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Cyanobacteria and seasonal death: A new taphonomic model for the Eocene Messel lake

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with 6 figures

Kurzfassung: Zwei neue Beobachtungen verändern das Bild der Taphonomie von Messel: Zum einen gibt es bei den Pferden und Schildkröten eindeutige Hinweise, dass viele dieser Tiere zu einer bestimmten Jahreszeit umgekommen sind, obwohl sie aus ganz unterschiedlichen Horizonten stammen. Zum anderen gleichen spezielle Strukturen im Sediment solchen aus Neumark-Nord in hohem Maße, die dort durch Blüten von Cyanobakterien verursacht wurden. Diese Bakterien können bei hoher Konzentration das Oberflächenwasser zeitweise vergiften. Wie Rezentbeobachtungen zeigen, treten bei Tieren, die dieses Wasser trinken, sehr schnell Lähmungen und Krämpfe auf, und sie sterben meist sehr schnell im Wasser oder in dessen unmittelbarer Nähe. Das würde auch erklären, warum im ganzen Profil von Messel so viele Vögel und Fledermäuse überliefert sind, weil diese Tiere von der Wasseroberfläche trinken. Im Gegensatz zu bislang angenommenen vulkanischen Exhalationen treten derartige Cyanobakterienblüten immer wieder auf, meist im Frühsommer oder Herbst.

Schlüsselwörter: Messel, Taphonomie, Cyanobakterien, Vergiftung, Algenblüten

Abstract: Two new observations lead us to reconsider the taphonomy of Messel. First, several horses as well as turtles indicate death at a specific season although they come from different horizons. Second, specific structures in the sediments are very similar to those found in Neumark-Nord. There they could be related to Cyanobacteria. Blooms of Cyanobacteria may poison the surface water. From actual observations it is known that animals drinking such poison water collapse immediately and die mostly near or within the water soon. This model might explain why birds and bats are so frequent throughout the entire profile of Messel. Both drink from the water surface during flight. In contrast to volcanic exhalations, assumed so far, such algae blooms occur repeatedly and always during early summer and autumn.

Keywords: Messel, taphonomy, cyanobacteria, toxification, algal blooms

Introduction

The abandoned oil shale pit of Messel near Darmstadt (Germany) is famous for its excellent preservation of vertebrate skeletons from the Middle Eocene (MP 11) (FRANZEN 1977; SCHAAL & ZIEGLER 1988; von KOENIGSWALD & STORCH 1997). The oil shale was deposited in an ancient freshwater lake. The beds are about 160 m thick and the majority is well laminated. The laminae are about 0.01 mm thick and are considered as representing annual layers (IRION 1977; GOTH 1990). Due to its high water content the oil shale weathers immediately, and it is therefore impossible to follow single layers over a larger distance in order to check the density of the fossils per layer. Fossils are generally rare, but well preserved when present. The high quality of preservation is due to a stable lower water layer almost free of oxygen which did not allow scavengers to approach carcasses once they had sunken to the lake floor.

One of the main problems concerning this locality is the reason why the terrestrial, arboreal, or flying animals came to death. Most of them were in good health and well nourished as seen from stomach contents. Flying animals like birds and bats, normally quite rare in lake deposits, are frequent in Messel. Most skeletons are intact and show no traces of scavenging.

The reason for the death of these animals was discussed in several models. RICHTER & STORCH (1980) argued for poison gasses which caused the death of animals, especially bats and birds flying over the lake. RIETSCHEL (1988) assumed that the basin in which the lake came into existence represents a crater and thus steep walls might have caused the sudden fall of animals directly into the lake. Influenced by Lake Nio catastrophe in Cameroon, where many animals were killed by the eruption of poison gasses from the volcanic "maar" structure, FRANZEN & KÖSTER (1994) postulated similar causes for the death of the animals preserved in the Messel lake. Gases may have been derived from the volcanic underground or from the sediments. Since the skeletons

are widely spread in the profile, a great number of such gas eruptions would have to be postulated. So far no experience is available on how often such catastrophes as in Lake Nio may occur. The eruption of volcanic gasses is unpredictable in its frequency and in its effect on the terrestrial fauna. Even if animals were killed in the surrounding area, the carcasses have to be transported into the lake without being attacked by scavengers. Poison gasses originating from the lake sediments may occur more regularly when an algal turnover occurs. This would affect primarily the fish fauna. The unusual frequency of birds and bats could be explained only if these gasses remained trapped above the water in high concentrations. It was argued that a high forest surrounding the lake might have provided such a trap (RICHTER & STORCH 1980; FRANZEN & KÖSTER 1994) but the former Messel lake had a surface area of distinctly more than 1.5 square kilometers, making this unlikely.

Two new observations shed a somewhat different light on the taphonomy of Messel. On the one hand, there is good evidence for seasonal death, and on the other hand some evidence for cyanobacteria were found.

Seasonal death

Only a few specimen deaths can be attributed to a specific season. The aquatic turtle *Allaeochelys crassesculptata* is well documented in Messel, but the precise number of specimens is not known. In the various collections, at least 5 slabs of oil shale are preserved in which two specimen were imbedded as a pair close together (Figs. 1 and 2). The following specimens are known to us, but more may have been found (Museum für Naturkunde, Karlsruhe: SMNK-Pal-2348; Hessisches Landesmuseum Darmstadt: HLMD-Me-7593 and HLMD-Me-14998/14999; Senckenberg-Museum Frankfurt: SMF-Me-2449; SMF-Me-2034; SMF-Me-3566). This preservation is extraordinary since the density of fossils is very limited in Messel. RIETSCHEL (1998) gave the first interpretation of this unusual occurrence assuming both animals died when fused by the penis during mating. The somewhat crushed carapaces do not allow to identify males and females so far. Except close to the equator, mating of turtles occurs during specific seasons. The period becomes shorter with increasing distance from the equator. During the Middle Eocene, Messel was situated at about 30–40° North, and thus a high seasonality of the mating activity can be assumed. Again, the turtles come from different localities and different levels, indicating that death occurred in the same season but in absolutely different years.

There is a second, even more convincing indication for seasonal death among mammals. The dawn horse from Messel, *Propalaeotherium parvulum*, is represented by several dozens of skeletons. Their number may be about 50 but the exact number is unknown. Among the finds are 5 pregnant mares (Figs. 3 and 4). They are

housed in the Hessische Landesmuseum Darmstadt: HLMD-Me-8989, in the Museum für Naturkunde Karlsruhe: SMNK-Pal-3170, in the Senckenbergmuseum Frankfurt: SMF + Me: – 1970, and in the Bayerische Staatssammlung München: BSP.1985.I.62 (von KOENIGSWALD 1987; von KOENIGSWALD & STORCH 1997; MAIER 2000). These four specimen found before 1998 were studied by MAIER (2000), and he found that all fetuses were in the same late stage of development. A fifth specimen, found in 2001 by the crew of the Senckenbergmuseum (SMF, Me-11034; SCHAAL 2001), again shows the same late stage of development (Fig. 4). Although the climate was paratropic, it can be assumed that pregnancy and time of delivery was related to the seasonal change. This indicates that all these animals died more or less in the same month. Due to predator pressure on newborn hoofed animals, all pregnant females give birth during a very short period, mostly in late spring (HEIDEMANN 1973; CLUTTON BROCK 1985, 1988). The finds come from very different levels and localities within the pit, indicating that the death occurred in very different years but in the same season.

After these first two examples for seasonal death in the lake of Messel, it would be worthwhile to test other taxa. A successful marker for the date of death in mammals is the eruption of teeth in young animals (von KOENIGSWALD & KUBIAK 1979). It is so far not applicable in Messel since the number of such finds is too rare.

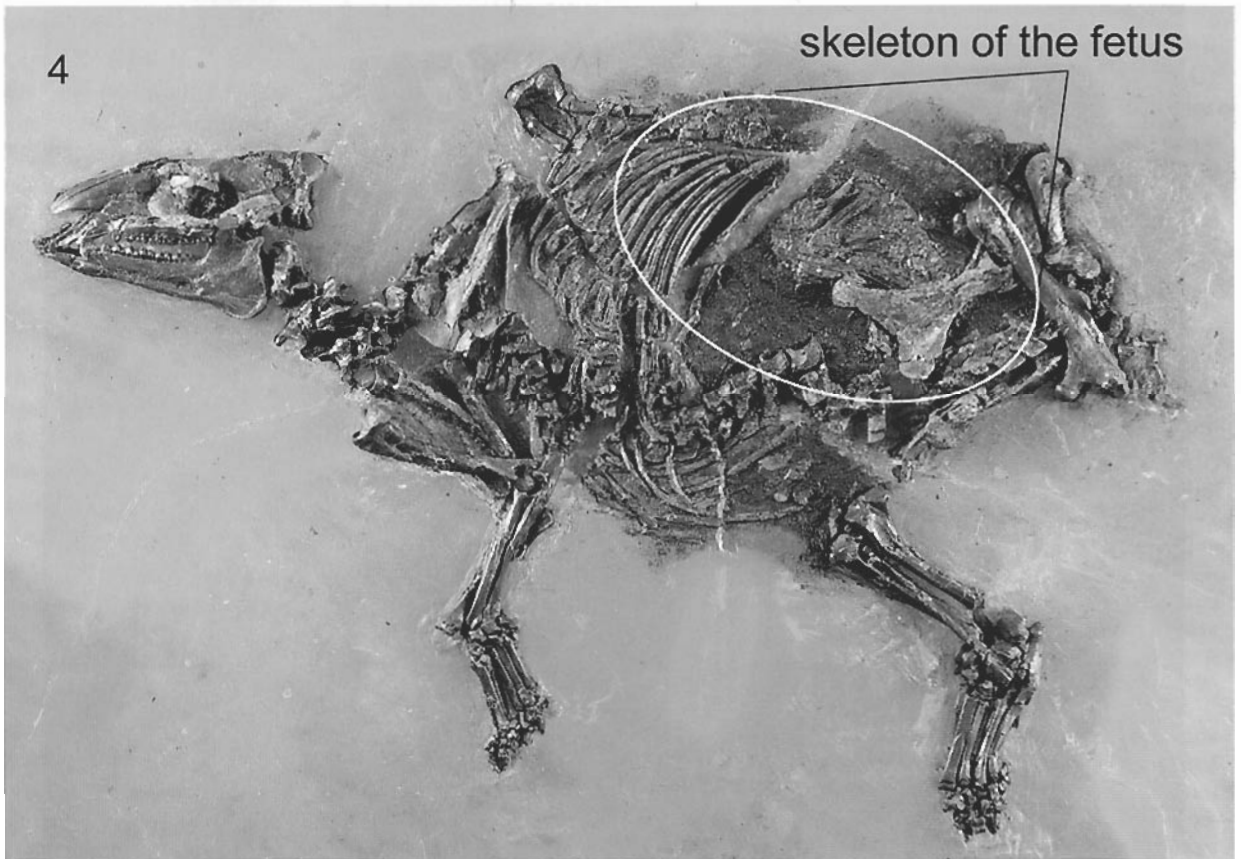
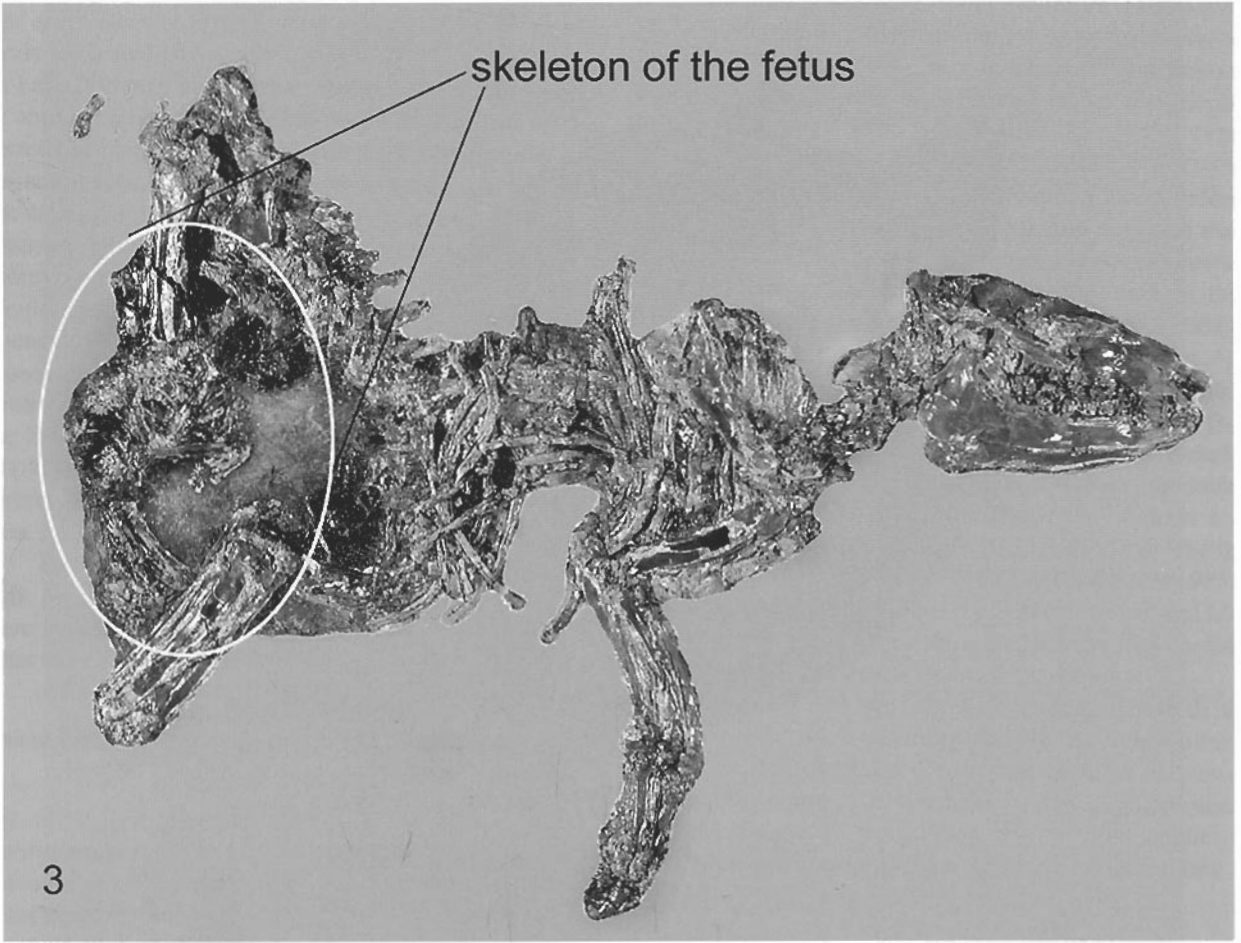
Cyanobacteria

The lamination of the Messel oilshale is connected with algal blooms (GOTH 1990). The specific proof of Cyanobacteria in fossiliferous sediments is difficult since their characteristic chemical traces are mostly destroyed by diagenesis. Recently BRAUN & PFEIFFER (2002) investigated Pleistocene lake sediments from Neumark-Nord (Geiseltal, Germany) (MANIA et al. 1990; PFEIFFER 1999), a locality, which yielded a multitude of well preserved and intact skeletons of large mammals. Within the varved sediments, the spring-early summer layer was packed with chrysophyceyan cysts. The subsequent autumnal layers are of limey composition which, compared to similar recent examples, have been interpreted as microbial carbonate mineralisation induced by benthic bacteria decomposing sunken cyanobacterial

Figs. 1–2. The turtle *Allaeochelys crassesculptata* is quite frequent in the Middle Eocene lake deposits from Messel. At least five times individuals are imbedded in pairs. This might be interpreted as a sudden death during mating. – 1: Darmstadt, HLMD-Me-7593. – 2: Karlsruhe, SMNK-Pal-2348.

Abb. 1–2. Die Schildkröte *Allaeochelys crassesculptata* ist relativ häufig im Mitteleozän von Messel überliefert. Mindestens fünf mal sind je zwei Individuen paarweise eingebettet worden. Dies kann durch einen plötzlichen Tod während der Kopulation bedingt sein. – 1: Darmstadt, HLMD-Me-7593. – 2: Karlsruhe, SMNK-Pal-2348.





blooms at the sediment-water interface (CHAEFZ & BUCZYNSKI 1992). The nature of the blooms could be identified at Neumark-Nord by biochemical analyses of pigments and toxins specific for Cyanobacteria (BRAUN & PFEIFFER 2002).

In Neumark-Nord, the death of many deer occurred mainly in autumn, with some exceptions in early summer according to antler development and skeletal characters (PFEIFFER 1999). The seasonal pattern occurred throughout the profile, indicating that such algal blooms occurred not every year but repeatedly during the several hundreds to thousands of years represented in the sequence.

There are strong taphonomic, preservational and sedimentological similarities between the Neumark-Nord lake sediments and those at Messel. Due to compaction and diagenesis, the vertical differentiation of the individual varve layers is not preserved in detail at Messel. But layers of densely packed chrysophyceans are well documented immediately below fine layers of siderite. The latter are here considered as derived from microbial calcium carbonate as preserved in the much younger varves from Neumark-Nord (Figs. 5 and 6; BRAUN & PFEIFFER 2002). Blooms of Cyanobacteria and their effect are well known from observations in modern lakes (HENNING & KOHL 1981; SIVONEN 1989; WECKESSER & MARTIN 1990; CARMICHAEL 1992, 1994). Reports for Lake Suwa (Japan) document the seasonal changes in species composition of *Microcystis* and concentration of toxic heptapeptide microcystins (PARK et al. 1993). High amounts of microcystin were estimated during the exponential growth phase of the bloom from June to July. The production of the toxins by *Microcystis* seems to be associated with the dissolved inorganic nitrogen (DIN) concentration. After the collapse of the summer algal bloom which removed much nitrogen from the water, nitrifying Cyanobacteria may attain a selective advantage. The sinking bloom together with the generally high organic content of the water causes poor light in the lake and favours phototrophic Cyanobacteria exclusively drifting near the surface with the aid of gas vacuoles in the late summer. Therefore high amounts of microcystin could be detected also in autumn.

It is observed that terrestrial animals drinking the poisoned water die almost instantly (PYBUS et al. 1986; WECKESSER & MARTIN 1990; EDWARDS et al. 1992; NEHRING 1993). Predators obviously avoid such poisoned carcasses (WECKESSER, personal communication).

A new taphonomic model for Messel

For the reconstruction of the taphonomy in a fossil site, it is important to understand why the taphocoenosis is biased compared to the species composition in the habitat. Therefore the attempt has to be made to understand the cause of the death and the course of the carcass into the sediment. For Messel, the proof of seasonal death linked with the most probable occurrence of blooms of Cyanobacteria sheds new light on taphonomy and allows the following scenario for the taphonomy of the Messel lake.

We distinguish between normal conditions which occur most of the time and unusual conditions, the results of which are the extremely well preserved fossils.

Most of the time – that is for many years – life was normal. Fish and crocodiles lived in the uppermost part of the water body, while the lower part was almost free of oxygen. Animals which might have died near the lake were washed into the lake. Thus life within the Messel lake was nevertheless limited, since water insects were extremely rare (LUTZ 1987). This is the only obvious restriction documented in the fossil record.

Unusual conditions were postulated earlier to explain the exceptional preservation of the terrestrial, arboreal, and flying animals. We suggest blooms of Cyanobacteria as a major cause for such conditions. Poisoning algal blooms may occur during specific seasons not each year, but every couple of years – as necessary to explain the occurrence of excellent fossils throughout the entire observed sedimentary sequence. A volcanic origin of gas eruptions as in the Lake Nio would not match any of these patterns. A gas eruption from lake sediments requires a deep lake which certainly was present in Messel. However, such a turnover primarily would have caused the massive death of fishes and other animals in the water. It would not have effected terrestrial, arboreal or flying animals in the same way. The model that poison gasses arising from the water may be kept stable by the surrounding forest is highly improbable since the surface of the lake was at least 1.5 or 2 square kilometers.

During a bloom of Cyanobacteria the surface water may be enriched with poisoning microcystins. A slight wind may even enrich the poisoning cells in some shore areas. Such water becomes highly dangerous for any animal drinking from the lake. That would effect mammals feeding on animals from the water like *Macrocranion* and *Buxolestes* which had fish remains in their intestines (SCHAAL & ZIEGLER 1988). Effected are all terrestrial and arboreal mammals drinking from the water. Others not drinking from the lake will be underrepresented in the fossil record. Therefore this model might provide a new understanding why many of the larger mammals known from that time period are missing in Messel. Concentrated poison on the water surface would be especially dangerous for animals drinking from the water in flight, such as bats and some birds. Others not drink-

Figs. 3–4. From the Middle Eocene of Messel near Darmstadt, Germany five pregnant mares of *Propalaeotherium parvulum* are known so far. The fetuses all show the same degree of maturity. – **3:** Darmstadt, HLMD-Me-8989. – **4:** Frankfurt, SMF-Me-11034. **Abb. 3–4.** Aus dem Miozän von Messel sind fünf tragende Stuten von *Propalaeotherium parvulum* bekannt, die alle den gleichen Reifegrad des Fötus zeigen. – **3:** Darmstadt, HLMD-Me-8989. – **4:** Frankfurt, SMF-Me-11034.

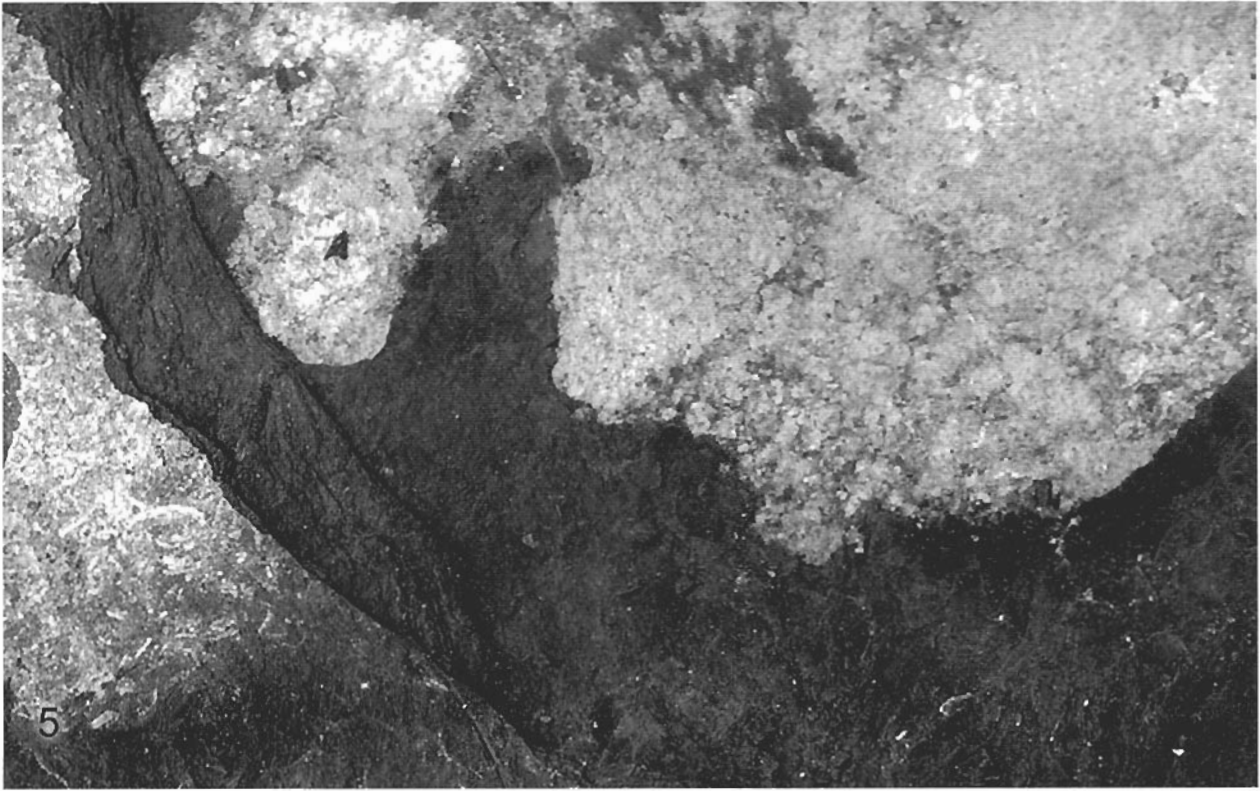


Fig. 5. Light thin layers of siderite in the Messel oil shale. Thickness, appearance and distribution of the layers in the laminated sediment shows great similarity to the carbonate layers in the Pleistocene lake sediment of Neumark-Nord and are probably of similar origin. – Magnification: $\times 6$.

Abb. 5. Helle dünne Lagen aus Siderit im Ölschiefer von Messel. Dicke, Erscheinungsbild und Verteilung der Lagen in dem feinschichtigen Sediment zeigt große Übereinstimmung mit den Karbonatlagen im Pleistozän von Neumark-Nord und sind möglicherweise gleichen Ursprungs. – Vergrößerung: $\times 6$.

Fig. 6. White, thin carbonate layers in the warped silty lime mud, Pleistocene, ?Eemian interglacial or interstadial of the Saale glaciation, Neumark-Nord, Geiseltal, Sachsen-Anhalt. The origin of the carbonate layers is most probably due to bacterial action during decompo-

ing from the lake will be underrepresented in the fossil record. So our model would explain why some groups are much better represented in Messel than in any other site so far known.

This idea that the fossil record in lakes may be strongly effected by Cyanobacteria poisoning the water, first postulated for Neumark-Nord (BRAUN & PFEIFFER 2002), may be the clue for other sites as well. Recently independent and additional observations indicating the presence of repeated algal blooms in Tertiary lakes have been published. FELDER et al. (2004) discuss algal blooms as the most likely cause of fine lacustrine carbonate laminae in the Oligocene lake sediments of "Grube Stöbchen", Westerwald. They publish SEM micrographs showing carbonate crystal aggregates corresponding morphologically to the carbonates found at Neumark-Nord (BRAUN & PFEIFFER 2002). A short notice of RICHTER & CLAUSING (2004) about freshwater dinoflagellates from Messel lead to the assumption that there was repeated algal blooms of this (dinoflagellate-) species. The presence of microbial communities in Tertiary oil shale lakes and their possible ecological effect lakes has been discussed also by WUTTKE & RADTKE (1993, 1994). The major problem is that the toxic microcystins traced back some hundred thousand years into the Pleistocene are much more difficult to prove in much older or coarser sediments.

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sition of sunken blooms of Cyanobacteria at the sediment surface. – Magnification: $\times 6$.

Abb. 6. Weiße, dünne Karbonatlagen in der jahreszeitlich geschichteten siltigen Kalkmudde, Pleistozän, ?Eem-Interglazial oder Interstadial der Saale-Vereisung, Neumark-Nord, Geiseltal, Sachsen-Anhalt. Die Bildung der Karbonatlagen ist wahrscheinlich auf bakterielle Tätigkeit an der Sedimentoberfläche beim Abbau abgesunkener Cyanobakterien-Blüten zurückzuführen. – Vergrößerung: $\times 6$.

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