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Taphonomy of trace fossils at omission surfaces (Middle Triassic, East Germany)

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Abstract

In shallowing-upward cycles of the East German (Thuringian) Muschelkalk (Middle Triassic), sedimentological (probably storm) events interrupted longer periods of low net-sedimentation. The ichnofauna changed with the diagenesis of the substrate; it does not represent an ecological succession. The presence of both firmground and hardground traces in the same samples indicates superimposed *Trypanites* and *Glossifungites* ichnofacies. The ichnofabric of burrows was 'frozen' by cementation during omission, the amount of erosion controlling the preservation of the upper tiers (borings). In general, both burrowing and boring has been intense but patchy, and recruitment of tracemakers had been almost monospecific. A hostile environment, perhaps due to high salinity and/or erosion, may thus be assumed. The type of preservation was governed by different reactions to sulphide production in different chemical microenvironments during early diagenesis. In absence of significant amounts of iron, H_2S escaped into burrows or borings from the adjacent anaerobic sediment. Depending on local physicochemistry, this resulted in calcite or pyrite precipitation. Well-aerated parts of burrows facilitated the formation of celestite after reoxidation of sulphide. On goethite-encrusted hardgrounds, pyrite rings were formed around numerous borings, trapping the active H_2S immediately after its formation. These haloes were previously mistaken as excrements.

Keywords: taphonomy; diagenesis; trace fossils; Muschelkalk; Triassic; Germany

1. Introduction

Despite the widely recognized importance of trace fossils for the reconstruction of ancient sedimentary environments, their value for chemical ecology and diagenesis of both host rock and organic inclusions has so far been underestimated. Differing from body fossils by their exclusively autochthonous and more or less complete preservation (except for example some borings and coprolites), trace fossils permit different research approaches to their taphonomy. To the author's knowledge these have mostly been limited to reworking and overprinting processes; very few studies consider geochemical processes in diagenesis, e.g. of a prominent Chalk trace fossil (Bromley et al., 1975; Clayton, 1986; Zijlstra, 1995; and others).

The diagenesis of calcareous sediments representing a phase of omission (non-deposition) is particularly interesting since it usually implies the transition from soft or firm to hard substrate. Suites like this have been studied repeatedly (see Pemberton and Frey (1985) for a Recent example, and

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Goldring and Kažmierczak (1974) for a conceptual and stratigraphical review) but chemical processes were hardly considered. To this end and in order to exclude effects of biological interaction, an omission horizon was selected from a period of still rather limited diversity in this environment. Triassic hardgrounds generally are poorly colonized compared with those of other epochs (e.g. Müller, 1956; Wilson and Palmer, 1990), and in addition the European Muschelkalk represents a facies of harsh ecological conditions (e.g. salinity, storm disruption). Therefore it could be expected to see trace fossil taphonomic phenomena, especially diagenetic ones, clearly expressed.

Within the German Muschelkalk Basin, the so-called Oolithbank may be traced over hundreds of kilometres as a marker bed. It consists of two prominent horizons of dense hard limestone, the lower one named alpha, the upper one beta, within the surrounding Wellenkalk formation (Fig. 1); this is made up of impure micrites with secondarily undulating bedding planes (e.g. Jubitz, 1959).

The lithology of the horizon studied varies strongly in Thuringia, East Germany. The regional geology is well known for decades and its most frequent trace fossils have been studied by Mägdefrau (1932). Müller (1956) described *Trypanites* in detail and verified its boring nature; his findings are fully confirmed by the present study. Lacking continuity of outcrops, however, precludes the investigation of transitional taphonomic phenomena associated with facies change. For this reason, case studies of two extreme situations are presented here.

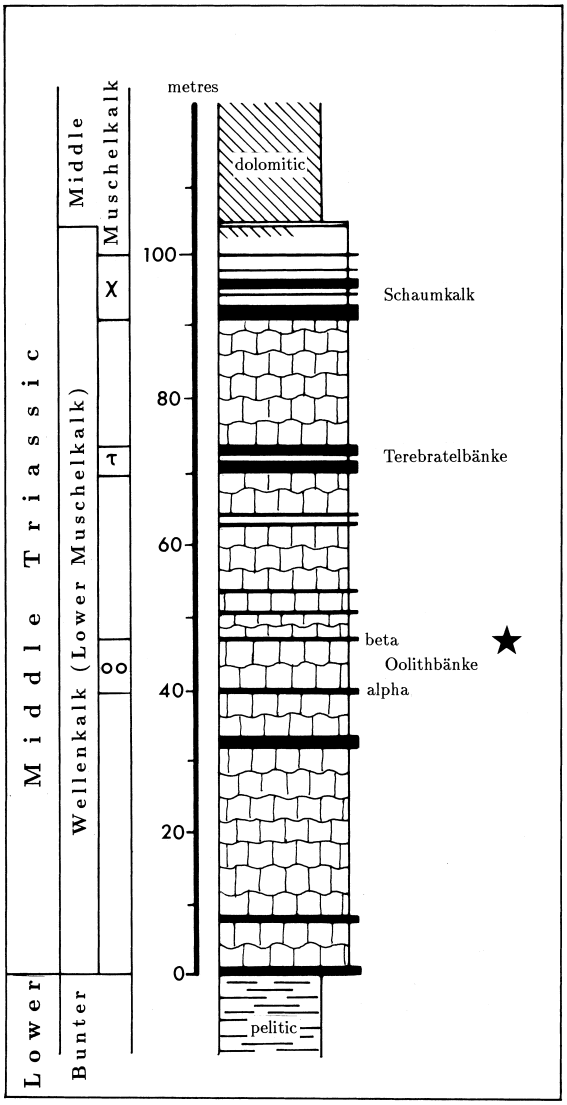


Fig. 1. Schematic log of Lower Muschelkalk Fm. near Jena (Thuringia, Germany): dense hard limestones (black) in impure micrites with undulating bedding planes. ⋆ = sampling horizon.

2. Materials and methods

The Oolithbank was investigated in several active quarries in Thuringia but only two of them yielded enough material for comprehensive study (Fig. 2). At Dorndorf–Steudnitz north of Jena, large fresh as well as weathered blocks could be removed, sectioned and polished. Thin-sections were prepared from selected samples, and additional specimens collected by Mägdefrau (1932) were considered. This locality is also very close to the type locality of Mägdefrau's newly established ichnogenus *Trypanites* with the type species *T. weisei*.

The Obermöllern quarry west of Naumburg rendered much less and worse preserved specimens. The situation is less complex on the other hand, so even rather small quantities of samples give an accurate picture. Because of the different type of preservation, the material was treated in another way: samples were split open vertically and sectioned horizontally, as well as resin-casted to display the borings' morphology and fill.

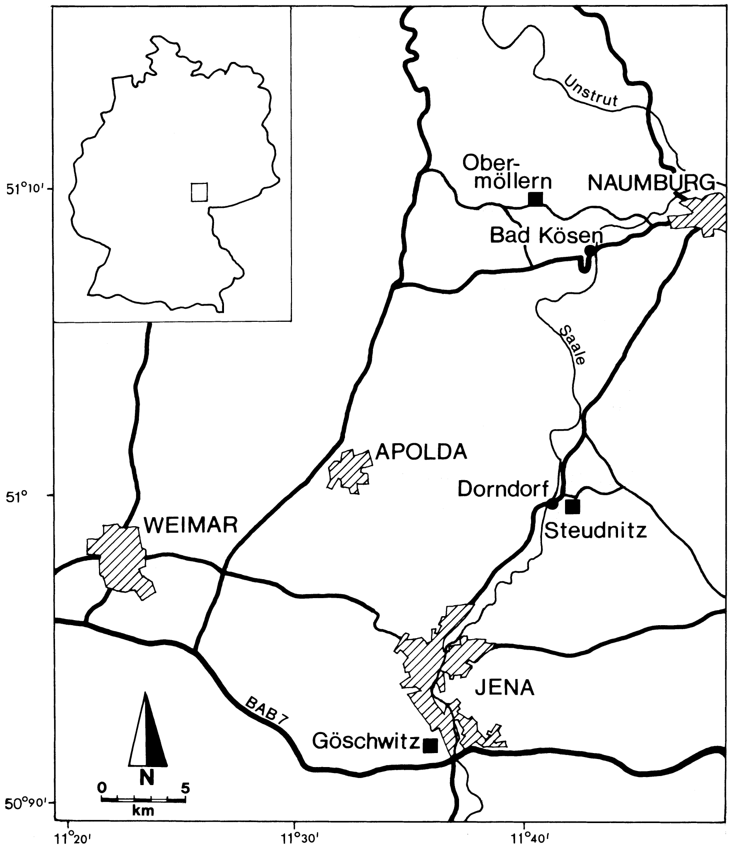


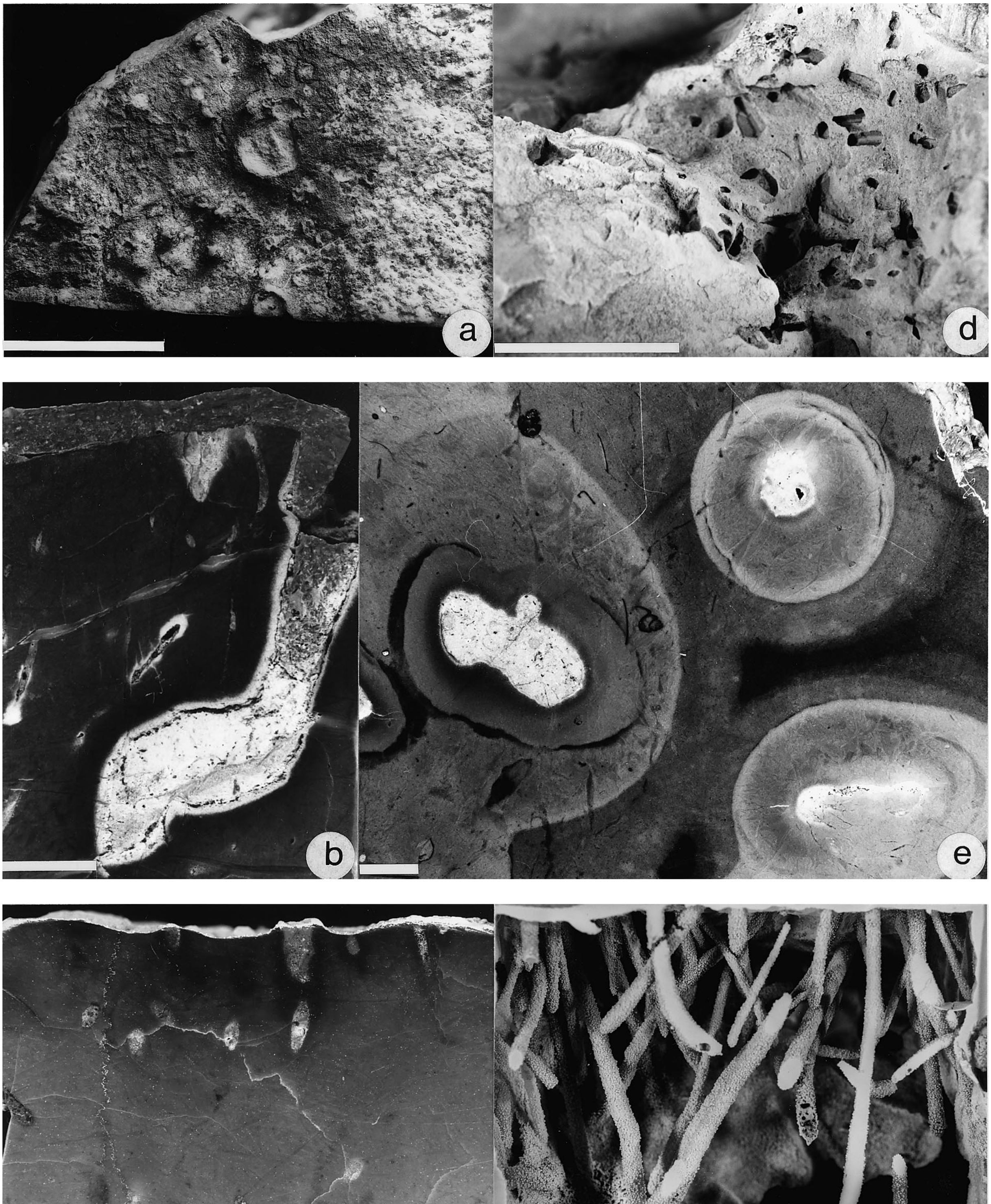
Fig. 2. Map of localities (■) in Thuringia, Germany.

3. Results: type of preservation

3.1. Steudnitz locality

At Steudnitz the Oolithbank beta consists of a pelmicrite reaching some 25 cm in thickness. Isolated large shell fragments and ooids occur. The unit's rugged hardground surface is intensely but patchily bored with *Trypanites* reaching a diameter of more than 1 mm, and it is encrusted by the oyster-like bivalve *Placunopsis ostracina* Schlotheim preserved with its original shell. The bivalves sometimes grew over the apertures of borings, indicating a later larval settlement. Most specimens show a brownish goethite cover but this can be shown to be due to weathering of an originally pyritic encrustation. This crust is thickened to an irregular rim around some of the borings' apertures (Fig. 3a) which Mägdefrau (1932) interpreted as 'Kothäufchen' (= excrement piles). His erroneous assumption had led Vogel et al. (1987) to conclude that *Trypanites* is a burrow, not a boring.

The borings are filled by a dolomitized sparite rich in bioclasts. Below a depth of 3 cm (measured from the surface), sulphide replacement is common within the fill (Fig. 3b), both in bioclasts and finer-grained sediment. Other borings are filled by pelitic material; it is unclear whether they represent a second colonisation phase. The margin of the borings is black in fresh samples, brown when weathered, suggesting disseminated iron sulphides as the colourant (Fig. 3c). The black margin sometimes extends up to 2 mm above the hardground, forming a chimney-like ring around the boring's aperture (Fig. 3a, c). The matrix surrounding the borings is discoloured dark grey; when weathered it first turns brownish, but later displays a cream white halo.


a
d
b
e
c
f

In addition to the borings, irregularly wound burrows named *Balanoglossites triadicus* by Mägdefrau (1932) may be observed. Branched shafts frequently reach the surface again by U turns, but may as well be dug obliquely into the sediment. As can be judged from fully preserved specimens at other localities, at least the funnel-like top 3 cm have been eroded away. The margins sometimes collapsed or were flattened by the surrounding matrix but normally they are circular in cross-section (Fig. 3e). Intact shell fragments occasionally stick out from the margins, especially when weathered. Amalgamation of adjoining burrows has not been detected but this may be due to the unfavourable type of preservation. The shafts are filled by a dense dolomitic calcarenite rich in rolled bioclasts (Fig. 3b). Sometimes a gradation from small pebbles at the base to pure calcite at the top can be seen. The infill is becoming softer only in an advanced stage of weathering, slowly disintegrating and turning brownish. Mägdefrau's (1932) material was of this latter type and thus tends to give a distorted impression.

The most spectacular feature of the *Balanoglossites* preservation is best visible in polished section (Fig. 3e): the 1 cm wide burrows are surrounded by haloes with a radius of 2 to 3 centimetres. These haloes are zoned in a more or less identical way: the dark grey burrow margin fades into light grey initially but later becomes medium brownish grey. With a sharp boundary, a narrow black ring of iron sulphide follows, giving way outward to light brownish grey colours. After another sharp boundary a more greyish-brown sediment is seen, and finally with a distinct change the black matrix joins. The latter is very rich in coarse-grained pyrite.

3.2. Göschwitz locality

A different type of preservation of *Balanoglossites* occurs in the slightly younger Terebratelbänke of the Göschwitz area southeast of Jena (Figs. 1 and 2). In this horizon of hard micrites, the burrow infill consists of a sandy micritic limestone which weathers porously. Already Mägdefrau (1932) noted numerous casts of isolated idiomorphic crystals in such weathered specimens (Fig. 3d). They morphologically correspond to celestite, a mineral ($SrSO_4$) which is common in druses and fissures throughout the area and southern Germany alike (Schwarz, 1975). If not very densely packed the casts are oriented obliquely to the burrow margin. They are frequently stained yellowish by goethite whereas the dark grey matrix is invariably bleached cream white in contact with *Balanoglossites*. The casts of celestite crystals may concentrate on certain parts of the burrow, especially on the margins of the funnel-like aperture but may also be found throughout the burrow interior. At first sight, they look like a second generation of tiny traces fossils (e.g. *Chondrites*) but close study shows the limited stretch and their sharp edges, even when weathered.

3.3. Obermöllern locality

The Oolithbank at Obermöllern shows less features than its counterpart at Steudnitz: it is represented by an almost pure whitish oolite; fresh material could not be obtained from the quarry walls, however. The ooids are dissolved frequently, except when close to the top of the unit. This is a conspicuous hardground with many borings and few

Fig. 3. Details of trace fossil preservation in Thuringian Lower Muschelkalk carbonates; scale bars 1 cm. (a) Surface of Oolithbank beta, Steudnitz: pyrite crusts of variable thickness around *Trypanites* apertures; note intact pyrite knobs in depression at left centre (Geologisches Museum, Münster, sample No. B4.B.7-1). (b) Polished vertical section of Oolithbank beta, Steudnitz: partially weathered bioclastic infill of *Balanoglossites* (right) also on hardground; weathered haloes around *Trypanites* with dark pyrite fill (left centre) (Geologisches Museum, Münster, sample No. B4.B.7-2). (c) Polished vertical section of Oolithbank beta, Steudnitz [specimen as in (a)]: cut through pyrite chimney around *Trypanites* individual at lower centre in (a), borings with bright dolomitic infill. (d) Oblique view of *Balanoglossites* funnel on bedding plane of Terebratelbänke horizon, Göschwitz: impressions of coffin-shaped celestite crystals in bleached burrow margin (Thüringer Landesanstalt für Bodenforschung, Weimar, Mägdefrau collection No. 215). (e) Polished horizontal section 7 cm below top of Oolithbank beta, Steudnitz: zoned redox haloes around *Balanoglossites*; black colours due to sulphide impregnation, collapse of burrow at lower right (Geologisches Museum, Münster, sample No. B4.B.7-3). (f) Resin cast of Oolithbank beta top, Obermöllern: subparallel *Trypanites* borings cutting through each other (right centre) or bivalve shell (far right); note warty surface of casts due to previous ooid dissolution in matrix at contact with boring depression at left centre (Geologisches Museum, Münster, sample No. B4.B.7-4).

encrusting bivalves, although surface iron impregnations and truncated *Balanoglossites* are missing.

Trypanites apertures and shafts may cut each other occasionally but normally their course within the substrate is roughly parallel (Fig. 3f). They obviously avoided contact by thigmophobotaxis but penetrated isolated shell fragments. The variable reaction to obstacles may have depended on the presence of a living inhabitant of a conspecific boring. Deviations of the generally vertical orientation occur mostly after the top centimetre. The borings hardly are longer than 3 cm, with 5 cm depth as the maximum. Most borings are empty but show goethite-impregnated margins, partially fading when strongly weathered. Rarely their top millimetres have been filled by a blob of clay or marl; in this case, lumps of iron sulphide (now goethite) or sugary calcium carbonate may be seen in the lower part of the boring. Some rounded bioclasts of the coated-grain type occur in the fill as well. Independent of the presence of a pelitic blob, the ooids bordering the boring are dissolved, even if they are still preserved in the adjacent matrix.

4. Interpretation of the phenomena

4.1. Taphonomy of Balanoglossites *(Steudnitz)*

The sediment was firm but not completely solid when the producers entered. This is suggested by the unbored and unabraded shell fragments protruding from the inner margin of the burrows. The duration of the unlithified phase cannot be assessed at the moment. It must have continued throughout the formation of the haloes discussed below, and even after the final infill, the matrix collapsed locally, strongly distorting burrow outline and adjacent haloes.

The concentric haloes around the burrows indicate an alteration of the matrix with the burrows as the origin of the processes involved. No simple one-stage explanation may be put forward, however, since two rings of iron sulphide impregnation occur at different positions within the haloes, i.e. in differing distances from the burrow. Sediment colour has to be taken as the only available clue for the redox state of the matrix before lithification: brownish tinges suggest oxic or suboxic conditions whereas the intensity of blackening is controlled by the pyrite content due to oxygen deficiency. The various redox states of the matrix remained 'frozen' during early diagenesis because all available sulphide within the matrix had been consumed by melnikovite/pyrite formation before.

The intense precipitation of sulphide in the sediment unaffected by bioturbation shows that the matrix was essentially anoxic when the *Balanoglossites* producers entered. With their burrows, an open connection to the well-aerated seawater above was established despite some probable mucus cover (depending on the nature of the animals) of the wall interior (Fig. 4a). The former is shown by the strong and continuing activity of the animals. Oxygen could diffuse into the sediment adjacent to the burrows, and a zonation of microbially mediated chemical reactions was established. Close to the burrow, ferrous iron (Fe^{II}) was oxidized to ferric iron (Fe^{III}) and sulphur probably existed as sulphate instead of sulphide. Suboxic conditions prevailed in a zone further outward where the sediment colour was changed to light greyish brown.

After the producers' death, the redox state around the burrows changed drastically. The decaying corpses consumed all oxygen infiltrating the burrows from above and released hydrogen sulphide and ammonia into their surrounding (Fig. 4b). This altered the previously oxic areas into suboxic ones, simultaneously raising the pH because of the ammonia-related dissociation:

$$NH_3 + H_2O \rightarrow NH_4^+ + OH^-$$

Still within the light brown zone, HS^- saturation was achieved which caused iron sulphide to precipitate. According to Drobner et al. (1990), this process is independent of sulphate reduction since H^+ may be used as oxidant, liberating hydrogen:

$$2HS^- + Fe^{2+} \rightarrow Fe(SH)_2 \rightarrow FeS_2 + H_2$$

The resulting black rings mark the contact to the outward anoxic (previously suboxic) conditions. The situation of anoxic overprint only existed for a limited time until the animals had decayed; for this reason only the inner parts of the haloes around the burrows were reduced.

With the decomposition of their producers, the burrows regained access to seawater. During this

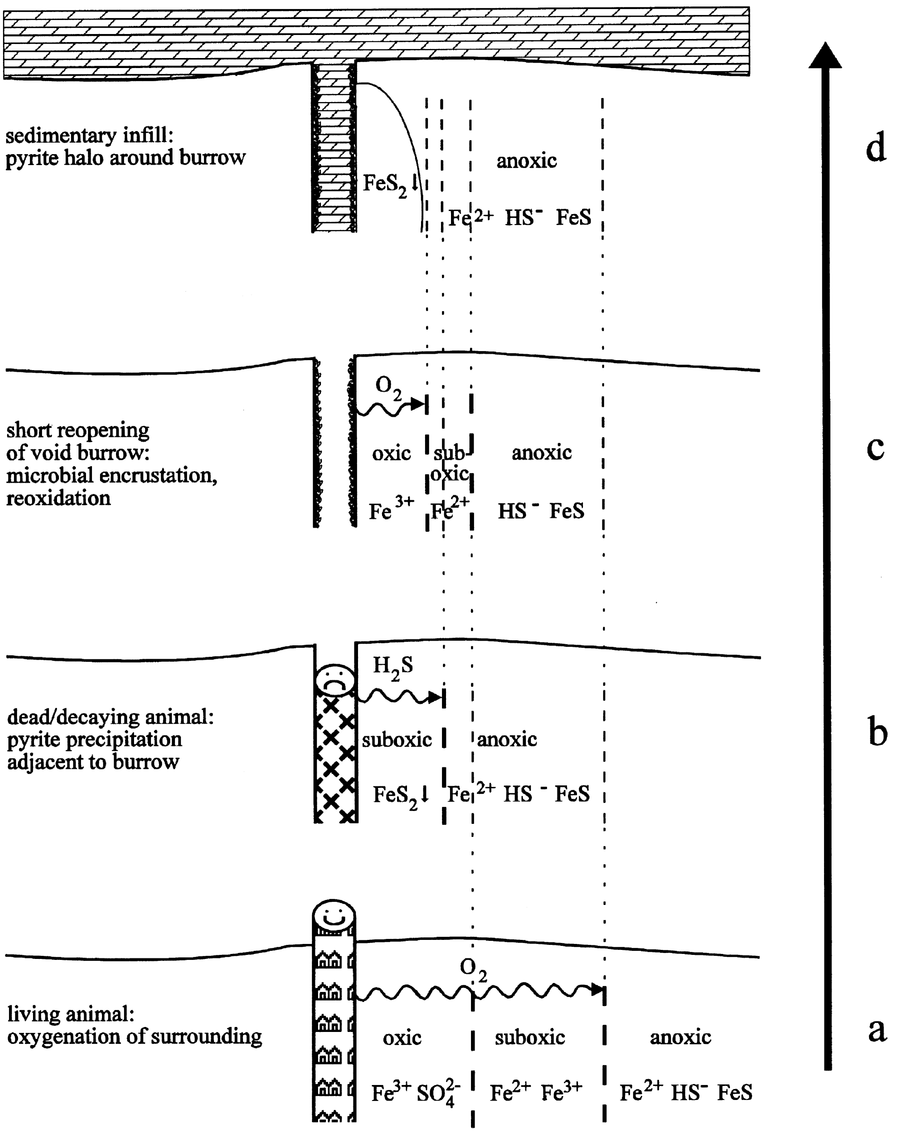


Fig. 4. Schematic sketch of taphonomic history of *Balanoglossites* at Steudnitz; see Section 4.1 for details.

reopening period, oxygen again penetrated into the adjacent matrix and reoxygenated the inner part of the suboxic zone (Fig. 4c). Lateral diffusion of oxygen turned the intermittently blackened zone brownish, indicating the reoxidation of ferrous iron. It did not reach the outer limit of the previous zone of sulphide precipitation in most places, however. Therefore this zone is now preserved as a black ring of variable thickness and contour. While the burrows were flushed by seawater, the remaining organic matter of the margins sustained microbial colonisation.

The burrows were abruptly filled by an event of calcareous sedimentation. In due course the microbial mats decayed in situ, producing local anoxic conditions (Fig. 4d). Diffusing hydrogen sulphide precipitated pyrite around the burrows but essentially remained confined to the margins themselves. As a consequence, a second set of narrow, inner pyrite rings formed at the burrow margins, with sharp contacts to the infill but a blurred transition to the inner suboxic light brown zone. The microbial biomass was consumed too quickly to have resulted in a more significant alteration. The burrow infill was not affected because it still contained small amounts of 'connate' oxygen.

The presumable lifetime of the burrowers suggests that the intravital and postmortal processes mentioned above occurred during at least two or three years. The time elapsed between decay of organic matter and infill of the burrows, however, is hard to substantiate. As frequently observed in shallow marine carbonates ascending cementation occurred during a period of continuous sedimentary cover. *Balanoglossites* shafts were filled at this time since no *Trypanites* borings starting from their margins have been observed. The rising cementation front is nowadays mirrored by the hardground morphology. This phase was terminated by an erosion event which removed all unlithified cover material; it resulted in the loss of top layer of the sediment, including the funnel openings of *Balanoglossites*. By comparison with fully preserved specimens from other horizons, a minimum erosion of 4 cm is suggested.

4.2. Taphonomy of Balanoglossites *(Göschwitz)*

The formation of celestite crystals within the *Balanoglossites* burrows and associated *Thalassinoides* deserves special attention. Since the shafts penetrated anoxic sediments the most plausible explanation is the oxidation of hydrogen sulphide: it diffused from the matrix and upon encounter with oxygenated seawater in the burrows, thiobacilli produced sulphate (see Clayton, 1986). Because of the burrows' sand content their permeability must have been much higher; the connection with open seawater even after infill probably has provided sufficient aeration.

In this context the isotopically light sulphur in barite of Liassic concretions is remarkable; it equally suggests provenance from sulphide oxidation (Hesselbo and Palmer, 1992). Strontian ions instead of barium probably stemmed from ascendent pore water flow during very low water depths or even emersion (Schwarz, 1975). In modern sabkhas with these conditions, celestite may precipitate:

$$HS^- + 2O_2 + Sr^{2+} + H_2O \rightarrow SrSO_4 + 2H_3O^+$$

The accompanying liberation of hydronium ions resulted in sinking pH which in turn facilitated carbonate dissolution (see Zijlstra, 1995). This may be the cause for the porous appearance of the burrow fills. The pore fluids in the burrows were not saturated with oxygen, however, since the minor amounts of ferrous iron remained in the reduced state. Only upon recent weathering it is oxidized, resulting in yellow goethite stain of the burrow fill.

As can be seen from compacted burrows, infill and oxidation occurred early in diagenesis, similar to the situation at Steudnitz. The producer of the burrow was no longer present, however, because this would have limited precipitation to the apertural region. Sedimentary cover during celestite formation must not have exceeded very much the position of the apertures because otherwise downward oxygen diffusion would have been hampered. The assumption of a firmground seafloor with infilled burrows in direct contact to seawater is even more plausible.

4.3. Taphonomy of Trypanites *(Steudnitz)*

Two remarkable features of the borings' preservation require a detailed explanation: black haloes in the matrix and occasional raised black rims above the hardground surface. The black colour is reflecting iron sulphide content, as is shown by localized brassy patches.

During a time of coverage with at least several centimetres of unknown sediments, ascending pore fluids rich in hydrogencarbonate cemented the micritic sediment below, including the burrows, and a hardground with uneven upper borderline formed (Fig. 5a). After its exhumation by an erosion event, the *Trypanites* animals entered a still suboxic substrate with pH below 7. Their metabolic activities released carbon dioxide into the surrounding (Fig. 5b), raising the pH by the establishment of a buffer system with (hydrogen)sulphide:

$$CO_2 + S^{2-} + H_2O \rightarrow HCO_3^- + HS^-$$

and

$$HCO_3^- + H_2O \rightarrow H_2CO_3 + OH^-$$

Due to the elevated pH, iron sulphides were precipitated around the borings; because the reduced sulphur stages only exist as S^{2-} at lower pH, e.g. pyrite

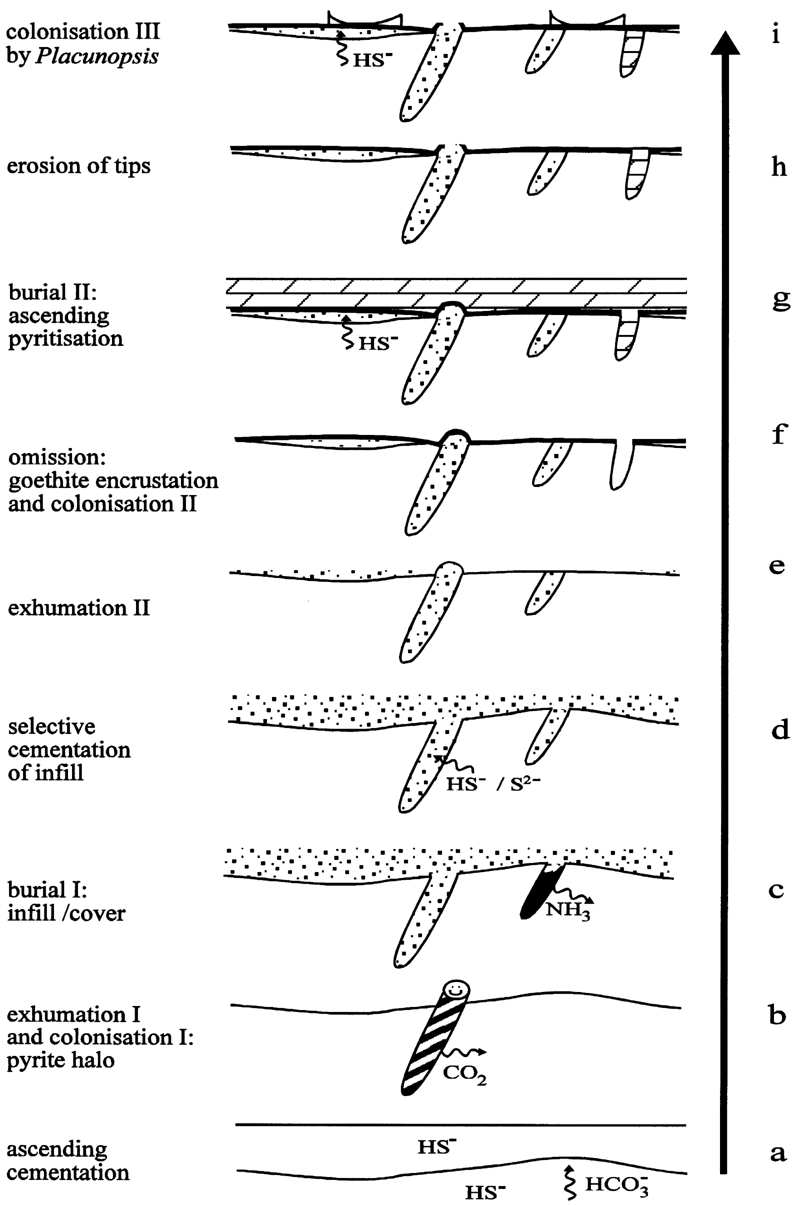


Fig. 5. Schematic sketch of taphonomic history of *Trypanites* at Steudnitz; see Section 4.3 for details.

cannot form in acid environments. Higher pH provides conditions for the stability of HS^- and still higher pH even of H_2S. Thus haloes of finely disseminated melnikovite/pyrite formed as long as the burrows were occupied. (If the matrix had been oxic, carbon dioxide production would have lowered pH via hydrogencarbonate formation; as an effect, calcite solution would be expected, but this is not observed.)

Death and decomposition of the producers had little effect on the borings' margins. The probable release of ammonia also triggered the formation of pyrite haloes, as did carbon dioxide by raising pH. Very soon afterwards, the borings were filled in by a coarse bioclastic sediment covering the whole hardground. A significant part of the borer population was buried alive, as is indicated by the numerous narrow and short borings (Fig. 5c): obviously juveniles could not mature, and their corpses then produced the intense haloes observed already around very small perforations.

Under the bioclastic cover, the boring fill was selectively cemented (Fig. 5d): hydrogensulphide (or even sulphide) from the neighbouring matrix diffused into the slightly alkaline pore fluids of the carbonate sediment and with calcium ions certainly present reacted to precipitate aragonite:

$$HCO_3^- + HS^- + Ca^{2+} \rightarrow CaCO_3 \downarrow + H_2S$$

Simultaneously the pH was raised because this reaction removes hydrogencarbonate, shifting the solution equilibrium of calcite:

$$CaCO_3 + H_2O \rightarrow Ca^{2+} + HCO_3^- + OH^-$$

(represented by the bioclasts) towards the right side. This effect allowed for even stronger aragonite precipitation and thus cementation than in the surrounding matrix or the overlying sediment. It extended a short distance into the wallrock, however, producing an intensely lithified blob there.

Except for small relics, the overlying sediment was later eroded again (Fig. 5e), and a longer period of non-deposition set in. During this time, the frequently observed impregnation with ferric iron (Fe^{III} as goethite) occurred, forming a more or less coherent crust on the hardground including the blobs protruding from the borings (Fig. 5f). This phase must have lasted much longer than the other stages described here since iron accumulation from seawater tends to require large time spans. Within these, a second generation of annelid spat settled and bored through the goethitic encrustation.

The omission was ended by the sedimentation of a fine-grained marl, sealing off the encrusted hardground against the seawater above and filling in the few *Trypanites* which had been made.

Hydrogensulphide ascended from the matrix below and reduced the goethite to iron-sulphides (Fig. 5g):

$$2FeOOH + 3H_3O^+ + 3HS^- \rightarrow FeS + FeS_2 + 7H_2O$$

This process may also have operated in the British Coinstone formation if the model of Hallam (1969) is correct, instead of the alternative sulphate reduction hypothesis suggested by Hesselbo and Palmer (1992).

The reaction is proton-consuming and facilitated further precipitation of melnikovite/pyrite where hydrogensulphide could percolate well. Most probably this was the case at the boring apertures with their permeable fill, resulting in the increment of the (former goethite, now) iron sulphide caps on them. This model is suggested by very similar conditions on the bottom of modern Sulu Sea (A. Wetzel, pers. commun., 1995). The formation of narrow pyrite rims around *Trypanites* in the British Lias (Hesselbo and Palmer, 1992) is hardly comparable because from the supposed pore fluid direction and chemistry there is no reason to assume any large-scale activity of sulphate-reducing thiobacilli here, especially not on the seafloor. In addition, Thuringian pyrite rims are much thicker and wider.

The period of reducing conditions at the hardground was probably rather short; otherwise ascendent cementation would have proceeded above it.

A second erosion event swept the hardground free again; the pyritic caps of the apertures were broken off in numerous cases, especially on the more exposed hillocks (Fig. 5h). In protected areas, they had good potential of preservation. After this event, the apertures of the borings stood out like short chimneys surrounded by an irregular mass of pyrite. The surface was settled by spat of oyster-like *Placunopsis* (Fig. 5i). There is also some indication of a fourth generation of *Trypanites* which has been filled by a type of sediment differing from the others. It is not clear how the pyritic encrustation could ‘survive’ this oxic phase but perhaps it was first oxidized, and later reduced a second time during the final sedimentary cover.

4.4. Taphonomy of Trypanites *(Obermöllern)*

The situation at Obermöllern differs from Steudnitz regarding the substrate and the lack of raised rims; the basic taphonomic processes were very similar, however (Fig. 6a). Although the oolite is nowadays very lightly coloured, it has to be concluded that it once contained fluids rich in sulphide and iron, as is shown by the pyrite impregnation of some borings’ infill and the weathered brown halo around the tubes.

A largely lithified oolite with reducing pore fluids was bored by the *Trypanites* animals (Fig. 6b). The

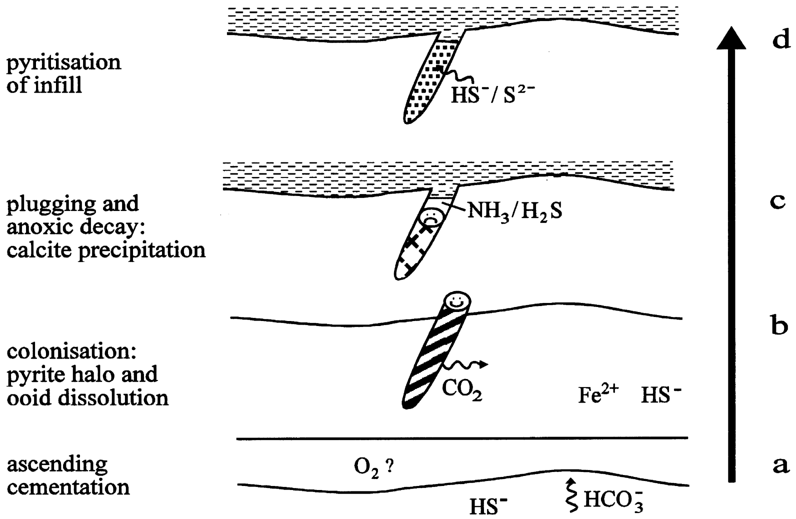


Fig. 6. Schematic sketch of taphonomic history of *Trypanites* at Obermöllern; see Section 4.4 for details.

carbon dioxide produced by their metabolic activities entered the adjacent matrix, formed a buffer system by reaction with sulphide, and raised pH there (see Section 4.3). With pH above 7, iron sulphides were precipitated from the surrounding pore waters (see Section 4.1). The precipitation is strongest at the borings' margins and fades out away from it. The metabolic carbon dioxide had yet another effect: it facilitated the dissolution the marginal ooids after their partial mechanical removal by the boring action.

$$CaCO_3 + CO_2 + 2H_2O \rightarrow 2HCO_3^- + Ca^{2+}$$

A physical abrasion by the worms' setae is highly unlikely since ooids must have been harder than the early cement around them.

A major sedimentation event caused the borers' death; their decomposition took place under a plug of marly sediment (Fig. 6c). Despite its small grain size this marl did not fill in the borings completely which shows their occupation by the dead producers. In this situation their corpses released hydrogensulphide which reacted with the omnipresent calcareous pore fluids to form aragonite in and around the borings' lumina:

$$HCO_3 + HS^- + Ca^{2+} \rightarrow CaCO_3 \downarrow + H_2S$$

Perhaps pore fluids account for more sulphur than the decaying corpses; in this case the release of ammonia and the subsequently raised pH was the trigger for carbonate precipitation.

Sulphidic pore fluids entering the borings could locally precipitate pyrite/melnikovite when enough iron was present as well (Fig. 6d); the controlling factor again was the alkaline solution within the borings. No further erosion or sedimentation events seem to have affected the preservation of the borings, drastically different from the history of the Steudnitz hardgrounds.

5. Conclusions

5.1. Control factors of taphonomy

The taphonomy of the Oolithbank trace fossils was controlled by sedimentological and chemical factors. Sedimentologically, the onset of low sedimentation rates (omission) facilitated stiffening of the soft sediment to a firmground. This could be used by the *Balanoglossites* producers but soon afterwards the top was eroded. The same event may also have filled the hitherto open burrows, e.g. during a ceasing storm. A prolonged phase of sedimentary cover caused the cementation by upward pore water flow. With a second major erosional event the cemented surface was exposed as a hardground. This was colonized by borers, encrusted by bivalves, covered by sediment and eroded again. Situations like these are typical of the tops of shallowing-upward cycles (e.g. Zwenger, 1993), i.e. during lowstand phases.

There were frequent changes of environmental conditions, but only during the transitional phase from firmground to hardground they triggered a different set of biota. The temporally varying colonisation must not be mistaken as an ecological succession, as this has repeatedly happened before (see e.g. Goldring and Kažmierczak, 1974; Bromley, 1975; Gruszczyński, 1979). This would imply a biologically induced change of the environment which results in the settlement of new taxa; this cannot be substantiated in any of the cases mentioned.

The taphonomically most important chemicals were iron, oxygen and sulphide. Oxygen was (almost?) absent from the sediment, only locally being introduced by open burrows or borings as pathways. Most reactions occurred at the boundary between aerated and anaerobic/dysaerobic regions. Hydrogen sulphide liberated from the sediment was trapped as pyrite with iron present under anaerobic conditions. With iron absent, calcite could form within the borings' fill while the sulphide escaped. Under aerobic conditions and lack of iron, it was oxidized to sulphate, allowing celestite precipitation.

The permanent sulphide production in the matrix differs from most other situations where diagenetic pyritisation has been discussed (e.g. Clayton, 1986; Hesselbo and Palmer, 1992); there, sulphate reduction in an aerobic to dysaerobic environment was the driving force. In the case studied, however, the reactions of hydrogensulphide depend on the presence or absence of iron and oxygen in the same microenvironment. A pH control (buffering) is not achieved by hydronium consumption during sulphate reduction but by the hydrogencarbonate/hydrogensulphide system. Iron obviously was generally present in abundance, as could be expected from the significant clay mineral content in the matrix (see Clayton, 1986). Iron concentrations were lower in the bioclastic infill of burrows and borings, however. Since these were the sites of oxygen availability at the same time, absence of iron and presence of oxygen was frequently (but by no means permanently) coupled. The patchiness of celestite occurrence in burrows may thus be due either to the amounts of iron available for sulphide trapping, or oxygen presence for sulphide oxidation (strontian was distributed much more evenly). Oxygen was consumed soon in shafts isolated from the seawater above and may have persisted in others, resulting in a highly variable preservation of even neighbouring burrows or borings.

5.2. Ichnology (ichnofacies and ichnofabric)

Firmground and hardground trace fossils occurring in the same bed have been described from the Recent (Bromley and Allouc, 1992), Late Cretaceous (Bromley, 1975), Jurassic (Goldring and Kažmierczak, 1974), and Triassic (Zwenger, 1993). Burrows tend to remain open for some time after their producers' death, even during the hardground phase, which has not been observed in the case studied. The sequence of colonisation corresponds well to the examples cited by Goldring and Kažmierczak (1974) for their type 3a hardground, closely reflecting the substrate transition.

The ichnofacies accordingly is an overprinted *Trypanites* on *Glossifungites* facies. The latter one is characterized by U- and J-shaped domichnia of suspension feeders (shrimp, crabs, polychaetes, etc.). It is typical of non-lithified firm substrates especially in intertidal or supratidal positions and it frequently shows evidence of exhumation (Frey and Seilacher, 1980; Pemberton and Frey, 1985). According to Bromley (1975), it represents the first stage of an omission suite which, however, need not reach its climax. Pollard (1981) groups *Balanoglossites* within the *Cruziana* ichnofacies and only mentions *Arenicolites* from typical *Glossifungites* facies. This trace has not been observed in the horizons studied, so a regrouping of at least *Balanoglossites* seems advisable. *Thalassinoides* and *Rhizocorallium* occur in the Oolithbank as well; they too have been placed in the *Cruziana* facies by Pollard (1981).

The ichnofabric is characterized by intense but patchy burrowing and boring. Because of the size of the *Balanoglossites* animals, burrowing is more conspicuous even with its top layer being removed by subsequent erosion. It forms the lower tier in the composite fabric but does not seem to have controlled the settlement of the borers in any way. This is probably due to the infill and cementation of the burrows; it 'froze' their ichnofabric and rendered them equal to the adjacent substrate for the succeeding borers. The preservation of the upper tiers (borings) depends on the amount of erosion (see e.g. the abraded sulphide chimneys at Steudnitz) but at least *Trypanites* is nonetheless continuously present. From the lack of very shallow borings which have been described by Jahnke (1966) from the Terebratelbank horizon, it may be surmised that a top tier above *Trypanites* might have been present in Thuringia as well.

In the material studied, burrowers and borers seem to have been monospecific in most cases. Although the situation regarding borings cannot be fully clarified, the apparently low diversity of burrowers is remarkable. Pollard (1981) mentions seven ichnotaxa from European Muschelkalk carbonates, and according to personal observations some more are present in other beds even in Thuringia. In this context the cumulative nature of such listings has to be considered, probably representing variable environments through time. For the very limited time represented by the Oolithbank, microfacies and regional studies suggest hostile conditions: hypersalinity, emersion, erosion, sporadic sedimentation, and/or elevated temperatures (?) may have accounted for low diversity in trace fossils and encrusters.

5.3. Regional comparison

A regional comparison is hindered by the scarcity of other studies concerned with Triassic omission suites. The basic pattern of *Trypanites* boring before *Placunopsis* encrustation once a hardground is formed was found in southern Germany as well (Schwarz, 1975). The works of Jahnke (1966) and Hagdorn and Simon (1983) prove the ecological and taphonomical similarity of conditions some 150 km to the northwest. Given the facies uniformity of the Muschelkalk basin, this is not surprising although the authors do not mention burrows of the *Balanoglossites* type. The roughly synchronous hardgrounds near Göttingen house a richer assemblage of shallow borings, however, which suggests stronger erosion in Thuringia. A detailed study of these traces from southern Poland was performed by Kažmierczak and Pszczółkowski (1969). Their description of the preservation match the Thuringian samples well but the authors do not give an interpretation of diagenetic phenomena. Erosion seems to have played a stronger role, however.

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