

Exceptional preservation of Late Jurassic trace fossils in a modern cave (Mühlbachquellhöhle, S Germany)

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With 6 figures and 1 table

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Abstract: From the unusual outcrop of an active river cave (Mühlbachquellhöhle, S Germany), well-preserved Late Jurassic (Kimmeridgian) trace fossils, produced by soft-bottom dwelling organisms in an epicontinental sea, are reported. Three types of vertical burrows are exposed by corrosion on the cave's ceiling and walls: less than 1 mm thick, rarely branching tubular structures (ichnogenus *Trichichnus*), 3–5 mm thick vertical traces (*Skolithos*) with rare horizontal protrusions or Y-shaped branching (*Polykladichnus*), and 10–20 mm thick irregular vertical structures with affinities to *Skolithos*. They exhibit a range of preservational styles, comprising combinations of voids and sediment-, spar-, or pyrite infills. The trace fossil genesis is interpreted as deep burrowing, reaching down to reducing levels in the seafloor, with the presence of an organic lining preventing collapse and catalysing the development of a pyrite infill. Remaining voids were partly filled with calcite spar, possibly during early burial diagenesis in the zone of anaerobic methanogenesis by the re-precipitation of dissolved aragonite. Subsequent stages of differential burial diagenesis led to the development of the limestone-marlstone alternation with a compaction of the trace fossils only in the marlstone layers. The potential of caves as natural outcrops, where well-preserved fossils and trace fossils can be studied in situ is emphasised, and the obligation of a non-destructive approach is pointed out.

Key words: Ichnology, burrows, preservation, cave, Mühlbachquellhöhle, Upper Jurassic, Kimmeridgian.

1. Introduction

Soft-bottom trace fossils in calcareous sequences are often difficult to address, owing to their limited preservation potential and the wealth of potential trace makers and respective behavioural spectra involved. One of these limestone sequences was deposited in the central and western European ancient epicontinental sea during the Late Jurassic. From these strata, only a few trace fossil assemblages have been studied, e. g. in the boreal deposits in England and the Normandy by FÜRSICH (1974), in the Upper Jurassic Lusitanian Basin in Portugal (FÜRSICH 1981), or the detailed

observations by SCHLIRF (2000) of the Boulonnais in northern France.

As for the extensive outcrop of the classical Upper Jurassic limestone sequence exposed in the Swabian Alb and Franconian Alb in the south of Germany, observations on trace fossils other than the xiphosuran trackways and other trace fossils in the famous *Archaeopteryx*-bearing Solnhofen Limestone and equally conspicuous Nusplingen Limestone (e. g., SCHWEIGERT 1998) are limited to a few brief notes (e. g., RIETH 1932; SCHNEID 1938; V. FREYBERG 1964, 1966; WAGENPLAST 1972; MEYER 1984; WINGS 2000; PAWELLEK 2003).

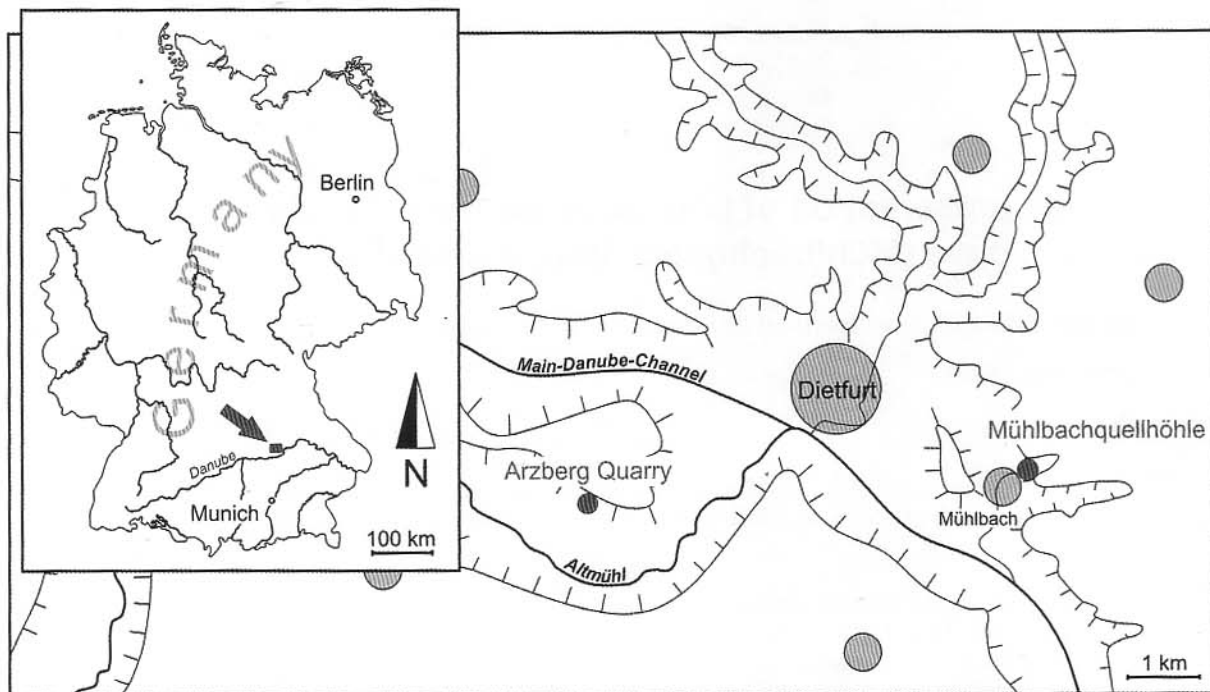


Fig. 1. Location of the Mühlbachquellhöhle and the Arzberg quarry in the Altmühl Valley in Bavaria, southern Germany.

In this paper, we want to report an unusual Late Jurassic trace fossil occurrence where exceptionally well preserved trace fossils were encountered in the ceiling and walls of a limestone cave in the Franconian Alb. This natural underground outcrop features a wide range of well preserved fossils, comprising ammonites, bivalves, belemnites, gastropods and echinoids among others. In this setting, the karst water with its weak acidity (carbonic acid plus humic acids) fulfils a role of a gentle and patient preparator, freeing delicate features of fossils from the surrounding rock matrix via corrosion. In this process, the somewhat more corrosion resistant fossils become coated with iron/manganese oxides, further enhancing their protection from corrosion and leading to the preservation of delicate and brittle fossils such as the vertical tubular trace fossils reported herein.

2. The “outcrop” and its stratigraphic framework

The Mühlbachquellhöhle was discovered in 2001 in the valley of the Altmühl River near Dietfurt, Bavaria (Fig. 1), and has since been explored to a total length of 7.1 km by the local cave research group “Karstgruppe Mühlbach e.V.” (Fig. 2A). Behind the gated

entrance, an artificial tunnel, dug through the talus deposits of the valley slope, leads to the complex entrance region of the cave where the underground river forms a branched underground outlet delta, feeding several springs in the village of Mühlbach with about 300 l/s water supply (GLASER et al. 2003; GLASER 2005, 2007). The main passage is in average 8 x 5 m in dimension and heads for about 1 km in north-easterly direction to a junction where the cave and its river splits into the “East Gallery” and the “North Gallery”. Up to date, both continuations have yielded several kilometres of passage with open ends in deeply sumped regions (STRAUB & WALTER 2006). While the East Gallery carries the main portion of the water, the North Gallery has a greater extension and ramifies into three sub-branches at its known end. The main passages of the cave display the well known features of fine river caves, such as lakes, streamways, waterfalls, sumped obstacles and delicate flowstone decorations. Sediments and breakdown blocks are abundant on the floor, but walls and ceiling exhibit unhindered insight into the characteristics of the limestone layers of the Upper Jurassic host rock.

The stratigraphic position of the cave (Fig. 2B) is – for speleogenetic reasons related to differential permeability – linked to the Platynotamergel (= marls



Fig. 2. **A** – Overview map of the Mühlbachquellhöhle (survey: “Karstgruppe Mühlbach e. V.”) with the investigated trace-fossil bearing sites as listed in Table 1. **B** – Relevant stratigraphic section logged in the Mühlbachquellhöhle (modified after GLASER 2005) alongside the Franconian standard section from the Arzberg quarry (introduced by v. FREYBERG 1939 and STREIM 1960) with bed numbers and stratigraphic position of the documented trace fossils.

with *Sutneria platynota*, *platynota* Zone, Arzberg Formation, Lower Kimmeridgian, Upper Jurassic). These are usually developed as an intercalation of limestone beds and thin marlstone layers with grey to greenish-grey colour, containing an astonishing richness of fossils, particularly ammonites (STREIM 1960, 1961). Within the cave, the *Platynotamergel* reach a thickness of about 10 m, starting with a more calcareous section at bed #234 (referring to the Franconian standard section as introduced by v. FREYBERG 1939). The marly layers are dominant in the middle part (bed #243 to #252) whilst the top is again more calcareous. Above these layers, the cave reaches the *hypselocyclum* Zone and in some chimneys the *divisum* Zone of the Kimmeridgian Stage. The deepest parts of the cave cut into the *planula* Zone of the Oxfordian Stage (Dietfurt Formation).

3. The palaeoenvironment

The limestone sequence in question was deposited during the Late Jurassic in the central and western

European epicontinental sea, marginal to the Tethys in the south and separated from the northern Boreal Sea by an island archipelago. Protected from the shallower northern part of the Franconian Platform by the Parsberg Reef Barrier (MEYER & SCHMIDT-KALER 1989), soft carbonate ooze was deposited on a moderately deep epicontinental carbonate ramp, giving way to the present well-bedded limestone-marlstone alternation. The other major facies association within the Upper Jurassic are massive microbial/sponge buildups that are not exposed within the outcrop of the Mühlbachquellhöhle.

4. Material and methods

Hundreds of well preserved, three-dimensionally exposed trace fossils were observed in the walls and especially the ceiling of the Mühlbachquellhöhle (Fig. 2; Table 1), where they were studied and photographed in situ. The density of trace fossils per surface area was determined by marking and photographing a square metre of cave ceiling at typical occurrences in the cave and counting all trace

fossils on site. A number of samples was taken from loose breakdown blocks for further work in the laboratory, where they were cleaned in an ultrasonic bath and investigated and photographed in detail under an incident light microscope (Leica® M420 + DC320 digital unit) applying image analysis software (Leitz® IM) with extended focal imaging. In addition, several thin-sections were prepared and photographed with a transmission light microscope (Zeiss® Axio-phot) with non-polarised light.

Additional observations were carried out in the nearby Leibrecht quarry, Arzberg, where the very same limestone beds are exposed and numerous trace fossils in a wide range of preservation types were photographed and sampled. Several thin-sections of these samples were prepared and photographed in order to reveal fine details of the matrix, the lining and the sedimentary infill of the fossil burrows.

All studied samples and thin-sections will be deposited in the 'Karstinfozentrum', an exhibition and speleological laboratory currently being built near the cave's entrance in Mühlbach, Bavaria.

5. Results

5.1. The trace fossil assemblage

Three different types of vertical tubular trace fossils are recognised, which are preliminarily distinguished according to their size and branching pattern but share common preservational characters (see below). All three types often co-occur in the same limestone beds together with other fossil remains such as ammonites, bivalves or belemnites.

The first, comparatively rare type is best addressed as ichnogenus *Trichichnus* FREY, 1970a, and comprises simple straight vertical to sub-vertical tubular structures of very small diameters in the range of 0.5 to 1 mm at a maximum exposed length of 30 mm and an unlined pyrite infill (Fig. 3C). Only very few downward facing Y-shaped bifurcations were recorded for *Trichichnus*.

The by far most common type of vertical trace fossil is characterised by simple vertical to sub-vertical tubular structures, with a generally uniform diameter in individual specimens ranging from 3 to 5 mm, three-dimensionally exposed on the cave's ceiling or walls, traceable for several centimetres (Figs. 3A-B, D-G, I-J, 5A-F, 6A-F). These structures are assigned to the ichnogenus *Skolithos* HALDEMAN, 1840. The maximum recorded length is 40 cm. Some structures of equal size as the *Skolithos* trace fossils feature upward facing Y-shaped bifurcations with a branching angle of ~ 40 to 60° (Fig. 3H) and are then most appropriately attributed as *Polykladichnus* FÜRSICH, 1981. Also rarely, short protrusions of a smaller diameter emerge horizontally from the main gallery (Fig. 5B). Only occasionally, trace fossils were found with a sub-horizontal course (Fig. 4A-B), whereas several trace fossils bending towards a sub-horizontal orientation in their lower part forming J-shaped tubular structures (Fig. 3E) were observed. True U-shaped structures are not developed.

The third type of vertical tubular trace fossil – assignable as *Skolithos* only where lacking bifurcations – is distinguished from the former two by a distinctly larger diameter of 15 to 20 mm and a globular to

Table 1. Selected sites within the Mühlbachquellhöhle (as indicated in Fig. 2A), where trace fossils were documented, with the corresponding survey shot stations and the bed based on the local fine-scale stratigraphic analysis by V. FREYBERG (1939).

site #	passage name	survey point #	bed #	Figs. #
1	Southwest area in the 'Mühlbachpromenade'	22-23	~ 195	3I
2	Southwest area at 'Rentnersiphon'	33-34	~ 226	4C
3	North Gallery at the 'Augentropfenschlot'	132-133	252	3C, 4B
4	North Gallery just after the 'Maulwurfsiphon'	503-505	~ 261	4D, I
5	North Gallery in the 'Traumpfad'	508-509	266	3A-B, D-E, H, J, 4A
6	North Gallery in the 'Grand Canyon'	589-590	~ 231	3F
7	North Gallery at the 'Zauberberg'	563-564	~ 228	3G
8	East Gallery in chamber just after the 'Stiller Kanal'	236-237	264	5A-F
9	East Gallery just before the first sump.	236-237	252	

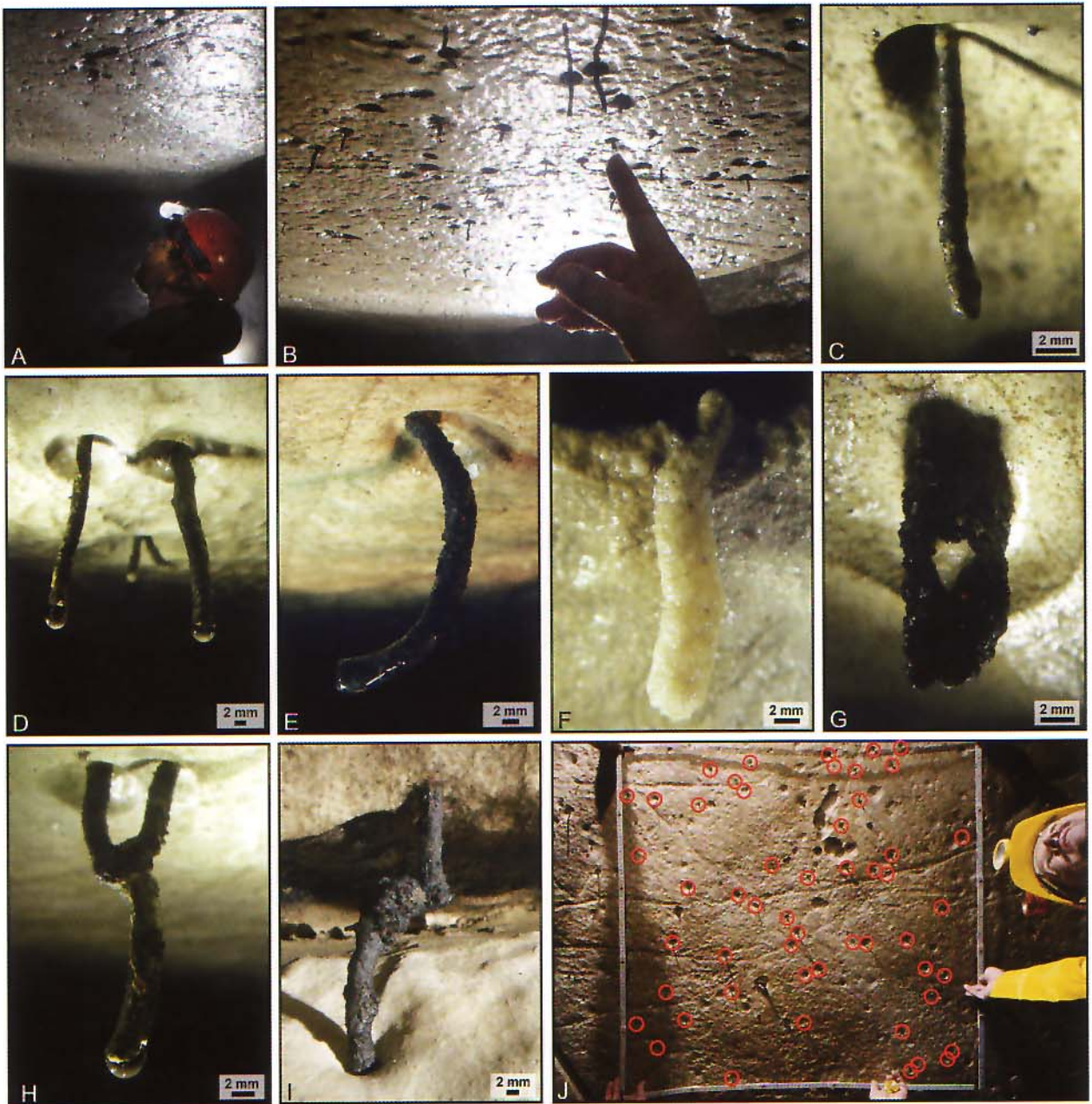


Fig. 3. Tubular trace fossils exposed by corrosion as full relief on the ceiling of the Mühlbachquellhöhle. **A** – Typical ceiling formed by the bottom of a homogenous limestone layer, exhibiting dozens of vertical trace fossils. **B** – Detail showing the high density of trace fossils and corrosion scours where they emerge from the host rock. **C** – Very thin trace fossil of the ichnogenus *Trichichnus*. **D** – Two *Skolithos* trace fossils. **E** – Bend variation of *Skolithos*. **F** – *Skolithos* preserved with sparite infill and lacking a pyrite lining. **G** – *Skolithos* with limonitised pyrite lining and spar core. **H** – *Polykladichnus* with upward directed, Y-shaped bifurcation pattern. **I** – *Skolithos* emerging and entering a limestone bed, crossing a compacted marlstone interlayer, thereby showing compression features in form of a swelling and slight offset. **J** – One square metre of cave ceiling with some 52 specimens of *Skolithos* aside other fossil remains.

irregular surface texture (Figs. 4C, 5F). The trace fossils also exhibit a dominating vertical orientation and occasionally feature Y-shaped bifurcations which are, in contrast to the common type, always found

diverging downwards. In addition, horizontal side branches of smaller diameter (<10 mm) were observed (Fig. 4C). Some of the trace fossils exhibit irregularly shaped swellings along their course.

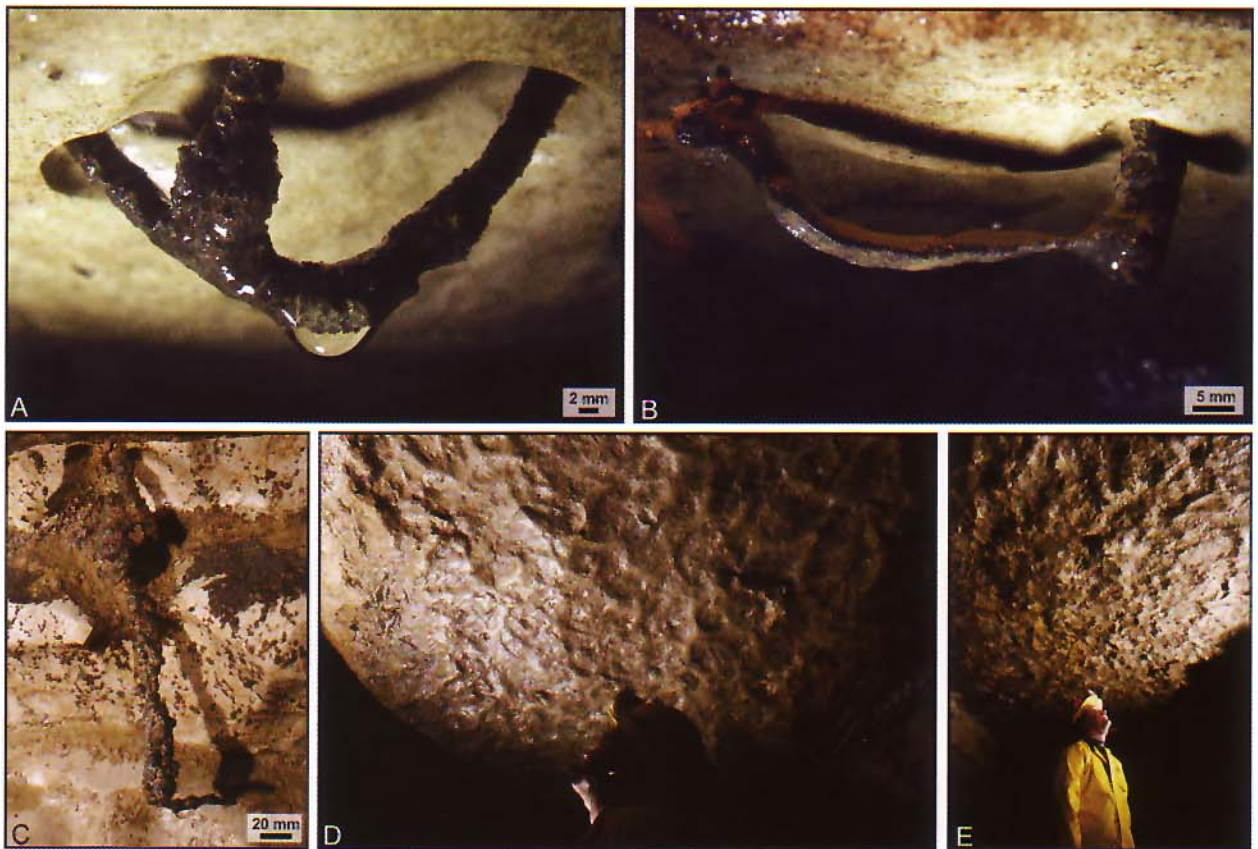


Fig. 4. Tubular trace fossils exposed by corrosion as full relief on the ceiling of the Mühlbachquellhöhle. **A** – Rarely observed sub-horizontal course with slightly swollen branching point. **B** – Another sub-horizontal gallery with inhomogeneous diameter. **C** – Irregular, thick vertical gallery with a short horizontal branch at its base. **D-E** – Ceiling with exposed indistinct networks of *Thalassinoides*.

Apart from these vertical trace fossils, large horizontal networks of *Thalassinoides* EHRENBERG, 1944 with a polygonal branching pattern are exposed in various places of the cave but not in the same beds as the vertical trace fossils (Fig. 4D-E). The individual tubes are up to several centimetres in diameter and the entire network often spans many dozens of square metres on the cave's ceiling.

5.2. Preservational spectrum

The abundant thin *Skolithos* and *Polykladichnus* exhibit a wide range of preservational styles as there are:

- (1) hollow forms
- (2) forms with a sediment infill and no recognisable lining (e.g., Fig. 6C)
- (3) forms with a calcareous infill and a thin, dark lining

- (4) hollow forms with a prominent pyrite lining (e.g., Fig. 5D-E)
- (5) forms with a prominent pyrite lining filled with coarse calcite spar (e.g., Figs. 3G, 5C)
- (6) forms completely filled with massive pyrite (e.g., Fig. 6F)
- (7) forms completely filled with blocky calcite spar (e.g., Figs. 3F, 6A, D).

While all of these preservation types were encountered in the quarry, the types four to seven are the most prominent ones encountered in the cave. Occasionally, the preservation types integrate along the trace fossil's vertical axis.

Trichichnus was only encountered with a massive pyrite infill (type six) and the thick variants of *Skolithos* are predominantly found in preservational types five and six.

A prominent, yet not all-prevailing character for all vertical trace fossils is the appearance of a distinct

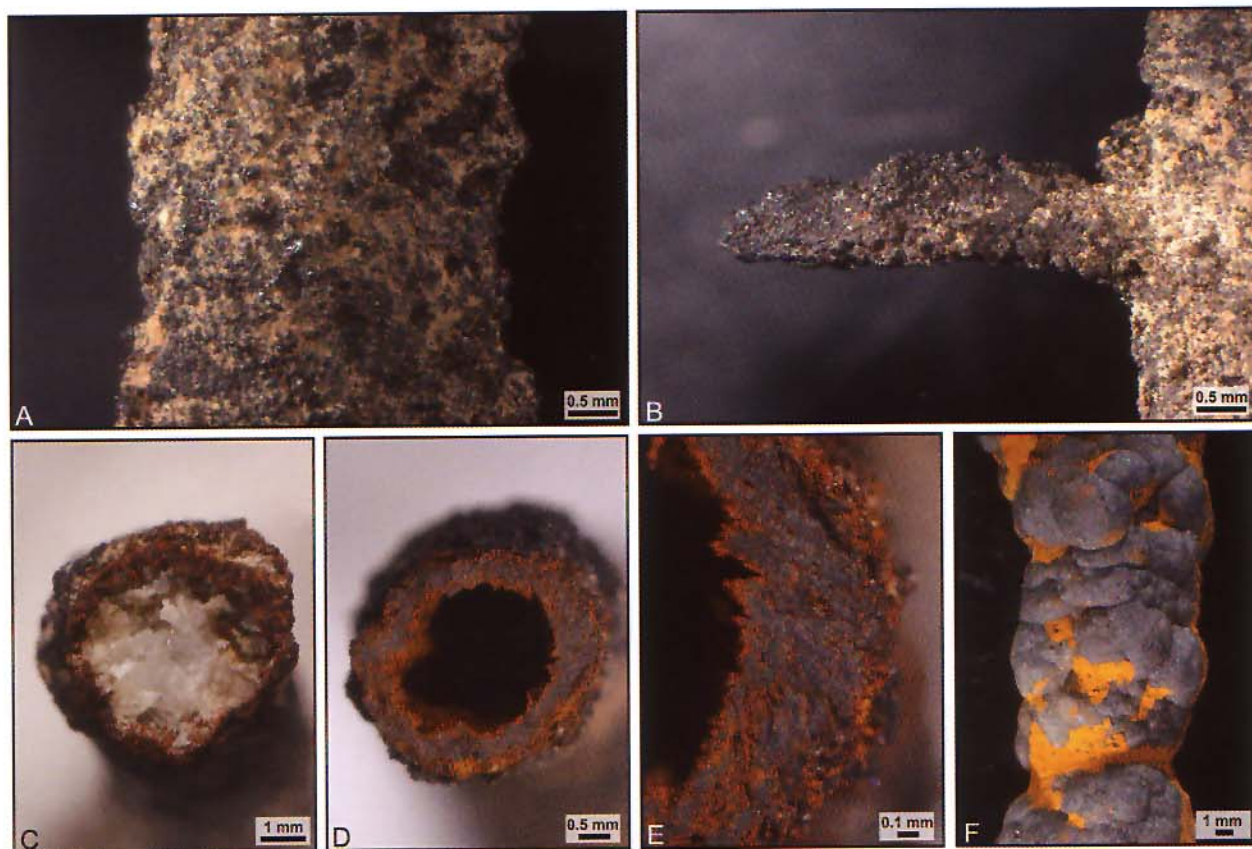


Fig. 5. *Skolithos* isolated from a breakdown block in the Mühlbachquellhöhle. **A** – Surface texture of limonitised pyrite wall. **B** – Short horizontal protrusion. **C** – Cross section with limonitised pyrite lining and calcite spar infill. **D-E** – Cross-section of hollow limonitised pyrite tube. **F** – Irregular knobby appearance of massive framboidal pyrite infill of a thick variant.

corrosion scour (solution cups), ca. 20 to 40 mm in diameter at a relief of 10 to 20 mm, where the trace fossils emerge from the ceiling.

The horizontal networks of *Thalassinoides* do not show mineral infills but are exclusively preserved with micritic infill and lack a recognisable lining.

5.3. Spatial patterns

The trace fossils are not evenly distributed but appear to be better preserved in parts of the carbonate sequence where the limestone beds are intercalated with more distinct marlstone layers, such as encountered in the Platynotamergel. The most prominent layers in which the trace fossils occur are underlain by marlstone layers of several centimetres in thickness, as for instance beds #252 and #266. They are, however, not restricted to this stratigraphic level but appear at least throughout the Upper Oxfordian and Lower Kimmeridgian limestones exposed in the cave and in

the nearby Arzberg quarry. As regards of the lateral distribution, the trace fossils show an inhomogeneous pattern and occur locally concentrated in high numbers. The three-dimensional exposure of the trace fossils in the cave ceiling provided the unique chance to determine representative densities of the limonitised trace fossils per surface area. Several prominent spots in the cave were analysed in this respect, yielding densities ranging from nine specimens/m² at site #8 and 21 specimens/m² at site #9 to maximum values of 50 and 52 specimens/m² at site #5 (Fig. 3J). When smaller areas of only 20 x 20 cm were considered at the latter site, specimen densities reach a maximum of an extrapolated 225 specimens/m². Considering the co-occurrence of other preservational types, which are not enhanced by corrosion (e.g., trace fossils filled with sedimentary matrix), these values represent minimum numbers of trace fossils at the given sites.

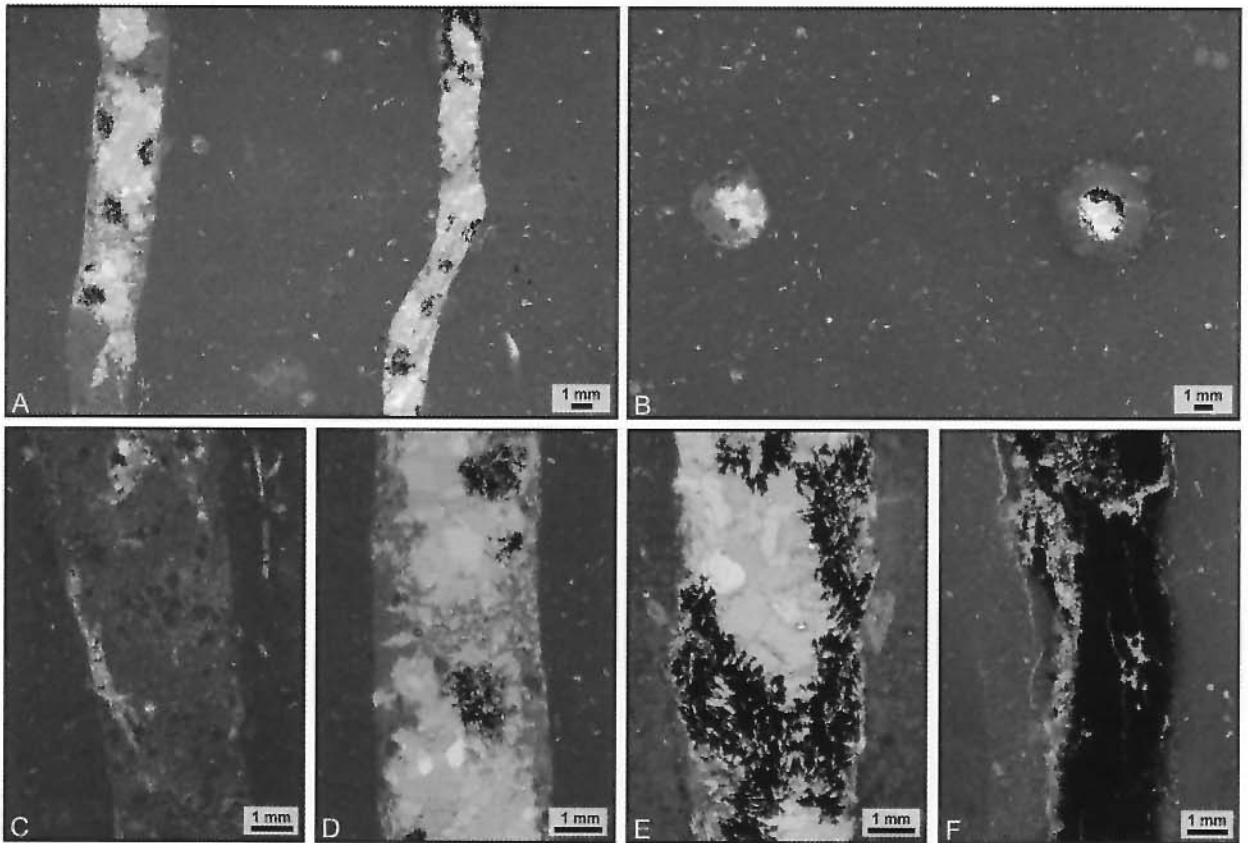


Fig. 6. Thin-sections of *Skolithos* from the Arzberg quarry, illustrating the wide spectrum of preservational styles. **A** – Micritic host rock with two sharply incised vertical tubular structures filled predominantly with calcite spar. **B** – Horizontal section of **A**. **C** – Trace filled with sedimentary matrix. **D** – Trace fossil filled with calcite spar and some limonitised pyrite. **E** – Trace fossil filled with spar interfingered with limonite. **F** – Trace fossil chiefly filled with limonitised pyrite.

6. Discussion

6.1. The trace makers

Considering the lack of body fossil evidence within the present – most likely domichnial – trace fossils, the question concerning the potential trace makers of these structures is limited to indirect reasoning in concert with a comparison to similar traces from the Recent.

The producers may be found among endobenthic worms, among which many groups are known to produce vertical burrow structures. Deep, narrow, vertical burrows, similar to the ichnogenus *Trichichnus*, for instance, were reported from extant sipunculan worms in the deep sea from the Norwegian continental margin (ROMERO-WETZEL 1987; see UCHMAN 1999 for a review on this ichno-

genus). Thicker vertical burrows corresponding to the ichnogenus *Skolithos* are known or interpreted to be produced by phoronid and annelid worms (e.g., ALPERT 1974; FÜRSICH 1974; SCHLIRF & UCHMAN 2005). Among the latter, polychaetes are known to produce J-shaped burrows addressed as ‘mineral filled burrows’ by FREY (1970a). Y-branching *Polykladichnus*-like traces are also known to be produced by polychaetes (e.g., HOWARD & FREY 1975; FÜRSICH 1981) but are additionally known from burrowing cerianthid actinians (FREY 1970b; SCHLIRF & UCHMAN 2005). All of these trace makers may well have been present in the palaeoenvironment of the Late Jurassic epicontinental sea but lack a fossil record due to their minute preservation potential.

The origin of the large *Thalassinoides* networks is well documented as being the work of (mostly

decapode) crustaceans (see FÜRSICH 1973, 1974; UCHMAN 1995; BROMLEY 1996; SCHLIRF 2000 for reviews) and is supported by direct body fossil evidence specifically in the Upper Jurassic by the finding of a cephalothorax of the decapod crustacean *Glyphea rostrata* in a *Spongiomorpha suevica* (RIETH, 1932) trace fossil (*Spongiomorpha* SAPORTA, 1887 sensu FÜRSICH 1973 and SCHLIRF 2000 = *Thalassinoides* = *Ophiomorpha*), reported by FÜRSICH (1974).

6.2. Trace fossil genesis, taphonomy and diagenesis

The fact that the vertical burrows are often filled with calcite spar and limonitised pyrite, or that they are still hollow (not a weathering effect as indicated by hollow traces found within freshly formatted blocks in the quarry), is contradicting the assumption of a soft-bottom calcareous ooze as a sedimentary environment – on first sight. This fact can be explained by two means: the traces were not produced before the sediment was reasonably semi-consolidated, or the burrows were stabilised by a thin organic lining such as a mucus film, preventing collapse.

We can deduce a comparably late genesis of the trace fossils in question in a given sediment layer, since they are well preserved and undisturbed relative to the often heavily bioturbated host sediment. Following this line of reasoning this simply means that the traces were deeply penetrating, or in other words were part of the deeper tiers within the present ichnocoenosis architecture (such as the corresponding Recent sipunculans; see above). Thereby, the traces were likely to penetrate down to reducing zones within the sedimentary profile, as there are the nitrogen reduction zone and the zone of sulphate reduction below (CANFIELD & RAISWELL 1991a). In these zones, the genesis of pyrite catalysed by the decay of the organic lining is strongly promoted (CANFIELD & RAISWELL 1991b). By the time the traces were subjected to the upward migrating (due to ongoing sedimentation) lower sulfate reduction zone, the anaerobic methanogenesis resulted in a considerable increase in alkalinity (CANFIELD & RAISWELL 1991a) promoting the early diagenetic infill with calcite spar cement where the traces had not yet been filled with intruding overlying sediment or autogenous pyrite. Sufficient dissolved carbonate species were potentially present due to

diagenetic dissolution of aragonitic skeletal elements during early burial diagenesis (MUNNECKE & WESTPHAL 2004). Alternatively, a much later cementation with sparry calcite induced by meteoric waters is well conceivable. In any way, cementation was not readily taking place, and some of the trace fossils remained in the state of open voids. In this way, all preservational types recognised in the material can be explained.

During subsequent stages of burial diagenesis and specifically the development of the present day limestone-marlstone alternation, the trace fossils were compacted in the marlstone layers while they stayed undisturbed in the limestone layers – a common phenomenon for fossils in corresponding limestone sequences. The genesis of the limestone-marlstone alternation during early burial diagenesis as a result of aragonite dissolution and migration leading to selective re-precipitation of calcite cements (differential diagenesis) has been well demonstrated in recent years (MUNNECKE & SAMTLEBEN 1996; MUNNECKE & WESTPHAL 2004; WESTPHAL et al. in press), opposing the earlier models of a primary environmental cyclicality (as introduced by SEIBOLD 1952). The process of the resulting selective compression is nicely evidenced by one specimen of the present trace fossils, where a *Skolithos* is emerging from a limestone bed, crossing a compacted marlstone interlayer, thereby showing compression features in form of a swelling and slight offset, and entering the underlying limestone bed (Fig. 3I).

6.3. Trace fossils and speleogenesis

A prominent feature of the present trace fossils is the corrosive scours (solution cups) at the point where the trace fossils emerge from the cave's ceiling. Two alternative processes are conceivable to explain this feature:

Firstly, the local permeability of the limestone beds for migrating surface water should be better at the place of a vertical fossil trace. The tubes of the trace fossils, especially the limonitic ones that are not filled with spar, are forming veritable water channels. On the contact to the underlying water body of a completely water filled cave passage or a thin moist water film, a progressive corrosion effect is formed by mixing two waters with different saturation states (mixing corrosion sensu BÖGLI 1963), leading to a small solution cup around the trace fossils.

Secondly, the oxidation from the pyrite inside the trace fossils into limonite under the influence of water and air locally produces sulphuric acid (e.g., JANTSCHKE 1989). The sulphuric acid reacts with the surrounding limestone to form readily soluble gypsum. This process may also play a role in the initial phase of the cave's speleogenesis, as the Platynotamergel are known to contain considerable amounts of pyrite (GLASER 2005). The occurrence of gypsum in marly beds on the wall of a big hall within the East Gallery, high above the spring flood level, evidences this effect.

6.4. Caves as valuable natural outcrops

With the present study we want to emphasise the potential of caves as natural outcrops where – given adequate spelunking skills and equipment – fossils and trace fossils can be studied in situ, often in excellent and unique preservation. However, it needs to be stressed that a recovery of these fossils must not be attempted for reasons of cave conservation unless the fossils are encountered in loose breakdown blocks or in caves incised in quarries which are facing complete destruction. In other words, caves should be treated as vulnerable museum collections as opposed to a quarry.

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References

- ALPERT, S. P. (1974): Systematic review of the genus *Skolithos*. – *Journal of Paleontology*, **49**: 509-512.
- BÖGLI, A. (1963): Beitrag zur Entstehung von Karsthöhlen. – *Die Höhle*, **14**: 63-68.
- BROMLEY, R. G. (1996): Trace fossils: biology, taphonomy and applications. – 361 pp.; London (Chapman & Hall).
- CANFIELD, D. E. & RAISWELL, R. (1991a): Carbonate precipitation and dissolution – its relevance to fossil preservation. – In: ALLISON P. A. & BRIGGS D. E. G. (Eds.): *Taphonomy – Releasing the data locked in the fossil record*, 411-453; New York (Plenum Press).
- (1991b): Pyrite formation and fossil preservation. – In: ALLISON P. A. & BRIGGS D. E. G. (Eds.): *Taphonomy – Releasing the data locked in the fossil record*, 338-387; New York (Plenum Press).
- EHRENBERG, K. (1944): Ergänzende Bemerkungen zu den seinerzeit aus dem Miozän von Burgschleinitz beschriebenen Gangkernen und Bauten dekapoder Krebse. – *Paläontologische Zeitschrift*, **23**: 354-359.
- FREY, R. W. (1970a): Trace fossils of Fort Hays Limestone Member of Niobrara Chalk (Upper Cretaceous), West-Central Kansas. – *The University of Kansas Paleontological Contributions*, **53**: 1-41.
- (1970b): The Lebensspuren of some common marine invertebrates near Beaufort, North Carolina. II. Anemone burrows. – *Journal of Paleontology*, **44**: 308-311.
- FREYBERG, B. v. (1939): Geologische Aufnahmeergebnisse zwischen Auerbach und Pegnitz. – *Sitzungsberichte der Physikalisch-Medizinischen Sozietät zu Erlangen*, **71**: 209-218.
- (1964): Geologie des Weißen Jura zwischen Eichstätt und Neuburg/Donau (Südliche Frankenalb). – *Erlanger Geologische Abhandlungen*, **54**: 3-97.
- (1966): Der Faziesverband im Unteren Malm Frankens – Ergebnisse der Stromatometrie. – *Erlanger Geologische Abhandlungen*, **62**: 3-104.
- FÜRSICH, F. T. (1973): A revision of the trace fossils *Spongiomorpha*, *Ophiomorpha* and *Thalassinoides*. – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1973**: 719-735.
- (1974): Corallian (Upper Jurassic) trace fossils from England and Normandy. – *Stuttgarter Beiträge zur Naturkunde, (B)*, **13**: 1-51.
- (1981): Invertebrate trace fossils from the Upper Jurassic of Portugal. – *Comunicações dos Serviços Geológicos de Portugal*, **67**: 153-168.
- GLASER, S. (2005): Geologische und hydrologische Erkenntnisse aus der Mühlbachquellhöhle (Südliche Frankenalb, Bayern). – *Geologische Blätter für NO-Bayern*, **55**: 1-30.
- (2007): Die Mühlbachquellhöhle – erste Einblicke in das unterirdische Gewässernetz der Frankenalb (Bayern). – *Laichinger Höhlenfreund*, **42**: 61-72.
- GLASER, S., SCHÖFFEL, C., SCHOBERT, R. & STROBL, C. (2003): Die Mühlbachquellhöhle bei Mühlbach im unteren Altmühltal, Fränkische Alb. – *Mitteilungen des Verbandes der deutschen Höhlen- und Karstforscher*, **49**: 66-69.
- HALDEMAN, S. S. (1840): Supplement to number one of "A monograph of the Limniades, and other freshwater bivalve shells of the apparently new animals in different classes, and names and characters of the subgenera in *Paludina* and *Anculosa*." – 3 pp.; Philadelphia (J. Dobson).
- HOWARD, J. D. & FREY, R. W. (1975): Estuaries of the Georgia Coast, USA: sedimentology and biology. II. Regional animal-sediment characteristics of Georgia estuaries. – *Senckenbergiana Maritima*, **7**: 33-103.

- JANTSCHKE, H. (1989): Das Mordloch (7325/01) im Roggental bei Eybach und seine Mineralbildungen. – *Laichinger Höhlenfreund*, **24**: 71-84.
- MEYER, R. K. F. (1984): Erläuterungen zur Geologischen Karte von Bayern 1:25 000, Blatt 6635 Lauterhofen, 96 pp.; München (Bayerisches Geologisches Landesamt).
- MEYER, R. K. F. & SCHMIDT-KALER, H. (1989): Paläogeographischer Atlas des süddeutschen Oberjura (Malm). – *Geologisches Jahrbuch*, (A), **115**: 3-77.
- MUNNECKE, A. & SAMTLEBEN, C. (1996): The formation of micritic limestones and the development of limestone-marlstone alternations in the Silurian of Gotland, Sweden. – *Facies*, **34**: 159-176.
- MUNNECKE, A. & WESTPHAL, H. (2004): Shallow-water aragonite recorded in bundles of limestone-marlstone alternations – the Upper Jurassic of SW Germany. – *Sedimentary Geology*, **164**: 191-202.
- PAWELLEK, T. (2003): Fazies, Sequenz-Analyse und stratigraphische Architektur im höheren Oberjura der Schwäbischen Alb (SW Deutschland). – *Jahreshefte der Gesellschaft für Naturkunde in Württemberg*, **159**: 29-75.
- RIETH, A. (1932): Neue Funde spongeliomorpher Fucoiden aus dem Jura Schwabens. – *Geologisch-Paläontologische Abhandlungen, Neue Folge*, **19**: 257-294.
- ROMEO-WETZEL, M. B. (1987): Sipunculans as inhabitants of very deep, narrow burrows in deep-sea sediments. – *Marine Biology*, **96**: 87-91.
- SAPORTA, G. DE (1887): Nouveaux documents relatifs aux organismes problématiques des anciennes mers. – *Bulletin de la Société Géologique du France*, **15**: 286-302.
- SCHLIRF, M. (2000): Upper Jurassic trace fossils from the Boulonnais (northern France). – *Geologica et Palaeontologica*, **34**: 145-213.
- SCHLIRF, M. & UCHMAN, A. (2005): Revision of the ichnogenus *Sabellarifex* RICHTER, 1921 and its relationship to *Skolithos* HALDEMAN, 1840 and *Polykladichmus* FÜRSICH, 1981. – *Journal of Systematic Palaeontology*, **3**: 115-131.
- SCHNEID, T. (1938): Über eine interessante neue fossile Lebensspur aus dem mittleren Malm Frankens (*Xenohelix suprajurassica* n. sp.). – *Zentralblatt für Mineralogie, Geologie und Paläontologie*, (B), **1938**: 312-315.
- SCHWEIGERT, G. (1998): Die Spurenfauna des Nusplinger Plattenkalks (Oberjura, Schwäbische Alb). – *Stuttgarter Beiträge zur Naturkunde*, (B), **262**: 1-47.
- SEIBOLD, E. (1952): Chemische Untersuchungen zur Bankung im unteren Malm Schwabens. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **98**: 28-86.
- STRAUB, R. & WALTER, M. (2006): Tauchforschungen in den Nordost-Siphons der Mühlbachquellhöhle bei Mühlbach im Altmühltal. – *Mitteilungen des Verbandes der deutschen Höhlen- und Karstforscher*, **52**: 114-117.
- STREIM, W. (1960): Geologie der Umgebung von Beilngries (Südliche Frankenalb). – *Erlanger Geologische Abhandlungen*, **36**: 1-49.
- (1961): Stratigraphie, Fazies und Lagerungsverhältnisse des Malm bei Dietfurt und Hemau (Südliche Frankenalb). – *Erlanger Geologische Abhandlungen*, **38**: 1-49.
- UCHMAN, A. (1995): Taxonomy and palaeoecology of flysch trace fossils: The Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). – *Beringeria*, **15**: 3-115.
- (1999): Ichnology of the Rhenodanubian Flysch (Lower Cretaceous – Eocene) in Austria and Germany. – *Beringeria*, **25**: 67-173.
- WAGENPLAST, P. (1972): Ökologische Untersuchungen der Fauna aus Bank- und Schwammfazies des Weißen Jura der Schwäbischen Alb. – *Arbeiten des Institutes für Geologie und Paläontologie der Universität Stuttgart, Neue Folge*, **67**: 1-99.
- WESTPHAL, H., MUNNECKE, A., BÖHM, F. & BORNHOLDT, S. (in press): Limestone-marlstone alternations in epeiric sea settings – witnesses of environmental changes, or of rhythmic diagenesis? – In: HOLMDEN, C. & PRATT, B. R. (Eds.): Dynamics of epeiric seas: sedimentological, paleontological and geochemical perspectives, Geological Association of Canada, Special Paper, **48**.
- WINGS, O. (2000): Ein Hartgrund als neuer Aspekt bei der Interpretation der untertithonischen Solnhofener Plattenkalke. – *Archaeopteryx*, **18**: 75-92.

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