

The ecological role of immature phantom midges (Diptera: Chaoboridae) in the Eocene Lake Messel, Germany

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ABSTRACT

Autochthonous aquatic arthropods are only rarely found in the sediments of the Eocene Lake Messel. This has led to the assumption that certain abiotic conditions prevented a stable colonisation of aquatic groups. In recent years, the analysis of small fossil fish coprolites has shown that aquatic life was present in the former Lake Messel. A food web of different taxa of aquatic insect larvae and crustaceans was traced. Very abundant among the remains in the coprolites are larvae and pupae of phantom midges (Diptera: Chaoboridae). This article focuses on the survey of identified remains of immature chaoborids in the coprolites. In addition, it gives an outline of the major role that large populations of phantom midges can play in the pelagic ecosystem of a lake. Chaoborids are important both as prey for planktivorous fish and as predators of the smaller zooplankton. Via comparison with extant meromictic lakes, one can infer that the older phantom midge larvae displayed a vertical diurnal migration behaviour. They probably remained during the day within the anoxic water layers of the monimolimnion of the former Lake Messel to minimise the effect of predation by planktivorous fish. Lakes with large chaoborid populations are known to exist since the Jurassic.

KEY WORDS: Diptera, Chaoboridae, Tertiary, Eocene, Messel, palaeoecology, palaeolimnology, fish coprolites.

INTRODUCTION

The sediments of the fossil Lake Messel yield many exquisitely preserved fossils (e.g. Schaal & Ziegler 1992; Koenigswald & Storch 1998), among them thousands of insect remains. The insects are represented mostly by terrestrial groups (e.g. Lutz 1986, 1987, 1990; Tröster 1991, 1993a, 1994, 1999; Hörnschemeyer & Wedmann 1994; Wedmann & Hörnschemeyer 1994; Wappler 2003a; Wappler & Engel 2003; Wappler & Andersen 2004; Wedmann 2005). Analysis of the insect fossils provided interesting clues to the terrestrial environment of the former lake. Body fossils of autochthonous aquatic arthropods are rare (Lutz 1991; Tröster 1993b). Thus, the ecosystem of the lake itself was largely unknown for a long time.

In some other Palaeogene fossil sites aquatic insects also seem to be quite rare. For example, this appears to be the case in the volcanic basins of Eckfeld (Eifel, Germany) and Enspel (Westerwald, Germany), where the insect oryctocoenoses were analysed by Wappler (2003b) and Wedmann (2000). The size and shape of the sedimentary basin had a very important effect on the composition of the taphocoenosis.

The geographic position of Lake Messel is illustrated in Fig. 1. Today, the locality is situated about 8 km north-east of Darmstadt in Germany. Until some ten years ago the Messel pit was destined to become a rubbish tip. Since 1995, it is on the World Heritage List, mainly because of its wealth of fossil mammals. The fossils are embedded in the so-called “oil shale” sediments. This is a siltstone that contains kerogen mainly originating from algae. The sediments were formed under anaerobic conditions in a deep meromictic lake (Goth 1988, 1990). The lake was permanently stratified, where a

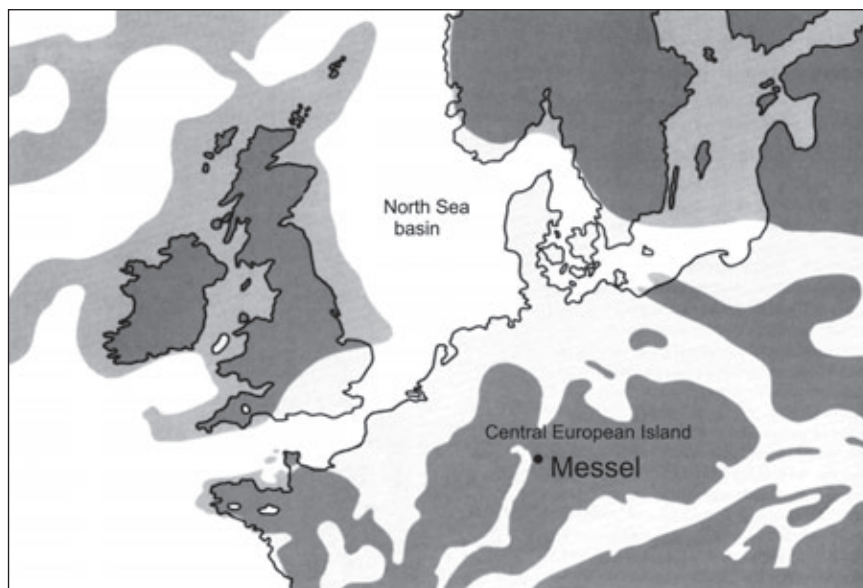


Fig. 1. The geographic position of Lake Messel during the Eocene. White indicates sea, grey indicates land during the Eocene. The outlines of present-day northern Europe are superimposed. Modified after Franzen (1992).

chemocline separated the upper part of the water body, also called mixolimnion, from the lower part, the monimolimnion. Life was possible only in the mixolimnion. The monimolimnion was anoxic and also had a higher salinity.

A core drilled in 2001 revealed that Lake Messel was a maar lake with an initial diameter of about 1.5 km (Harms 2002). Maar lakes have their origin in a volcanic steam explosion. According to recent research, the sediments of Messel were deposited about 47 million years ago (Mertz *et al.* 2004).

Until some years ago, the rarity of autochthonous water-living arthropods in the sediments of Lake Messel seemed to support the assumption that special abiotic conditions prevented colonisation of the lake by aquatic groups (Lutz 1987, 1990; Rietschel 1988). Autochthonous insects and water fleas were first reported by Lutz (1991). Richter and Krebs (1999) identified nymphs of mayflies (Ephemeroptera) from the sediments and interpreted their presence as indicating that Lake Messel had not been as hostile as supposed previously. As further studies showed, the scarcity of body fossils of aquatic arthropods did not indicate an absence of aquatic life in the lake. Through the analysis of small fish coprolites, that can be found quite frequently in the sediments, it was possible to discover a food web in the pelagic zone of Lake Messel (Richter & Baszio 2001a, 2002). Examination of gut contents showed that the main producer of the so-called 'type A' coprolites were small fish of the species *Thaumaturus intermedius* Weitzel, 1933 or juvenile stages of other fish species occurring in the lake (Richter & Baszio 2001b). Specimens of *T. intermedius* reached a maximum length of 90 mm in Lake Messel, however most fossils recovered are 30 to 70 mm long (Micklich 2002). Fossils of this fish species are found quite often in the sediments. Type A coprolites contain a variety of chitinous remains of different aquatic invertebrates. Identified

structures belong to the larvae and pupae of phantom midges (*Chaoboridae*), larvae of mosquitoes (*Culicidae*) and chironomid midges (*Chironomidae*), mayfly nymphs (*Ephemeroptera*) and small crustaceans (*Cladocera* and juvenile *Conchostraca*) (Richter & Baszio 2001*a*, 2002; Richter & Wedmann 2005). Many other fragments remain to be identified. An absence of small fish coprolites from basal sediments of the core of the 2001 drilling project indicates that apparently no significant planktivorous fish population existed during the initial stages of Lake Messel (Richter & Wedmann 2005).

The aim of this paper is to discuss the ecological significance of chaoborid remains found in the type A coprolites.

MATERIAL AND METHODS

About 500 small fish coprolites were studied. Some of the fish coprolites come from sediments with a stratigraphic range of a few meters around the key horizon alpha, where excavation is currently taking place. The remaining coprolites originate from the drilling core of the 2001 Messel pit research drilling project.

The coprolites of type A are very flat, not mineralised and flexible when humid. They are either round with a diameter of up to 12 mm or elongated and ribbon-shaped, up to 25 mm long (Fig. 2). Freshly collected coprolites can be separated from the sediment matrix quite easily.

The coprolites were dehydrated and embedded in Canada balsam (Richter & Baszio 2001*a*). When investigated with transmitted-light microscopy many interesting structures are visible (Fig. 3; Richter & Baszio 2001*a*).

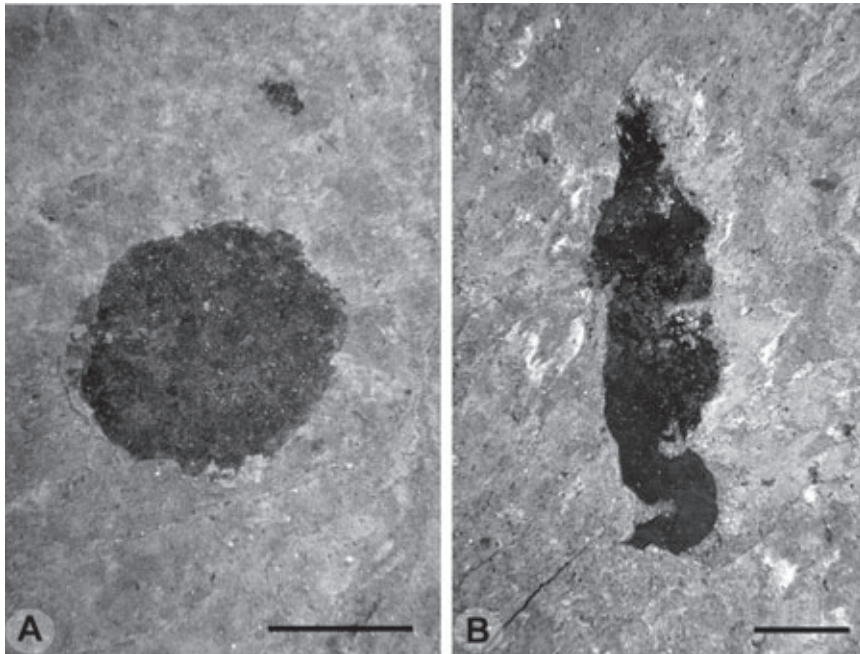


Fig. 2. Coprolites of so-called type A which exclusively contain remains from aquatic living invertebrates: (A) round coprolite; (B) elongated coprolite. Incident light microscopy. Scale bars 5 mm.

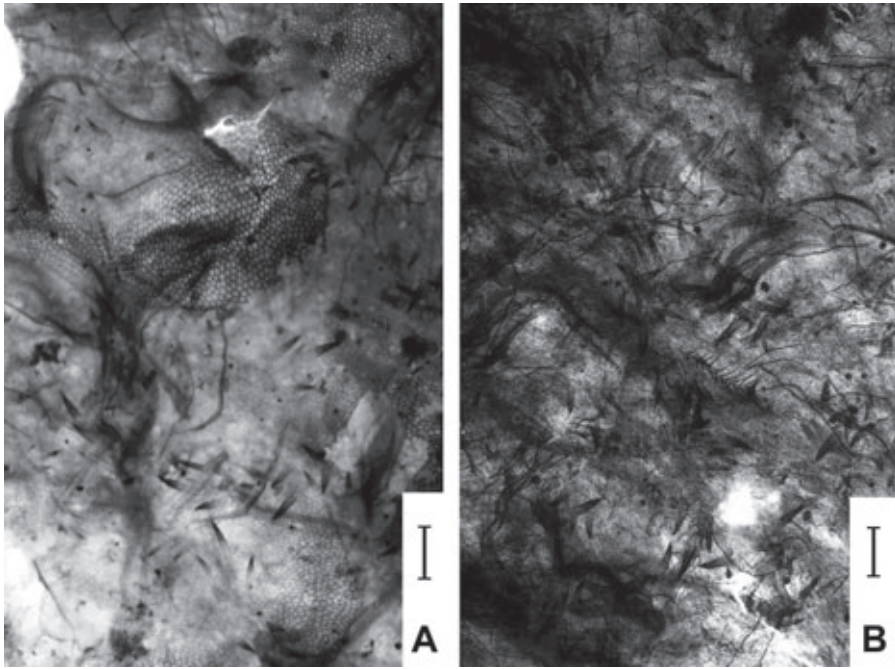


Fig. 3. Isolated type A coprolites viewed using transmitted-light microscopy. Scale bars 100 μm .

The number of identifiable remains in coprolites was roughly estimated. It must be noted that many remains that are present in the coprolites are not yet identified, so the results of this analysis are preliminary.

RESULTS AND DISCUSSION

Remains of immature phantom midges are common in the coprolites from Messel. More than 90% of the coprolites studied contain them.

The mandibles of *Chaoborus* larvae are particularly common (Richter & Baszio 2001a). They consist of a characteristic set of four dark-coloured spines (Fig. 4). The mandibles are often found in pairs (Fig. 4A). In some coprolites, mandibles of different sizes are present (Fig. 5). This indicates that different larval instars of chaoborid midges coexisted in the ancient lake (see discussion of chaoborid life cycle below). Figure 6 shows characteristic groups of cirri, which constitute a part of phantom-midge mandible bases (Richter & Baszio 2001a). Structures difficult to find are pairs of small, transparent caudal hooks (Fig. 7A), which are located on the last abdominal segment of *Chaoborus* larvae. Remains with a fan-like row of setae (Fig. 7B) can also be found (Richter & Baszio 2002). Unambiguous assignment of this structure to phantom midge larvae is impossible because such anal fans are known in larvae of three nematoceran families, i.e. Corethrellidae, Culicidae, and Chaoboridae (Wood & Borkent 1989). Another rare find is a paddle-like structure in a coprolite (Fig. 7C). Similar structures can be found at the apex of the abdomen of pupae of chaoborid midges (see Fig. 9B). This kind of membranous paddle with a supporting midrib and additional ribs on each side is characteristic of *Chaoborus* pupae (Sæther 1997).

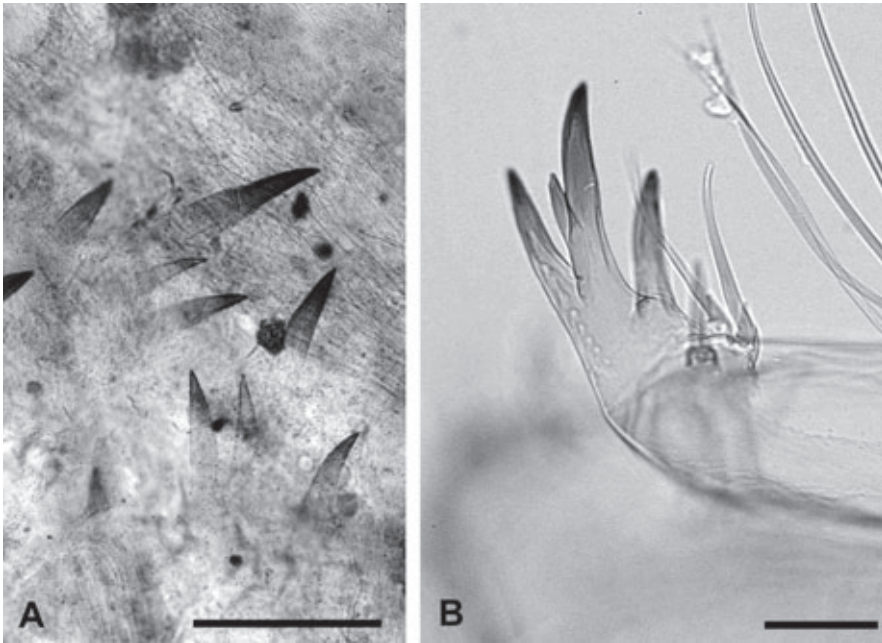


Fig. 4. Parts of mandibles of phantom midge larvae (Chaoboridae): (A) fossil structure in a coprolite; (B) part of a mandible from extant *Chaoborus* sp. Transmitted-light microscopy. Scale bars 100 μm .

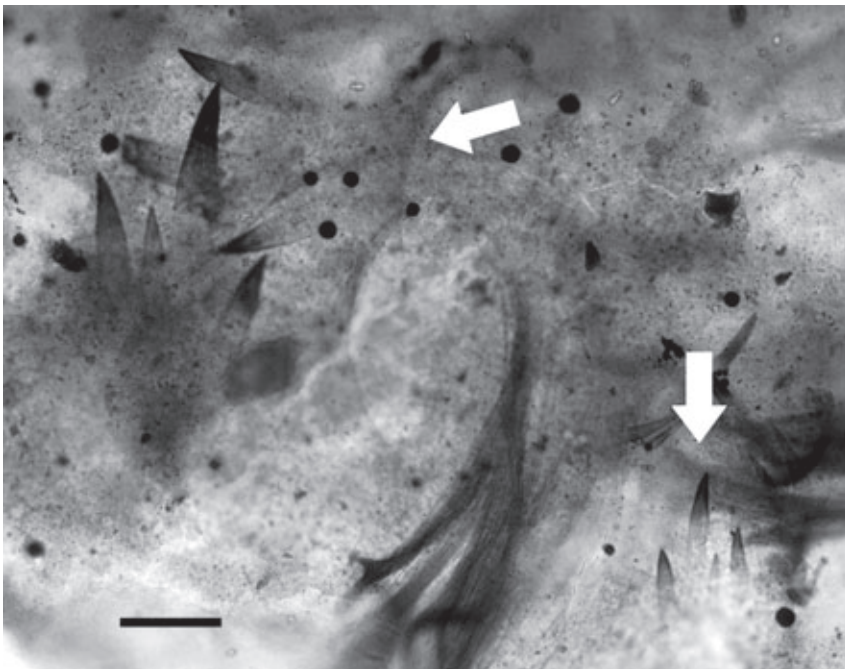


Fig. 5. Different sizes of fossil chaoborid mandibles, found in one coprolite. Transmitted-light microscopy. Scale bar 50 μm .

Figure 8A shows a structure with reticulate wall patterns and a short appendix. These remains are found moderately often in 25 to 50% of the coprolites. They are often associated with pairs of compound eyes and tarsal claws. Comparison with extant structures (Fig. 8B) shows that these are parts of the respiratory horns of chaoborid pupae which were identified by Richter and Wedmann (2005). Their frequency is rather high when it is considered that especially the fourth larval instars are subject to such a strong predation pressure that only a fractional amount of them gets around to pupation (Irvine 1995). Pupal organs are markers of a short period in the life cycle of chaoborid midges. The duration of metamorphosis of tropical *Chaoborus* species is two to a maximum of four days, and, in extant tropical lakes, one complete life cycle including four larval instars and the pupa generally takes about two months (MacDonald 1956; Cressa & Lewis 1986; Irvine 1995). It was found in extant tropical lakes that the larval stages of each *Chaoborus* species form two separate size-groups (MacDonald 1956). Larvae of one generation develop into pupae within a two-week period (Irvine 1995). Pupation and emergence of adult chaoborids in the tropics are synchronised and seemingly associated with the period of the new moon. So, in the tropics, roughly synchronised emergences occur at monthly intervals (MacDonald 1956; Irvine 1997). Possibly a scenario like this can be transferred to the former Lake Messel.

The abundance of phantom-midge structures in the coprolites shows that both larvae and pupae were present in large quantities and were an important component in the food web of Lake Messel. In many extant lakes, chaoborids play a major ecological role in the pelagic food web, as demonstrated, for example, by Carpenter and Kitchell (1993) for some lakes in Wisconsin, USA, and Menz (1995) for Lake Malawi, Africa.

The larvae of phantom midges float in the pelagic zone of a lake. They are translucent and, except for their two pairs of hydrostatic tracheal sacs, almost invisible while motionless.

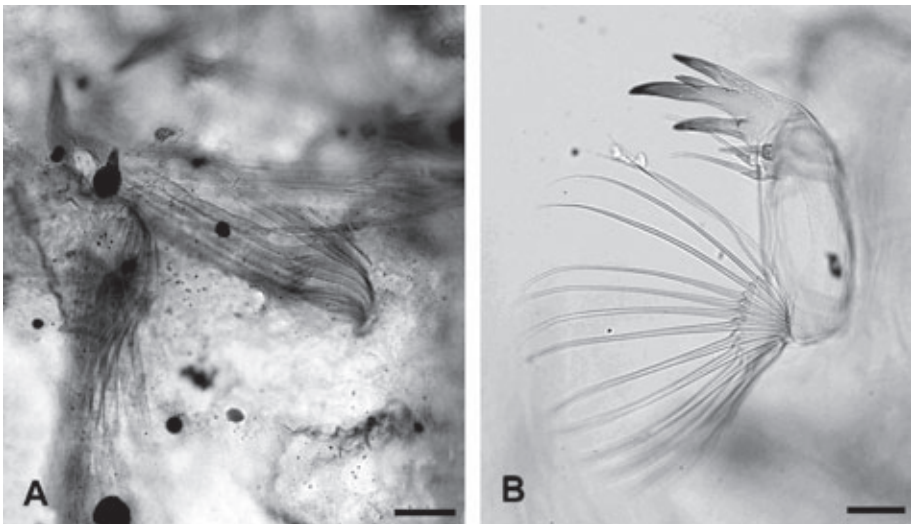


Fig. 6. Mandibles of phantom midge larvae (Chaoboridae): (A) fossil structure in a coprolite; (B) mandible from extant *Chaoborus* sp. Transmitted light microscopy. Scale bar 25 μm in Fig. 6A and 100 μm in Fig. 6B.

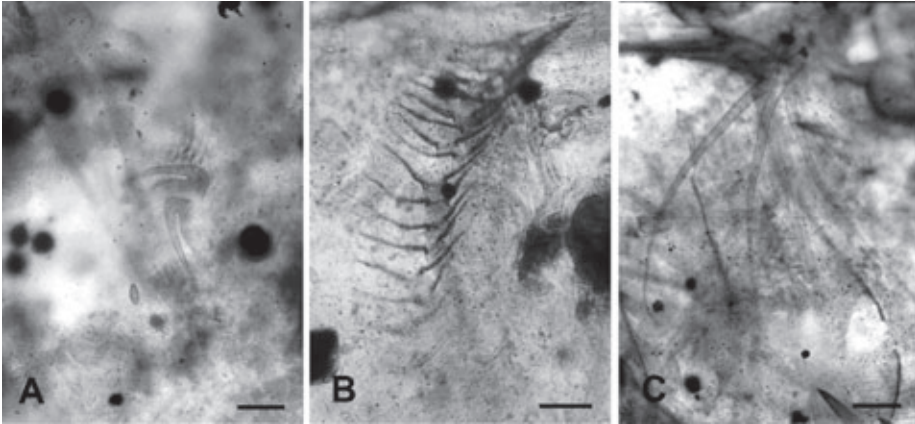


Fig. 7. Fossil structures: (A) pair of caudal hooks, remains of a chaoborid larva; (B) T-shaped bases of setae of an anal fan, remains of a culicoid larva; (C) paddle with supporting midrib, remains of a *Chaoborus* pupa. Transmitted-light microscopy. Scale bars 25 μm .

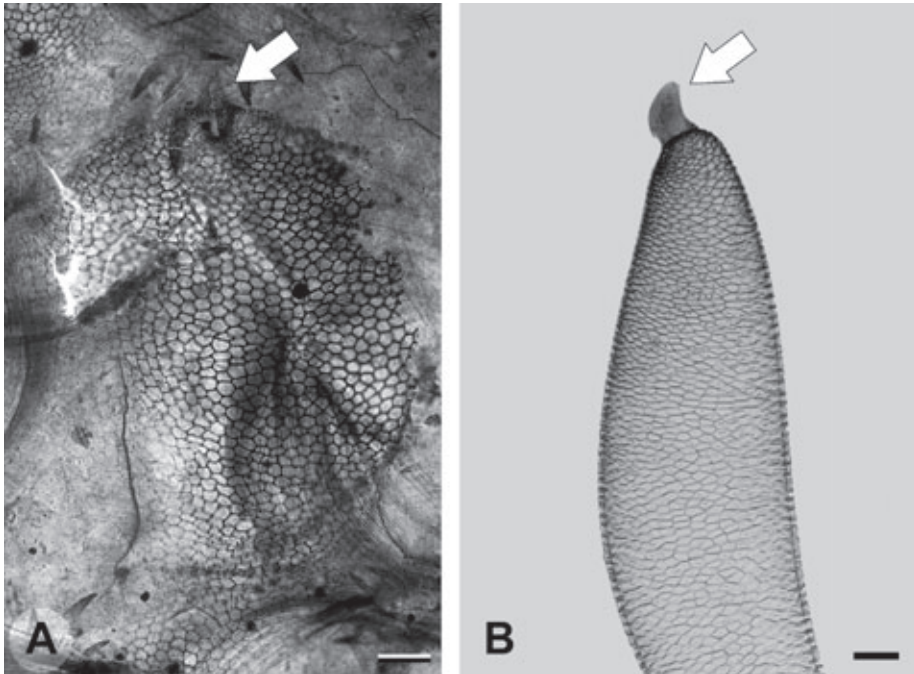


Fig. 8. Parts of respiratory horns of phantom midge pupae (Chaoboridae): (A) upper part of fossil respiratory horn in a coprolite; (B) upper part of a respiratory horn from extant *Chaoborus* sp. The appendices of the respiratory horns are arrowed. Transmitted-light microscopy. Scale bars 50 μm .

Their altered antennae together with the strong mandibles serve for capturing their prey (Fig. 9A). The pupae hover in an upright position in the water (Fig. 9B).

Chaoborid larvae are important both as prey for planktivorous fish and as predators. Diet studies of tropical *Chaoborus* larvae show that the older larval instars feed mainly on small planktonic crustaceans, such as copepods or waterfleas, and only occasionally ingest phytoplankton (Lewis 1975; Moore *et al.* 1994; Irvine 1997). This implies that large populations of chaoborids might have a measurable effect on zooplankton population dynamics (Cressa & Lewis 1986; Lehman *et al.* 1998). Small roundish clusters of phytoplankton are found regularly in the coprolites. These particles may well represent gut contents of prey animals. Moore *et al.* (1994) pointed out that, when present in high density, phytoplankton forms a substantial part of the diet of *Chaoborus* larvae. It is obvious from our study that *Thaumaturus intermedius* from Messel preyed heavily on these larvae. Studies on the food consumption of fish in Lake Malawi show that these insects are an important part of the diet of several pelagic fish species in extant lakes with large chaoborid populations (Allison *et al.* 1995). The possible importance of chaoborids as prey for fish is also shown by He *et al.* (1993).

The presence of these immature stages of chaoborid midges prompts different interesting hypotheses on the former lake ecology. Studies on extant populations of chaoborid larvae in both temperate and tropical lakes show that when planktivorous fish are present, a vertical diurnal migration of the third and fourth larval instars generally occurs (e.g. Sardella & Carter 1983; Irvine 1997). During the night the later instars of chaoborid larvae stay in the upper horizons of the lake to capture their prey (Fig. 10). During the day, in meromictic lakes the chaoborid larvae stay in the upper anoxic horizons of the monimolimnion, where they take refuge from planktivorous fish (Sardella & Carter 1983). A refuge with low oxygen concentration might be essential for the stable presence of high numbers of phantom midge larvae in lakes where they coexist with fish (Irvine 1997).

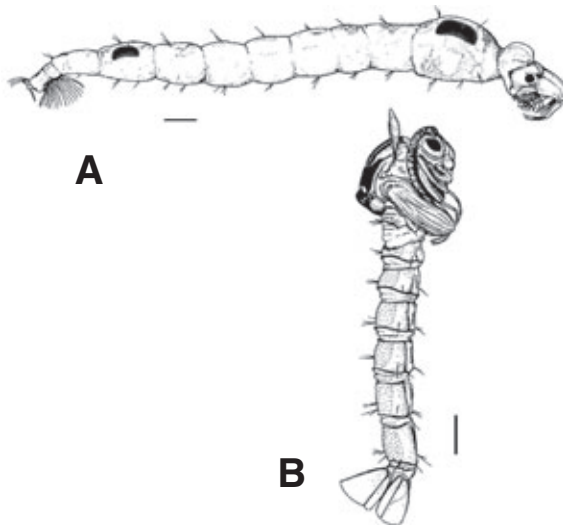


Fig. 9. Immature stages of extant *Chaoborus* sp. in lateral view: (A) larva; (B) pupa. Scale bars 1 mm. Drawings modified after Sæther (1997).

Moreover, Rahel and Nutzman (1994) found that planktivorous fish in extant meromictic lakes venture during the day into the anoxic water zone in search of prey. One can only speculate whether the fossil *Thaumaturus* species in Messel displayed the same behaviour or whether the *Chaoborus* species had no migration behaviour at all.

The investigation of coprolites has confirmed the presence of a great variety of invertebrate organisms in the limnic food web of Lake Messel (Richter & Baszio 2001a, 2002). Without analysis of the small fish coprolites, the detection of significant populations of phantom midge larvae would not have been possible. Analysis of the drilling core confirmed the stable presence of *Chaoborus* populations throughout the life span of the former Lake Messel (Richter & Wedmann 2005).

Large populations of immature chaoborid midges also played an important role in other fossil ecosystems. Sinitshenkova (2002) and Zherikhin and Sinitshenkova (2002) gave an overview of assemblages of aquatic insects in lacustrine deposits through time and they distinguished between different assemblage types. Immature stages of chaoborids are preserved, sometimes in huge numbers, in many Mesozoic lakes in Siberia, Mongolia and China. For example, fossils of Chaoboridae are moderately abundant in Lower Jurassic to Lower Cretaceous sediments of several former lakes in Transbaikalia (type A of Sinichenkova & Zherikhin 1996; Jurassic assemblage 2 of Sinitshenkova 2002). In numerous Lower Cretaceous lacustrine deposits from Siberia, Mongolia and China, Chaoboridae are very abundant (types C, D, and E of Sinichenkova & Zherikhin 1996; Cretaceous assemblage types 3, 4, 5, 7, and 8 of Sinitshenkova 2002). Their diversity in these deposits was generally low, with usually only one species occurring in each locality (Sinitshenkova 2002). Immature chaoborids are also quite common in the Lower Cretaceous Koonwarra fossil beds of Australia (Jell & Duncan 1986). Chaoborids and other autochthonous aquatic insects seem to be lacking in Upper

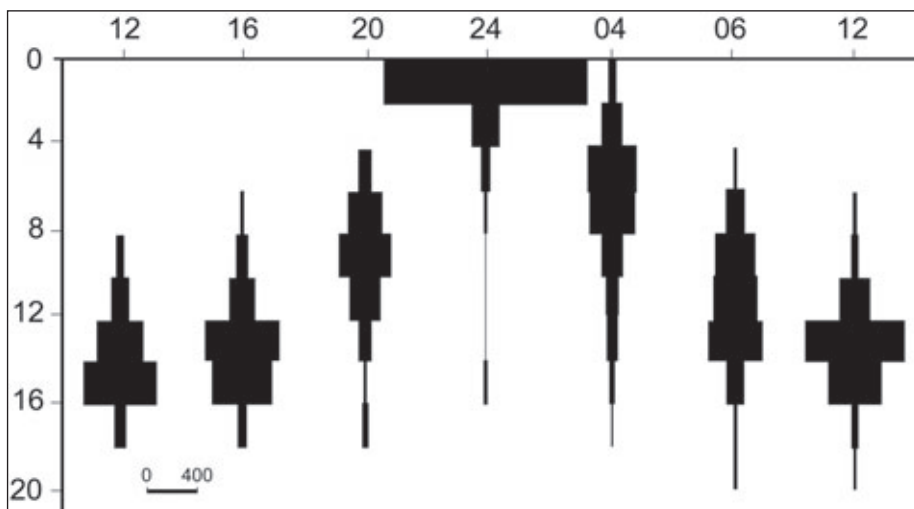


Fig. 10. Vertical diurnal migration of the last larval instar of *Chaoborus punctipennis* in the extant meromictic Crawford Lake, Canada. Crawford Lake is continuously anoxic below 14 m, but the anaerobic boundary may vary seasonally from 11 to 14 m. The hours are plotted horizontally, the depth in metres is plotted vertically. Horizontal scale shows number of individuals/m³. Modified after Sardella and Carter (1983).

Cretaceous deposits. This is interpreted as that an extinction event of insects which inhabit stagnant water habitats possibly occurred at the end of the Early Cretaceous (Sinitschenkova 2002). Abundant fossils of chaoborid pupae from Cainozoic deposits have been reported by Johnston and Borkent (1998) from the Middle Eocene Tallahatta Formation in Mississippi, USA.

These examples show that lakes with large populations of chaoborid midges existed for a long time. A major difference between all these deposits and Messel is that in all the other deposits body fossils of chaoborids have been found, whereas in Messel the presence of chaoborids is proven almost only via investigation of fish coprolites. Only after close examination some seemingly isolated mandibles of the larvae were also found directly in the sediment. The lack of complete body fossils is possibly due to very weak sclerotisation of the larvae. It is likely that the larvae are preserved in the sediment but cannot be seen because of their translucent body. The lack of body fossils of adult chaoborid midges shows the importance of taphonomic influences on the taxonomic composition of fossil assemblages. In general, body fossils of dipterans (midges and flies) are very rare among thousands of insect fossils from Messel.

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REFERENCES

- ALLISON, E.H., THOMPSON, A.B., NGATUNGA, B.P. & IRVINE, K. 1995. The diet and food consumption rates of the offshore fish. In: Menz, A., ed., *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*. Chatham, UK: Natural Resources Institute, pp. 233–278.
- CARPENTER, S.R. & KITCHELL, J.F. 1993. *The Trophic Cascade in Lakes*. Cambridge: University Press.
- CRESSA, C. & LEWIS, W.M., JR. 1986. Ecological energetics of *Chaoborus* in a tropical lake. *Oecologia* **70**: 326–331.
- FRANZEN, J.L. 1992. Europe in the Eocene: Messel in time and space. In: Schaal, S. & Ziegler, W., eds, *Messel. An Insight into the History of Life and of the Earth*. Oxford: Clarendon press, pp. 13–15.
- GOth, K. 1988. Origin of Messel oil shale kerogen. *Nature* **336**: 759–761.
- 1990. Der Messeler Ölschiefer – ein Algenlaminit. *Courier Forschungsinstitut Senckenberg* **131**: 1–143.
- HARMS, F.-J. 2002. Steine erzählen Geschichte(n): Ursachen für die Entstehung des Messel-Sees gefunden. *Natur und Museum* **132**: 1–4.
- HE, X., KITCHELL, J.F., HODGSON, J.R., WRIGHT, R.A., SORANNO, P.A., LODGE, D.M., COCHRAN, P.A., BENKOWSKI, D.A. & BOUWES, N.W. 1993. Roles of fish predation: piscivory and planktivory. In: Carpenter, S.R. & Kitchell, J.F., eds, *The Trophic Cascade in Lakes*. Cambridge: University Press, pp. 85–102.
- HÖRNSCHEMEYER, T. & WEDMANN, S. 1994. Fossile Prachtkäfer (Coleoptera: Buprestidae: Buprestinae) aus dem Mitteleozän der Grube Messel bei Darmstadt, Teil 1. *Courier Forschungsinstitut Senckenberg* **170**: 85–136.

- IRVINE, K. 1995. Ecology of the lakefly, *Chaoborus edulis*. In: Menz, A., ed., *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*. Chatham, UK: Natural Resources Institute, pp. 109–140.
- 1997. Food selectivity and diel vertical distribution of *Chaoborus edulis* (Diptera, Chaoboridae) in Lake Malawi. *Freshwater Biology* **37**: 605–620.
- JELL, P.A. & DUNCAN, P.M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. In: Jell, P.A. & Roberts, J., eds, *Plants and Invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria*. Sydney: Association of Australasian Palaeontologists, pp. 111–205.
- JOHNSTON, J.E. & BORSENT, A. 1998. *Chaoborus* Lichtenstein (Diptera: Chaoboridae) pupae from the middle Eocene of Mississippi. *Journal of Paleontology* **72**: 491–493.
- KOENIGSWALD, W. VON & STORCH, G. 1998. *Messel. Ein Pompeji der Paläontologie*. Sigmaringen: Jan Thorbecke.
- LEHMAN, J.T., HALAT, K., BETZ, B., NDAWULA, L.M. & KIGGUNDU, V. 1998. Secondary production by the lake fly *Chaoborus* in Lake Victoria, East Africa: Implications for trophic dynamics of the modern lake. In: Lehman, J.T., ed., *Environmental Change and Response in East African Lakes*. Dordrecht, Boston, London: Kluwer Academic Publishers, pp. 135–145.
- LEWIS, W.M., JR. 1975. Distribution and feeding habits of a tropical *Chaoborus* population. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* **19**: 3106–3119.
- LUTZ, H. 1986. Eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mittel-eozänen Ölschiefer der “Grube Messel” bei Darmstadt (Deutschland, S-Hessen). *Senckenbergiana lethaea* **67**: 177–218.
- 1987. Die Insekten-Thanatocoenose aus dem Mittel-Eozän der “Grube Messel” bei Darmstadt: Erste Ergebnisse. *Courier Forschungsinstitut Senckenberg* **91**: 189–201.
- 1990. Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg* **124**: 1–165.
- 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.
- MACDONALD, W.W. 1956. Observations on the biology of chaoborids and chironomids in Lake Viktoria and on the feeding habits of the elephant-snout fish (*Mormyrus kannume* Forsk.). *Journal of Animal Ecology* **25**: 36–53.
- MENZ, A. 1995. *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*. Chatham, UK: Natural Resources Institute.
- MERTZ, D.F., HARMS, F.-J., GABRIEL, G. & FELDER, M. 2004. Arbeitstreffen in der Forschungsstation Grube Messel mit neuen Ergebnissen aus der Messel-Forschung. *Natur und Museum* **134**: 289–290.
- MICKLICH, N. 2002. The fish fauna of Messel pit: A nursery school? *Courier Forschungsinstitut Senckenberg* **237**: 97–127.
- MOORE M.V., YAN, N.D. & PAWSON, T. 1994. Omnivory of the larval phantom midge (*Chaoborus* spp.) and its potential significance for freshwater planktonic food webs. *Canadian Journal of Zoology* **72**: 2055–2065.
- RAHEL, F.J. & NUTZMAN, J.W. 1994. Foraging in a lethal environment: Fish predation in hypoxic waters of a stratified lake. *Ecology* **75**: 1246–1253.
- RICHTER, G. & BASZIO, S. 2001a. Traces of a limnic food web in the Eocene lake Messel – a preliminary report based on fish coprolite analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology* **166**: 345–368.
- 2001b. First proof of planctivory/insectivory in a fossil fish: *Thaumaturus intermedius* from the Eocene Lake Messel (FRG). *Palaeogeography, Palaeoclimatology, Palaeoecology* **173**: 75–85.
- 2002. Beiträge zur Ökologie des tertiären Messelsees. *Natur und Museum* **132**: 137–149.
- RICHTER, G. & KREBS, G. 1999. Larvenstadien von Eintagsfliegen (Insecta: Ephemeroptera) aus Sedimenten des eozänen Messelsees. *Natur und Museum* **129**: 21–28.
- RICHTER, G. & WEDMANN, S. 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.
- RIETSCHEL, S. 1988. Taphonomic biasing in the Messel Fauna and Flora. *Courier Forschungsinstitut Senckenberg* **107**: 169–182.
- SÆTHER, O.A. 1997. Diptera Chaoboridae, Phantom midges. In: Nilsson, A., ed., *Aquatic Insects of North Europe* 2. Stenstrup: Apollo, pp. 149–161.

- SARDELLA, L.C. & CARTER, J.C.H. 1983. Factors contributing to coexistence of *Chaoborus flavicans* and *C. punctipennis* (Diptera, Chaoboridae) in a small meromictic lake. *Hydrobiologia* **107**: 155–164.
- SCHAAL, S. & ZIEGLER, W. 1992. *Messel. An Insight into the History of Life and of the Earth*. Oxford: Clarendon Press.
- SINITSHENKOVA, N.N. 2002. Ecological history of the aquatic insects. In: Rasnitsyn, A.P. & Quicke, D.L.J., eds, *History of Insects*. Dordrecht etc.: Kluwer Academic Publishers, pp. 388–417.
- SINICHENKOVA, N.N. & ZHERIKHIN, V.V. 1996. Mesozoic lacustrine biota: Extinction and persistence of communities. *Paleontological Journal* **30** (6): 710–715.
- TRÖSTER, G. 1991. Eine neue Gattung der Elateridae (Insecta: Coleoptera) *Macropunctum* gen. n. aus der Messel-Formation des unteren Mittel-Eozän der Fundstätte Messel. *Courier Forschungsinstitut Senckenberg* **139**: 99–117.
- 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.
- 1993b. Wasserkäfer und andere Raritäten – Neue Coleoptera-Funde aus den mitteleozänen Tonsteinen der Grube Messel bei Darmstadt. *Kaupia – Darmstädter Beiträge zur Naturgeschichte* **2**: 145–154.
- 1994. Fossile Elateridae (Insecta: Coleoptera) aus dem Unteren Mitteleozän (Lutetium) der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg* **170**: 11–64.
- 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** (1): 11–20.
- WAPPLER, T. 2003a. 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.
- 2003b. Die Insekten aus dem Mittel-Eozän des Eckfelder Maares, Vulkaneifel. *Mainzer Naturwissenschaftliches Archiv, Beiheft* **27**: 1–234.
- WAPPLER, T. & ANDERSEN, N.M. 2004. Fossil water striders from the Middle Eocene fossil sites of Eckfeld and Messel, Germany (Hemiptera, Gerromorpha). *Paläontologische Zeitschrift* **78**: 41–52.
- WAPPLER, T. & ENGEL, M.S. 2003. The middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera: Apoidea). *Journal of Paleontology* **77**: 908–921.
- WEDMANN, S. 2000. Die Insekten der oberoligozänen Fossilagerstätte Enspel (Westerwald, Deutschland) – Systematik, Biostratonomie und Paläoökologie. *Mainzer Naturwissenschaftliches Archiv, Beiheft* **23**: 1–154.
- 2005. Annotated taxon-list of the invertebrate animals from the Eocene fossil site Grube Messel near Darmstadt, Germany. *Courier Forschungsinstitut Senckenberg* **255**: 103–110.
- WEDMANN, S. & HÖRNSCHEMEYER, T. 1994. Fossile Prachtkäfer (Coleoptera: Buprestidae: Buprestinae und Agrilinae) aus dem Mitteleozän der Grube Messel bei Darmstadt, Teil 2. *Courier Forschungsinstitut Senckenberg* **170**: 137–187.
- WOOD, D.M. & BORKENT, A. 1989. Phylogeny and classification of the Nematocera. In: McAlpine, J.F. & Wood, D.M., eds, *Manual of Nearctic Diptera*, Volume 3. Monograph No. 32. Ottawa: Research Branch Agriculture Canada, pp. 1333–1370.
- ZHERIKHIN, V.V. & SINITSHENKOVA, N.N. 2002. 3.3.7. Cainozoic. In: Rasnitsyn, A.P. & Quicke, D.L.J., eds, *History of Insects*. Dordrecht etc.: Kluwer Academic Publishers, pp. 417–426.