992) for the species *Electrobates spinipes* ANDERSEN & POINAR from Dominican amber. The fossil species from Eckfeld differs from *Electrobates* by the following characters:

1. First antennal segment without spinous hairs.
2. Antennal segments 2–4 subequal in length (segment 2 shortest in *Electrobates*).
3. Ventral margin of femora not armed with spines.
4. Female mesonotum not divided by a median, longitudinal sulcus into two sclerites connected by a hairy membrane.
5. Metanotum without a secondary, transverse line in front of the first abdominal tergum.

Additionally, the female abdomen is unusually short in *Electrobates*. In our opinion, the Eckfeld fossil does not belong to the extinct subfamily Electrobatinae.

Most members of the extant subfamily Trepobatinae have a very characteristic middle leg structure, where the femur is distinctly shorter than the tibia. This character is less pronounced in the tribe Metrobatini, but in this group the fore tibia has a distal process or "spur" not found in the Eckfeld fossil. The three distal antennal segments are, however, distinctly shorter in these trepobatines as well as in members of the subfamily Halobatinae. The fossil species does not reveal the spine-like hairs on the first antennal segment and spinous hairs on the tibiae and tarsi which characterize most members of the subfamily Eotrechinae. In conclusion, it is impossible to place the Eckfeld water strider in any of the known subfamilies of Gerridae, extant as well as extinct. We nevertheless describe it as a new genus and species to facilitate future reference.

Lutetiabates eckfeldensis n. sp.

Figs. 2–3

Derivatio nominis: Name after the Middle Eocene (Lutetian) fossil lagerstaette Eckfeld Maar (Germany, Eifel).

Holotype: PE 1990/472-LS, nearly complete, apterous female, preserved as a compression fossil, deposited in the NHMM (Figs. 2A, 3A).

Type locality: Eckfeld Maar near Manderscheid, Eifel Mountains, Germany.

Paratypes: Specimens no. 1 (PE 2000/1a+b-LS), incomplete, apterous specimen, preserved as a compression fossil in two blocks; no. 2 (PE 2000/823-LS), incompletely preserved specimen, apical part of abdomen partly covered with a thick layer of sediment; no. 3 (PE 1992/472a+b-LS), incomplete specimen, preserved as a compression fossil in two blocks; no. 4 (PE 2000/542a+b-LS), almost complete specimen, preserved as a compression fossil in two blocks.

Additional material probably belonging to *Lutetiabates* n. gen.: PE 1992/589a+b-LS, although clearly identifiable as a species of *Lutetiabates* sp. based on the dorsal structure of the abdomen; PE 2000/543-LS, the individual is preserved as almost a pale, reddish-brown apparition on light brown matrix; PE 1992/454-LS), very incompletely preserved apterous specimen, compressed laterally.

Stratigraphic distribution: Middle Eocene (Middle Lutetian, ELMA Geiseltalian, MP13, 44.3 ± 0.4 Ma).

Diagnosis: As for genus (see above).

Description: Small to medium-sized, apterous gerrids, total length (from tip of head to end of abdomen) 3.1–4.4 mm, greatest width (across thorax) 1.7–2.1 mm. Body elongate oval, length (from tip of head to end of abdomen) 1.8–2.2x greatest width. Head relatively short (0.40 mm), eyes large, globular, located close to the anterior margin of prothorax. Antennae long (2.74 mm), about 0.75x total length: segment 1 longest (0.85–1.00 mm), about twice as long as head; segments 2–4 sub-

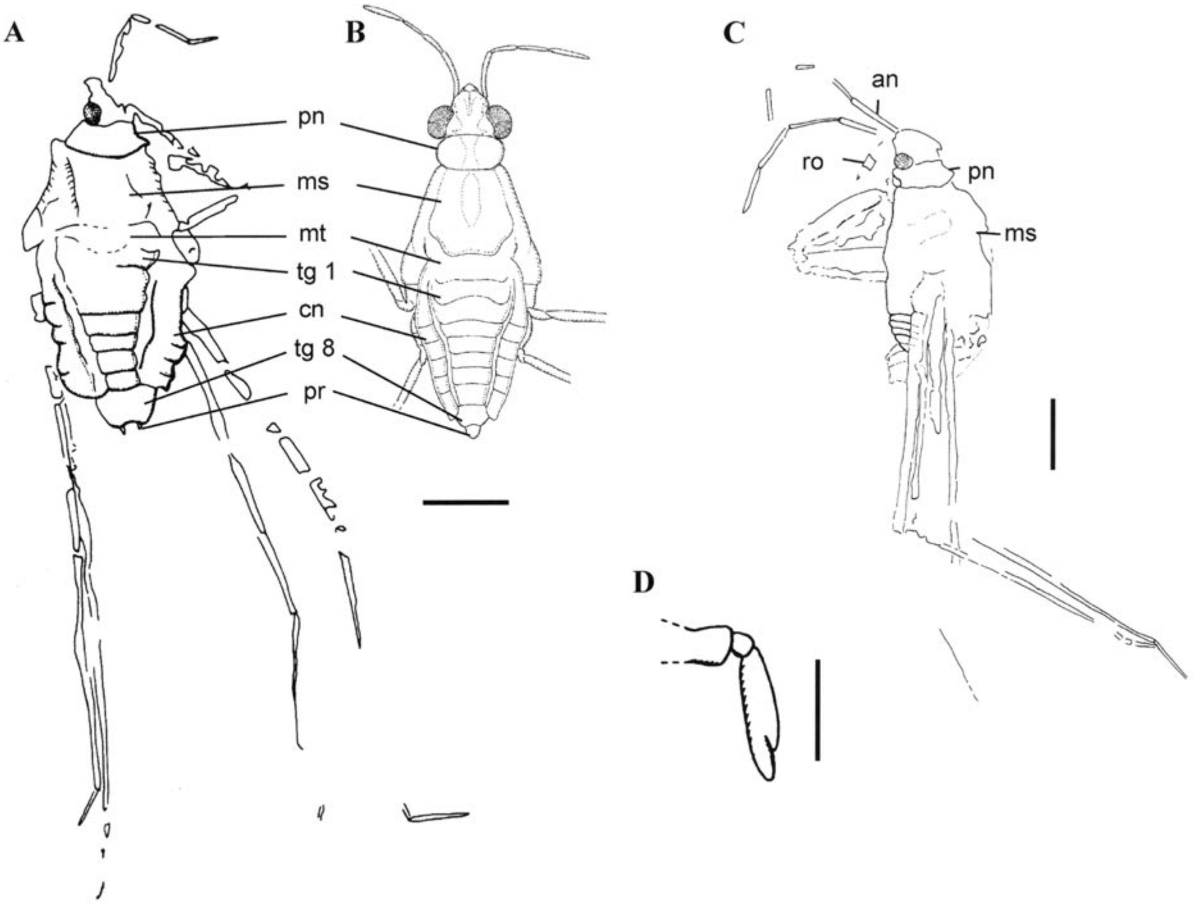

Fig. 2. – **A**: *Lutetiabates eckfeldensis* n. gen. et n. sp. Dorsal view of an apterous female from the Eckfeld Maar (PE 1990/472, LS) (holotype). – **B**: *Electrogerris kotashevichi* ANDERSEN, 2000; dorsal view of an apterous female (holotype) from Baltic amber (adapted from ANDERSEN 2000: 261). – **C–D**: *Lutetiabates eckfeldensis* n. gen. et n. sp. **C**. Ventrolateral view of an apterous specimen from the Eckfeld Maar (PE 2000/542a+b, LS) (paratype no. 4). **D**. Apex of left fore tarsus (PE 2000/542a+b, LS). – Abbreviations: an, antennae; cn, connexivum; ms, mesothorax; mt, metathorax; pn, pronotum; pr, proctiger; ro, rostrum; tg, tergum. – Scale bar = 1 mm (Figs. A–C), 0.3 mm (Fig. D).

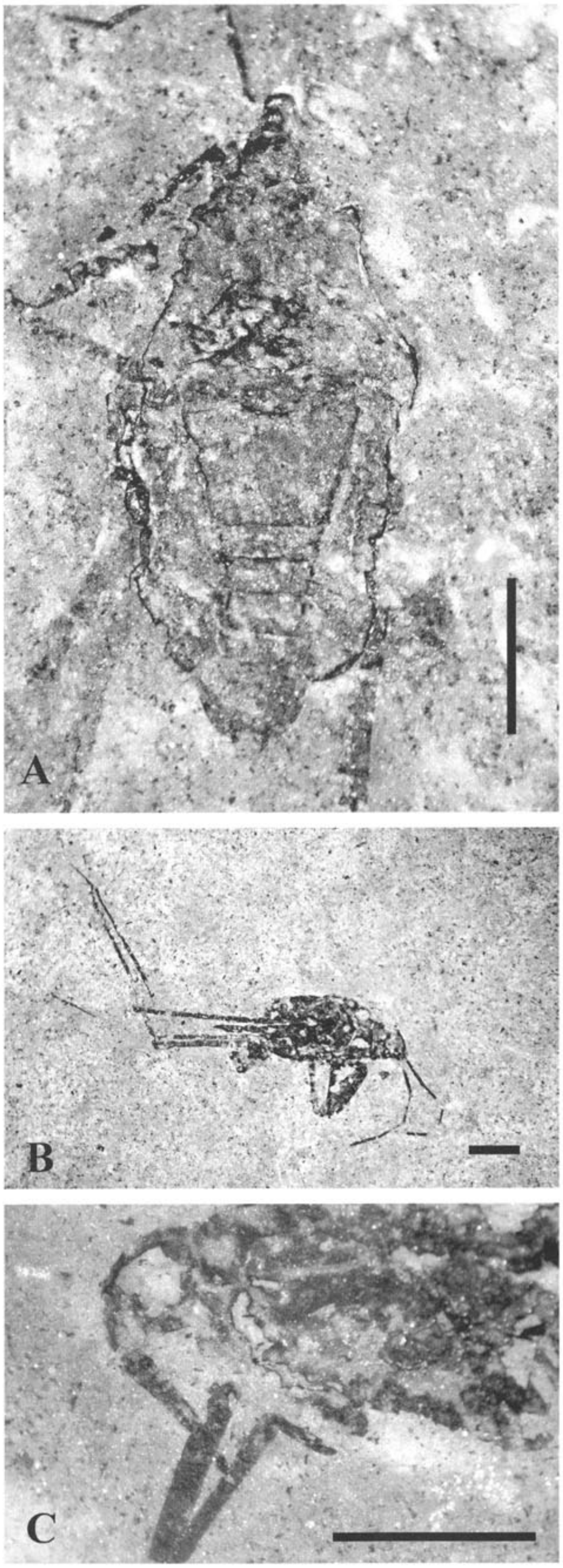

Fig. 3. *Lutetiabates eckfeldensis* n. gen. et n. sp. – **A**: Apterous female (PE 1990/472, LS) (holotype). – **B**: Ventrolateral view of an apterous specimen from the Eckfeld Maar (PE 2000/542a+b, LS) (paratype no. 4). – **C**: Left fore tarsus and distal part of tibia (PE 2000/542a+b, LS) (paratype no. 4). – Scale bar = 1 mm.

equal in length (0.60–0.70 mm), relatively slender. Rostrum slender and moderately prolonged (labial segments 3 + 4 = 1.13 mm), about 0.3x total length, reaching anterior part of mesosternum. Pronotum very short, shorter than head, with sides and posterior margin rounded. Mesonotum prolonged, length 0.85 mm; metanotum very short, length 0.19 mm. Forelegs short and robust; fore femur 1.21–1.43 mm, thickened; fore tibia 0.88–1.20 mm, almost straight, without distal process; fore tarsus 0.55 mm, first segment very short (0.10 mm), second segment much longer (0.45 mm), with preapical cleft (claws not visible). Middle and hind legs long and slender, inserted laterally on thorax. Middle femur 2.97–3.64 mm or 0.8–0.9x total length; middle tibia 3.30–3.57 mm, or subequal in length to middle femur; length of middle tarsus at least 1 mm, hind legs slightly shorter than middle legs; hind femur 3.18–3.50 mm; hind tibia 1.78–2.09 mm; length of hind tarsus unknown. Abdomen relatively short, length (from the point of insertion of hind legs to abdominal end) 1.82 mm, or only about 0.5x total length; mediotergites 1–7 subequal in length (0.18–0.25 mm); laterotergites (connexiva) very broad. Genital segments (female?) relatively large; abdominal segment 8 (first genital segment) 0.27 mm; proctiger incomplete but button-like, protruding.

Comments: See under genus (above).

Gerris FABRICIUS, 1794 (nymphs)

* 1794 *Gerris* FABRICIUS: 188.
1856 *Hydrometra* (nymph). – GERMAR & BERENDT: 19, pl. 2 fig. 7.
1856 *Holobates* (nymph). – GERMAR & BERENDT: 19, pl. 2 fig. 8.
1978 Gerroidea (nymph). – LARSSON: 119, pl. 8 fig. A.
1998 *Gerris* sp. (nymphs). – ANDERSEN: 34–35, figs. 24, 116–117.

Type species: *Cimex lacustris* LINNAEUS, 1758; subsequent designation (LATREILLE 1810).

Diagnosis: SEE ANDERSEN (1998: 33).

Distribution: Representatives of *Gerris* have a chiefly holarctic distribution. The majority of the 42 extant species are distributed in Eurasia and North America (ANDERSEN 1993). They are exclusively confined to stagnant freshwater like pools, ponds, and smaller lakes. In particular, gerrid nymphs often aggregate in more protected areas of the water surface than adult water striders. Such places are usually close to the shore (e.g., ANDERSEN 1982, 1993).

Gerris sp. indet. (nymph)
Fig. 4

Material: Very incomplete specimen, probably also an nymphal instar, preserved as a compression fossil, deposited in the NHMM (PE 1993/216a+b-LS). Almost complete specimen, probably the 4th or 5th nymphal instar, preserved as a compression fossil, deposited in the NHMM (PE 2000/2-LS).

Stratigraphic and geographical distribution: Eckfeld Maar near Manderscheid, Eifel Mountains, Germany; Middle

Fig. 4. *Gerris* sp. indet. (PE 2000/2, LS), probably 4th or 5th nymphal instar. – Scale bar = 2 mm.

Eocene (Middle Lutetian, ELMA Geiseltalian, MP13, 44.3 ± 0.4 Ma).

Description: The specimen (PE 2000/2-LS) is dorsally compressed and probably a nearly completely preserved 4th or 5th nymphal instar. Ventral surface of the specimen dark to pale brown. Forelegs directed anteriorly alongside and above head and pronotum. Mid and hind legs extended out from the body. Total length (abdomen extended) 3.43 mm, greatest width 1.38 mm. Antennae a little more than 0.67× length of insect; length of segments 1–4: 0.75, 0.48, 0.58, 0.50 (segment incomplete). Mesonotum length 1.48 mm, with two elongated, oval structures visible. It is possible that these are superimposed structures of wing pads from the dorsal site. Length of leg segments (femur, tibia, tarsus. front leg: 1.08, 0.90, and 0.33 mm; middle leg: 2.40–2.48, 2.58–2.98, and 1.43 mm; hind leg: 2.38–2.68, 1.78 mm (incomplete). Front femur relatively short; middle femur longer than hind femur and all of equal width. Abdomen extended and slightly tapering at the apex.

Comments: Until now only two specimens of gerrid nymphs are known from Baltic amber (ANDERSEN 1998, 2000). Based on comparisons with descriptions of all nymphal instars of western Palaearctic *Aquarius*, *Gerris*, and *Limnoporus*, ANDERSEN (1998) classified these fossil gerrids as belonging to the genus *Gerris* s. lat. Based on characters of the antennae (second and third segments together longer than first segment), their moderate size, and rather robust body we believe that the Eckfeld Maar specimens belong to the genus *Gerris* s. lat.

Subfamily incertae sedis

Cylindrobates n. gen.

Derivatio nominis: The generic name is combined after the cylindrical body shape and "bates" (meaning gliding). The gender is masculine.

Type species: *Cylindrobates messelensis* n. sp.

Diagnosis: Medium-sized, apterous gerrids. Body elongate and slender. Head relatively short, eyes large, globular, located close to the anterior margin of prothorax. Antennae long; segment 1 longest; segment 2 distinctly shorter; segments 3–4 subequal in length. Pronotum shorter than head, with sides rounded and posterior margin sinuated. Mesonotum prolonged. Forelegs short and robust, without distal process. Middle and hind legs long and slender. Hind legs slightly shorter than middle legs. Abdomen long; laterotergites (connexiva) relatively narrow. Genital segments (female?) relatively large; proctiger probably button-like, protruding.

Comments: The general structure and in particular the prolonged mesothorax, relatively short forelegs, and very long middle and hind legs (which are inserted laterally on thorax), unequivocally place this new fossil species in the gerromorphan family Gerridae. The fossils from Messel do not reveal many of the characters which are used to identify gerrids to subfamily level (see above). The Messel species represents another of the general body shapes found in extant Gerridae, where the mesothorax is prolonged but narrow, and the abdomen prolonged and relatively narrow (MATSUDA 1960; ANDERSEN 1982). The fossils thus resemble species of the extinct genus *Palaeogerris* ANDERSEN, known from the Danish Mo Clay (Fur and Ølst formations, Upper Paleocene – Lower Eocene transition). The thorax of *Palaeogerris*, however, is never as narrow as that seen in the Messel fossils. The almost cylindrical body is characteristic of the extant genus *Cylindrostethus* FIEBER which is tropicopolitan in distribution. The antennal structure is similar in that the first antennal segment is about as long as segments 2–4 combined. The structure of the fore leg of the Messel species is rather different, however, especially the relatively short fore tibia. It is therefore impossible to place the Messel water strider in any of the known subfamilies of Gerridae. Nevertheless, we describe it as a new genus and species to facilitate future reference.

Cylindrobates messelensis n. sp.

Fig. 5

Derivation nominis: Name after the Middle Eocene fossil lagerstaette "Messel", now in the world heritage list of the UNESCO.

Holotype: SMF MeI 4763, a complete individual, dorsoventrally compressed with venter exposed, mid and hind legs are extending away from the body, deposited in the SMF (Figs. 5A–B).

Type locality: Grube Messel near Darmstadt, Grabungsstelle grid square E89.

Paratype: SMF MeI 6264, a complete individual, dorsoventrally compressed with venter exposed, abdomen twisted, forelegs lying alongside the head, mid and hind legs extending away from the body.

Stratigraphic distribution: Lower Middle Eocene (Lower Lutetian, ELMA Geiseltalian, MP11), Messel Formation; 1.75–2.05 m below marker horizon α (holotype), and 3.54–4.50 m above marker horizon α (paratype).

Diagnosis: As for genus (see above).

Description: Medium-sized, apterous gerrids, total length (from tip of head to end of abdomen) 7.6–8.7 mm, greatest width (across thorax) 1.25–1.6 mm. Body elongate and slender, length 5.4–6.1× greatest width. Head poorly preserved, but seemingly relatively short, eyes large, globular, located close to the anterior margin of prothorax. Antennae long (3.44 mm), about 0.4× total length: segment 1 longest (1.70 mm); segment 2 distinctly shorter (0.73 mm); segments 3–4 subequal in length (0.43–0.58 mm), relatively stout. Rostrum not visible. Pronotum short (0.48–0.60 mm), shorter than head, with sides rounded and posterior margin sinuated. Mesonotum prolonged, length 1.25–2.25 mm; metanotum indistinct, but probably very short. Forelegs short and robust; fore femur 1.95 mm, thickened; fore tibia short, 0.88 mm, almost straight, without distal process; fore tarsus very short 0.33 mm, segmentation and claws indistinct. Middle and hind legs long and slender, inserted laterally on thorax. Middle femur 5.53–7.02 mm (holotype) or 2.97 mm (paratype), thus 0.4–0.8× total length; middle tibia 3.64–4.05 mm, or distinctly shorter than middle femur; length of middle tarsus at least 1.21 mm. Hind legs slightly shorter than middle legs; hind femur 3.91–4.86 mm; hind tibia 2.83–2.97 mm; length of hind tarsus unknown. Abdomen long, almost parallel-sided, length (from the point of insertion of hind legs to abdominal end) 4.45–4.86 mm, or about 0.55–0.6× total length; length of abdominal terga 2–6: 0.94, 0.94, 0.81, 0.81, and 0.67 mm; length of tergum 7: 0.24 mm; laterotergites (connexiva) relatively narrow, width 0.13 mm. Genital segments (female?, paratype) relatively large; abdominal segment 8 (first genital segment): 0.33 mm; proctiger indistinct but probably button-like, protruding. Entire specimens covered with a pubescence of tiny fine hairs.

Comments: See under genus (above).

Discussion

Fossil history

As pointed out earlier, at present 38 fossil species of Gerromorpha belonging to six families have been described, spanning more than 120 Ma of geological history (e.g., ANDERSEN 1998, 2000, 2001; ANDERSEN & GRIMALDI 2001; PEREZ GOODWYN 2002). ANDERSEN (1998) recently monographed the fossil Gerromorpha. The best preserved specimens are found in fossiliferous resin. From the Mesozoic only five gerromorphan fossils have been described (Tab. 1). The only one in Mesozoic amber, *Carinametra burmensis* ANDERSEN & GRIMALDI, is also the most completely preserved Mesozoic fossil of the infraorder. *Carinametra* shares many characters with the Heterocleptinae, the most primitive subfamily of Hydrometridae (ANDERSEN & GRIMALDI 2001).

The most ancient members of the family Gerridae belong to the genus *Palaeogerris* ANDERSEN with three species in the Fur and Ølst formations of Denmark (Paleocene – Eocene transition), which constrain the minimum age of the entire family back to 55–54 Ma. A possible veliid fossil from the Lower Cretaceous of Australia suggests that their sister group, the Veliidae, evolved even more than 120 Ma ago.

Biology and taphonomy

As is typical for the gerromorphan bugs in general, they possess long legs covered by hydrofuge hair layers to

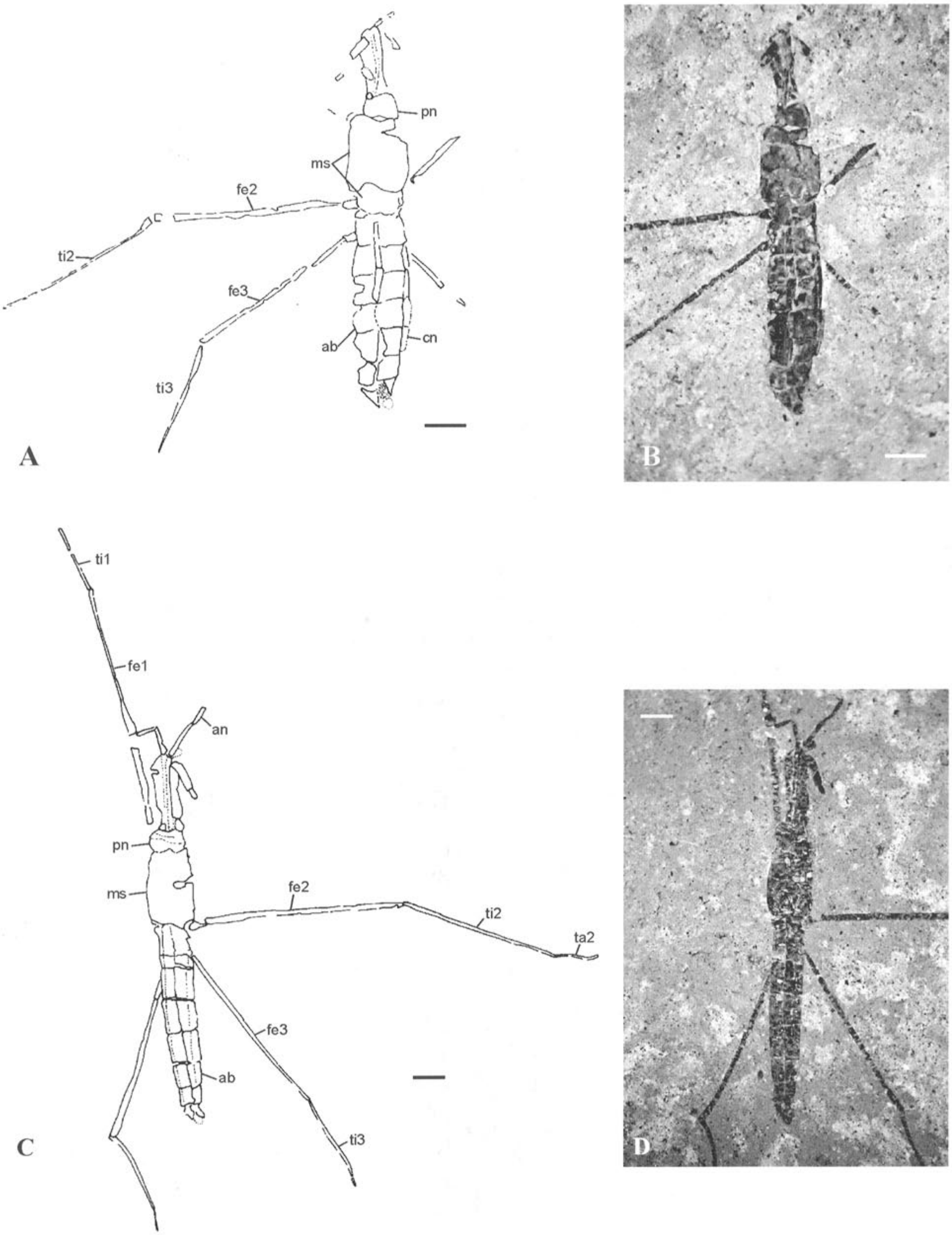

Fig. 5. *Cylindrobates messelensis* n. gen. et n. sp. – **A–B**: Dorsal view of an apterous specimen from Messel (MeI 4763) (holotype). – **C–D**: Dorsal view of an apterous specimen from Messel (MeI 6264) (paratype). – Abbreviations: ab, abdomen; an, antennae; cn, connexivum; ms, mesothorax; pn, pronotum; fe, femur; ta, tarsus; ti, tibia. – Scale bar = 1 mm.

prevent wetting, and well-developed pairs of trichobothria on the head (ANDERSEN 1982). In particular, species of the family Gerridae are highly specialised (e.g., morphological structures associated with locomotion and feeding) for life on the water surface. Some are winged and others are wingless. *Gerris* is usually fully winged and a good flier, but short-winged individuals are regularly found in most populations. They feed on various small insects that fall on the water surface. The genus *Halobates* deserves mention as one of the few insect groups that have conquered marine environments. These insects are found on floating seaweed, and on the water surface itself in mainly tropical and subtropical seas (ANDERSEN 1998).

Because the Gerromorpha form a very distinct ecological group specially adapted for life on the water surface they are preferentially fossilized in lacustrine/marine fossil beds rather than in resin (Tab. 1). In Eckfeld and Messel, they constitute approximately less than 0.5 % of the whole entomofauna. This can mainly be explained on the one hand by individual and taxon-specific factors and on the other hand by abiotic and biotic factors. In particular, the effects of the maximum possible length of transport and the water density and viscosity considerably affect the composition of insect taphocoenoses in meromictic lakes (e.g., LUTZ 1997, 1998b; WILSON 1980; WAPPLER 2003a). In case of these locally restricted fossil lagerstaetten, Eckfeld and Messel, with a relatively small diameter-range between 700–1500 m, especially "filigreed" taxa like gerrids with long and slender legs were preadapted for long post-mortem surface drifting and an accumulation ashore where the fossilization potential was very low. Moreover, Eckfeld and Messel were deep meromictic lakes. Meromictic lakes are those in which complete overturn is prevented by density stratification because of dissolved substances in the lower water layer (monimolimnion). Water circulation in meromictic lakes is therefore limited to the upper water layer (mixolimnion). This would slow down the sinking velocity of dead insects. It is especially true that taxa which have long legs and/or large wings causing a high frictional resistance while compact forms with a lower frictional resistance like most Coleoptera are less biased (e.g., NACHTIGALL 1998). Weakly sclerotized taxa can even be destroyed within the chemocline by intensive bacterial activity or may even be transported to the surface again (LUTZ 1997, 1998a, b). This is probably a reason why "filigreed" taxa are under-represented in sediments of meromictic lakes, in contrast to marine deposits, e.g., of the Fur and Ølst formations where the Gerromorpha yield an unusually rich and diverse fauna of semiaquatic bugs (ANDERSEN 1998).

Biogeography and palaeoenvironment

Although the exact taxonomic relationships of the taxa from Eckfeld and Messel are unclear, the morphological structures clearly show that they belong to the Gerridae. Extant Gerridae are cosmopolitan in distribution. They comprise eight subfamilies with 60 genera and approximately 500 species (ANDERSEN 1982). Today the northern temperate latitudes are dominated by representatives of the genera *Aquarius* (15 species), *Limnoporus* (6 species), and *Gerris* (42 species). The fossil data suggest that during the Paleogene Europe, in particular northern Europe, was inhabited by a rather diverse fauna of gerrids as compared to the present (ANDERSEN 1995). The gerromorphan bugs of the Baltic amber and the Fur and Ølst formations seem to have their closest extant representatives in Palaearctic, Neotropical, and central Pacific regions (ANDERSEN 1998, 2000). The specimens from Eckfeld and Messel show close affinities to genera from Baltic amber and the Fur and Ølst formations (see "Comments"). In the case of *Cylindrobates* n. gen. there may be a close relationship to the extant genus *Cylindrostethus* FIEBER which is tropicopolitan in distribution. Lastly several other taxa, like Isoptera (Mastotermitidae), Auchenorrhyncha (Fulgoridae: *Lycorma* sp.), and Coleoptera (Buprestidae, Elateridae) are found at Eckfeld and Messel, whose Recent distribution is disjunct or restricted to southern temperate regions, especially South-East Asia.

Many bioindicators like palms and reptiles are present in the fossil record at Eckfeld and Messel and point towards a humid paratropical climate. Correspondence between fossils and Recent taxa in their systematics and especially their morphology suggests that they also correspond in their ecological requirements.

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