

# Remarkably preserved benthic organisms and their traces from a Middle Triassic (Muschelkalk) mud flat

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# LETHAIA



Knaust, D. 2010: Remarkably preserved benthic organisms and their traces from a Middle Triassic (Muschelkalk) mud flat. *Lethaia*, Vol. 43, pp. 344–356.

A new Fossil-Lagerstätte is reported from the Middle Triassic of Germany, preserving Foraminifera, Nematoda, Platyhelminthes, Nemertea, Annelida and a range of Arthropoda together with their traces. This is the oldest fossil record of free-living nematodes and turbellarians, and the first occurrence of nemerteans in the Mesozoic. The rare preservation of the benthic associations together with their traces is unique; especially the abundant occurrence of different phyla as meiofauna (organisms with shortest dimension between 0.06 and 1 mm) provides an insight into the palaeoecological conditions of a 240-Ma-old muddy tidal flat. The preservation of benthic animals at the termination of their traces offers the exclusive opportunity to assign producers to the trace fossils. The results show that the discussed phyla were already established in the early Mesozoic in a similar diversity and composition as in modern analogues. The new Fossil-Lagerstätte has the potential to prove a number of soft-bodied taxa immediately after the end-Permian mass extinction, which has wide-ranging implications for phylogenetic interpretations.  $\Box$  Benthos, soft-bodied organisms, Fossil-Lagerstätte, Muschelkalk, trace fossils, Triassic.

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The study of exceptionally preserved biota has contributed much to our understanding of the development of life and evolutionary processes. Fossil-Lagerstätten with different content and preservation have been described from numerous times in Earth history but only few are known from the Triassic (Allison & Briggs 1993). Phylogenetic research on the origin of bilaterians (including a number of phyla, such as nemerteans and platyhelminths) is in progress but is hampered by a patchy geological record of soft-bodied animals.

The Middle Triassic (Muschelkalk) marginal-marine carbonates of the Germanic Basin were deposited in a vast epicontinental sea. They contain a rich fauna, which has been long known from hard parts (Schmidt 1928), whereas fossils with soft-tissue preservation have been only reported recently (Knaust 1991; Klug et al. 2004, 2005; Tucker & Marshall 2004). Temporary outcrops in the county Thuringia (Germany) have provided abundant material of a new Konservat-Lagerstätte, containing a rich benthic faunal association (Fig. 1). Although the soft-bodied organisms are generally preserved by mineral replacements and cavity fills following decay, their outlines document taxa of different phyla from the beginning of the Mesozoic. Moreover, many benthic animals are preserved together with their traces (Knaust 2007a), a fact that adds more value to the ichnotaxonomical importance of trace fossils. This circumstance is rare in FossilLagerstätten described so far and provides potentials for ethological and palaeobiological interpretations of those trace fossils and their trace makers. A combination of microbial overgrowth of fine-grained sediment with soft to firm consistency, followed by gentle obrution, allows the excellent preservation of delicate traces (Trace Fossil-Lagerstätte; Mangano & Buatois 1995) together with their producers.

This article is intended to present the newly discovered Konservat-Lagerstätte in the light of its stratigraphical and sedimentological context, to outline the main groups of animals together with their traces, their style of preservation and to discuss the taphonomic history leading to the exceptional preservation. A detailed description and taxonomic treatment of certain body fossils and trace fossils is beyond the aim of this paper and will be published elsewhere.

## Study area and material

Many thousand specimens of macro- and meiobenthic soft-bodied fossils were collected and studied from the Triassic Upper Muschelkalk, just below the Anisian/Ladinian boundary. Almost all material comes from the outcrops Troistedt and Gelmeroda in the vicinity of the town of Weimar in Thuringia (Central Germany), whereas sporadically collected



*Fig. 1.* Palaeogeography of the Germanic Basin during the Middle Triassic, and location of the studied sections (Gelmeroda: 50°56′42″N, 11°17′20″E; Troistedt: 50°56′44″N, 11°14′57″E) near the town Weimar (Thuringia). After Knaust (2007a).

samples from other parts of the Germanic Basin indicate a widespread distribution of the described fossils. The studied interval is characterized by marlstone/limestone alternations, organized into metrescale coarsening- (shallowing-) upward cycles (Knaust & Langbein 1995). Oolitic and bioclastic limestone beds are common and are interpreted as high-energy event deposits (proximal tempestites, *cf.* Aigner 1985). Most portions of the succession in the central part of the Germanic Basin were deposited under subtidal conditions, whereas the proximal facies along the basin margins exhibit intertidal to supratidal features.

The benthic fossils occur in many stratigraphic intervals of the Upper Muschelkalk, but most specimens were collected from the *Ceratites compressus*, *C. evolutus* and *C. spinosus* zones between the Trochitenkalk Beds and the *cycloides* Bed (Fig. 2). They are preferably preserved on bedding planes of fine-grained (micritic) limestone beds in the uppermost (shallowest) part of the coarsening-upward cycles (parasequences). Sedimentary structures such as wrinkle structures, millimetre ripples, voids, mud cracks and fractures are evidence of temporary emersion (desiccation) of a muddy tidal flat, whereas brecciation, minifaults and calcretes indicate subsequent supratidal conditions (Knaust 2007a; Fig. 3).

### Benthic taxa and their traces

#### Involutinidae foraminifera

Involutinidae foraminifera are often preserved at the end of their traces (Fig. 4). The tests (0.3–0.8 mm in size) consist of white, grey or transparent microspar (calcite) with an irregular flat to elliptical shape.



*Fig. 2.* Stratigraphy and lithostratigraphic marker beds of the studied section, Gelmeroda. After Knaust (2007a).

Because Involutinidae were originally aragonitic, their tests are very commonly recrystallized (Hohenegger & Piller 1975) thus preventing exact systematic determinations. These foraminifers are widespread in the studied interval (Pérez-López *et al.* 2005), but their trace making activity has been unknown as yet.

Within the benthic association, traces of foraminifers are most common. They occur preferably on upper and lower bedding planes in form of straight to gently curved trails or burrows and show a wide variability in morphology and size. The unbranched traces are about 0.3–1.0 mm wide and up to several centimetres long. In general, the described foraminifer traces are strongly controlled by primary substrate conditions. Specimens with a sharp outline reveal crudely transverse annulations and are flanked by narrow marginal grooves produced by irregularly spaced



*Fig. 3.* Lithology and sedimentary features in the studied interval of the Upper Muschelkalk (*Ceratites compressus* to *C. spinosus* zones). A, marlstone/limestone alternation with thickening and coarsening upward trend. B, wrinkle structures on bedding surface, indicative of microbial activity. C, bedding surface with polygonal patterns of limonite-stained fractures with sharp crests, similar to incipient prism cracks as developed on modern mud flats under microbial modification. D, the same bedding surface as in C, sectioned and in oblique view, exhibiting a narrow, deep prism crack within biolaminated micrite. A sub-vertical corkscrew-shaped burrow (limonite-filled, arrows) probably left by a nemertean follows the course of this weakened zone. E, marlstone with limestone beds (top) and embedded calcrete nodules. F, bedding plane with early-diagenetically re-precipitated limestone in form of crystallaria (calcrete feature). Scale bars = 1 cm.

constrictions referable to *Torrowangea* Webby (1970), (Fig. 4B, C). They may grade into loosely arranged traces with spherical aggregates (Fig. 4A).

*Torrowangea* includes random, sinuous to meandering trails, from 1 to 2 mm wide, with irregularly spaced transverse constrictions (Webby 1970). It is



*Fig.* 4. Involutinidae Foraminifera in microsparitic calcite preservation and their trace fossils. A, crowded trails of (mainly) foraminifers in negative and positive epirelief, irregularly spaced constrictions and loosely arranged traces with spherical aggregates. B, foraminifer (white arrow) leaving a trail with irregularly spaced constrictions referable to *Torrowangea*, associated with a pyritic and limonitized nematode and its sine-wave trail (red arrow). C, two foraminifers (arrows) together with *Torrowangea*. Scale bars in A and B = 5 mm, scale bar in C = 1 mm.

commonly reported from the Precambrian (e.g. Webby 1970) to Permian (Van Amerom *et al.* 1993), where it occurs in marine and continental deposits (Głuszek 1995; Kim *et al.* 2002). The producer of *Torrowangea* is generally assumed to be a vermiform animal (Narbonne & Aitken 1990; Van Amerom *et al.* 1993). However, Severin *et al.* (1982) demonstrated in experiments that individuals of the benthic foraminifer *Quinqueloculina impressa* Reuss produce *Torrowangea*-like surface trails, which confirms the findings from the Triassic and has implications for the interpretation of the *Torrowangea* trace maker. In recent sediments, benthic foraminifers produce such traces with the aid of their pseudopodia (Kitazato 1988; Groß 2002).

#### Platyhelminthes (flatworms)

Platyhelminthes may be preserved at the termination of their trails (Fig. 5) or occur in isolation on the bedding plane. They consist of a flattened, unsegmented body with a rounded anterior region (up to 10– 15 mm long and 5–7 mm wide) and belong to freeliving turbellarians. Turbellarians are mainly preserved as calcitic casts of moulds (Fig. 5A, B), but occasionally contain limonite mineralization around it (Fig. 5C, F), representing the multilayered and complex body wall (Ruppert *et al.* 2004). In well-preserved specimens, the limonitic body wall is broken-up by intercellular space and vacuoles filled with calcite (Fig. 5D, E). Calcareous spicules are concentrated around some specimens, as they are known from modern marine turbellarians to originate from the basal lamina (Rieger & Sterrer 1973). The unsegmented nature of the fossil remains (in contrast to annelids occurring on the same bedding planes, see below), their dorsoventrally flattened appearance and the general body shape (which becomes especially obvious in slightly contorted specimens) allow an interpretation as platyhelminthes. The local occurrence of vacuoles and calcareous spicules (in association with the body wall), and the connection of the body fossils with traces characteristic of platyhelminthes support this interpretation.

Trails of turbellarians are occasionally preserved on upper bedding planes (Fig. 5C, F). The more or less straight traces are a few millimetres wide and some centimetres long. Typically, they consist of paired ridges along the trail margins, which are accompanied by a number of minute and poorly defined sub-parallel ridges, furrows and pustules as a result of microbial overgrowth. These characteristic trails were produced in experiments with polyclads, which glide over the surface and entrain sedimentary particles by means of mucociliary locomotion (Collins *et al.* 2000).

Seilacher (2007) argues that *Curvolithus* could potentially be produced by platyhelminthes and, indeed, *Curvolithus* isp. is reported from the same interval (Knaust 2007b). Furthermore, tripartite surface trails occur also in association with turbellarians preserved as calcite-filled moulds at the end of such



*Fig.* 5. Turbellarians (platyhelminthes, flatworms). A, four turbellarians are preserved as slightly distorted calcitic casts of moulds within the living chamber of a *Ceratites* sp. steinkern (Ammonoidea), partly leaving groove-like trails behind them. B, close-up view of A. C, contracted individual preserved by crystalline calcite with a trail similar to the ones produced by modern polyclads. D, part of a sediment-filled individual with the epidermis preserved in limonite, characterized by intercellular space and vacuoles. Calcareous spicules are concentrated in an external zone around the epidermis (arrows). The turbellarian is associated with minute foraminifers and their traces. E, close-up view of D, showing the vacuoles (arrow heads) and the accumulation of spicules (arrows). F, turbellarian preserved as calcitic and dolomitic cast of a mould together with its trail consisting of paired lateral ridges and minute sub-parallel ridges as known from modern polyclads. Scale bars = 5 mm.

traces (Fig. 6). The shortened outline of the body fossil indicates the contraction of the organism during its last movement, which led to the preservation of a tail print just behind the animal. Subsequently, the bedding surface including the *Curvolithus*-like traces became modified by microbial activity and the tripartition became blurred.

A third group of turbellarian traces is described as *Terricolichnus permicus* Alessandrello *et al.* (1988) from Permian continental deposits and is attributed to the activity of terrestrial flatworms of the Order Tricladida. *T. permicus* consists of a linear sequence of individual elongated imprints (ca. 1 mm long, 0.1 mm wide and about 0.5 mm away from each other) with a curved shape. *Terricolichnus* isp. is also abundant in the Muschelkalk material, where it occurs as irregularly curved minute trails, typically with impressions 0.5 mm long, 0.1 mm wide and in intervals of about 1 mm (Knaust 2007a). These traces are a few millimetres in length, straight to irregularly curved and often characterized by abrupt changes of direction (Fig. 7). Some



*Fig.* 6. Photograph (A) and interpretative line drawing (B) of a microbially modified bedding surface, which is cross-cut by an initial tripartite *Curvolithus*-like trace (C), the outline and longitudinal ridges of which have been blurred due to microbial overgrowth (pustules). At the front of the trace, a calcite aggregate seamed with limonite is preserved, the shape of which represents a contracted flatworm (f) that leaves a tail print behind it (tp). This part of the trace is flanked by marginal grooves. A diverse meiobenthos fauna is scattered over the surface and their traces incise the micrite. Scale bar = 1 cm.

of them preserve their producer at the last imprint, represented by a tiny sulphide aggregate of undeterminable nature.

#### Nemertea (ribbon worms)

Nemertea and their traces occur in close association with platyhelminthes (Figs 7–10). They are more robust and elongated than the flatworms and have a solid body that is cylindrical anteriorly and flattened posteriorly. Nemerteans lack segmentation and are circular in cross-section, although some specimens are slightly flattened. The diameter of the often sinusoidally curved aggregates is between 1 and 5 mm, with a length of up to several centimetres. The common preservation style consists of



*Fig. 7.* Photograph (A) and interpretative line drawing (B) of a micritic bedding plane preserving nemertean remains as sulphide aggregates (red fill) and their casts (dashed line) within their traces, which reflect the peristaltic movement and probing blind sidebranches by means of the proboscis (arrow heads). A foraminifer (F) and numerous minute meiobenthic animals such as a nematode (n) together with their traces are associated with the nemerteans. Note the occurrence of the tiny trace fossil *Terricolichnus* isp. (T) in the central part of the image. Scale bar = 1 cm.

a dolomitic or limonitic rim, the remains of two or three well-developed layers of body wall muscles, surrounding a spar calcite core, corresponding to the rhynchocoel (a fluid-filled cavity, (Figs 7, 8A, 9A). In many cases, however, only the moulds of the soft-bodied worms are preserved and details of the tissues (such as ciliated epidermis and gland cells) are lacking. A few specimens bear a calcareous element in their frontal region, interpreted as a stylet apparatus (barb) within the proboscis (Ruppert et al. 2004; Fig. 9C), or leave a trace of the proboscis in the anterior region (Fig. 9A). One specimen preserves a slightly sinuous faecal string on its posterior end within its trail (Fig. 9B), indicating a digestive system including anterior mouth and posterior anus characteristic for nemerteans and rules out an interpretation as platyheminths and sipunculids.



*Fig.* 8. Specimens with nemerteans (ribbon worms) and their traces. A, bedding surface with pustules and fractures (prism cracks) originated by microbial activity. Nemerteans are preserved as limonite-filled moulds (arrows) at the end of their traces and preferably follow the weak zones of cracks. B, microbially altered bedding surface with numerous burrow entrances. Scale bars = 1 cm.

The traces produced by nemerteans are complex and modern forms of these remarkable extensible worms are known for peristaltic burrowing and crawling over the surface (Ruppert et al. 2004; Fig. 7). On the studied bedding surfaces and in vertical sections, trails and burrows with an irregular to sinusoidal course are common (Fig. 3C), of which some resemble a compressed corkscrew and refer to Cochlichnus anguineus (Knaust 2007b). Most common are surface traces, about 2-3 mm wide, which sharply incise the microbially modified sediment surface. In crosssection, these trails are V- or U-shaped and display irregularly spaced annular ridges. The traces preferably follow sediment-filled cracks, which had acted as weak zones of a gradually drying mud flat (Figs 8, 10). Subsurface, the trails change into long, straight and sub-vertically oriented burrows (Skolithos isp.) with a circular cross-section, whereas others show short off-branches or are repeatedly branched and build complex burrow systems including shallow U- and Y-shaped tunnel parts similar to Polykladichnus isp. and Thalassinoides isp. (Bromley 1996; Hauck et al. 2009; Fig. 10).

#### Nematoda (roundworms)

Nematoda are abundant and represent the most common metazoan meiobenthos in the studied interval (Figs 4B, 11). They are preserved in sulphide minerals (probably mobilized by the activity of bacteria that initiate decay) or brown limonite and thus contrast to the bright limestone beds. Nematodes have a cylindrical shape and are only fractions of a millimetre in cross-section, with length of a few millimetres. However, several size classes indicate that a number of different populations and species are preserved in the meiobenthic association.

Most of the nematodes occur together with their traces, sinusoidal trails known in the fossil record as *Cochlichnus anguineus* (Moussa 1970; Metz 1998; fig. 13A). The reason for these characteristic traces is the unique body plan of nematodes, consisting of lon-gitudinal muscles only but without antagonistically acting circular muscles. Therefore, nematodes move by compression and stretching of the cuticle with support of the high hydrostatic pressure in the pseudocoel and leave sinusoidal trails.

In addition to lateral sine wave traces, vertical or oblique sine wave traces are also common and probably result from the activity of parapodia-bearing nematodes (Fig. 11A, B). In this way of crawling, the nematode alternates attachment of its adhesive toe and bristles on the trunk (Ruppert *et al.* 2004).

#### Annelida (segmented worms)

Annelida can be occasionally identified if the preservation is sufficient (Fig. 12). Most common are worms with a length of *ca*. 20 mm and a diameter of *ca*. 2 mm, which contain numerous (50–60) segments (Fig. 12A, B). They are circular in cross-section and resemble eunicid polychaetes, of which the jaw elements (scolecodonts) are abundant within the same beds (Kozur 1974). Other annelids exhibit faint bristles and thus also testify as polychaetes.

Eunicid-like polychaetes were found in association with the complex trace fossil *Balanoglossites* (Fig. 12C) and can be regarded as the producer of this trace fossil. *Balanoglossites* is highly variable in morphology and size and consists of grooves or irregularly winding tunnels along the upper bedding surface, galleries with dichotomous branching, and short off-branches and bulbous to lance-like terminations (Knaust 2008).

#### Arthropoda

Many traces were produced by arthropods but they are usually poorly preserved in various sulphide minerals or limonite and thus hinder a more specific



*Fig.* 9. Nemerteans and their traces. A, large nemertean in dolomite preservation together with its posterior moving trace (t) and a short anterior trace left by the proboscis (p). The wrinkled (microbial) sediment surface is scratched with *Radulichnus* isp. (encircled). B, limonitic remain interpreted as a nemertean within its microbially modified trail and preserving a slightly sinuous faecal string on its posterior end (arrow). C, anterior part of a dolomitic nemertean (natural cast of a mould) with a calcareous element in its frontal region, interpreted as the stylet apparatus (barb) within the proboscis. Scale bars = 1 cm.

determination (Fig. 13A, B). Exceptions are ostracods (crustaceans), of which the soft parts were enclosed by a bivalved calcareous carapace, together with their bilobated traces. Elongated trails with striations and segmented traces (Fig. 13C) could be the result of malacostracan crustaceans, but the associated aggregates do not justify a clear assignment.

#### Mollusca

Although bivalves, gastropods and cephalopods in the studied succession are commonly poorly preserved as steinkerns or with recrystallized shells, some bivalves were found in connection with their traces. Figure 13D shows a bedding surface with two bivalves (?*Nucula* sp.), one leaving an actively filled burrow similar to *Planolites* behind it. Depending on the substrate and preservation, there is a continuum between smooth *Planolites* and sculptured *Protovirgularia* (Knaust 2007b).

# Taphonomy and fossil preservation

The described soft-bodied animals and their traces record their last movements before they died (mortichnia, Seilacher 2007). The sedimentological context indicates a marginal-marine (peritidal) depositional



*Fig. 10.* Vertical section along a prism crack with a limonite-filled nemertean burrow system (*Polykladichnus* isp.). Scale bar = 1 cm.

environment, in which microbial mats and biofilms flourished. Wrinkle structures, pustules, blisters and features like elephant skin occur on several bedding surfaces and were formed underneath microbial mats similar to their Precambrian counterparts. The widespread occurrence of such biolaminates documents extensive mud flats with regular exposure. An intertidal interpretation is also evident from the preservation of many traces, which change their shape over short distances (and thus over a short period of time) on a rapidly drying mud flat.

Therefore, the stressing factors for the benthos in the intertidal zone are a combination of a hostile (micro-) environment with low oxygen because of the growth of microbial mats and their frequent emersion



*Fig. 11.* Nematoda in sulphide mineral preservation and their traces. A–B, Nematoda within their oblique to vertical sinusoidal trails on a micritic bedding plane. C, long individual within a marlstone layer. Scale bars = 1 mm.



*Fig. 12.* Annelida in limonite preservation. A, posterior part of a multi-segmented annelid resembling a eunicid polychaete. Note the cross-cutting relationship with *Radulichnus* isp. on the microbially modified sediment surface. B, almost complete annelid with numerous segments. C, eunicid-like polychaetes preserved in limonite within their burrows (frame and arrow, close-up upper right corner), which are linked to a complex *Balanoglossites* burrow system (B). Scale bars = 5 mm.

under arid conditions. Many nemerteans and annelids incise the wrinkled surface and suggest an activity as undermat miners beneath microbial mats. This interpretation is also supported by their cross-cutting relationship with *Radulichnus*, which results from the activity of organisms scraping on microbial mats. Dysaerobic bottom conditions, probably enhanced by biofilms, can also be postulated for the subtidal environment as indicated by the abundance of nematodes.

In general, a palaeoenvironmental distribution of body and trace fossils can be reconstructed based on

observations made on the substrate consistency, the microbial overgrowth and relationship of trace fossils. Thus, nematodes are abundant in marly sediment deposited in the subtidal environment under dysoxic and reducing conditions. Foraminifers are common on the surfaces of micritic beds deposited in the subtidal to intertidal transition zone and many of their traces document drying-out ponds. Platyhelminthes are typically preserved on originally soft- and water-saturated mud surfaces which became subsequently modified by microbial overgrowth in the lower intertidal zone. Arthropods and annelids are also best preserved on microbially modified sediment surfaces and occur in the intertidal environment. Nemerteans clearly show the sharpest traces with deep incisions into the microbially modified sediment as it is common in the upper intertidal zone.

In addition to dysaerobic bottom conditions and exposure, rapid burial enabled the favourable fossilization of soft-bodied organisms living on the mud flat. The occurrence of benthic organisms at the end of their traces documents the final stage in their life and is suggesting burial of the fauna while in life position. The faunas are best preserved along micritic bedding planes which are covered by thin marly veneers. Change of size, outline and sharpness of traces indicates a rapid shift of sediment consistency from soft to firm because of emersion. Frequent input of fine-grained sediment probably rapidly buried the faunas. Although coarse-grained storm layers are common in the succession, exceptional fossil preservation is more or less independent of those but seems to be controlled by waning turbiditic currents such as tides.

In many cases, rapid burial and specific earlydiagenetic circumstances may have enhanced the preservational potential especially of meiobenthic trace fossils and their producers. This becomes obvious when thick bioclastic event beds (tempestites) preserve a thin pre-event micrite veneer at their basis, on which numerous traces are conserved in hyporelief. Fast and intense event bed cementation may include the underlying marly substrate by forming so-called underbeds just below the bioclastic event beds (Ricken & Eder 1991).

The rapid sediment burial and bacterial activity may have generated dysaerobic to anaerobic microenvironments around the organisms. Depending on the original anatomy and subtle variations in the chemistry of the organisms, complex taphonomic scenarios played a role in the fossilization process, with fossils preserved in calcite, siderite, dolomite, pyrite, chalcopyrite or limonite (Wilby *et al.* 1996; Briggs 2003).



*Fig. 13.* Arthropoda, in sulphide and limonite preservation, and Mollusca. A, two arthropods preserved in sulphide mineral and associated with a trackway consisting of numerous ellipsoidal imprints. Meiobenthic traces include *Cochlichnus anguineus* (arrows). B, arthropod with an initially interrupted trail changing into a continuous trail with stacked conical segments due to substrate changes from soft to firm. C, various arthropoda on a micritic bedding plane, associated with striated and plait-like traces with changing appearance owing to the increasing firmness of the substrate. Note the imprints in front of the arthropod (crustacean, malacostracan?) to the left, interpreted as having been produced by its appendages. D, two molluscs (bivalves, *?Nucula* sp., arrows), one producing a *Planolites*-like trace on the bedding surface. Scale bars in A, B and D = 1 cm, scale bar in C = 5 mm.

Sulphide cementation in particular may be indicative of bacterial involvement due to these complex processes. As a result of decay and early diagenetic modifications such as pyrite replacement, the internal structure is commonly destroyed and only the outlines of the soft-bodied animals are preserved. In many instances, only the moulds of the previous organisms were filled with cement.

### Conclusions

Benthic communities in marginal-marine environments represent sensitive ecosystems with a wealth of (palaeo-) ecological information. The described remarkably preserved benthic organisms meticulously document the palaeoecological conditions of a 240-Ma-old carbonate mud flat and offer its qualitative and quantitative comparison with similar modern and ancient systems. The value of this new Fossil-Lagerstätte is not the detailed preservation of the organisms themselves but the proof that the discussed phyla were already established in the early Mesozoic. This has implications for the radiation especially of soft-bodied organisms after the end-Permian mass extinction. Moreover, the co-occurrence of benthic organisms together with their traces is an exception in the fossil record and offers the possibility to unequivocally



*Fig. 14.* Meiobenthic traces, mainly made by foraminifers, from a micritic bedding plane from the Middle Triassic of Germany (A) and from a modern muddy carbonate tidal flat in the southern Arabian Gulf north of Dohar, Qatar (B). Scale bars = 5 mm.

assign producers to trace fossils, which has wide-ranging ichnotaxonomic implications.

Most of the described phyla have a poor geological record owing to their soft-bodied nature and low preservation potential. Turbellarians are important research subjects because they are believed to belong to the most primitive representatives of the Bilateria. However, remains of platyhelminthes are very rare and questionable in the geological record (e.g. Fedonkin 1990; see reviews in Conway Morris 1985, and Poinar 2003). Early Cambrian vermiforms have possibly an affinity to platyhelminthes and nemerteans (Chen et al. 2005). As yet, the oldest body fossil of a turbellarian is described from 40-Ma-old Baltic amber (Poinar 2003), but the turbellarians presented here together with their characteristic traces indicate that platyhelminthes were already established in the Triassic.

Convincing nemerteans are only known from the Carboniferous Mazon Creek ironstone nodules (Schram 1973) and possibly Bear Gulch Limestone in Montana (Schram 1979; Conway Morris 1985), so the Triassic benthic community of nemerteans adds some valuable information regarding phylogeny and behaviour. Remains of Palaeozoic nematodes (e.g. Schram 1973, 1979) remain controversial (Conway Morris 1985), so that the Triassic material represents the oldest occurrence of free-living nematodes, which are otherwise only conserved in Cenozoic amber.

Foraminifers are common and abundant in many strata because of their hard tests, but their preservation together with their traces is unique in the fossil record. Annelids and arthropods have an extensive fossil record from the Phanerozoic because the presence of various hard tissues, however, additional information of these complex phyla can be gained from the remarkably preserved specimens.

The composition of the Middle Triassic benthic association contains about 99% meiobenthic organisms, of which foraminifers numerically dominate. Subdominant are nematodes, followed by arthropods, turbellarians, nemerteans and annelids. The composition of the 240-Ma-old meiofauna communities is strikingly similar to meiofauna associations of modern tidal flats, in which foraminifers dominate over nematodes, arthropods (mainly harpacticoida) and platy-helminthes (turbellarians) (Giere 1993; Kotwicki *et al.* 2005; Fig. 14).

Acknowledgements. – I would like to express my thanks to many colleagues (ichnologists, palaeontologists and sedimentologists) who gave me constructive feedback during the last years, foremost as response to my presentations on the 33. International Geological Congress in Oslo (2008) and the Second International Congress on Ichnology in Cracow (2008). I am indebted to Alfred Uchman (Kraków) and anonymous reviewers who provided valuable comments on the manuscript. Peter Doyle and Alan Owen are thanked for their editorial work.

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