Revision and description of Keuper (Middle Ladinian to Rhaetian) invertebrate trace fossils from the southern part of the Germanic Basin and studies of related material

300 pages, 135 figures, 5 tables

Dissertation zur Erlangung des
naturwissenschaftlichen Doktorgrades
der Bayerischen Julius-Maximilians-Universität Würzburg

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Würzburg, Januar 2005

Dedicated to my love

Silke and Jan-Niklas

PREFACE

§. 1.

Es iſt keine unter allen mineralogiſchen Wiſſenſchaften mit mehreren Muthmaaßungen angefüllet, als diejenige, welche von den verſteinerten Dingen handelt. Dieſes zeiget ſich inſonderheit, wenn man die urſprünglichen Körper ausfindig machen will, welche zu verſchiedenen Verſteinerungen den Grund geleget haben, indem man, unter den verſteinerten Dingen, Arten anſichtig wird, deren natürliche Körper uns entweder ungemein ſelten zu Geſichte kommen, oder die noch zur Zeit völlig unbekannt ſind.

From: CHRISTIAN FRIEDRICH SCHULZE: Betrachtung der versteinerten Seesterne und ihrer Theile, 1760.

Abstract

The invertebrate trace fossils from the Keuper (Upper Triassic) of the southern part of the Germanic Basin are revised. The Keuper sediments of the Germanic Basin are predominantly composed of rocks representing various nonmarine environments dominated by red-bed facies. The Würzburg Formation, the Stuttgart Formation, and the Hassberge Formation, all representing deposits of extended river systems, contain the richest ichnofauna. Trace fossil abundance is generally low and their occurrence is scattered. The studied material can be assigned to 28 ichnogenera, 38 ichnospecies, and 6 vernacular forms. Among the described trace fossils are one new ichnogenus and three new ichnospecies.

Apart from the revision of the invertebrate trace fossils from the Keuper numerous related ichnotaxa from various localities and ages have been studied and revised. In the course of these studies several ichnotaxa are synonymised, lowered in rank, and new ichnogenera, subichnogenera, and ichnospecies are suggested.

In addition, general guidelines for naming, and methodologies for studying invertebrate trace fossils are presented.

The palaeoecology of three ichnocoenoses, one from the Würzburg Formation and two from the Hassberge Formation in Lower Franconia are briefly discussed.

Key words: Upper Triassic, Germanic Basin, nonmarine deposits, ichnotaxonomy, nomenclature.

Zusammenfassung

Die Invertebratenspuren aus dem Keuper (Obere Trias) des südlichen Germanischen Beckens werden revidiert. Die Sedimente des Germanischen Keupers bestehen zum überwiegenden Teil aus verschiedenen nichtmarinen Rotsedimenten. Die Würzburg Formation, die Stuttgart Formation und the Hassberge Formation werden als Ablagerungen ausgedehnter Flusssysteme interpretiert und enthalten die reichhaltigsten Spurenfaunen. Die Häufigkeit von Spurenfossilien ist generell niedrig und ihre Verbreitung ist punktuell. Das untersuchte Material kann 28 Ichnogattungen und 38 Ichnoarten zugewiesen werden. Sechs Spurenfossiltypen konnten taxonomisch nicht zugewiesen werden.

Neben der Revision der Keuperspuren wurden zahlreiche verwandte Spurentaxa verschiedener räumlicher und zeitlicher Herkunft detailiert revidiert. Im Zuge dieser Revision wurden einige Taxa synonymisiert oder in ihrem taxonomischen Rang erniedrigt sowie neue Ichnogenera, Unterichnogenera und Ichnospezies vorgeschlagen.

Darüber hinaus werden Leitlinien zur Nomenklatur von Spurenfossilien sowie generelle Verfahrensweisen zum Studium von Invertebratenspurenfossilien vorgestellt.

Die Palökolgie dreier Ichnozönosen aus Unterfranken, eine aus der Würzburg Formation und zwei aus der Hassberge Formation werden kurz diskutiert.

Schlüsselwörter: Obere Trias, Germanisches Becken, nichtmarine Ablagerungen, Ichnotaxonomie, Nomenklatur.

CONTENT

INTRODUCTION

Trace fossils are very important in palaeoenvironmental studies, and often serve as sole biogenic tools for this purpose. In many cases, body fossils are not preserved in sandstones, the rock type in which most trace fossils occur. This sometimes led to irritations in the past because, for instance, rocks bearing *Cruziana* were barren of trilobites and vice versa (e.g., SEILACHER 1970). The importance of trace fossils for palaeoenvironmental reconstructions in the marine realm is long known and well used (e.g., SEILACHER 1955, 1967; FÜRSICH 1975; HOWARD & FREY 1984). With increasing knowledge on trace fossils in general and sedimentological and/or stratigraphical tools, new methods were incorporated in marine palaeoenvironmental reconstructions (e.g., PEMBERTON et al. 2001, MCILROY 2004); even a new ichnologic tool was invented, called "ichnofabric analysis". TAYLOR et al. (2003) give a detailed overview on ichnofabric analysis. Ichnofabric analysis is not as different from classical ichnological studies as often believed. Much more is it an attempt to come to the same conclusions as classical studies, but with less information on one side and additional information on the other. Less information because the information available for ichnofabric analysis usually comes from core material, and thus is somewhat limited concerning the entire trace fossil morphology. More information because in ichnofabric analyses cross cutting relationships, tiering and the degree of bioturbation is always considered. However, neither of the methods could be called the better one. As usual there are pros and cons on each side, the strongest tool remains the one that incorporates all available data. The biggest progress in the last decades was made in studies of subaquatic and non-aquatic invertebrate trace fossils of the non-marine realm (BOWN 1982, GENISE 2004, GENISE & BOWN 1994, BUATOIS & MÁNGANO 1995, 2004). The bases of all these much-respected studies of 'applied' ichnology are the much less respected and often disliked disciplines of nomenclature, taxonomy, and systematics. This is not really new but no less true. Only well-defined trace fossils can be used as tools in palaeoenvironmental studies. Besides many other differences (see below) trace fossils fundamentally differ from body fossils as they usually are not bound to stratigraphy. Thus, while reviewing trace fossils, publications dealing with ichnotaxa from various geological ages have to be consulted. In order to get a consistent and complete picture of each ichnotaxon related forms also have to be studied. For this reason various trace fossils that do not occur in Keuper deposits also are discussed and revised in this study. The aim of this study is, to revise and document all previously reported invertebrate trace fossils from Keuper (Middle Ladinian to Rhaetian) deposits of the southern part of the Germanic Basin, and to provide information on how to study trace fossils in general. The ethology of the trace fossils is discussed. This is important not only for future palaeoenvironmental studies but also builds the fundaments of the evaluation of ichnotaxobases (FÜRSICH 1974a, b).

GEOLOGICAL SETTING

The Germanic Basin was located approximately 30° N of the equator and was part of the Central European basin (ZIEGLER 1990). The main source areas from which the siliciclastic deposites of the Keuper derived were the Fennoscandian High (Balto-Scandia) and the Vindelician-Bohemian Massif.

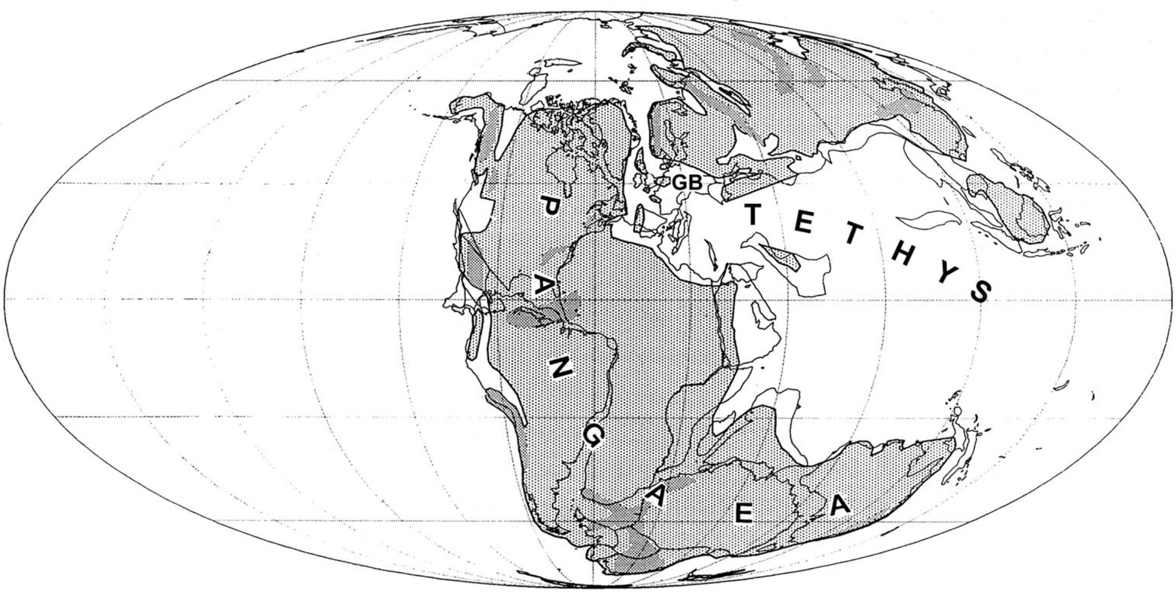

Figure 1: Palaeogeography and positions of coastlines during the Late Triassic; dotted areas were terrestrial, and dark grey indicates the main denudation areas; GB indicates the position of the Germanic Basin. Modified after SMITH et al. (1994).

The Keuper beds (Upper Triassic) of southern Germany are predominantly composed of rocks representing various nonmarine environments dominated by red bed facies. In the following the Upper Triassic (Keuper) formations relevant for the southern part of the Germanic Basin are described. The data is compiled after GEYER & GWINNER (1986), BEUTLER (1998), and GEYER (2002).

The Lower Keuper (**Erfurt Formation**) is characterized by a gradual transition from marine to nonmarine. The marine deposits consist of dolomites, and the nonmarine deposits are made up of continental shales and dominantly fluvial sandstones of Fennoscandic provenance. The Lower Erfurt Formation is unconformably overlain by the Werksandstein (Bavaria) and his equivalent, the Hauptsandstein (Baden-Württemberg; Figs 6-7). The Werksandstein/Hauptsandstein represent fluviatile deposits deriving from the Fennoscandian High, and their facies are highly variable. The Werksandstein/Hauptsandstein can be subdivided into two major facies types: 1) fluvial channel deposits (Flutfazies) and 2) overbank deposits (Stillwasserfazies). The fluvial channel fills are made up of 2-8m thick, trough cross-bedded, yellow-greenish to yellow, subordinately light grey, purple, or

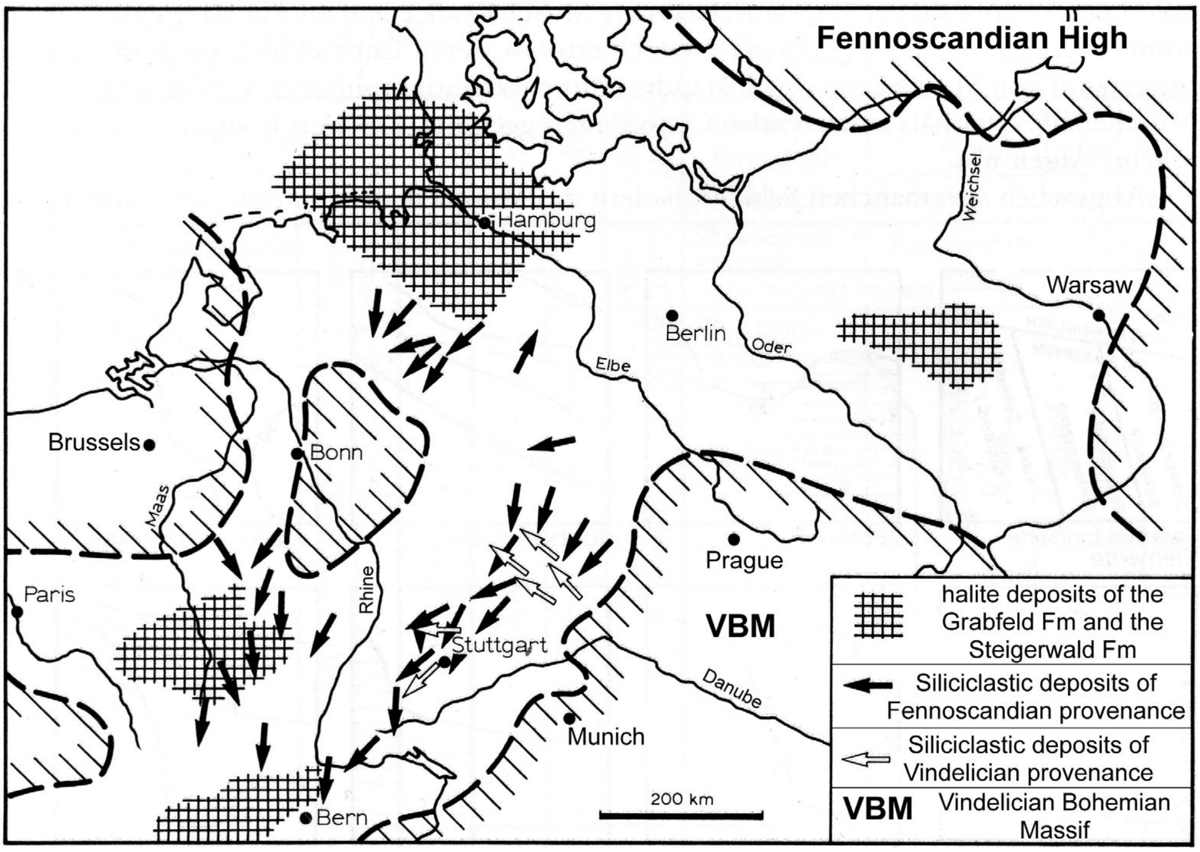

Figure 2: Palaeogeography of Middle Europe during the Late Triassic. Modified after WURSTER (1964) and SCHRÖDER (1982).

brownish, moderately well sorted, mica rich (predominantly occurring on parting surfaces), fine sandstones with a clay matrix. The overbank deposits are characterized by thin bedded, up to 2.5m thick, yellowish to brownish, cross-bedded, fine sandstones, with a clay matrix. Intercalated are greyish to brownish silt and claystones. The sandstones are occasionally overlain by multicoloured claystones and sandstones. The dominating environment was nonmarine but marine incursions are also documented by faunal remains such as shark teeth (e.g., SANDBERGER 1890).

The Werksandstein/Hauptsandstein of the Lower Keuper is genetically equivalent to the Schilfsandstein of the Middle Keuper. GEYER (2002) therefore suggested the introduction of the **Würzburg Formation** in analogy to the Stuttgart Formation for the Schilfsandstein. This suggestion is followed here.

The lower Middle Keuper (**Grabfeld Formation**) is characterized by playa deposits with marine incursions into the basin centre, and represents the first evaporitic unit of the Keuper (lower Gipskeuper). The sediments are redbeds, grey or multicoloured shales with numerous massive or nodular gypsum/anhydrite and dolomite intercalations. The equivalent at the southern basin margin of

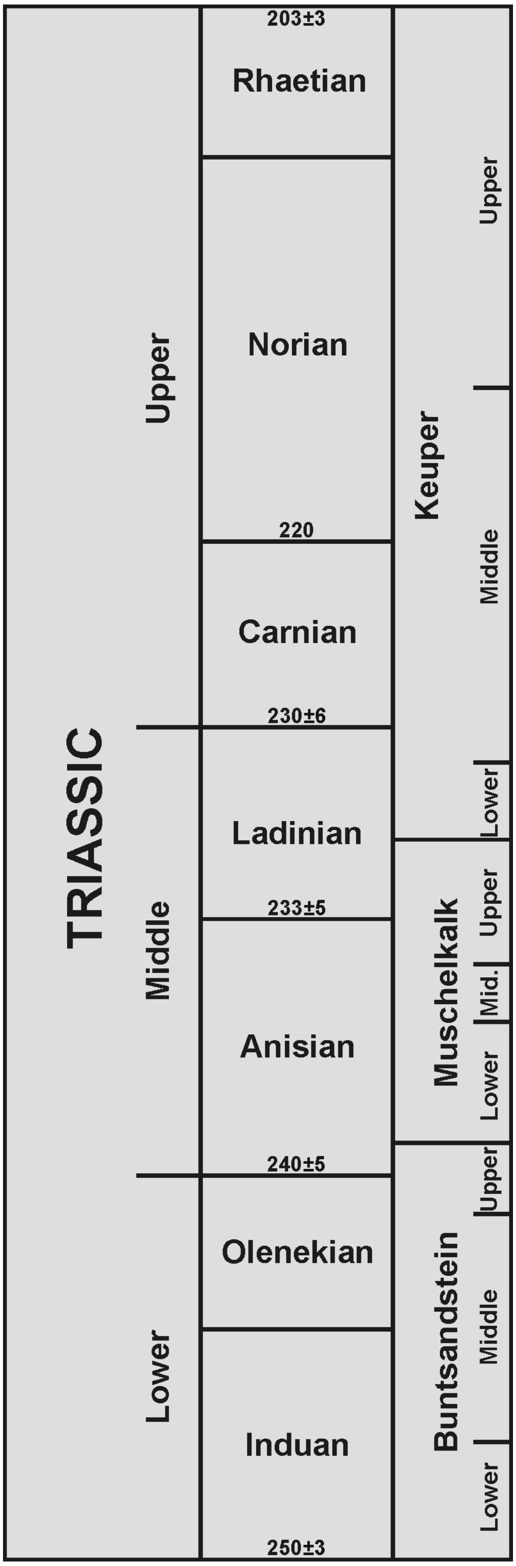

Figure 3: Triassic time scale. Modified after BEUTLER (1998).

the Grabfeld Formation is the **Benk Formation**, which is made up of typical coarsening upward cycles of multicoloured shales, and fine-grained to coarse grained arkosic sandstones. The deposits of these formations are unconformably overlain by the Schilfsandstein (**Stuttgart Formation**). The Schilfsandstein, the genetical equivalent of the Werksandstein, was deposited in a large fluvial system

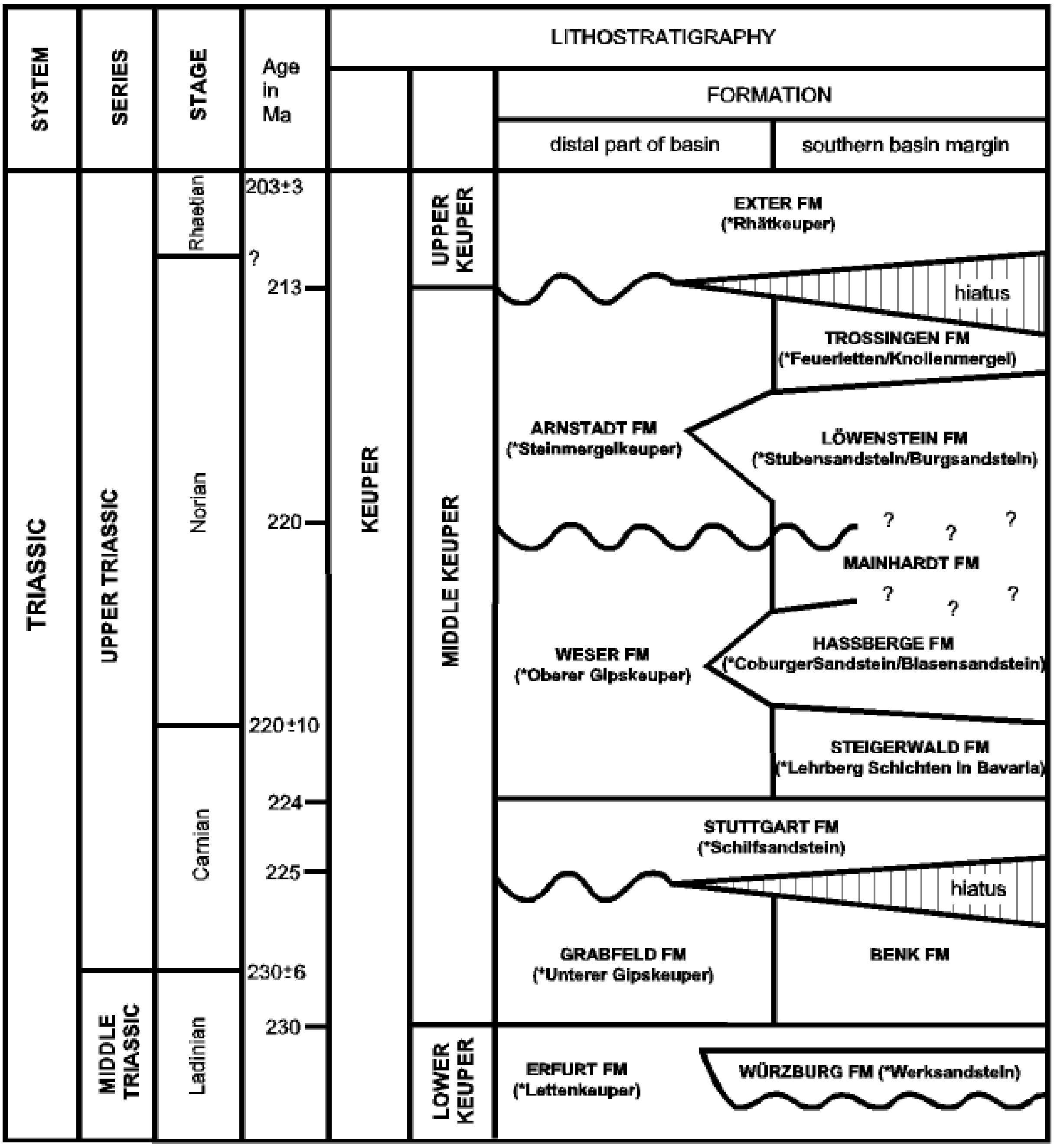

Figure 4: Chrono- and lithostratigraphy of the studied rock sections. Modified after BEUTLER (1998); age dates for stages from International Stratigraphic Chart; absolute ages on right site of the column from BEUTLER (1998); * traditional lithostratigraphic names.

covering the entire Germanic Basin. The sediments derived from Fennoscandia and are highly variable. Two major facies are distinguished: 1) fluviatile channel facies (Flutfazies) and 2) overbank deposit facies (Stillwasserfazies). The channel fills commonly are greywacke-like sandstones with grey and red shale intercalations. The overbank deposits consist of pelites with generally thin sandstone intercalations. In parts, the deposits of the Schilfsandstein have a high content of glauconite (autochthonous and allochthonous), which indicates at least short termed marine incursions. The following deposits of the **Steigerwald Formation** (Lehrbergschichten in Bavaria;

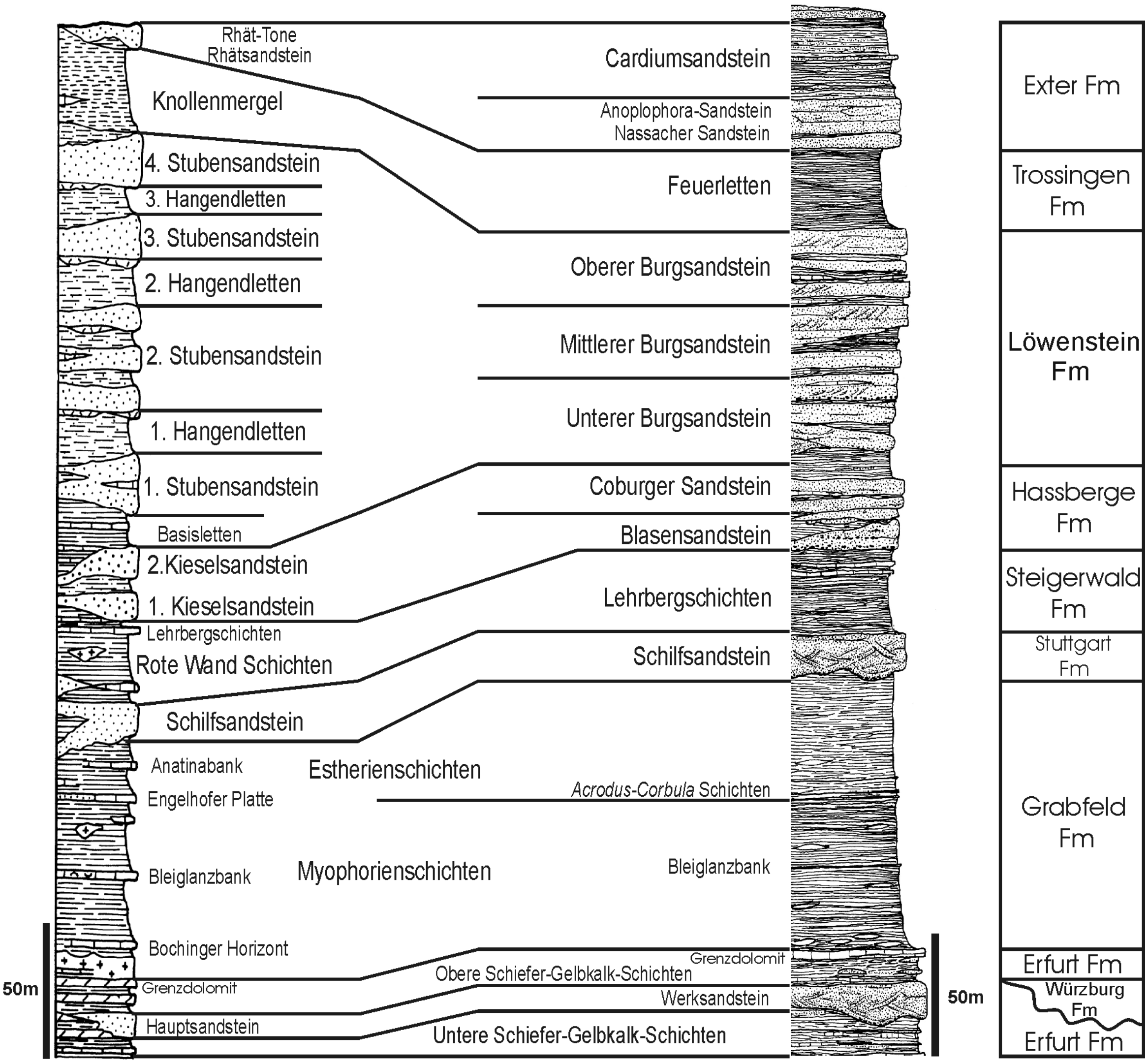

Figure 5: Generalized lithostratigraphic logs of the Upper Triassic (Keuper) in Baden-Württemberg and eastern Lower Franconia. Right column gives currently used Formation names for the Germanic Triassic, including the Würzburg Formation as suggested by GEYER (2002). Modified after GEYER & GWINNER (1986) and GEYER (2002).

Rote Wand and Lehrbergschichten in Baden-Württemberg) are made up of red-brown, occasionally green shales, subordinately with dolomite and gypsum/anhydrite intercalations; finally they grade into red, occasionally green, shales and siltstones and marly shales, interpreted as overbank deposits and deposits of shallow lakes. The overlying deposits of the **Hassberge Formation** (Blasensandstein and Coburger Sandstein in Bavaria; Kieselsandstein in Baden-Württemberg) have a Vindelician-Bohemian provenance. The deposits are fine-grained to coarse-grained, in parts conglomeratic arcosic sandstones with high mica content. The sediments are interpreted as high-energy fluvial channel deposits, indicated by large-scale cross-bedding, mud-pebbles and frequent erosional bases. Intercalated are reddish to brownish shales and dolomite beds, interpreted as overbank deposits. The Hassberge Formation is followed by the **Löwenstein Formation** (Burgsandstein in Bavaria; Stubenandstein in Baden-Württemberg) which consists of alternating fine-grained to

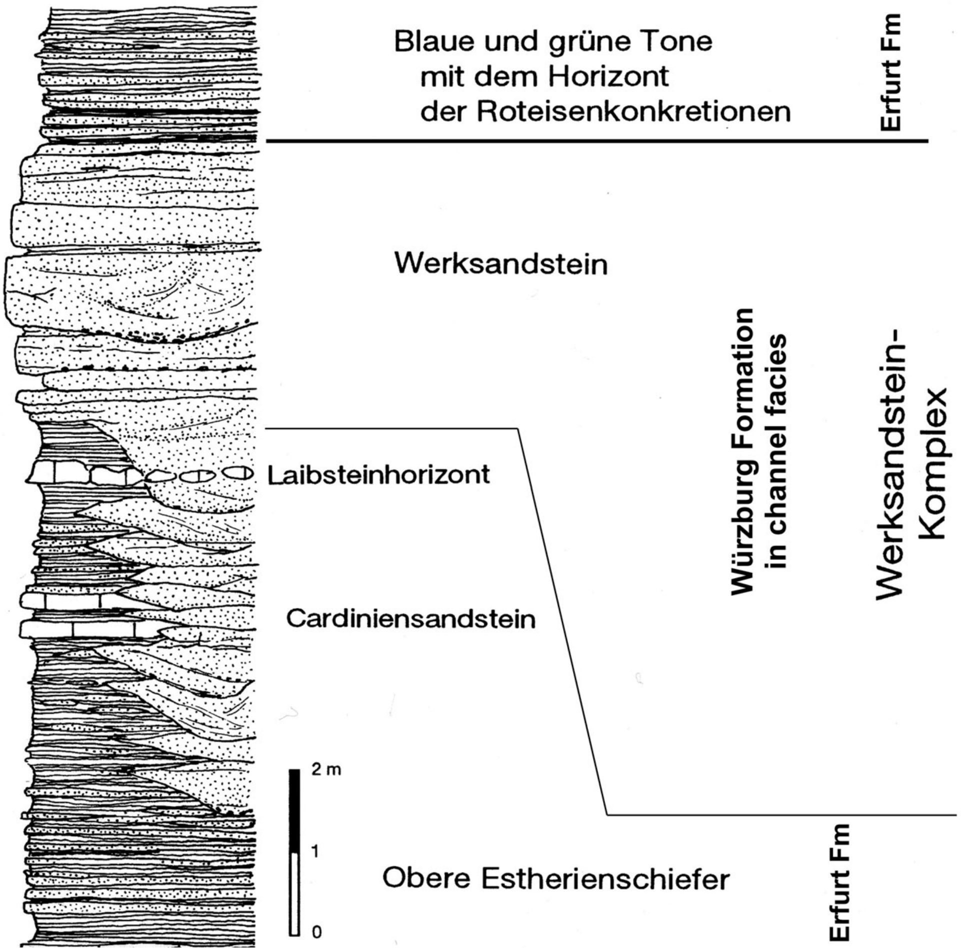

Figure 6: Generalized lithostratigraphic log of the Werksandstein, Würzburg Fm, and parts of the Erfurt Fm in Lower Franconia, Bavaria. Modified after HOFFMANN (1962).

coarse-grained, partly conglomeratic arcosic sandstones, and multicoloured shales. Intercalated are pedogenic dolomites. The overlying **Trossingen Formation** (Feuerletten in Bavaria; Knollenmergel in Baden-Württemberg) is made up of red to brown, brownish purple silt to claystones with nodules and beds of dolomite.

The Upper Keuper (**Exter Formation)** is separated from the Middle Keuper by an unconformity and shows considerable marine influences. In the study area the deposits of the Exter Formation are made up of reddish, brownish and yellow, medium grained sandstones overlain by black or purple claystones to siltstones, followed by red to violet claystones. The top is build by either massive or trough cross-bedded sandstones (channel facies), or thin bedded, fine sandstones with high mica content and intercalated claystones (overbank facies).

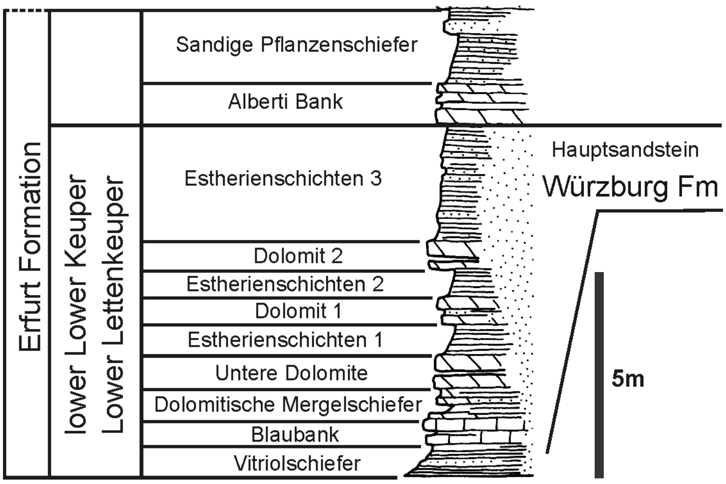

Figure 7: Generalized lithostratigraphic log of the Hauptsandstein, Würzburg Fm, and the lower part of the Erfurt Fm in Baden-Württemberg. Modified after BRUNNER (1980).

PREVIOUS STUDIES

Although invertebrate ichnological data on Keuper deposits are quite scattered in the literature (KUHN 1937; LINCK 1949a, b, 1961; FREYBERG 1968; SEILACHER 1981, SCHLIRF et al. 2001) the material described herein includes a variety of trace fossils, which in parts are useful for the palaeoenvironmental interpretation of the rock sequence.

A great variety of trace fossils has been found in the Coburger Sandstein, Hassberge Formation, Middle Keuper, around Eltmann, and in the Werksandstein, Würzburg Formation, Lower Keuper, between Seubrigshausen and Thundorf in Unterfranken (abbreviated “i. Ufr.” in the following). Both localities are in Lower Franconia, Bavaria, southern Germany. In addition, well-preserved trace fossils from the Kieselsandstein, Hassberge Formation, Middle Keupeer, from various localities in Baden-Württemberg; the Schilfsandstein, Stuttgart Formation, Middle Keuper, at the Stromberg and Heuchelberg Nature Park; and from the Rhätsandstein near Nürtingen were studied. Large parts of this material have been collected and previously described by LINCK (1942, 1949a, b, 1961). This material has been revisited under modern ichnotaxonomical aspects. Additional material from museum collections in Stuttgart and Würzburg has been stuied.

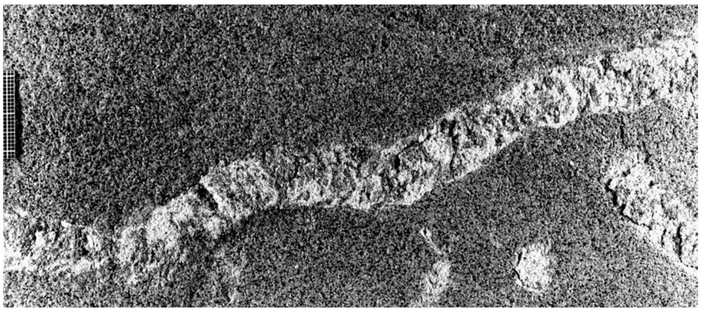

Figure 8: Well preserved specimen of *Taenidium barretti* (BRADSHAW, 1981), fullrelief, top view, Coburger Sandstein, Hassberge Fm, Haßberge, Bavaria. Millimetre grid for scale.

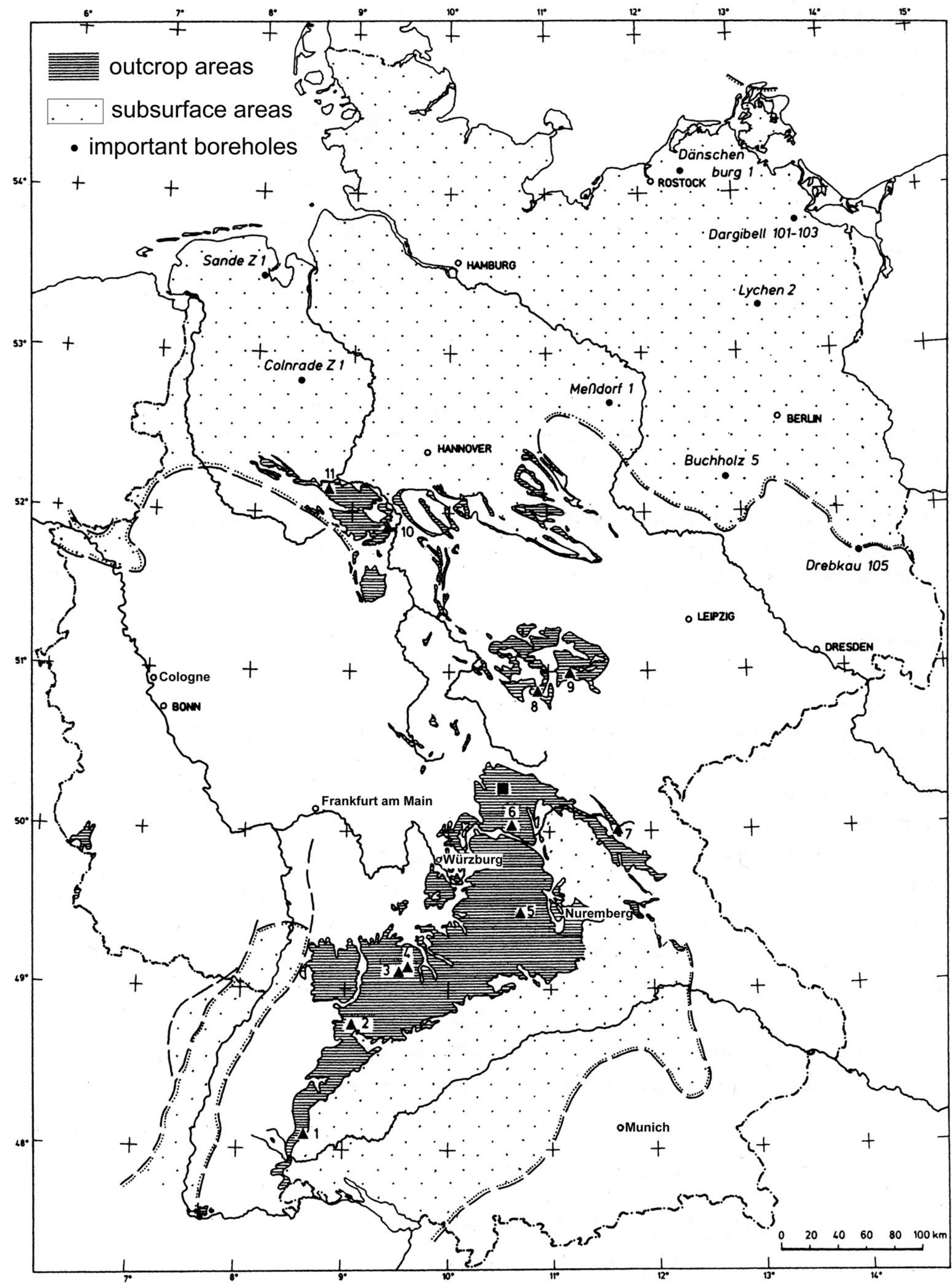

Figure 9: Keuper distribution in Germany. Numbers 1-11 indicate stratotype localities: 1) Trossingen; 2) Stuttgart; 3) Löwenstein; 4) Mainhardt; 5) Steigerwald; 6) Haßberge; 7) Benk; 8) Arnstadt; 9) Erfurt; 10) Weser; 11) Exter; black square) Grabfeld. Modified after BEUTLER (1998).

Figure 10: Outline map of the study area.

Next page:

Figure 11: Generalized graphic logs of the studied outcrops in the Haßberge area.


Eltmann quarry
10
5
1
cm cm
10-15°
dm-m
cm mm
40-60°
lake
fluvial
lake margin
lake
fluvial
lake margin
c s fs ms cs
Schleifsteinwerke quarry
10
5
1
10-15°
dm-m
mm cm
fluvial
lake and lake margin
fluvial
c s fs ms cs
Schönbach quarry
5
1
cm mm
cm dm
OF cm-dm
OF mm-cm
dm dm
lake margin
lake
fluvial
lake margin
c s fs ms cs
Dörflis quarry
10
5
1
cm mm
cm cm
dm
10 m
10-15°
dm-m
lake margin
lake
fluvial
c s fs ms cs
stacked channel fills
pinching, isolated channel
trough bedding
tabular cross bedding
irregular, wavy bedding
desiccation cracks
bioturbation
dm
dm-scale
C
carbonate concretions
intraclasts
rootlets
structureless, massive
horizontal bedding
dm
dm-scale horizontal bedding
siltstone
arcosic sandstone
sandstone
soil (Recent)
cm cm
intercalation of subarcose and siltstone, cm-scale
cm
channelled subarcoses (cm-scale) in siltstone matrix

HASSBERGE AREA

Remarks: The varying spelling of Haßberge area and Hassberge Formation in this paper is due to nomenclatural reasons. When BEUTLER (1998) first introduced the Hassberge Formation he transcibed the original German spelling of the Haßberge area into English, thus resulting in an *ss* instead of *ß*. However, whenever talking of the Haßberge area one should keep the original spelling, and when talking of the Hassberge Formation the originally introduced spelling of BEUTLER (1998) should be used.

The exposed Late Triassic rocks of the Haßberge area and north-eastern part of the Steigerwald belong to the sedimentary fill of a half-graben, located between the Franconian platform in the SW and the Bohemian Massif in the NE (ZIEGLER 1990). This half-graben is divided into several fault blocks, which are directed orthogonally toward the half-graben fault. The deposition was mainly controlled by tectonic activitiy along the Thuringian Fault or the Franconian Lineament, representing the active half-graben fault. There is no evidence of eustatic sea-level fluctuations in the studied sections, although elsewhere they have been well documented in Triassic sediments of the Germanic Basin (AIGNER & BACHMANN 1992). Possibly, the continuous sediment supply from the Bohemian Massif and the tectonic regime overprinted any eustatic signals. During the Keuper interval, the half-graben, situated at the margin of the Germanic Basin, was filled with non-marine sediments of fluvial and lacustrine origins, which in places, contain a great variety and abundance of trace fossils (Fig. 11). The studied sections are about 40m thick and belong to the Hassberge Formation (Coburger Sandstein and Blasensandstein in Bavaria) and the Löwenstein Formation (Burgsandstein in Bavaria) (BEUTLER 1998). The precise age of the exposed rocks is difficult to determine since the sediments are devoid of any index fossils and no volcanic rocks suitable for age dating by physical methods are known. BEUTLER (1998) suggests a latest Carnian to early Norian age for the mentioned formations, whereas the upper and lower boundaries of the Hassberge Formation are diachronous (Fig. 4).

STUDY AREA

Keuper trace fossils from various localities in Baden-Württemberg and Bavaria have been studied. For an outline map of the study area see Fig. 10. Detailed maps of outcrop positions are given in Appendix III: Detailed locality maps.

TRACE FOSSILS

Explanation of used terms (only the most relevant terms are explained, in general the terms used in this study follow BROMLEY 1996):

burrow – space within sediment occupied and maintained by an animal (BROMLEY 1996).
bioglyph – ornament on a burrow wall produced by the life activity of the occupant (BROMLEY et al. 1984).
mottling – biodeformational structure, which prohibits the identification of an ichnotaxon (TAYLOR et al. 2003).
wall – burrow boundary.
wall-lining/**lining** – material applied to the burrow wall by the occupant or passively accumulated material, which adhered to the wall wile the burrow was open (BROMLEY 1996).
constructed wall-lining – where possible, actively and deliberately formed wall-linings should be distinguished from passive wall-linings; only constructed wall-linings qualify as ichnotaxobases (e.g., pelleted wall-linings in *Spongeliomorpha*, *Gyrolithes* etc.).
passive wall-lining – material adhered to the burrow wall while burrow was open and did not result from active deliberate behaviour; such passive wall-linings do not qualify as ichnotaxobases (e.g., thin clay film in some *Scoyenia*).
ichnotaxobase – recurrent morphological element useful for taxonomic classification.
tunnel – usually cylindrical burrow with two openings.

BIOLOGY AND NOMENCLATURE OF TRACE FOSSILS

Trace fossils, because they are sedimentary structures after all, are somewhat difficult to deal with in a biological sense. Although receiving binominal treatment there are fundamental differences between trace and body fossils. A name in the biological sense is not just a name; rather, it is a particular biological entity with affinities and relationships to other such entities. Sedimentary structures have no such biological background. As a result, a consequent use of a biology-based binominal nomenclature for trace fossils will turn out as a dead end road in the long run. It should become clear that trace fossils are androgynous because trace fossils are simultaneously both biogenic and abiogenic. Thus they need an independent treatment. Currently there is no majority of ichnologists supporting an independent code of ichnological nomenclature. However, in the near future, with more and more problems arising, such an independent code will certainly be tailored and find general acceptance. There is hardly any second discipline in geosciences, which suffers from such an ambivalence than ichnology. Being too sedimentologic for purist zoologists and too biologic for many sedimentologists, ichnology, although meanwhile a well respected discipline, faces typical problems of being neither fish nor fowl.

Science at first glance seems to have to do something with classification. Humans tend to classify anything. In many respects, this is helpful but one should always keep in mind that any classification scheme is an artificial tool helping us to see things apparently clearer. In order to make sure that certain classification schemes are uniformly used we have even invented ratified laws on how to do it. One important set of such rules is the International Code of Zoological Nomenclature (e.g., ICZN 1999). This invention goes back to the style of LINNÉ'S classification (e.g., LINNAEUS 1758). The magic of LINNÉ'S work is the invention of binominal nomenclature; an apparently perfect system for the classification of organisms, and indeed it works very well, if there were not something called ichnology. One may say, no, it does not only work apparently well because trace fossils are not organisms. This statement is not really new but no less true, and important while trying to classify and especially name trace fossils with the help of the ICZN. Maybe someone like SIGMUND FREUD would have been a more suitable person than a natural scientist in order to invent a classification scheme for behaviour. On the other hand, one has to keep in mind that although trace fossils are a reflection of behaviour, they are not behaviour themselves but sedimentary structures resulting from behaviour.

Only rarely can this behaviour be reconstructed exactly. No one has ever observed a trilobite producing a *Cruziana*. There can be no doubt about the fact that nobody ever will. Admittedly it sounds very reasonable that most Palaeozoic *Cruziana* specimens were produced by crawling trilobites although evidence for producers other than trilobites are well documented (e.g., PRATT 1993; HAGADORN & HOLLINGSWORTH 2004). With *Rusophycus* the story becomes even more complicated. For quite a long period common belief was that *Rusophycus* was a resting trace. Among the large variety of *Rusophycus* ichnospecies there certainly exist resting traces but the majority of *Rusophycus* seems better explained as ploughing, feeding or hunting traces, at least something more active than just resting. Anyway, all this is behaviour and is not important for the classification at first glance. A bird is not classified by its way of flying but by anatomical features. No doubt, those anatomical features mostly are closely related to the living habits, but this again is a different story. Anatomy is what counts, not behaviour. What is the anatomy of a trace fossil? That seems to be quite simple: its morphology. Trace fossils are classified by morphology; in fact it is the only reasonable possibility. Trace fossils are made by organisms; they have a morphology, and for morphology we have a classification scheme. This seems to solve all problems. However, the scheme was made for living creatures, and it already is difficult enough to place body fossils into that scheme but it appears to be nearly impossible to fit sedimentologic remains of behaviour into this scheme because it was not meant for this purpose.

Maybe because one of the first systematicists among ichnologists, and certainly one of the most influential ichnologists, WALTER HÄNTZSCHEL, belonged to this rare species of Prussian soldiers full of ideals, in a positive sense, ichnologists have developed a certain kind of stubbornness to become accepted among bioscientists. This finally led ichnology out of the dark anarchy into the light and under the shade of the law of the ICZN – apparently a great victory in the battle of acceptance. After the one and the other additional smaller fights, ichnology has finally made it. In 1999, with the latest and fourth edition of the ICZN, ichnology became fully integrated into the zoological system of nomenclature, irrespective of the fact that actually sedimentary structures are classified. Certainly this framework of rules has led to a broad acceptance of ichnology, and finally this discipline became a strong tool in reconstructing palaeoenvironments. However, this is the applied part of our subject and its success is founded on the often so much hated and dismissed disciplines of nomenclature, taxonomy and systematics. Nomenclature in fact is the only discipline in palaeozoology, which is nearly free of subjectivity. Taxonomy in general is not free of subjectivity, although, the principle of typification helps to minimize this subjectivity. We may not share the same opinion on the behaviour represented by *Rusophycus*, but there can be hardly any discussion on the morphology of the holotype. The value of the certain features we observe is a different story again and very often an unfortunate one. Since ichnology deals with sedimentary structures there are many purely sedimentologic facts that have to be kept in mind while evaluating certain morphological features. At this stage the weakness of the system in use becomes obvious. Zoologists compare their animals or animal remains, respectively, and undoubtedly have evolutionary lineages helping them in evaluating anatomical features much less subjective than ichnologists have to. Certainly, behaviour also evolved over the time, but the evolution of behaviour is by far less helpful in evaluating morphological features for trace fossil taxonomy. Since currently no better concept than the ICZN exists, and even more important, no other legal instrument is available to treat the nomenclature of trace fossils, one has to arrange with the given system. The onus lies with us ichnologists to use this system to the very last consequence and finally to show the weaknesses of this system for trace fossil nomenclature. After such an attempt, which will certainly take another one or two decades, a group of active ichnologists will then have the duty to write up an ichnocode that should be imbedded in the ICZN to guarantee its legal status. However, binominal nomenclature for sediment structures certainly cannot be the last word in this debate.

SUBJECTIVITY IN TAXONOMY

In his meanwhile classic paper, FÜRSICH (1974b) established a system of significant and accessory features for ichnotaxonomy. There can be no doubt that FÜRSICH'S concept bears some kind of subjectivity. However, which system dealing with fossils does not? The best and most logical species definition is that of fertile descendants. Two animals able to produce fertile descendants belong to one species. A brilliant concept, but it is very difficult to apply to fossil material, and often even to recent animals. Body fossils having extant relatives can at least be compared morphologically with their recent counterparts. This certainly helps in establishing more-or-less objective criteria for their taxonomic and systematic treatment. However, even where this possibility exists it seems to be only theoretical and often it is disregarded. If it comes to Mesozoic brachiopods, for instance, the vast majority of rhynchonellids is still classified by exterior shell morphology only although it is well known from studies on recent material that exterior shell morphology among most rhynchonellids is of minor importance (ROWELL & GRANT 1987) – one more example that emphasizes the subjectivity of animal systematics.

The only more-or-less 'natural' unit appears to be the species. All supraspecific classifications only show relationships. Members of a supraspecific rank are not as similar as members of one species. The degree of similarity, or better the relation, differs on the various supraspecific levels of classification. Are members of one genus 90 percent similar, or more, or less? It depends on definition – albeit subjective definition. Such definitions are of course generally based on detailed studies of a group. Even if we were about to define members of one genus as follows: members of one genus must be 90 percent similar, automatically the question arises: 90 percent of what? Is it exterior morphology, interior morphology, or DNA? In modern times DNA seems to be the answer. Analyses of DNA data show that this similarity may be less than once supposed. *Homo sapiens sapiens* differs in less then 3 percent of the genetic code from *Pan troglodytes* subspp. (chimpanzee). Accordingly members of one genus should be more than 97 percent DNA similar. This is certainly no scientific argumentation. Why? There are 'important' genes and 'unimportant' genes, which are responsible for the differences. It is certainly not the simple percentage that counts. However, again this is a subjective decision. We define which gene is important and which not. A truly consequent person may argue that the DNA results proof that man and chimpanzees belong to one genus. On the other hand DNA sequences are so unique, unique as a fingerprint, that each human on this planet can be identified by a DNA sequence, which means that every member of the subspecies *Homo sapiens sapiens* differs in gene sequences.

THE NATURE OF TRACE FOSSILS

When the species concept was introduced it was somewhat similar to the introduction of the atom concept, which was introduced as the smallest physical unit, thought to be indivisible. As history has shown this was a wrong assumption. In analogy to the atom, a species also is no indivisible entity, but nevertheless it is a very useful tool for classification. However, what is an ichnospecies? There is no answer available because no one has yet defined the ichnospecies concept. Binominal nomenclature in ichnology is a historic burden. Most trace fossils were once introduced as fossil remains of animals or plants, and thus received generic and specific names according to the understanding of the particular group to which they were thought to belong (e.g., ‘worms’, sponges, corals, algae etc.). Thus, the morphological similarities to such groups automatically defined our understanding of ichnogenera and ichnospecies.

Not alone do we actually not know what an ichnogenus or ichnospecies is we do not even know what a trace fossil is if it comes to a definition. Hitherto there has been no exact definition of what a trace fossil is. The basic definition in the ICZN (1999) sounds plausible at first glance. A trace fossil is the fossilized work of an animal. This sounds convincing and easy but upon close examination this definition is insufficient. What is ‘fossilized’ and what exactly is the ‘work of an animal’. This also is in need of a definition. A completely bioturbated substrate certainly was the work of an animal (or plant etc.) but cannot be a trace fossil. Soils are the work of organisms but again do not qualify as trace fossils. The point that only trace *fossils* are to be named, and no *recent* traces, is another fundamental difference to body fossils, which are considered to be equal to recent biotaxa. BERTLING et al. (2003) proposed a definition for ‘trace fossil’, which did not find general acceptance among ichnologists and zoologists (e.g., TUBBS 2003). As a consequence GENISE et al. (2004) proposed an emendation of this definition followed by a refinement by BERTLING et al. (2004). Resulting from years of discussion BERTLING et al. (2003) define ‘trace fossil’ as follows: “Morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate”. They also give recommendations for a uniform treatment of trace fossils. Such a uniform treatment of trace fossils, however, appears to be as far away as peace on earth. There are morphological criteria that have to be considered equally among various trace fossil groups, but there also are morphological details that have to be treated differently among various trace fossil groups. SCHLIRF & UCHMAN (in press) discuss this problem at the example of simple, vertical and horizontal tubular burrows. The knowledge about possible producers may help in defining the value of various ichnotaxobases. Thus, the producer relation is very important for ichnologists. In the history of trace fossil treatment there were times when a trace fossil name only was valid when its producer could be identified; an impracticable attempt. It became clear that various widely different morphologies may be produced by one particular animal, as there are also various widely different animals that may produce morphologically identical structures. These facts build the foundation of modern ichnology. As a consequence, trace fossil nomenclature as well as ichnotaxonomy shall be producer-independent, but knowledge about possible producers should affect the evaluation of ichnotaxobases. Data on possible producers help evaluating morphological features according to their significance. This is a long and stony path to travel and open to all kinds of subjectivity.

ICHNOFAMILIES

As stated above, there are certainly useful concepts in the ICZN. However, ichnofamilies seem by far too much. A family is a concept developed for the relationship of organisms. Of course, there also are relationships between trace fossils such as similar behaviour, same or similar producer, similar morphology, same cross-section, same size, etc. A family in the zoological context is a grouping of biologically/phyllogentically related genera and accordingly is usually well defined. One positive example for the use of an ichnofamily concept was shown by GENISE (2004). This author could convincingly show that with terrestrial insect trace fossils such a suprageneric classification may make sense. However, this model is not applicable to marine invertebrate trace fossils. What about an ichnofamily based on U-shaped spreite structures, as an example. As there are no evolutionary lineages and hardly any stratigraphic limitations the resulting ichnofamily will be purely based on morphological criteria. *Rhizocorallium*, *Diplocraterion*, *Phycosiphon*, *Fuersichnus*, *Zoophycos*, to name a few, show U-shaped spreite morphologies. In the case of *Zoophycos* it becomes difficult because U-shaped, J-shaped and mixed forms currently belong to this ichnogenus. By the way: *Zoophycos* is an ichnogenus without a single defined and used ichnospecies! This is a rather strange fact: an ichnogenus without a single ichnospecies.

Other examples are networks. Structures such as the one called *Spongeliomorpha* could be placed in an ichnofamily with *Paleodictyon*. Both show polygonal networks. However, close examination reveals that the structures have not much in common.

If one argues that ichnofamilies are not families in a biological sense, and hence one ichnogenus may belong to more than one ichnofamily, than the question may be allowed, what then are ichnofamilies good for? If one would favour ichnofamilies based on wall-linings it certainly has the same value as an ichnofamily based on general morphology. A wall-lining would at least serve the same purpose in all occurrences, stabilizing the structure, regardless whether this was the primary intention of the producer or not. This is at least something, which is generally accepted of being highly significant in trace fossil taxonomy. Certainly such a concept would put together structures of various morphologies.

Any suprageneric classification should be left open according to the needs of various authors. The history of ichnology taught us that often there are hardly any two ichnologists having the same opinion on one ichnogenus. What then will be the precept for ichnofamilies? If we can hardly agree on ichnogenera, how should we ever be able to agree on ichnofamilies? The authors of the upcoming revised trace fossil Treatise are well advised not to use ichnofamilies. No one would think of building ripple families, although ripples are also sedimentary structures and could be grouped at a higher rank.

For "ordinary" marine trace fossils, UCHMAN (1995) considered an additional formal suprageneric classification as unnecessary ballast. This view is supported here. Systems such as those introduced by FREY (1973) and KSIĄŻKIEWICZ (1977), later modified by UCHMAN (1995), are absolutely sufficient. These authors introduced informal groupings based on general morphological principles such as 'simple straight vertical burrows' or 'meandering structures'. Such basic morphological groups are easy to understand and can be modified according to the needs of each particular author. If an author wishes to emphasize the fact that his form-group should be understood in the same way as a previously used one, an additional comment like '*sensu* author X' clearly expresses this fact. No formal, typified suprageneric hierarchies are necessary. According to the Code (ICZN 1999) ichnofamilies are formally allowed and must be typified. Especially since we still are at the dawn of ichnotaxonomy and ichnosystematics it is not wise to introduce ichnofamilies based on the current understanding of ichnogenera. In addition, many ichnofamilies have already been introduced (e.g., FUCHS 1909; RICHTER 1926; VIALOV 1968, 1972) and have to be varified before new ichnofamilies are introduced. The higher the supraspecific ranks are the more complicated it will be to group trace fossils. It already is very difficult to handle ichnogenera and ichnospecies without having true relationships, and introducing even higher ranks would not improve the situation. Until there is at least a more-or-less uniform concept for ichnospecies and ichnogenera available and accepted, an additional higher systematic rank is almost impossible to define. For a discussion of various ichnofamily concepts see BROMLEY (1996).

PRIORITY OF NAMES

Some remarks are necessary on Article 23 of the ICZN (1999). This article rules the priority of names. The general aim of the ICZN is stability in nomenclature, and thus long-used names should not be abandoned in favour of unknown names. This article also clearly states that if an author recognizes that the use of an older synonym would disturb the universality and stability the case is to be referred to the Commission for a ruling. This guaranties that the case is published in the Bulletin of Zoological Nomenclature and the scientific community has the chance to reply. Proposed older synonyms can be suppressed only if an author can prove that the older synonym has not been used validly in a publication after 1899. In addition, the proposed younger synonym must have been used in 25 publications by at least ten authors over a period of the last 50 years in a period longer than ten years. A name not used validly in a publication after 1899 is considered a *nomen oblitum* (forgotten name). It becomes clear for these exceptions that it is rather difficult to consider a name a *nomen oblitum*. One valid use since 1900 does not amount to much and is easily overlooked. This in fact is the reason why all such cases should be reported to the Commission because who can consider herself or himself as having knowledge about the entire published literature. *Lockeia* JAMES, 1879 was also considered a *nomen oblitum* at first. However, after a short taxonomic note by MAPLES & WEST (1989) and its subsequent use it almost completely replaced the junior synonym *Pelecypodichnus* SEILACHER, 1953. A call of the Commission requires a great deal of effort. However, if an author wishes to suppress a senior synonym, it is the respect we owe to previous workers that demands such efforts.

ICHNOTAXA AND THE ICZN

The fact that the nomenclature of ichnotaxa is ruled by the International Code on Zoological Nomenclature (ICZN) certainly has positive effects and guarantees stability in the use of trace fossil names at least to some respect. The system of typification is one of the most powerful tools and one of the rare cases of pure objectivity in ichnology as for palaeontology in general. A type is a type, as simple as that. However, typification only works if taxonomists stick to type specimens and not to words. *Monocraterion* is a nice example. There is a nearly hopeless debate whether *Monocraterion* and *Skolithos* are synonyms, or not. In fact, this is no real question. One quick look at the type material of both will make it easy for anybody to distinguish these forms. No matter what they actually are: morphologically they are different (Fig. 64) and best kept distinctly separate.

Binominal nomenclature, typification etc. is excellent and undoubtedly the best and most practicable system yet invented. However, this system was invented for animals and not for their behaviour. This is the vulnerability of ichnology. Although the rules of the ICZN only deal with nomenclature, this nomenclature is the fundament on which ichnotaxonomy is built. If the base is weak, the whole building is also weak. In order to prevent this building from collapsing novel and unexpected architectonic constructions are necessary. I have to admit that currently no better system is available. However, a system that was and is made for animals cannot serve as an equally good system for the behaviour of animals. This should lead to a common effort to create a better one.

ICHNOTAXONOMY

As stated above, ichnotaxonomy should be producer-independent. However, there is one particular invertebrate trace fossil group in which producers always played an important role. It is the group of the so-called resting traces. The behavioural pattern represented by resting traces, as already indicated by the name, appears to be the same, resting, and to a certain degree this is correct. One may argue that the action performed by a brittle star to produce a resting trace (e.g., *Heliophycus*) is different from that of a bivalve (e.g., *Lockeia*), and again different from an arthropod (e.g., *Gluckstadtella*, *Tonganoxichnus*). However, in general the ichnotaxobases for distinguishing these forms at the ichnogeneric as well as at the ichnospecific level is nothing else than pure body (producer) morphology. One has to admit that this makes a lot of sense. Such trace fossils are almost as good as body fossils. They tell us a lot about the environment in which they were produced. Nevertheless, this should not affect their taxonomy and/or systematics. Such traces often reveal even more details about the body morphology of the producer than body fossils alone. In the case of *Tonganoxichnus*, a monuran insect resting trace, even appendages can be observed, which usually have a very low preservation potential.

How much should morphologic differences effect the classification of trace fossils? Let’s assume fossil human fingerprints were found, they all differ in their pattern. Were they different ichnospecies? Well, it depends, would be the usual answer. To differentiate between thumb and index finger for instance, seems to make sense. To differentiate between the index finger of individual A and individual B also seems to make sense, but certainly would not justify new names. The final decision on which level these distinctions should be made remains subjective.

EXAMPLES

The following examples should make clear how much substrate consistency influences ichnotaxonomy. If a brittle star rests on a soft substrate the resulting trace will be hardly recognisable. In another example we assume that the sediment was just so cohesive that the general outline of the brittle star was visible. There was no difference in behaviour between the first and the latter case. Exactly the same behaviour in an even more cohesive sediment will create a trace that shows nearly all morphological details of the brittle star, a fine grained sediment taken as prerequisite. In the first two examples one may name the resulting trace fossil *Heliophycus* isp., or even only cf. *Heliophycus* isp. In the third example one could identify the trace fossil as *Heliophycus* new ichnospecies. (see below). These three examples represent the same behaviour by the same producer, but show widely different results. The trace fossils in these examples were not even altered or modified by diagenesis. FORNOS et al. (2002) and MANNING (2004) have shown this for vertebrate tracks. However, trace fossils tell us a lot about substrate conditions. Morphology is the only tool we can use in ichnotaxonomy, there is no DNA, but as shown above, abiogenic facts have more influence on trace fossils than on body fossils (e.g., LUCAS 2001, MACNAUGHTON & PICKERILL 2003).

To which extent should these effects be considered in ichnotaxonomy? Many morphological details can only be observed under specific substrate conditions, e.g., scratch ornaments. Such delicate features can be observed only in fine-grained sediments. Are they therefore irrelevant? Certainly not, but one has to keep in mind their preservation potential while using them. True scratch ornaments are highly useful information and always related to producer behaviour. Scratch ornaments do not form abiogenically. Take a decapod crustacean producing a Y-shaped tunnel system. While burrowing in soft but cohesive medium- to coarse-grained sediment, the resulting wall will most probably neither show any scratch ornaments nor any wall-lining. If the sediment becomes finer-grained and more firm the resulting wall will most probably show scratch ornaments although the general behaviour has not changed at all. This example teaches two very important facts. Scratch ornaments are not absolutely behaviour-dependent and they tell us a lot about sediment cohesiveness. In addition, scratch ornaments can be removed again biogenically. BROMLEY (1967) and ASGAARD et al. (1997) have reported *Spongeliomorpha* burrows with scratch ornaments when newly dug. However, in places inhabited for a longer time period the scratch ornaments were removed again. If present, such features should certainly not be neglected, but they should also not be considered significant at a very high ichnosystematic level as already widely accepted for most trace fossils.

In soft and unstable substrates, irrespective of grain size one would make the following observations. A crustacean (and only certain species) will form pellets and press them into the wall of its burrow in order to stabilize its structure. Hence, the production and incorporation of pellets into a burrow wall appears to show more deliberate behaviour than scratch ornaments. In addition, the preservation of a wall-lining is much less dependent on grain size than are scratch ornaments. As a consequence, scratch ornaments should be less important ichnotaxobases than wall-linings. This concept is already used in the taxonomy of *Palaeophycus* and *Planolites*. Presence or absence of a wall-lining distinguishes these structures at the ichnogeneric level whereas finer details such as scratch ornaments are relevant at the ichnospecific level only (PEMBERTON & FREY 1982). What consequences would such a concept have for the taxonomy and systematic of *Spongeliomorpha*, *Ophiomorpha*, *Thalassinoides* (in the following abbreviated SOT)? *Spongeliomorpha* and *Thalassinoides* would belong to one ichnogenus and *Ophiomorpha* would remain a separate one, but also include forms with smooth wall-lining. Examples from the Upper Jurassic of the Boulonnais (SCHLIRF 2000, 2003) show forms with a smooth lining in *Ophiomorpha*. Does this make sense? Before making a final decision we should not forget the fact that these observations only count for Mesozoic and Cenozoic *Thalassinoides* because Palaeozoic

Thalassinoides were certainly not produced by decapod crustaceans (e.g., MYROW 1995). Thus we cannot be absolutely sure about the value of the ichnotaxobases.

This is a very strong argument in favour of general definitions of ichnotaxobases among certain groups. We have plenty of data on Recent SOT producers, which allow us to evaluate such ichnotaxobases, even though we are sure that in the Palaeozoic other producers were responsible for SOT structures. It would make no sense to treat Palaeozoic SOT differently from modern ones. This is supported by the fact that we do not definitely know the progenitors of Mesozoic SOT, admittedly decapod crustaceans are plausible candidates. However, studies on the deep-sea enteropneust *Stereobalanus canadensis* by ROMANO-WETZEL (1989) and JENSEN (1992) show that these animals also build networks of tubular burrows, which are morphologically very close to *Spongeliomorpha*. SELLWOOD (1971) and BROMLEY & ASGAARD (1972) reported finds of the decapod *Glyphea* in SOT burrows, which seem to prove a crustacean producer origin. However, fish remains also have been found in SOT structures (see BROMLEY 1996), but of course not taken as a prove for a possible fish origin.

The gross morphology is the most important feature we can observe and use. Smaller details, however, can make ichnology a nuisance. It is not immediately easy to understand why. For instance, a conical shaped mound can be more relevant than its ‘negative counterpart’ a funnel. Upon close examination it becomes clear: both structures have a low preservation potential, and thus are poor ichnotaxobases. If one does not find either of the structures associated with a burrow it seems pointless to discuss why. The structures might have been eroded, or were never built. However, there is one major difference between both structures. Funnels, when present, can be produced abiogenically just by currents. A conical mound, by contrast, must be the result of behaviour (see new Ichnogenus 2). Surface structures always have a low preservation potential, but should not be totally neglected. Otherwise, in order to follow a consistent and uniform treatment of all trace fossils, tracks and trackways would have to be neglected as well.

It is generally accepted that *Rhizocorallium* is synonymous with *Glossifungites*. Below, a new classification scheme for U-shaped spreite burrows is presented, which will show that *Glossifungites* is synonymous with *Diplocraterion*. In the Middle Triassic of the Germanic Basin specimens exist in which *Ilmenichnus* (previously assigned to *Rhizocorallium*) is attached to *Spongeliomorpha* (Fig. 77). Hence, they apparently were produced by the same animal, and thus the value of the various ichnotaxobases should be the same. As a consequence, we would either have to separate *Rhizocorallium* into two ichnogenera or we have to synonymise *Spongeliomorpha* and *Thalassinoides*. There are many *Rhizocorallium* specimens with scratch ornaments and many without. Yet, no *Rhizocorallium* with a knobby wall-lining has been reported. There are bedding parallel U-shaped spreite structures with knobby exterior, but the knobs are not the result of pellets pressed into a wall but rather are small cavities which were diagenetically superimposed (Fig. 81). The lack of otherwise knobby exteriors in U-shaped spreite structures may be explained 1) as a collection artefact; 2) the progenitors are unable to produce pellets; or 3) soft substrates are an unsuitable environment for 'U-shaped spreite behaviour'. *Diplocraterion* certainly belongs to this group of trace fossils. Knobby exteriors are unknown. However, smooth and scratched unlined forms can be distinguished from heavily lined forms (e.g., FÜRSICH 1974), which are currently not separated, not even at the ichnospecific level. Following the currently used SOT concept we would have to differentiate at least two ichnogenera for *Diplocraterion* structures; one with and one without wall-lining. What about *Gyrolithes*? Again the producers are similar to SOT and often connected to SOT burrow systems (see BROMLEY & FREY 1974 for numerous references). According to BROMLEY & FREY (1974) there is only one ichnogenus for *Gyrolithes* structures necessary although *Gyrolithes* is known as smooth, as scratched, and as knobby form. Similar traces should be treated equally. As a consequence we either need two ichnogenera for *Gyrolithes* structures or we have to re-arrange SOT. Wall-lining is a very useful tool, because even in fragments wall linings are still recognisable. Maybe this is the reason for their popularity among ichnotaxonomists.

CLASSIFICATION

In the following pages of the systematic ichnology the trace fossils are basically grouped according to the revision work. This is of course not always possible, but it was tried to follow this concept as strictly as possible in order to help the reader to follow the argumentations. The new Ichnogenus 2, for example, is discussed subsequently to *Arenicolites* because the type-ichnospecies hitherto was assigned to *Arenicolites*.

Basically this informal grouping follows SCHLIRF (2000) and UCHMAN (1995) who emended the classification scheme introduced by KSIĄŻKIEWICZ (1977). Their suprageneric classification scheme is based on general morphological patterns of trace fossils. Some authors prefer a strictly alphabetical listing of trace fossils (e.g., FILLION & PICKERILL 1990; JENSEN 1997). Lately ichnofamilies as a grouping tool are revived (e.g., MIKULÁŠ 1992, GENISE 2004). Ichnofamilies are discussed in detail above. I prefer an informal suprageneric grouping, based on general morphology because general morphology is free of interpretation, and thus appears to be the most stable basis. The three general categories of invertebrate trace fossils are borings (and pseudoborings), burrows/trails/tracks/trackways and coprolites (for a detailed discussion why this differentiation should be made see (BERTLING et al. in rev.). The stratinomic classification is that of SEILACHER (1964). The ichnotaxonomy is based on the concept introduced by FÜRSICH (1974b) who distinguished between significant and accessory features. This distinction is based on ethological studies of the trace fossils in order to define the value of particular morphological features (ichnotaxobases). Significant features (related to distinct behaviour) should be used as diagnostic at the ichnogeneric level and accessory features (reflecting minor behavioural changes) should be used as diagnostic at the ichnospecific level. The difficulties of this concept will be discussed by means of various examples, however, it is yet the best tool available.

MATERIAL

The studied material is housed in the collections of the Naturkundemuseum Senckenberg in Frankfurt am Main, acronym SMF, the Staatliches Museum für Naturkunde Stuttgart, acronym SMNS, the Naturkundemuseum Wiesbaden, acronym NMW, and the Institut für Paläontologie der Universität Würzburg, acronym PIW-####, if not otherwise stated.

SYSTEMATIC ICHNOLOGY

BORINGS

Ichnogenus *Anobichnium* LINCK, 1949a

Type ichnospecies: *Anobichnium simile* LINCK, 1949a: 185, fig. 1; by original designation.

1949a	*Anobichnium* n. g. LINCK.
1975	*Anobichnium* LINCK, 1949. – HÄNTZSCHEL: *W*124.

Emended diagnosis: Galleries of small, straight to slightly curved, unbranched or irregularly branched borings, with irregular to circular cross-section; wall smooth; orientation of galleries horizontal with respect to surface; with short, cylindrical openings (vertical with respect to surface) appearing as perforation on surface. Either with passive fill, or filled with small ovoid pellets.

Discussion: Previous diagnoses did not consider the galleries and a possible pelletal fill of *Anobichnium*. SELMEIER (1984) described wood borings from the late Tertiary. He did not assign the borings to a known ichnotaxon but described them informally as borings of *Anobium* sp. Morphologically they belong unequvivocally to *Anobichnium*. Most specimens described by SELMEIER (1984) are filled with faecal pellets of the progenitor. Although among the syntype material a pellet fill could not be identified by LINCK (1949a) a probable pellet fill is mentioned in the diagnosis. All material considered relevant by reviewing authors and information available from paratype material can enter the diagnosis, since the diagnosis should give the most complete information possible.

Anobichnium simile LINCK, 1949a

Not figured

*	1949a	*Anobichnium simile* n. g. n. sp. LINCK: 185, fig. 1-2.
	1975	*A. simile*. – HÄNTZSCHEL: *W*124, fig. 78.5.
	1984	Fraßgänge von *Anobium* sp. – SELMEIER: 22, fig. 7-14.
	1998	?*Anobichnium* isp. – RAJCHEL & UCHMAN: 221, fig. 2-3.

Diagnosis: As for ichnogenus (because of monotypy).

Description: Galleries of small (1-1.5mm in diameter), straight to slightly curved, unbranched or irregularly branched borings, with irregular to circular cross-section; wall smooth; with short, cylindrical to bowl-shaped openings, appearing as perforation on surface.

Discussion: The cylindrical to bowl-shaped openings are interpreted as escape holes of the adults, whereas the galleries are interpreted as feeding structures of the larvae.

From the Triassic *Anobichnium* was only reported once from nonmarine deposits of Thuringia in the original description by LINCK (1949a). RAJCHEL & UCHMAN (1998) described structures from Oligocene deposits, which they related (with restrictions) to *Anobichnium*. LINCK (1949a) pointed out the similarities between the fossil borings and the structures made by the Recent beetle *Anobium pertinax*. However, *Anobium pertinax* is unlikely to be the progenitor of the Triassic material. Triassic *Anobichnium* can be explained as borings of ephemerid (mayfly) larvae living in freshwater (pers. comm. BERTLING).

LINCK (1949a) also described a second form of wood borings occurring in the same wood fragment as *Anobichnium*. The structures are slightly larger (3-3.5mm in diameter), the walls are irregularly annulated, and the terminations often show a 5mm wide circular swelling. LINCK (1949a) compared these structures with the ones made by larvae of the Recent wasps *Sirex* ssp. RAJCHEL & UCHMAN (1998) reported similar structures from the Oligocene and referred them to borings of *Sirex* sp. However, their material lacks a chamber at the termination. Why LINCK (1949a) only named the smaller structures is unknown. Although no additional material has been discovered, *Anobichnium simile* is discussed in order to give a complete revision of hitherto reported Keuper trace fossils. If the specimen with the type material still exists is unknown.

PSEUDO-BORINGS

Ichnogenus new Ichnogenus 1

Type ichnospecies: *Cylindricum gregarium* LINCK, 1949b: pl. 1 fig.2 [= new Ichnogenus 1 new ichnospecies 1.1].

non	1961	*Cylindricum* LINCK 1948 [sic]. – LINCK: 8.
v, pt	1975	*Cylindricum* LINCK, 1949. – HÄNTZSCHEL: *W*57 [only reference to *Cylindricum antiquum* (PLIENINGER) fig. 35.4b; *non* fig. 35.4a = *Skolithos* isp.].

Diagnosis: Smooth, test-tube shaped, unbranched, slightly kink-bent, cylindrical structures, with circular openings and hemispherical terminations, dominantly perpendicular to the grain of the 'woody' substrate. Fill massive.

Derivatio nominis:

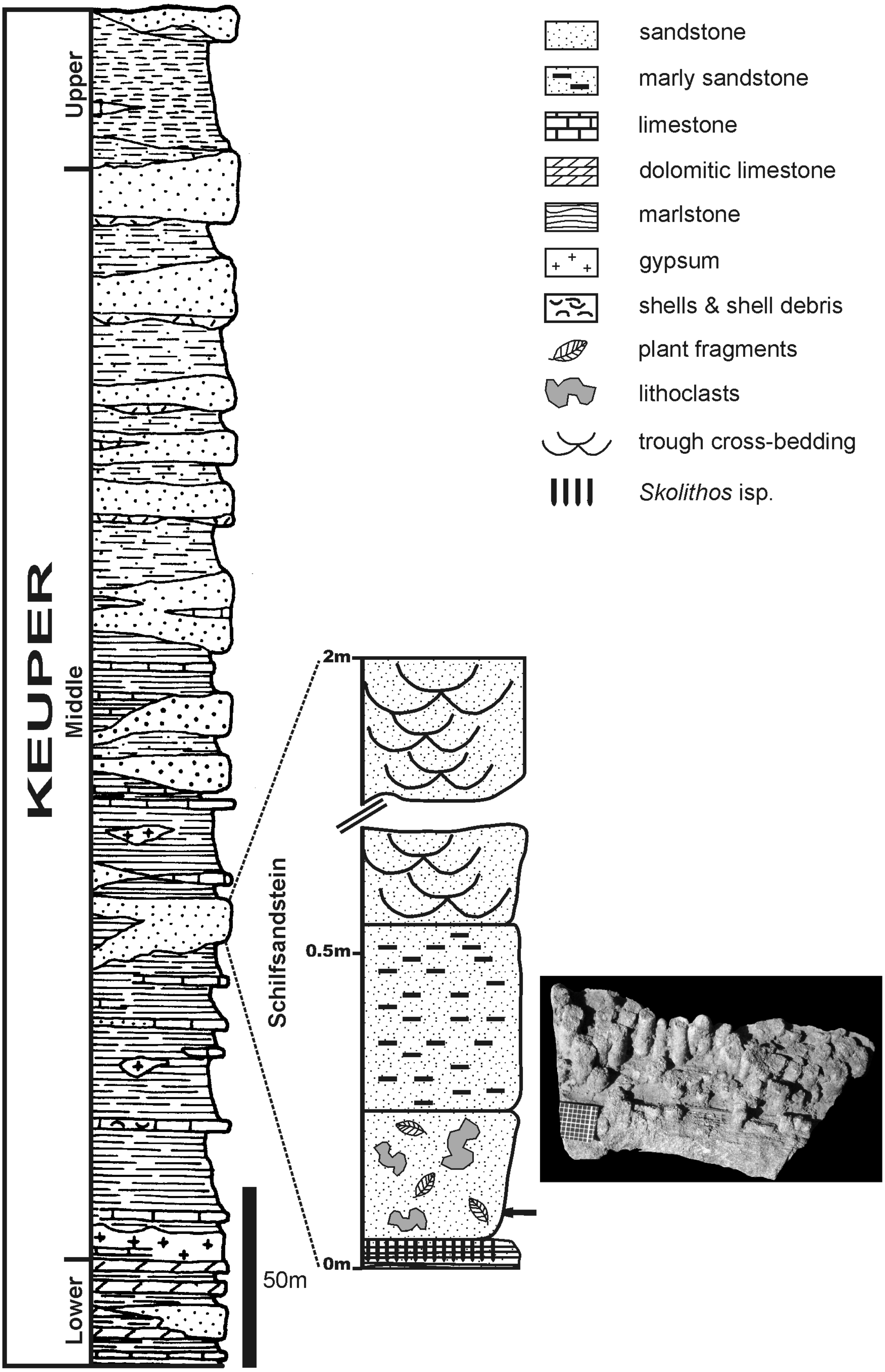

Figure 12: Lithostratigraphic log of the Upper Triassic (Keuper) of the Germanic Basin with a detailed log of the Schilfsandstein, Stuttgart Fm, near Stockheim, Baden-Württemberg, southern Germany. The Schilfsandstein is generally interpreted as deposits of a large delta system extended over the entire Germanic Basin, dominantly

deriving from Fennoscandia. Most of the sediments were deposited under nonmarine conditions. However, marine sediments are also known. Black arrow indicates the position of new Ichnogenus 1 new ichnospecies 1.1 in a plant fragment from the lower part of the section. Millimetre grid for scale in photograph. Log modified after LINCK, 1949b; GEYER & GWINNER, 1986.

Discussion: The structures are referred to borings with reservations only. The substrate in which the trace fossils were formed was not hard wood in a strict sense. Perhaps these structures are penetrating some strengthening tissue analogous to sclerenchyma or collenchyma. The stems of sphenophytes are only poorly lignified compared to trees. However, a classification as burrow would have been even more inappropriate. Certainly, the effort needed and the technique used to build a hole in a sphenophyte stem has something in common with boring. A problem for the classification is that wood in a botanical sense says nothing about its cohesiveness. Wood is just the result of lignification of plant cells. The various cells can be slightly or strongly lignified. As a result there is no strict line between soft/firm plant substrates and hard substrates. Time will show where it is wise to draw a line between borings *sensu stricto* (e.g. in the xylem of trees) and non-borings in softer plant substrates.

There is some confusion about the type material of *Cylindricum gregarium* LINCK, 1949b [= *Skolithos* isp.]. HÄNTZSCHEL (1975) figured one slab with numerous specimens of the type material of LINCK (1949b: pl. 1 fig. 2; Fig 13), which are not, as supposed by LINCK (1949b), burrows in clastic sediment but pseudo-borings in an id. There were good reasons for HÄNTZSCHEL (1975) for choosing this particular slab since it is the slab with the most complete specimens among the material collected by LINCK. LINCK (1949b) considered the specimens as being covered by a plant remain. However, close examination revealed that this specimen shows beautifully preserved borings in a nearly completely weathered sphenophyte stem fragment (Fig. 13). Such phenomena are well known from *Teredolites* borings in completely weathered wood fragments (e.g., KELLY & BROMLEY 1984; UCHMAN 1995; SCHLIRF 2000, 2003b). The test-tube shape with a kink is unknown from other trace fossils occurring in plant substrate. *Teredolites* as described by KELLY & BROMLEY (1984) differs from the proposed new ichnogenus in having a clavate shape and in occurring in true wood substrate. new Ichnogenus 1, by contrast, is cylindrical and occurs in poorly lignified plant substrate. According to BERTLING et al. (see BERTLING et al. in rev.) substrate as such is not a suitable ichnotaxobase, except for the general categories (sediment/rock and plant material, and soft/firm and hard). Because especially plant insect interactions frequently are very specific, even morphologies already known from the sediment/rock record should be kept separate. This can be justified by the fact that plant destruction for feeding, reproduction, or dwelling purposes certainly differs fundamentally from burrowing or boring in sediment/rock. In analogy to sediment/rock, true borings (in true wood) in plants can be distinguished from other feeding, biting, and gnawing structures in soft or firm plant substrates.

new Ichnogenus 1 new ichnospecies 1.1

Fig. 12-13

v, pt	1949b	*Cylindricum gregarium* n. g. n. sp. – LINCK: 19, pl. 1 fig. 2; [*non* pl. 1 fig. 1+3 = *Skolithos* isp.].
non	1961	*Cylindricum antiquum* (PLIEN.) [sic]. – LINCK: 9; [= *Skolithos* cf. *magnus*].
v, pt	1975	*Cylindricum antiquum* (PLIENINGER). – HÄNTZSCHEL: *W*58, fig. 35.4b; [*non* fig. 35.4a = *Skolithos* isp.].

Diagnosis: As for ichnogenus (because of monotypy).

Derivatio nominis:

Material studied: Numerous specimens on slab number SMNS 20956 [syntypes of New Ichnogenus 1 new ichnospecies 1.1 = original of LINCK, 1949b: pl. 1 fig. 2]; in addition, the other material collected by LINCK (1949b) was also studied: SMNS 22011 [holotype of *Cylindricum gregarium* LINCK, 1949b: pl. 1 fig. 1 = *Skolithos* isp.], SMNS 20957 [paratype of *Cylindricum gregarium* LINCK, 1949b: pl. 1 fig. 3 = *Skolithos* isp.].

Description: Smooth, unbranched, slightly kink-bent, cylindrical pseudo-borings, with circular openings and hemispherical terminations. Preserved as full relief in a completely weathered sphenophyte stem fragment. Orientation perpendicular to oblique to the grain of the woody substrate. Length: 4-16mm; width: 2-4mm.

Discussion: New Ichnogenus 1 new ichnospecies 1.1 differs from other ichnotaxa known from woody substrates by its test-tube shape and slight kink-bent.

Maybe the structures represent detritivorous habitation dwellings in an already-dead sphenophyte stem. However, the structures seem a bit too regular for that (pers. comm. CONRAD LABANDEIRA). Since no reaction tissues or other types of callus associated with the structures have been observed it is difficult to make a final statement. The fine-grained sandstone is still too coarse and too strongly weathered to allow such delicate structures to be preserved. Another possibility is that new Ichnogenus 1 new ichnospecies 1.1 are oviposition structures. Typically, oviposition structures are lenticular or ellipsoidal in cross-section, but scars that are rounded in cross section (surface features only) on equisetalean material from the Late Triassic of South Africa have been observed (pers. comm. CONRAD LABANDEIRA).

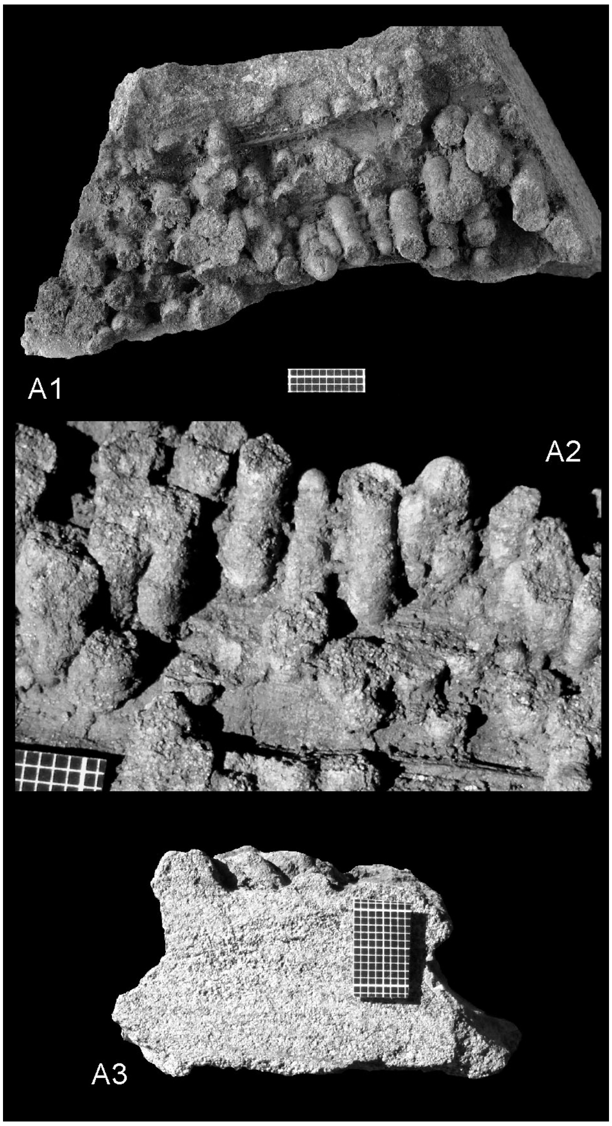

Figure 13: New Ichnogenus 1 new ichnospecies 1.1. **A1**. Syntypes, SMNS 20956, preserved as fullrelief in a completely weathered sphenophyte stem; Schilfsandstein, Stuttgart Fm, near Stockheim, Baden-Württemberg, southern Germany; hemispherical burrow terminations rarely preserved. **A2**. Detail of A1 in different view angle. **A3**. Side view of slab. Millimeter grids for scale.

BURROWS, TRAILS, TRACKS, TRACKWAYS, AND COPROLITES

Simple, horizontal, tubular structures

This form-group includes straight to curved, horizontal to slightly inclined, rarely branched burrows such as *Alcyonidiopsis*, *Halopoa*, *Palaeophycus*, and *Planolites*.

Ichnogenus *Alcyonidiopsis* MASSALONGO, 1856

Type ichnospecies: *Alcyonidiopsis longobardiae* MASSALONGO, 1856: 48, pl. 7 fig. 1-2; by monotypy.

Diagnosis: Straight to winding, seldom branching burrow, with small diameter, filled with small ovoid pellets, less than 1mm in diameter (UCHMAN 1995).

Discussion: *Alcyonidiopsis* is discussed by CHAMBERLAIN (1977), UCHMAN (1995) and SCHLIRF (2000). The stratigraphic range is Ordovician (CHAMBERLAIN 1977) to Miocene (UCHMAN 1995). The herein presented material is the first occurrence of an *Alcyonidiopsis*-related structure in nonmarine sediments.

cf. *Alcyonidiopsis* isp.

Fig. 14

Material: Two specimens on slab PIW-F795, Keuper, no place and no stratigraphical level given.

Description: Two short, up to 28mm long, 3-4mm wide, slightly concave, negative epireliefs, with small, 0.5-1.5mm long, irregularly arranged, ovoid moulds.

Discussion: The two specimens closely resemble *Alcyonidiopsis*. With ‘wrong’ light from lower right, as shown in Fig. 14A2, the pellet nature of the ovoid moulds becomes very clear. The irregularly arranged ovoid pellets are typical of *Alcyonidiopsis*. However, *Alcyonidiopsis* is essentially completely filled with faecal pellets. Due to the preservation of the specimens as negative epireliefs, a pelletal fill could not be proved, and the assignment to *Alcyonidiopsis* isp. is made with restrictions only.

Alcyonidiopsis is generally interpreted as burrow of an infaunal, deposit-feeding polychaete because of the relatively large size of the pellets in contrast to the burrow width (CHAMBERLAIN 1977).

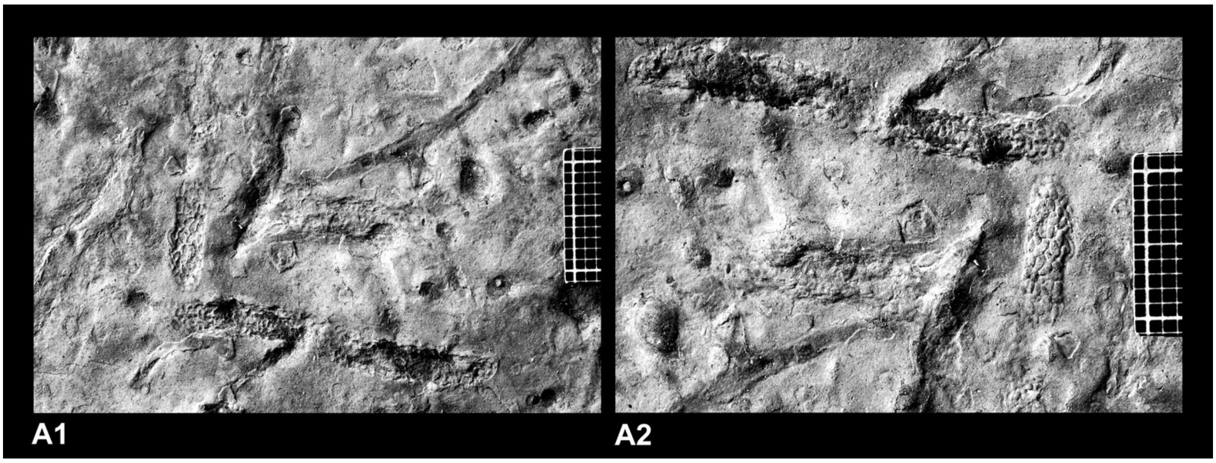

Figure 14: Cf. *Alcyonidiopsis* isp., negative hyporelief, bottom view, PIW-F795. **A1**. Assumed ovoid pelletal fill seen as moulds. **A2**. Same as A1 but slightly enlarged, and with light from right below. Assumed ovoid pelletal fill appearing as positive structures. Millimetre grids for scale.

Ichnogenus *Halopoa* TORELL, 1870

Type ichnospecies: *Halopoa imbricata* TORELL, 1870: 7; by subsequent designation (HÄNTZSCHEL 1975: *W*67).

Diagnosis: Long, generally horizontal trace fossil covered with longitudinal irregular ridges or wrinkles, which are composed of several imperfectly overlapping cylindrical probes (UCHMAN 1998).

Remarks: *Halopoa* has been extensively discussed by JENSEN (1997) and UCHMAN (1998). JENSEN argued that *Halopoa imbricata*, the type ichnospecies of *Halopoa*, was a passively filled tubular burrow, and placed *Halopoa* in synonymy with *Palaeophycus*. JENSEN (1997), among others (e.g., OSGOOD 1970, SEILACHER 1990a, UCHMAN 1998) believed that the striated exterior of *Halopoa* formed when the producer pushed its body through the sediment thus producing fractures, which were then filled with sediment. JENSEN argued that if this was true the striation was nothing else than a reaction of cohesive sediment to burrowing action and not the result of deliberate behaviour. As a consequence he did not consider the striate exterior pattern as an ichnotaxobase at the ichnogeneric level. UCHMAN (1998) stated that there is no indication that *Halopoa* were open burrows, and in addition, *Halopoa imbricata* lacks a wall-lining, typical of *Palaeophycus*. UCHMAN (1998) also interpreted the striation as tension faults, but in contrast to JENSEN (1997), argued that this is a reflection of deliberate behaviour, and thus a suitable ichnotaxobase. JENSEN (1997) is right in stating that the formation and the preservation of such tension cracks depends on sediment consistency, however, this is the case for most morphological features in trace fossils. Fine scratch ornaments can only be preserved in fine-grained sediments and also need sediment of certain stiffness to be produced. *Halopoa imbricata* seems to be a very distinctive form that can be identified without problems, and having a very distinct production history. For this reason the argumentation of UCHMAN (1998) is followed here and *Halopoa* is kept as a separate ichnogenus.

The exterior morphology of *Halopoa* may be mistaken for true scratch ornamentation of other ichnogenera such as *Scoyenia* (exteriorly striated meniscate backfill burrow). For this reason a study of internal structures is absolutely mandatory, especially in poorly preserved material, because otherwise the material may be misidentified. This again may lead to serious misinterpretations of the palaeoenvironment, since *Scoyenia*, for instance, is indicative of nonmarine deposits whereas *Halopoa* may occur in marine as well as nonmarine sediments.

Halopoa imbricata TORELL, 1870

Fig. 15A-E

Diagnosis: Unbranched *Halopoa* with horizontal, relatively long and continuous furrows and wrinkles (UCHMAN 1998).

Material: PIW2002-I-15, 16, 17, 18, 20, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

Description: Straight to gently winding, more-or-less tubular burrows, with very irregular, long ridges and grooves on the exterior; burrow fill massive; width: 2-4mm, length: 2.5-6cm; preserved as positive hyporeliefs or fullreliefs.

Discussion: The described structures show the typical morphology of *Halopoa*, they are relatively straight and have a striated exterior. As discussed above, the striation is interpreted as the result of fracture-building in the sediment while the progenitor was moving forward. No faecal pellets or other distinctive morphological features could be observed to identify the tracemaker. Tension faulting can be explained as result of peristaltic movement of the progenitor, thus making oligochaetes likely candidates for producing *Halopoa* in nonmarine settings. The structures are interpreted as deposit-feeder structures since no signs for an open burrow morphology are present.

Halopoa isp.

Fig. 15E-F

Material: PIW2002-I-6, 20, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

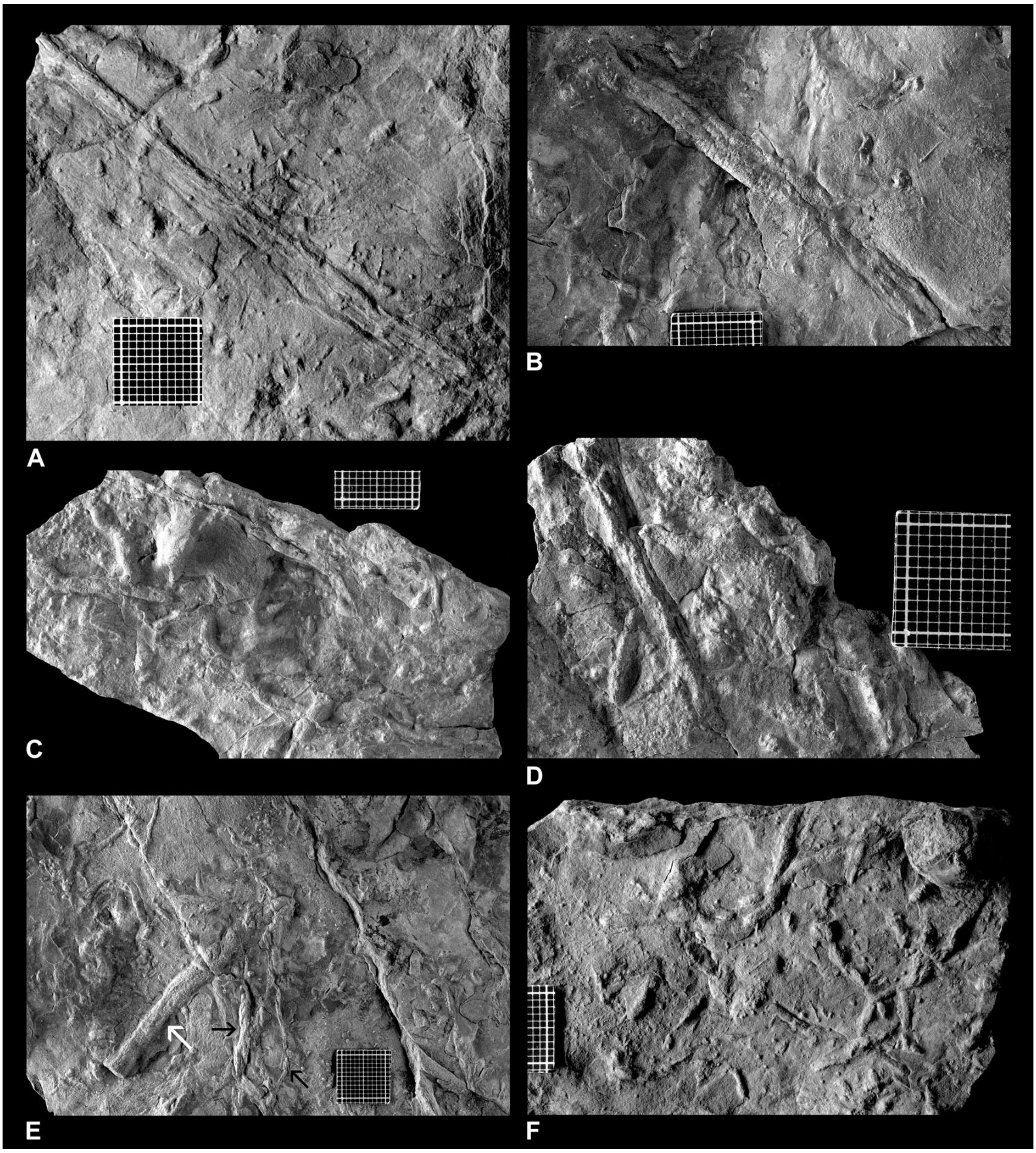

Figure 15: A-D. *Halopoa imbricata* TORELL, 1870. **A**. Straight habitus, and distinct, irregular longitudinal imbrication; PIW2002-I-15. **B**. Straight burrows with nearly smooth section and distinctly imbricated section; PIW2002-I-16. **C**. Small forms; PIW2002-I-17. **D**. Small specimen; PIW2002-I-18 **E**. Black arrows indicate imbricated *H. imbricata*, white arrow indicates almost smooth form of *Halopoa* isp.; PIW2002-I-20. **F**. *Halopoa* isp. Small irregular burrows with indistinct imbrication; PIW2002-I-6. All negative hyporeliefs, bottom view, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany. Millimetre grids for scale.

Description: Straight to very gently curved burrows with irregular striation on the exterior; burrow cross-section elliptical; burrow fill massive; width: 3-4mm, length: 4-7.5cm; preserved as fullrelief.

Discussion: The preservation of the structures does not allow a more precise assignment. The typical striate pattern is not distinct, but since these structures were found in the same beds where *Halopoa imbricata* occurs, an assignment to *Halopoa* seems justified.

Ichnogenus *Palaeophycus* HALL, 1847

Type ichnospecies: *Palaeophycus tubularis* HALL, 1847: 7, pl. 2 figs. 1-2, 4-5; by subsequent designation (MILLER 1889: 130 non BASSLER 1915: 939, see FILLION & PICKERILL 1990 for discussion).

Diagnosis: Straight to slightly curved to slightly undulose or flexuous, smooth or ornamented, typically lined, essentially cylindrical, predominantly horizontal structures interpreted as originally open burrows; burrow-fill typically massive, similar to host rock; where present, bifurcation is not systematic, nor does it result in swelling at the sites of branching (FILLION & PICKERILL 1990).

Palaeophycus striatus HALL, 1852

1959 archaeocyathid. – HAUGHTON: 57, pl. 3-4.
1963 *Archaeichnium haughtoni* n. g. n. sp. – GLAESSNER: 117, pl. 3 figs. 1-2.
1978 *Archaeichnium.* – GLAESSNER: 335, figs. 1-2.
non 2000 cf. *Archaeichnium* sp. – HAGADORN & WAGGONER: 351, fig. 3.5-3.6 (= unidentifiable trace fossil)
2000 *Palaeophycus striatus* HALL, 1852. – SCHLIRF: 153, fig. 7, pl. 1 fig. 5.

Diagnosis: Thinly lined burrows ornamented with fine, continuous, parallel, longitudinal striae (PEMBERTON & FREY 1982).

Discussion: GLAESSNER (1963) introduced a new ichnogenus and ichnospecies based on material previously published by HAUGHTON (1959). HAUGHTON (1959) introduced the material as new archaeocyathids from the Nama Group in Namibia. GLAESSNER (1963) studied gypsum casts of the material and came to the conclusion that these structures must be trace fossils according to their form and the lack of any of the morphological features typical of archaeocyathids. In 1978, GLAESSNER published an article on *Archaeichnium* in which he stated that after re-studying the original material of HAUGHTON (1959) the structures must be interpreted as fossils of unknown systematic position with agglutinated walls. Again, GLAESSNER (1978) was sure that the structures were no archaeocyathids. GLAESSNER (1978) was sure that the walls of the structures were agglutinated. However, he could not discover any organic material, especially no calcite cement that would justify an assignment to the kingdom of animals. The form of the structures, the varying diameters, and the wall-lining can well be explained by burrowing action. Wall-linings as described by GLAESSNER (1978), frequently occur in trace fossils and are a reaction of the trace maker to environmental conditions, in most of the cases to

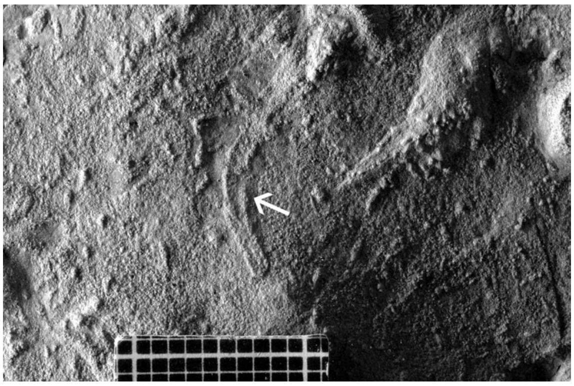

Figure 16: *Palaeophycus* isp. White arrow indicates wall-lining of burrow; PIW2002-I-9, positive hyporelief, bottom view, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany. Millimetre grid for scale.

instable sediment. In the case of *Archaeichnium* and *Palaeophycus striatus* it seems contradictory: On the exterior of these trace fossils longitudinal striations exist. The preservation of such an ornamentation (bioglyphs *sensu* BROMLEY 1990) indicates that the substrate must have had certain stiffness in order to preserve structures like these, thus it seems there was no need for a stabilisation of the burrow. However, the synonymy lists for *P. striatus* presented by PEMBERTON & FREY (1982) and by SCHLIRF (2000) clearly show that such forms are very common. After studying the works of GLAESSNER (1963, 1978), there are hardly any doubts that *Archaeichnium* is a trace fossil. The type material clearly shows a longitudinally striated wall, which exactly fits the diagnosis of *P. striatus*, and is thus considered a subjective junior synonym of the latter. HAGADORN & WAGGONER (2000) described structures from the Vendian-Cambrian of the Great Basin. Their figured material is poorly preserved and allows no assignment to a particular animal- or ichnotaxon, respectively. However, according to the description given by HAGADORN & WAGGONER (2000) it seems most likely that the structures are trace fossils.

Palaeophycus isp.

Fig. 16

Material: One specimen on slab PIW2002-I-9, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

Description: Poorly preserved, lined, short (1.4cm long), narrow (1.5mm wide), curved, positive hyporelief; lining preserved as distinct ridges at burrow margin.

Discussion: Although the material is incomplete and poorly preserved, the wall-lining allows an assignment to *Palaeophycus*.

Palaeophycus is generally interpreted as an open burrow, probably produced by polychaetes (PEMBERTON & FREY 1982). However, in the nonmarine realm polychaetes are unlikely progenitors since they prefer marine to brackish waters. Although only fragmentary preserved, the nature of curving is very smooth and suggests a soft-bodied organism, most likely vermiform. This can be insect larvae or oligochaetes. The structure is best explained as deposit-feeder structure.

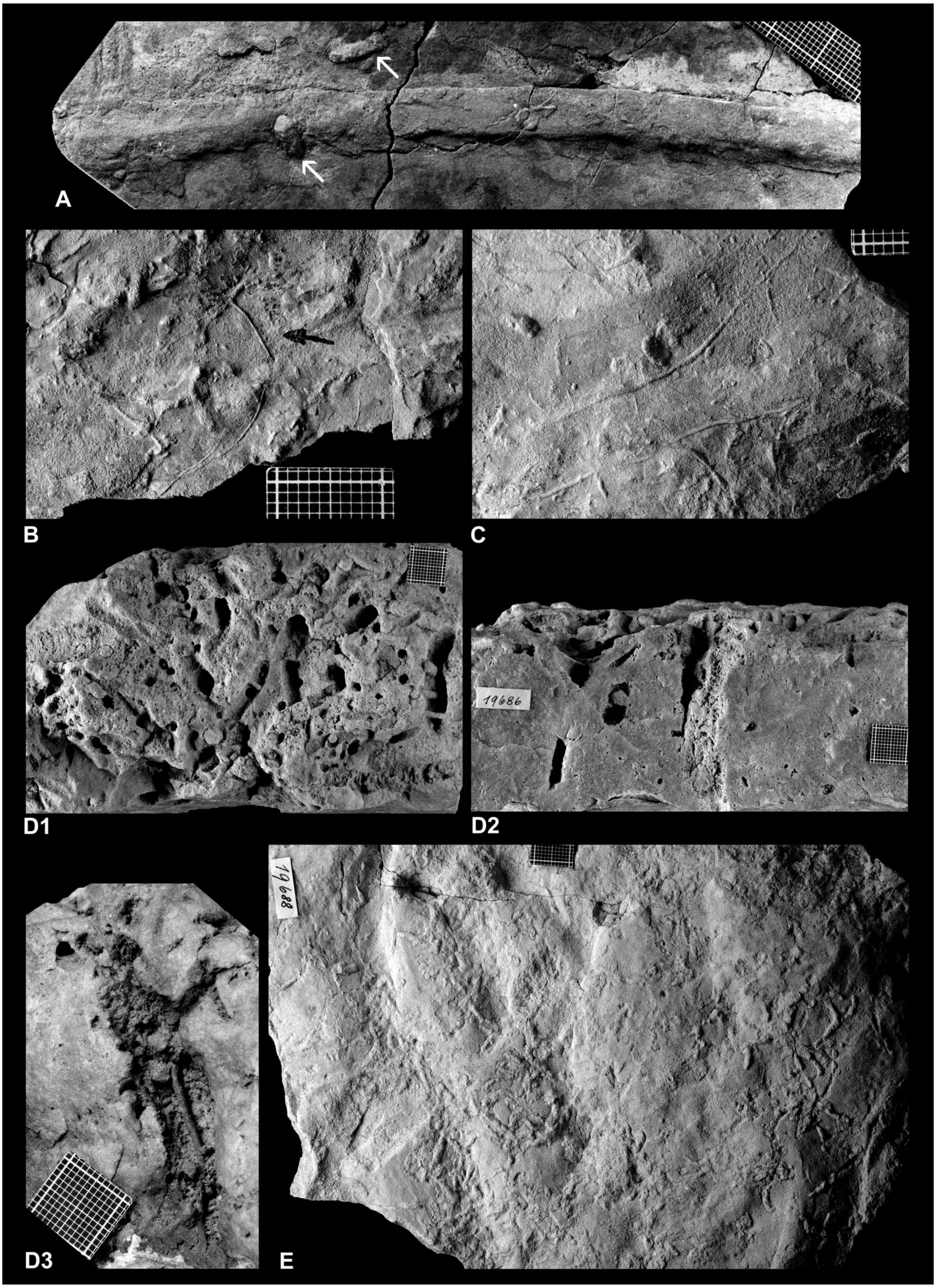

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Figure 17: **A-C**. *Planolites beverleyensis* (BILLINGS, 1862). **A**. Large form; white arrows indicate *P.* cf. *montanus* RICHTER, 1937; PIW1998-VIII-4, Coburger Sandstein, Hassberge Fm, Middle Keuper, Schleifsteinwerke quarry. **B-C**. Small specimens. **B**. PIW2002-I-5. **C**. PIW2002-I-7. Both Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen und Thundorf i. Ufr. **A-C**. Positive hyporeliefs, bottom view; Lower Franconia, Bavaria, southern Germany. **D-E**. *Planolites montanus* RICHTER, 1937. **D**. Large and small representatives, with the latter secondarily burrowing the larger forms, fullreliefs; SMNS 19686, Lower Stubensandstein, Löwenstein Fm, Middle Keuper, Eibensbach am Stromberg. **D1**. Top view. **D2**. Side view. **D3**. Side view. **E**. Small sized representatives, positive epireliefs and fullreliefs, top view; SMNS 19688, Middle Stubensandstein, Löwenstein Fm, Middle Keuper, Ochsenbach am Stromberg. **D-E**. Baden-Württemberg, southern Germany. Millimetre grids for scale.

Ichnogenus *Planolites* NICHOLSON, 1873

Type ichnospecies: *Planolites vulgaris* NICHOLSON & HINDE, 1875: 138-139; by subsequent designation (HOWELL, 1943: 17).

Diagnosis: Unlined, rarely branched, straight to tortuous, smooth to irregularly walled or ornamented, horizontal to slightly inclined burrows, circular to elliptical in cross-section, of variable dimensions and configurations. Burrow fill biogenic, essentially massive differing from host rock; where present, bifurcation is not systematic, nor does it result in swelling at the sites of branching (FILLION & PICKERILL 1990: 48).

Planolites beverleyensis (BILLINGS, 1862)

Fig. 17A-C

Diagnosis: Relatively large, smooth, straight to slightly curved or undulose cylindrical burrows (PEMBERTON & FREY 1982).

Material: One specimen PIW1998VIII-4, Coburger Sandstein, Hassberge Fm, Middle Keuper, Schleifsteinwerke quarry; Several specimens on slabs PIW2002-I-5, 7, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen und Thundorf i. Ufr. All Lower Franconia, Bavaria, southern Germany. Occasional field observations.

Description: Two size classes of *Planolites beverleyensis* occur. Hypichnial, horizontal, slightly curved, thinly lined, smooth, cylindrical burrows, about 1.1cm in diameter and up to 16cm long (size class 1). The second size class consists of very small forms with a width of 0.3-0.5mm in diameter and up to 7cm long.

Discussion: The observed thin lining in the figured specimen is no objection for an assignment to *Planolites*. The lining is very thin and can hardly be interpreted as a stabilization of the burrow. Thin linings may be formed by fine material adhering to a mucous film excreted by the progenitor. The rocks bearing *Planolites beverleyensis* are fine-grained sandstones with high clay content. While burrowing through such a substrate the clay components are brought into suspension and may then easily adhere to a mucous film.

Planolites montanus RICHTER, 1937

Fig. 17D-E, 18A

* 1937 *Planolites montanus* n. sp. RICHTER: 154, fig. 2.
? 1937 *Palaeophycus*-Typ – KUHN: 371, fig. 5.
v 1961 *Planolites* sp. – LINCK: 4, pl. 1, fig. 1
v 1961 *Palaeophycus* sp., kleine Form. – LINCK: 13, pl. 1, fig. 3
v 1961 *Taenidium* sp. Kleine, büschelige Form. – LINCK: 13, pl. 2, fig. 1

Diagnosis: Relatively small, curved to contorted *Planolites* (after PEMBERTON & FREY 1982).

Material: Numerous specimens on slab SMNS 19686, Lower Stubensandstein, Löwenstein Fm, Middle Keuper, Eibensbach am Stromberg; SMNS 19688, Middle Stubensandstein, Löwenstein Fm, Middle Keuper, Ochsenbach am Stromberg. Both Baden-Württemberg, southern Germany.

Description: Variably oriented, undulose, curved, unlined, cylindrical burrows, dominantly with massive fill identical to host rock, subordinately long meniscate packages exist; preserved as full relief or positive epireliefs. Two size classes can be distinguished: (1) large, 9-10mm across, between 4 and 6cm long, SMNS 19686, (2) small, 1-3mm across, between 0.5-5cm long. The small representatives are either found as separate occurrences (SMNS 19688) or occur as secondary burrowers in the large representatives (SMNS 19686).

Discussion: The variably oriented, undulose and curving nature of the burrows fits the diagnosis of *Planolites montanus*. The occasional meniscate fill is no objection for an assignment of the structures to *P. montanus* because *Planolites* is generally interpreted as an actively filled burrow (see below). However, the occasional meniscate fill does not allow an assignment of these structures to *Taenidium*, as supposed by LINCK, 1961. *Taenidium* is essentially dominated by meniscate backfill structures.

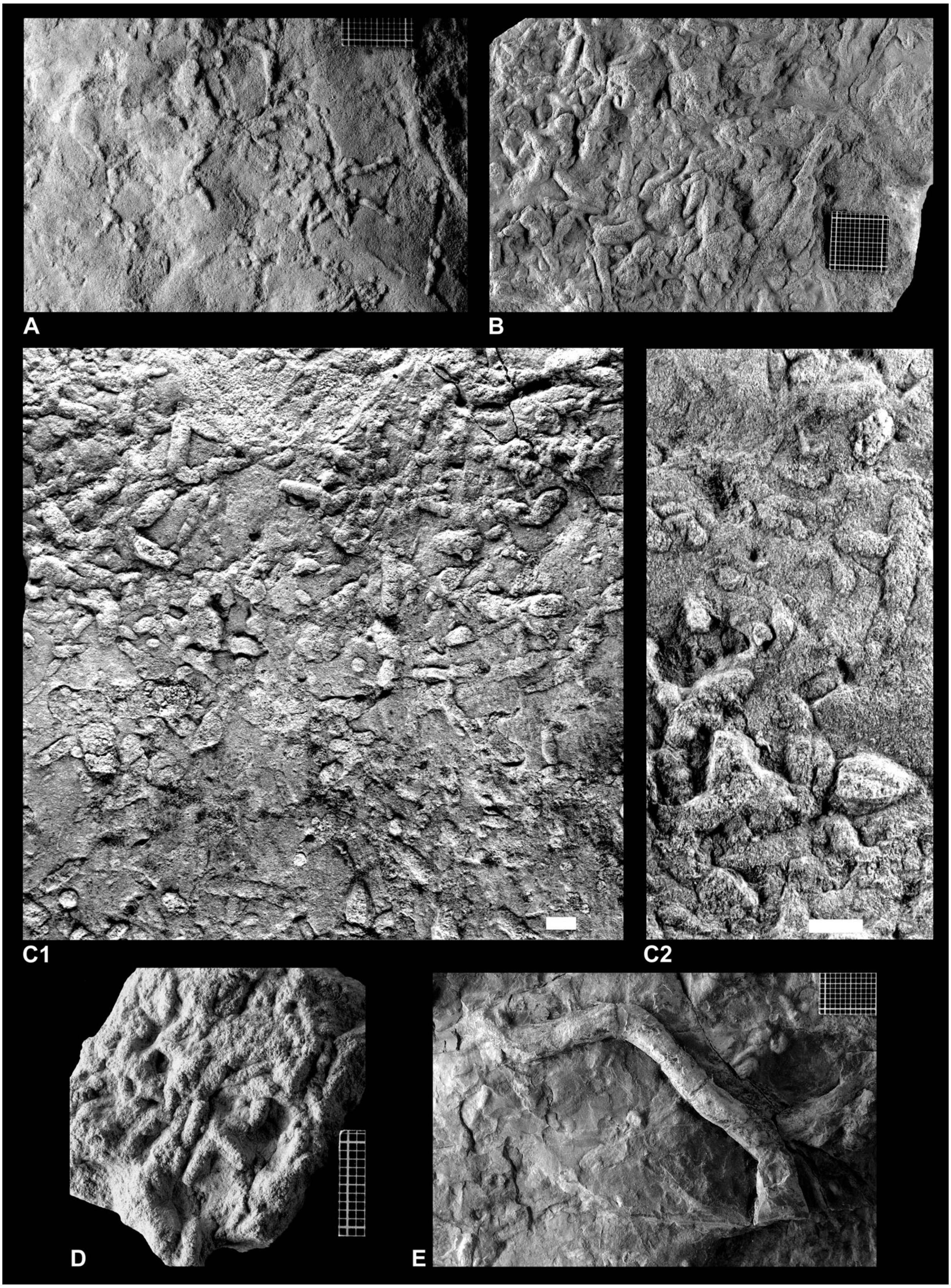


Figure 18: **A**. *Planolites montanus* RICHTER, 1937. Detail of Fig. 4E. **B-D**. *Planolites* cf. *montanus* RICHTER, 1937. **B**. PIW2002-I-32. **C1-2**. PIW1998-VIII-4, Coburger Sandstein, Hassberge Fm, Middle Keuper, Schleifsteinwerke quarry near Eltmann. **C2**. Detail of C1 **D**. PIW2002-I-33, near Effeldorf. **E**. *Planolites* isp.; PIW2002-I-36, between Seubrigshausen und Thundorf i. Ufr. **D-E**. Werksandstein, Würzburg Fm, Lower Keuper. **B-E**. Lower Franconia, Bavaria, southern Germany. All positive epireliefs and fullreliefs, top view. Millimetre grids for scale; scale bars: 1cm.

Planolites cf. *montanus* RICHTER, 1937

Fig. 18B-D

Material: Numerous specimens on slab PIW1998-VIII-4, Coburger Sandstein, Hassberge Fm, Middle Keuper, Schleifsteinwerke quarry near Eltmann; PIW2002-I-32, 33, Werksandstein, Würzburg Fm, Lower Keuper, near Effeldorf, Lower Franconia, Bavaria, southern Germany.

Description: Variably oriented, undulose, short, unlined, cylindrical burrows, preserved as fullreliefs or; 4-7mm across, mostly between 20 and 40mm long. Burrow margins uneven, with local change in width.

Discussion: The overall burrow morphology strongly resembles *Planolites montanus*, however, the uneven surface and changes in size are not typical of *P. montanus*.

cf. *Planolites* isp.

Fig. 18E

Material: Numerous specimens on slabs PIW1998VIII-19, 41 76, 81, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry, Schönbachsmühle and Natursteinwerke quarry, Dörflis. PIW2002-I-36. Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen und Thundorf i. Ufr All Lower Franconia, Bavaria, southern Germany. Numerous field observations.

Description: Short, straight, cylindrical, smooth ridges, either 2mm wide (PIW1998VIII-19) or 15mm wide (PIW1998VIII-41); or slightly winding, horizontal, cylindrical burrows, either 3-4mm wide (Fig. 5E and PIW1998VIII-81) or 6mm wide (PIW1998VIII-76).

Discussion: Preservation of the material does not allow a precise determination.

Planolites is an eurybathic, extremely facies-crossing form referred to vermiform deposit-feeders, which actively backfill their burrows (e.g., PEMBERTON & FREY 1982; FILLION & PICKERILL 1990; UCHMAN 1995). *Planolites* occurs from the Precambrian to the Recent (HÄNTZSCHEL 1975).

Simple, irregularly looping structures and irregular network structures

Ichnogenus *Helminthoidichnites* FITCH, 1850

Type ichnospecies: *Helminthoidichnites tenuis* FITCH, 1850: 868; by subsequent designation (HÄNTZSCHEL 1965: 45).

Diagnosis: Relatively thin, horizontal, irregularly meandering or winding trails with occasional loops (SCHLIRF et al. 2001).

Discussion: In contrast to *Gordia* EMMONS, 1844 in which loops are the most characteristic feature, and to *Helminthopsis* HEER, in which no loops occur (HOFMANN & PATEL 1989) *Helminthoidichnites* FITCH displays occasional loops. A computer simulation of trace fossils showed that the loops in *Helminthoidichnites* are a random pattern, whereas the loops in *Gordia* clearly show non-random signals (HOFMANN 1990). BUATOIS et al. (1998) considered *Helminthoidichnites* as a simple straight to curved structure with no self-overcrossing and no meandering pattern. This view is not supported here. Similar to *Cochlichnus*, *Helminthoidichnites* currently includes surface traces as well as endichnial forms. Distinction between them and relation of *Helminthoidichnites* to *Gordia* is pending a revision.

Helminthoidichnites ranges from the Precambrian (NARBONNE & AITKEN 1990) to the Lower Cretaceous (FREGENAL MARTINÉZ et al. 1995). It is interpreted as grazing trace produced by nematomorphs or insect larvae in marine environments as well as in non-marine environments (BUATOIS et al. 1997).

Helminthoidichnites tenuis FITCH, 1850

Fig. 19A

Diagnosis: As for ichnogenus (because of monotypy).

Material: PIW1998-VIII-75, Coburger Sandstein, Hassberge Formation, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Thin, irregularly winding, epichnial groove, with locally slightly elevated edges; 1mm in diameter.

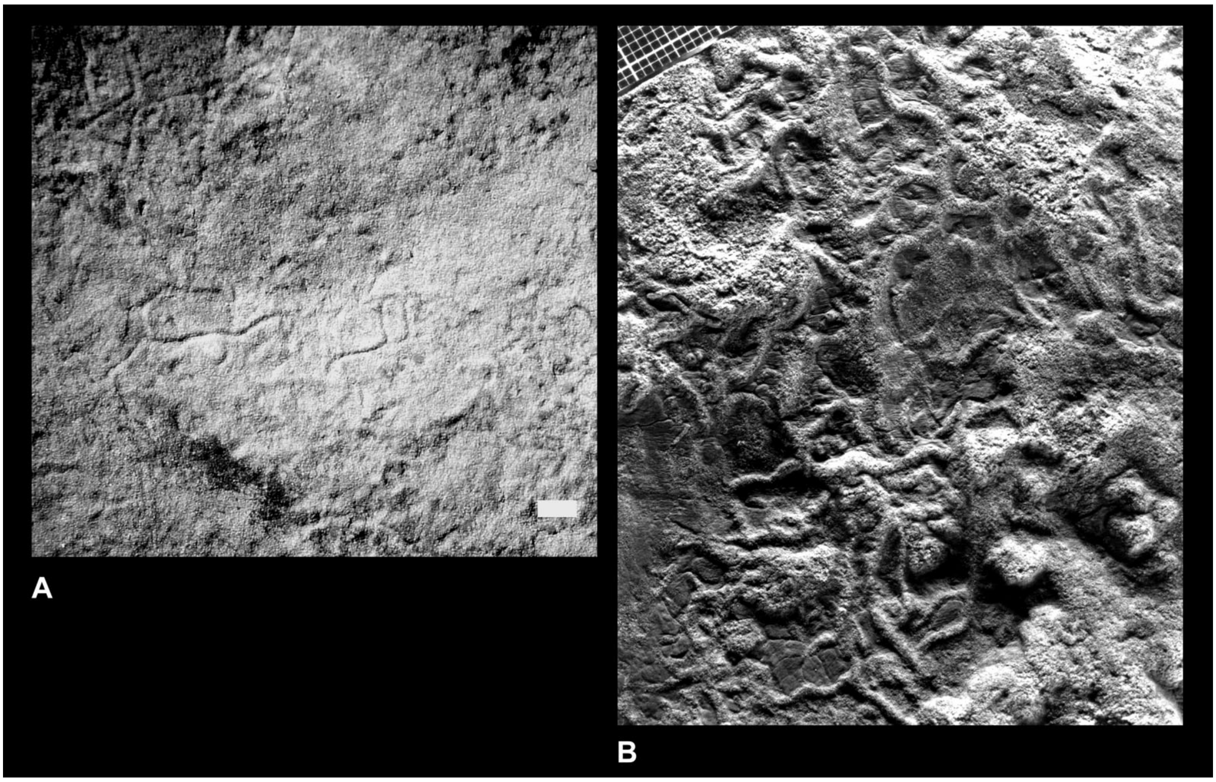


Figure 19: **A**. *Helminthoidichnites tenuis* FITCH, 1850. Negative epirelief, top view; Vetter quarry at Schönbachsmühle, field photograph. Scale bar: 1cm. **B**. cf. *Multina* isp. Positive epirelief/full relief, top view; PIW1998VIII-80; Natursteinwerk quarry near Dörflis. **A-B**. Coburger Sandstein, Hassberge Formation, Middle Keuper, Lower Franconia, Bavaria, southern Germany. Millimetre grid for scale.

Ichnogenus *Multina* ORŁOWSKI, 1968

Type ichnospecies: *Multina magna* ORŁOWSKI, 1968: 197-198, unnumbered fig. on p. 197, pl. 1 fig. 1-2; by original designation.

? 1969 *Pseudopaleodictyon.* – PFEIFFER: 674.
1985 *Olenichnus.* – FEDONKIN: Pl. 23 fig.2.
1995 *Vagorichnus.* – BUATOIS, MÁNGANO, WU & ZHANG: 269.

Diagnosis: Small, cylindrical burrows with meniscate filling structures, forming an irregular, horizontal network, in closely spaced, different levels (vertical distance 0.5-2mm), and locally undulating in the vertical plane. Vertical or oblique burrow parts can be present (SCHLIRF et al. 2001).

Discussion: *Megagrapton* KSIĄŻKIEWICZ, 1968 (see UCHMAN 1998) is referred to horizontal, more-or-less regular polygonal, open burrow systems. Generally it does not display a network of tunnels on different levels and active filling as does *Multina* (see ORŁOWSKI & ŻYLIŃSKA 1996) and its junior synonyms *Olenichnus* and *Vagorichnus*. The same may be true for *Pseudopaleodictyon* PFEIFFER (1969).

Multina is typified by *M. magna* ORŁOWSKI, 1968, found in marine Cambrian deposits of central Poland. *Olenichnus* is described from the Upper Precambrian-Cambrian (FEDONKIN 1985, 1990; JENSEN 1997). *Vagorichnus* was first described from lacustrine Jurassic turbidites in China (BUATOIS et al. 1995). Although the mentioned trace fossils have been recorded from different environments of different ages, their significant diagnostic features, particularly the active filling, are the same. For this reason they are synonymised under the oldest available name, *Multina* ORŁOWSKI 1968. Clarification of how many species belong to *Multina* requires a detailed revision of this ichnotaxon.

Well preserved wrinkle-marks may look very similar to *Multina* or even *Paleodictyon* (regular hexagonal networks). Most probably all reports of nonmarine *Paleodictyon* go back to wrinkle-marks rather than trace fossil origin. Figure 52 shows nice examples of wrinkle-marks that could be mistaken for trace fossils. Upon close examination of polished cross-sections the abiogenic origin becomes clear. However, this example shows that polished cross-sections often are needed to identify structures without doubt.

cf. *Multina* isp.

Fig. 19B

Material: PIW1998VIII-80, Coburger Sandstein, Hassberge Formation, Middle Keuper, Natursteinwerke quarry near Dörflis, Lower Franconia, Bavaria, southern Germany..

Description: Hypichnial, horizontal, irregular, more-or-less polygonal network composed of winding, cylindrical tubes with a diameter of 1.5mm; meshes 5-10mm wide. Occasionally with short ridges and knobs - comparable in size with tubes - associated with the network. The overall morphology strongly resembles *Multina*. However, due to the imperfect preservation and the sparse material a precise classification is impossible.

Discussion: *Vagorichnus* from Jurassic lacustrine turbidites is interpreted as a feeding structure, probably produced by amphipods or isopods (BUATOIS et al. 1995). The same interpretation can be applied to the material described here.

Meniscate backfilled burrows

This form-group includes meniscate backfilled, winding to meandering, horizontal to inclined structures such as *Scoyenia*, *Nereites,* and *Taenidium*.

Ichnogenus *Scoyenia* WHITE, 1929

Type ichnospecies: *Scoyenia gracilis* WHITE, 1929: 115; by monotypy.

Synonym: *Annelidichnium* KUHN, 1937: 368.

Emended diagnosis: Unbranched, unlined, straight to winding, vertical to horizontal, undulose, cylindrical structures with distinct meniscate fill; diameter of burrow slightly variable. Exterior with longitudinal or oblique, straight to slightly curving ridges and grooves. Cross-overs, intersections, or secondary successive branching may occur.

Discussion: The diagnosis provided by FREY et al. (1984) did not consider the orientation of burrows, the absence of branching, and the term ‘wall’ as used by FREY et al. (1984) is misleading, because he did not distinguish between lined and unlined walls. The diagnosis is therefore emended. MARCHÉ (1992) rediscovered material collected and described by HITCHCOCK (1833). He stated that *Fucoides shepardi* HITCHCOCK, 1833 is an older synonym of *Scoyenia gracilis* WHITE, 1929. From the material figured by MARCHÉ (1992) this is difficult to confirm. The material does not show any scratch ornaments on the exterior, diagnostic for *Scoyenia*. Following the currently used classification scheme the material presented by MARCHÉ (1992) is better assigned to *Taenidium* rather than to *Scoyenia*. Any nomenclatural consequences resulting from these rediscoveries need further investigation, which is beyond the scope of this study. MARCHÉ (1992) points out nomenclatural consequences from this situation but referred to a future article to tackle this problem. However, if it at all affects the ichnospecies of *Scoyenia* not the ichnogenus name. *Scoyenia* is the oldest available valid name for these structures and *Fucoides* is not applicable to trace fossils.

Annelidichnium KUHN, 1937 is considered to be a subjective younger synonym of *Scoyenia*. The tubular form and the exterior scratch ornaments are characteristic of *Scoyenia*. If *Annelidichnium* has a meniscate backfill structure cannot be answered because the type material is lost and such features are not visible in the photographs presented by KUHN (1937).

Scoyenia gracilis WHITE, 1929

Fig. 20

* 1929 *Scoyenia gracilis* n.g. et n. sp. WHITE: 115, pl. 4 fig. 3, pl. 5.
1937 *Annelidichnium triassicum* n. g. n. sp. – KUHN: 368, fig. 3.
1984 *Scoyenia gracilis* WHITE, 1929. – FREY et al.: 517, fig. 1B-C, 4A-B.
? 1992 *Fucoides shepardi*. – MARCHÉ: 15, fig. 1A-B, 2-5, 7.
2001 *Scoyenia gracilis* WHITE, 1929. – SCHLIRF et al.: 85, fig. 17A-B.
2001 *Scoyenia beerboweri* ichnosp. nov. – RETALLACK: 215, fig. 5A, 6-8.

Diagnosis: As for ichnogenus (because of monotypy).

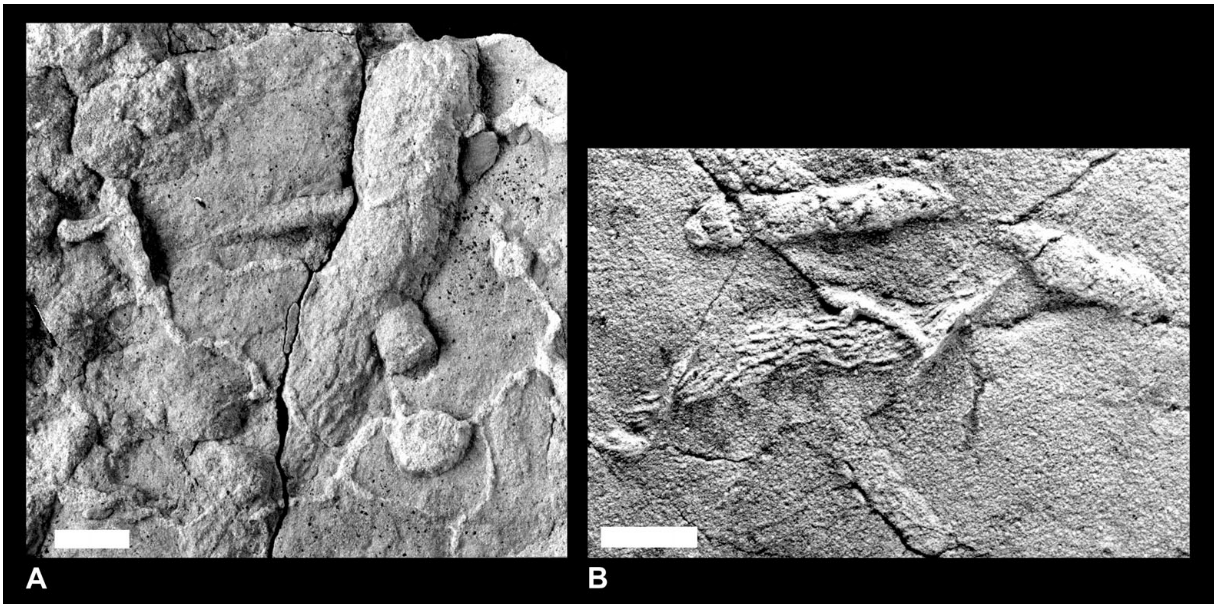


Figure 20: *Scoyenia gracilis* WHITE, 1929. **A**. *Scoyenia gracilis* (sculptured burrow), *Skolithos* isp. A (circular projections); positive epirelief, top view; PIW1998VIII-13A. **B:** *Scoyenia gracilis*. Positive epirelief, top view; PIW1998VIII-19. All Coburger Sandstein Hassberge Fm, Middle Keuper, Natursteinwerk quarry near Dörflis. Lower Franconia, Bavaria, southern Germany. Scale bars: 1cm.

Material: PIW1998VIII-13A-B, 19, 20, Coburger Sandstein, Hassberge Fm, Middle Keuper, Natursteinwerk quarry near Dörflis, Lower Franconia, Bavaria, southern Germany; numerous field observations.

Description: Short, slightly winding, undulose, tubular burrows, semi-circular in cross-section. Some ridges covered with five longitudinal winding, subparallel striae, each about 1mm wide; entire burrows 5-6mm wide and 20-35mm long. Slightly rugose ridges of comparable size, associated with the described form, are probably preservational variants of the same trace fossil.

Discussion: The external striation and the meniscate backfill are characteristic of *Scoyenia*. Although previously revised (e.g., FREY et al. 1984; D'ALESSANDRO & BROMLEY 1987; KEIGHLEY & PICKERILL 1994) a broadly accepted consistent concept for the classification of meniscate burrows is still missing. In order to avoid additional confusion the suggestions for the taxonomic treatment of *Taenidium* by KEIGHLEY & PICKERILL (1994) and *Scoyenia* by FREY et al. (1984) are followed here. The newly proposed ichnospecies, *S. beerboweri* RETALLACK, 2001 is considered a younger synonym of *S. gracilis*. The diagnosis and the figures provided by RETALLACK (2001) do not allow a separation of the material from *S. gracilis*. According to the diagnosis and the figures provided by RETALLACK (2001), the menisici are highly variable. The same is true for the holotype of *Scoyenia gracilis* (FREY et al. 1984). However, the reconstruction drawing by RETALLACK (2001) shows something different. Moreover, a diagnosis that includes the absolute position of a trace fossil in a palaeosol is not acceptable: "…burrows subhorizontal within upper 10cm of palaeosol, below that vertical and penetrating an additional 40cm down into the parent material" (RETALLACK 2001: 216). Host substrate and absolute positions are irrelevant and do not qualify as ichnotaxobases. The thin clay-lining observed in many *Scoyenia* is not considered ichnotaxonomically relevant. As shown by RETALLACK (2001) the clay lining may be present or absent in one particular specimen. The clay-lining is so thin that a deliberate formation by the progenitor seems unlikely. Such thin, non permanent clay-linings are better explained as passively formed due to adhesion of clay to a mucuous film, excreted by the progenitor (BROMLEY 1996). The formation and possible preservation of scratch ornaments is discussed in detail in the SOT section. The ropey external striation of some *Scoyenia* may lead to confusion with the exterior appearance of *Halopoa* (see discussion above).

Scoyenia is regarded as burrow of deposit-feeding organisms in different nonmarine environments, presumably in moist or wet substrates near water bodies, in periodically inundated areas, or in permanent, shallow subaqueous environments. According to BUATOIS & MÁNGANO (2004), *Scoyenia* is indicative of nonmarine firmgrounds. Arthropods are favoured as possible producers, but insects or adult crayfish can be excluded (FREY et al. 1984). *Scoyenia* occurs since the Permian (SCHWAB 1966).

While studying meniscate backfilled trace fossils with external striation (scratch ornaments) *Minichnium* PFEIFFER, 1969 came to the attention of the author and was subsequently revised (SCHLIRF 2002). *Minichnium* has been established based on material from the Kulm (Lower Carboniferous) of Thuringia (Germany). After a restudy of the type material the trace fossil nature of *M. wurzbachensis* can be confirmed. However, due to the poor preservation of the material there are no diagnostic features that would justify a separation at the ichnogeneric and ichnospecific level. Thus, *M. wurzbachensis* is regarded as a *nomen dubium*. Moreover, apart from the original description by PFEIFFER (1969) and the reference by HÄNTZSCHEL (1975) in the second edition of the Treatise Part *W*, *Minichnium* never entered the ichnologic bibliography.

The ichnogenus *Minichnium* PFEIFFER, 1969 is typified by *M. wurzbachensis* PFEIFFER (1969: p. 683, pl. 6 figs. 7-8; text-fig. 3 no. 13, by monotypy; holotype reposited at the Bundesanstalt für Geowissenschaften und Rohstoffe (BGR), Dienstbereich Berlin under the repository number X1851; refigured here Fig. 21A-B). In the following, PFEIFFER's (1969) original description is discussed and put into relation with the type material.

The diagnosis for *Minichnium* as introduced by PFEIFFER (1969; translated from German): *Minichnium* is characterized by relatively robust feeding tunnels, the filling of which consist of sediment particles of host sediment but with distinct bioturbation features. Tunnels not fully straight, in loose touch, spreading somewhat cluster-like from a starting point. Burrows slightly inclined towards the horizontal, dipping from starting point.

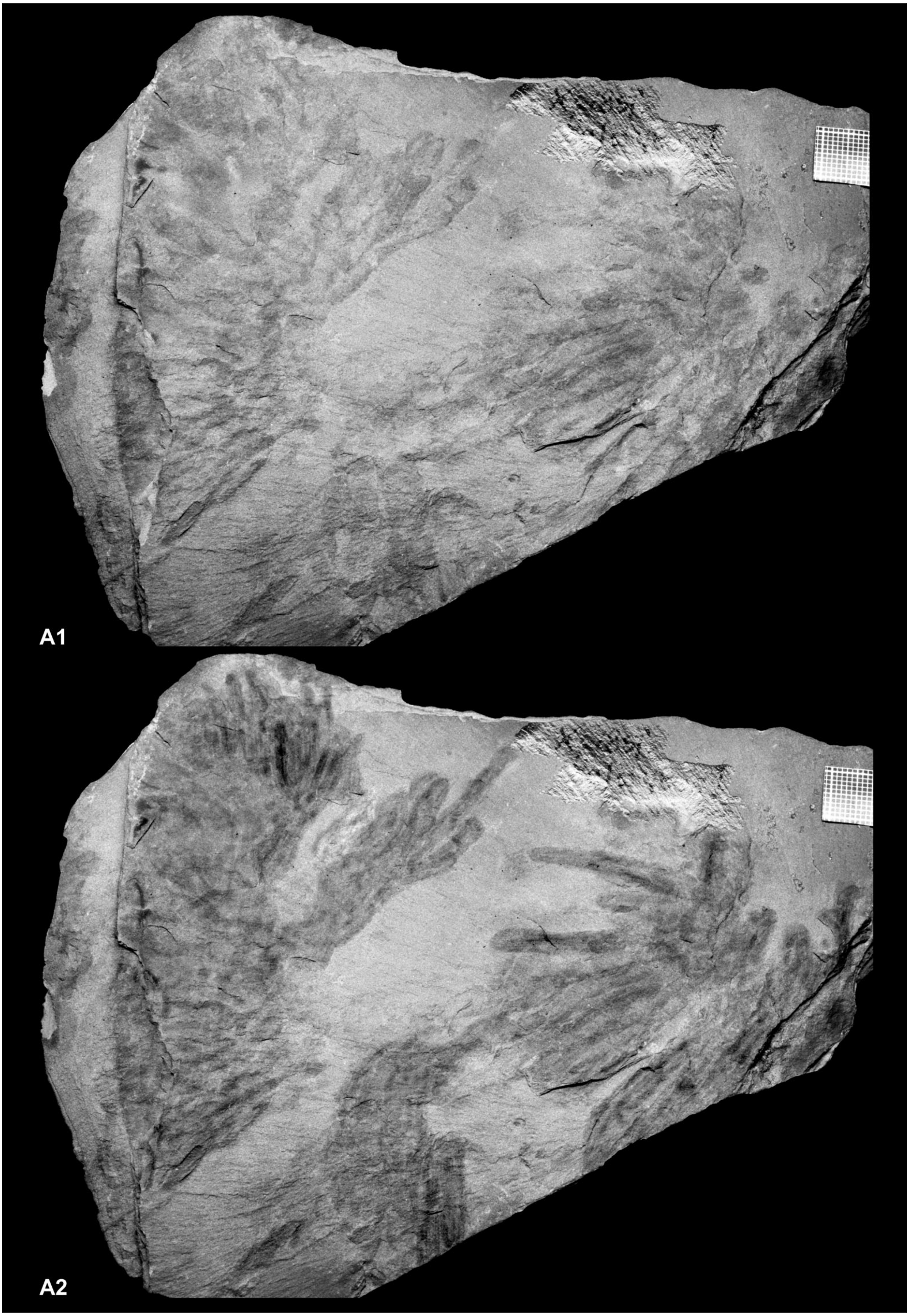


Figure 21: *Minichnium wurzbachensis* PFEIFFER, 1969. **A**. Holotype, X 1851, ordinary photographic reproduction. **B**. Same, but digitally modified in order to improve optical expression of the poorly visible trace fossil. Millimetre grids for scale.

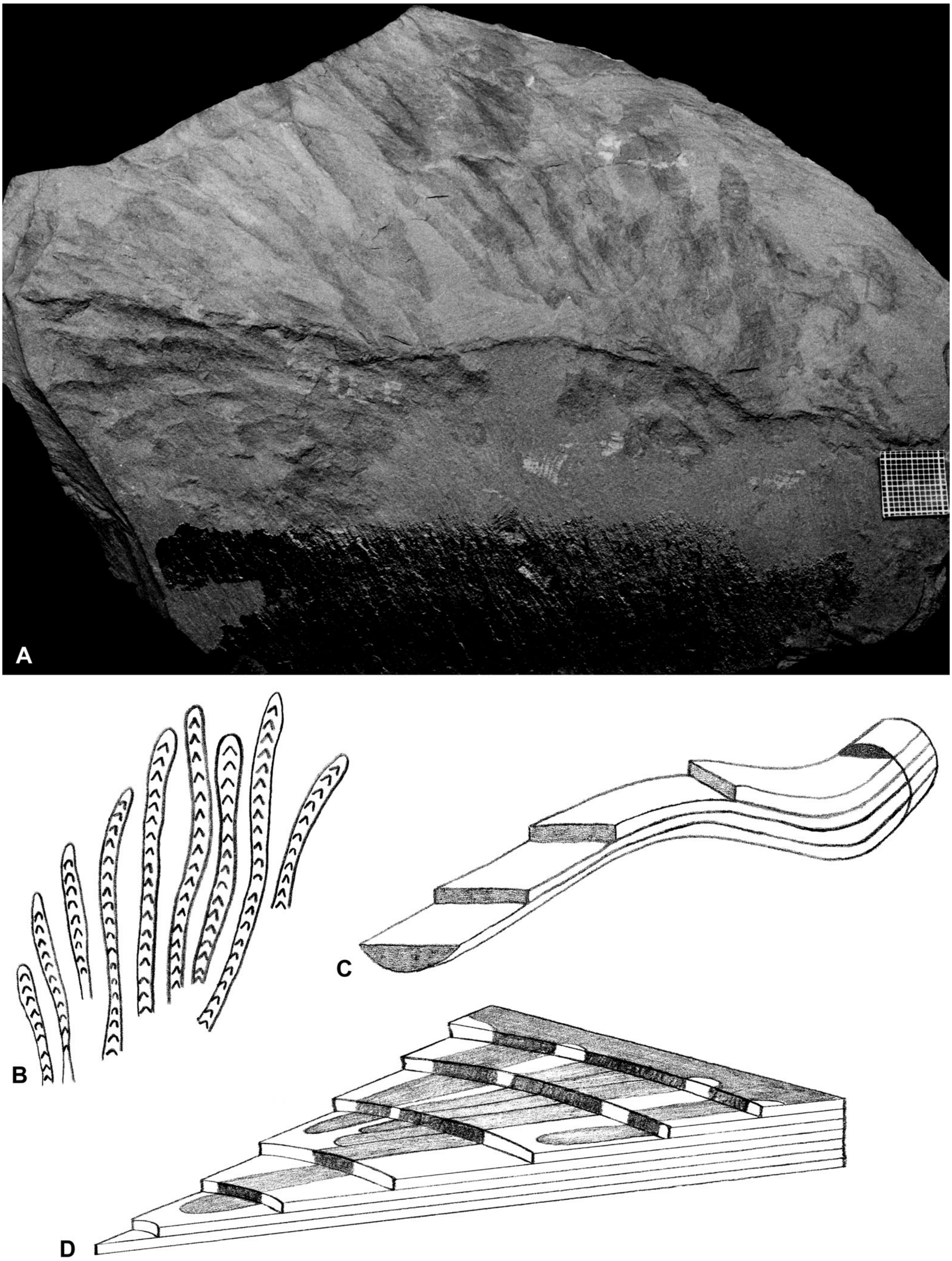


Figure 22: **A**. Paratype of *Minichnium wurzbachensis*, X 1852. Millimetre grid for scale. **B**. Enlarged reproduction of PFEIFFER's reconstruction of *M. wurzbachensis*, showing proposed chevron-shaped internal structures (Fig. 3-13 of PFEIFFER 1969). **C-D**. Sketch showing how the cutting of the cleavage of the sediment (black shales) in which the burrows occur may have produced artificial menisci. **B-D**. Not to scale.

PFEIFFER (1969) assumed a central shaft from which a bundle of tunnels emerged but this central tunnel is missing in the collected specimens and has never been observed. Each tunnel is more-or-less straight and becomes slightly curved towards the end. His reconstruction (Fig. 21B) shows chevron-shaped interior structures that resemble a meniscate burrow fill. While studying the type material these features could not be observed. There are some elements oriented perpendicularly to the long axis of the tubes, but these are artefacts of cutting the cleavage of the sediment (black shales) in which the burrows occur (Fig. 21C, D). Interestingly, the chevron-shaped internal structures were never mentioned by PFEIFFER (1969) in his description of *Minichnium*.

While studying the type material, neither a recurring pattern, nor internal structures, nor any significant diagnostic features could be observed. UCHMAN (1999) described various ichnospecies of *Phymatoderma* from Upper Cretaceous flysch deposits; *Minichnium* slightly resembles these forms. However, *Minichnium* does not offer enough details to justify an assignment to *Phymatoderma*, especially as no pellet-fill, oriented perpendicularly to the long axis of the burrow, could be observed, one of the most diagnostic features of *Phymatoderma*. Given the above reasons, *M. wurzbachensis* PFEIFFER, 1969 is considered a *nomen dubium* and any further use of this ichnotaxon is discouraged. The fact that *Minichnium* actually was never used after its introduction supports this view.

Ichnogenus *Taenidium* HEER, 1877

Type ichnospecies: *Taenidium serpentinum* HEER, 1877: 117, pl. 45 fig. 9, 10B; by subsequent designation (HÄNTZSCHEL, 1962: *W*162).

Diagnosis: Variably oriented, unlined, straight, winding, curved or sinuous, essentially cylindrical, meniscate backfilled trace fossils. Secondary successive branching may occur, but true branching is absent (after KEIGHLEY & PICKERILL 1994).

Discussion: Taxonomic problems of *Taenidium* and related meniscate backfilled burrows, and their formation were discussed in detail by D'ALESSANDRO & BROMLEY (1987), KEIGHLEY & PICKERILL (1994), UCHMAN (1995), and SCHLIRF (2000). In addition to gross morphology and composition of the meniscate packages, the shape of the latter is important for the classification of meniscate backfilled burrows. However, a revision of all meniscate burrows is beyond the scope of this study. Here some observations are given, which might be worth beeing considered by a future reviser. True wall-linings, and the presence or absence of scratch ornaments should be reconsidered concerning their ichnotaxonomic value. Following the herein presented classification scheme for SOT structures, *Scoyenia* and *Taenidium* could be assigned to one ichnogenus since most specimens are only differentiated by presence or absence of scratch ornaments on the exterior.

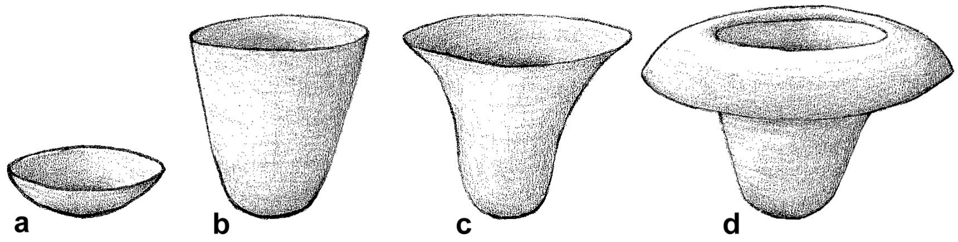


Figure 4: Various shapes of meniscate packages in *Taenidium barretti* (**a-c**); **a** is the typical form of a meniscate package of *T. barretti* in nonmarine environments (also see Fig. 5); **b-d** shows meniscate packages of *T. barretti* from marine Jurassic deposits as reported by SCHLIRF (2000), with **d** showing a sombrero-shaped meniscate package. Not to scale.

Taenidium occurs from the Lower Cambrian (CRIMES et al. 1992) to the ?Quarternary (WETZEL 1983; synonymised by D'ALESSANDRO & BROMLEY 1987).

Taenidium barretti (BRADSHAW, 1981)
Fig. 8, 24A-D

Diagnosis: Straight to variably meandering, unbranched, unwalled, meniscate backfilled burrow. Menisci are commonly hemispherical, deeply arcuate to bell-shaped, tightly packed or stacked, forming non-compartmentalised backfill or thin meniscate segments (SCHLIRF 2000: 182).

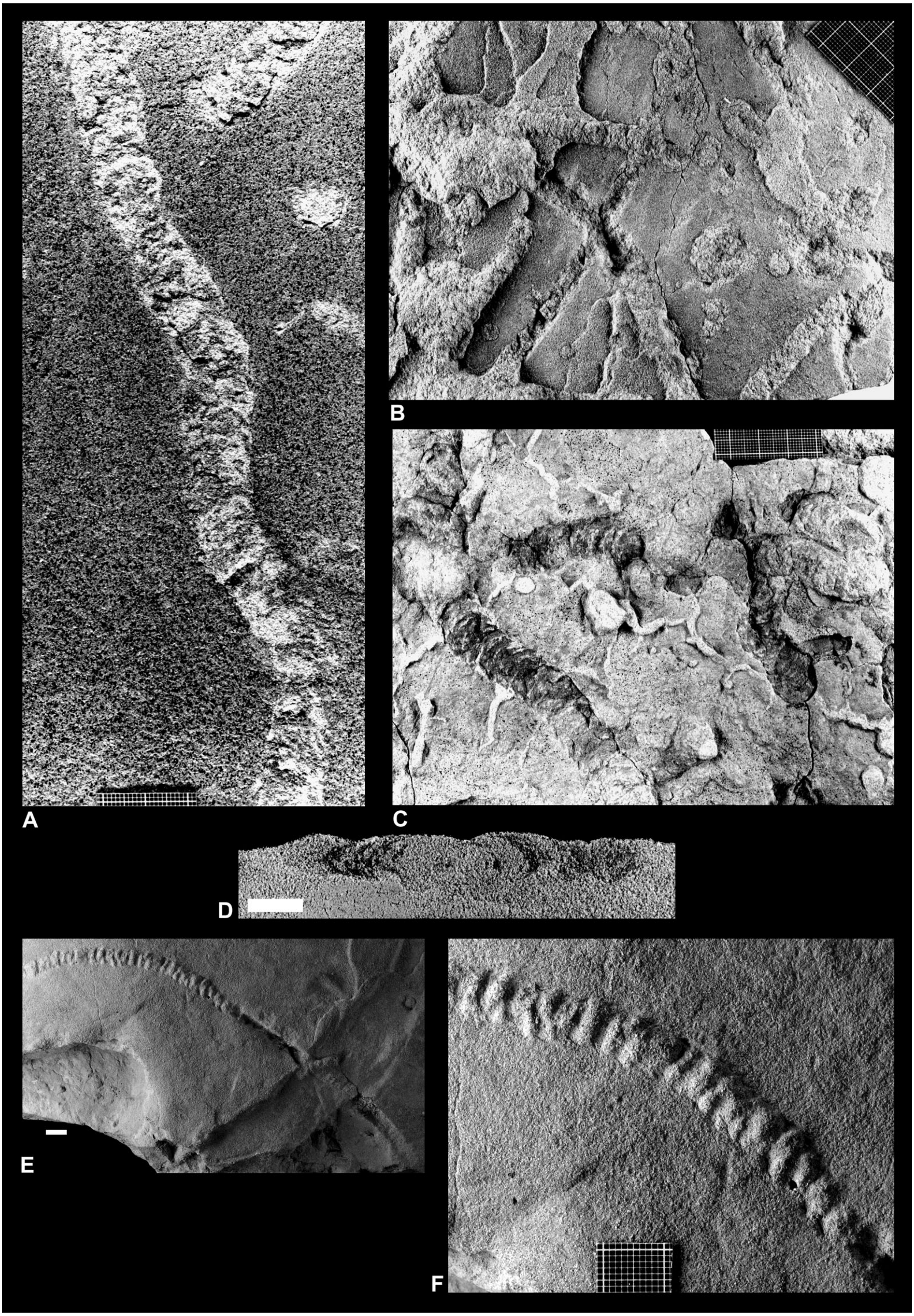
Material: PIW1998VIII-3A-F, 6, 13, Coburger Sandstein, Hassberge Fm, Natursteinwerk quarry near Dörflis; numerous field observations; numerous field observations.

Description: Endichnial, horizontal, oblique to vertical, slightly winding, cylindrical, unlined burrows with meniscate filling, 8-18mm wide and up to 35cm long. Menisci thin, arcuate, locally discontinuous, composed of alternations of fine and coarser-grained sediment. Burrow fill generally finer grained than host rock; number of menisci: about 5 per centimetre. Margin of burrows wavy. Occasionally desiccation cracks crosscut the burrows. In specimen PIW1998VIII-13 burrows crosscut desiccation cracks.

Taenidium barretti is associated with *Skolithos* isp. A.

Next page:

Figure 5: A-D. *Taenidium barretti* (BRADSHAW, 1981); fullrelief. Note heterogenous sedimentary composition of meniscate packages. **A**. PIW1998-VIII-3C, top view. **B**. High burrow density, PIW1998-VIII-6, top view. **C**. PIW1998-VIII-13B, top view **D**. Two specimens crossing each other; PIW1998-VIII-13C, lateral view;



Hassberge Fm, Natursteinwerke quarry near Dörflis. **E-F**. *Taenidium crinoidiforme* LINCK, 1949b. Holotype SMNS19687, Middle Stubensandstein, Löwenstein Fm, near Cleebronn, Baden-Württemberg, southern Germany. Note homogenous material of meniscate packages. **F**. Detail of **E**. Millimetre grids for scale in A-C and F; scale bars: 1cm D-E.

Discussion: Identical trace fossils, described as "horizontal feeding burrows" (= *T. barretti* in KEIGHLEY & PICKERILL 1994) were found in Triassic fluvial red beds of India (MAULIK & CHAUDHURI 1983). These burrows occur in a channel facies, and, like the Franconian material, they are associated with ‘vertical shafts’ (= *Skolithos*).

SQUIRES & ADVOCATE (1984) described *Taenidium barretti* (as ?*Muensteria* isp.) from a Miocene section in California from an environment in which a braided river entered a lake. These authors interpreted the meniscate burrows as traces of infaunal deposit-feeders, probably aquatic oligochaetes.

T. barretti occurs in different nonmarine environments from the Lower Ordovician to the Pleistocene (KEIGHLEY & PICKERILL 1994).

Taenidium crinoidiforme LINCK, 1961

Fig. 24E-F

**v* 1961 *Taenidium crinoidiforme* n. sp. LINCK: 6, pl. 1 fig. 2.
2001 *Taenidium* cf. *serpentinum*. – SCHLIRF et al.: 95, tab. 1.

Emended diagnosis: Straight to curved, unbranched, unlined, cylindrical burrow, with imbricated, serially to alternately arranged menisci; homogenous material of meniscate packages.

Material: Holotype SMNS19687, Middle Stubensandstein, Löwenstein Fm, near Cleebronn.

Description: Straight to curved, unbranched, unlined, cylindrical burrow, with imbricated, serially to alternately arranged menisci; menisci material homogenous. Burrow width: 7-9mm; length: ca. 28cm.

Discussion: The diagnosis provided by LINCK (1961) did not consider the stacking pattern and the arrangement of the menisci, thus the diagnosis is emended. The imbricated stacking pattern of the menisci and the serial and/or alternate arrangement of the menisci distinguish *Taenidium crinoidiforme* LINCK, 1961 from other known ichnospecies of *Taenidium*. For a detailed review of ichnospecies of *Taenidium* see KEIGHLEY & PICKERILL (1994), additional notes on the taxonomy of some ichnospecies of *Taenidium* are provided by SCHLIRF (2000).

In general, the same candidates are relevant progenitors of *Taenidium crinoidiforme* than for *Taenidium* ichnospecies in nonmarine environments. However, the imbricated stacking pattern of the menisci makes soft worm-like progenitors less likely. In order to produce imbricated menisci, an oblique burrowing position of the producer sounds plausible. If the burrowing position was oblique, the progenitor had a short body, because the diameter of *T. crinoidiforme* is small (max. 9mm). The angle of the long axis of each meniscus to the horizontal is approximately 20º, thus the resulting maximum length of a progenitor in an oblique position is 26mm. If each meniscus in *T. crinoidiforme* represents a single excretory event, as assumed for marine *Taenidium* (KEIGHLEY & PICKERILL 1994), is difficult to answer.

Ichnogenus *Nereites* MACLEAY, 1839

Type ichnospecies: *Nereites cambriensis* MACLEAY, 1839: 700, pl. 27 fig. 1; by original designation.

Diagnosis: Usually selectively preserved, winding to regularly meandering, approximately horizontal trails, consisting of median backfilled tunnel enveloped by even to lobate zone of reworked sediment. Generally, only external part of enveloping zone preserved as densely packed chain of uni-serial or multi-serial small depressions or pustules (UCHMAN 1995).

Nereites cf. *jacksoni* EMMONS, 1844

Not Figured

	1961	*Taenidium duplum* n. sp. – LINCK: 7, pl. 3 fig. 1.
?	1982	*Nereites jacksoni* EMMONS 1844. – BENTON: 76, fig. 6c, 6f3.
?, *pt*	1995	*N. jacksoni*. – UCHMAN: fig. 8B; [only 3rd fig. from left in second row].
	2001	unidentified trackways. – SCHLIRF et al.: 95, tab. 1.

Material: Specimen Ic1124, collection of the Geologisch-Paläontologisches Institut der Universität Tübingen.

Description: Horizontal, secondary successively branched negative hyporeliefs consisting of biserially arranged, opponing to alternating, circular or parallel to oblique elongate depressions, separated by a thin median ridge. Burrow width: 13mm; longest section: 55cm.

Discussion: The structures are assigned to *Nereites jacksoni* with restrictions only. Besides a centrally located meniscate backfilled tunnel, an even or lobate envelope zone is characteristic of *Nereites* (UCHMAN 1995). The material studied herein does not show a central meniscate backfill string. Due to preservation, only a biserially lobed envelope part is preserved. According to SEILACHER in LINCK (1961), such structures also occur in the Coconino Sandstone, Arizona, in the Lower Permian (Rotliegendes), Middle Triassic (Buntsandstein) and Upper Triassic (Rhaetic) of Germany.

The structures are probably made by a worm-like sediment-feeder probing the sediment for food, thus constructing the envelope zone and leaving behind a faecal string, represented by the median, meniscate backfilled string (CHAMBERLAIN 1971, SEILACHER 1986).

Simple almond-shaped, series of almond-shaped and club-shaped, and plaited structures

This form-group includes simple trace fossils with round or elliptical outline, preserved as hyporelief, epirelief, or fullrelief such as *Lockeia;* horizontal to inclined, almost straight, winding to meandering plaited burrows such as *Protovirgularia*, *Bolonia*, and *Gyrochorte* also are assigned to this group.

Ichnogenus *Lockeia* JAMES, 1879

Type ichnospecies: *Lockeia siliquaria* JAMES, 1879: 17; by monotypy.

Diagnosis: Bilaterally symmetrical, elongated, commonly almond-shaped, heart-shaped, club-shaped to dumbbell-like or rarely of triangular shape, with smooth margin; predominantly preserved as isolated or row-like arrangements of hypichnial mounds; single segments commonly with a distinct median crest. Vertical spreite may be present (SCHLIRF et al. 2001).

Discussion: Since the diagnoses for *Lockeia* given by RINDSBERG (1994) and SEILACHER & SEILACHER (1994) contain information on the possible producer, substrate, and ethology, they are considered to be too interpretative and thus have been modified by SCHLIRF et al. (2001).

Isolated *Lockeia* is commonly interpreted as a bivalve resting trace most probably produced by a wedge-like foot (SEILACHER & SEILACHER 1994). *Lockeia cunctator* is interpreted as a locomotion trace with a resting or probing component. *Lockeia* in general occurs in marine and non-marine environments since the ?Late Cambrian (FILLION & PICKERILL 1990). However, small crustaceans may have also produced such traces (BROMLEY & ASGAARD 1979; POLLARD 1981).

Lockeia cunctator SCHLIRF & UCHMAN, 2001

Fig. 25A-B

1992 *Treptichnus bifurcus* MILLER. – METZ: 31, fig. 6.

Diagnosis: Horizontal to oblique club-shaped or dumbbell-like to almond-shaped probes more-or-less arranged in a row. Clubs diverge laterally, bilaterally, or semi-radially from main axis of the row; all inclined in the same direction with respect to the row (SCHLIRF et al. 2001).

Material: Holotype PIW1998-VIII-17, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Hypichnial, horizontal, segmented, winding row or cluster composed of dumbbell-like, almond- or wedge-shaped, asymmetric ridges; terminations of ridges hemispherical or drop-like. Each dumbbell structure is 9-10mm long and up to 4.5mm wide. Wedge-like segments display a chevron-like pattern. One segment shows a calyx-like pattern.

Discussion: The club- to almond-shaped probes, arranged in a row, are somewhat transitional to typical isolated, almond-shaped *Lockeia* and the calyx-like segmentation in *Protovirgularia*. *Lockeia cunctator* shows locomotion as well as probing in various directions. The producer stopped at a spot from which it probed the sediment for unknown reasons and then moved on. This pattern is basically different from those of similar trace fossils. The enlargements of the dumbbells probably indicate an expansion of the foot during anchoring. If a single segment of *L. cunctator* is found, it may be confused with other *Lockeia* or *Protovirgularia* ichnospecies.

The chevron pattern, and particularly the calyx-like segment, resemble *Protovirgularia*, which, however, does not display dumbbell-like clubs or almond-shaped segments.

Similar asymmetric traces were produced experimentally as undertracks of the bivalve *Macoma* kept in an aquarium (SEILACHER & SEILACHER 1994: pl. 1 fig. c-d). Especially, the form illustrated in SEILACHER & SEILACHER (1994: pl. 1 fig. c) is very similar to the traces described herein, although *Macoma* is not considered a possible producer of the studied material, since it is a marine bivalve. SEILACHER & SEILACHER (1994) included this form in the resting trace *Lockeia*. However, the studied form is regarded as both pascichnial and cubichnial.

Treptichnus bifurcus described by METZ (1992) from the non-marine deposits of New Jersey, USA, displays a similar pattern, especially with respect to the clubs with enlarged terminations. Therefore, it is regarded as a synonym. However, the type material of *T. bifurcus* MILLER, 1889 does not display these features (BUATOIS & MÁNGANO 1993). It cannot be excluded that at least some *Phycodes curvipalmatus* POLLARD, 1981 belong to *Lockeia cunctator*. However, this problem requires a detailed analysis of hitherto documented *Phycodes curvipalmatus*, which is beyond the scope of this study. Bivalves, probably unionids, are suggested as possible producers of *Lockeia cunctator*.

Lockeia siliquaria JAMES, 1879

Fig. 25C-H

* 1879 *Lockeia siliquaria* JAMES: 17.
1954 *Pelecypodichnus amygdaloides* n. g. n. sp. – SEILACHER: 105, pl. 10 fig. 1, pl. 12 fig. 1-3.
1977 *Pelecypodichnus* sp. – HAKES: 223, pl. 1 fig. d.
1979 *Pelecypodichnus amygdaloides* SEILACHER. – BROMLEY & ASGAARD, p. 46, fig. 5A-C.
1984 *Lockeia siliquaria* JAMES, 1879. – ARCHER & MAPLES: 450, fig. 4D.
? 1984 *Pelecypodichnus elongatus* ichnosp. nov. – YANG: 713, pl. 3 fig. 9; [*nomen nudum*].
1990 *Lockeia avalonensis* ichnosp. nov. – FILLION & PICKERILL: 39, pl. 9 fig. 1-5, pl. 12 fig. 6.
1990a *Pelecypodichnus amygdaloides* SEILACHER 1953. – DAM: 138, fig. 9c.
1990b *Pelecypodichnus amygdaloides*. – DAM: fig. 8.
1994 *Lockeia siliquaria* JAMES 1879. – KIM: 222, fig. 4a, 5.
1994 *Lockeia amygdaloides* (SEILACHER 1953). – KIM: 223, fig. 4b, 6.
1994 *L. triangulichnus* nov. ichnosp. – KIM: 223, fig. 4-C, 5.
1995 *Lockeia siliquaria* JAMES 1879. – METZ: 45, fig. 3b.
For further synonymy see KIM (1994).

Diagnosis: Thin, elongated to stout, generally high-relief, almond-shaped, smooth hypichnial ridges, with strongly arcuate to almost obtuse terminations; occasionally showing vertical spreite (SCHLIRF et al. 2001).

Material: PIW1998-VIII-23, Coburger Sandstein, Hassberge Fm, Middle Keuper, old quarry in Eltmann. PIW1998-VIII-76, 77, 78, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle. PIW2002-I-8, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr. All Lower Franconia, Bavaria, southern Germany.

Description: Smooth, hypichnial, predominantly straight, variously oriented, gregarious, rarely single, almond-shaped mounds elongated in different degree, with pointed or obtuse terminations. Some of the mounds are slightly arcuate or winding. Three size classes can be distinguished: (a) about 26mm long, and about 7 mm across in the widest portion, (b) 5mm long and 2mm across, and (c) 1-3mm long and 0.5-2mm across.

Discussion: Kim (1994) tried to demonstrate the traditional distinction between pointed, more stout *Lockeia amygdaloides* (Seilacher, 1953) and narrower *Lockeia siliquaria* James, 1879. Furthermore, *L. avalonensis* Fillion & Pickerill, 1990 was introduced for relatively stout, but non-pointed forms. However, our material displays all morphological types covered by these ichnospecies on the same slab, including transitional forms. Upon close examination, the Ordovician forms of *L. amygdaloides* and *L. siliquaria* from Korea (Kim 1994: fig. 3, 6) show the same features, as does the material illustrated by Bromley & Asgaard (1979: 47, fig. 5A). Triangular forms of *Lockeia* described by Kim (1994) as *L. triangulichnus* appear to be preservational variants of *L. amygdaloides* instead of a proposed new ichnospecies. Therefore, *L. amygdaloides* (Seilacher, 1953), *L. avalonensis* Fillion & Pickerill, 1990, and *L. triangulichnus* Kim, 1994 are considered junior synonyms of *Lockeia siliquaria* James, 1879. *Lockeia elongata* (Yang, 1984) is considered a *nomen nudum* since no holotype was mentioned and figured.

Lockeia vagans (Książkiewicz, 1977)

Fig. 25I

v	1949	“Einzeilige reihenhöcker-Spur”. – Linck: 66, pl. 8 fig. 1-3.
**pt*	1977	*Tuberculichnus vagans* n. ichnosp. – Książkiewicz: 140, fig. 27 d-e, pl. 13 fig. 4; [*non* fig. 27 c, f-g].
pt	1977	*Tuberculichnus meandrinus* n. ichnosp. – Książkiewicz: 141, pl. 13 fig. 5; [*non* pl. 13 fig. 6 = ?*Saerichnites canadensis*].
?	1994	*Lockeia serialis* n. isp. – Seilacher & Seilacher: 10 [= *nomen nudum*].
	1998	*Protovirgularia vagans* Książkiewicz 1977. – Uchman: 166, fig. 70 A-B.

Diagnosis: Series of smooth almond-shaped, hypichnial ridges, having a strong carinate profile; distance between almond-shaped ridges variable.

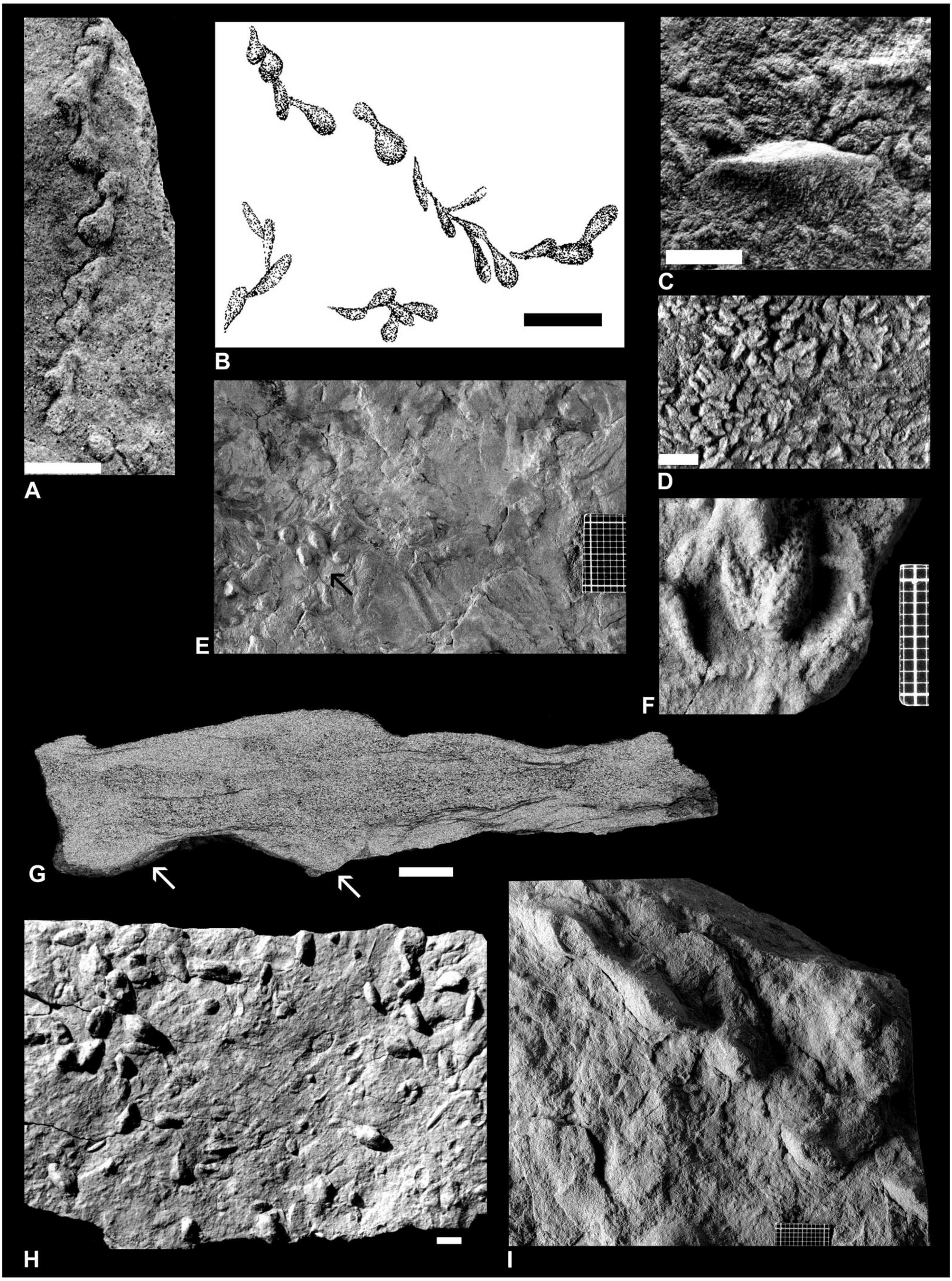


Figure 25: **A**. *Lockeia cunctator* SCHLIRF & UCHMAN, 2001. Positive hyporelief, Vetter quarry at Schönbachsmühle; holotype, PIW1998-VIII-17. **B**. Sketch of *L. cunctator*. **C-H**. *Lockeia siliquaria* JAMES, 1879. **C**. Positive hyporelief, Eltmann quarry; PIW-1998VIII-23. **D**. Dense occurrence, positive hyporeliefs, Vetter quarry at Schönbachsmühle; PIW1998-VIII-76. **A**, **C-D**. Coburger Sandstein, Hassberge Fm, Middle Keuper. **E**. Minute specimens (black arrow), positive hyporeliefs, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr.; PIW2002-I-8. **A**, **C-E**. Lower Franconia, Bavaria, southern Germany. **F**. Positive hyporelief, Rhätsandstein near Erlachsheim; SMNS65494. **G**. White arrows indicate almond-shaped,

polished cross-sections, fullreliefs; SMNS 19528. **H**. Positive hyporeliefs, SMNS65499 Hauptsandstein, Würzburg Fm, Lower Keuper, Epple quarry, Öffingen. **I**. *Lockeia vagans* (KSIĄŻKIEWICZ, 1977), Schilfsandstein, Stuttgart Fm, Middle Keuper, Sternenfels; SMNS 22189. **F-I**. Baden-Württemberg, southern Germany. Millimetre grids for scale; scale bars: 1cm.

Material: One slab SMNS 22189, Schilfsandstein, Stuttgart Fm, Middle Keuper, Sternenfels, Baden-Württemberg, southern Germany.

Description: Series of smooth almond-shaped, hypichnial ridges, having a strong carinate profile with variable distance between almond-shaped ridges.

Discussion: *Tuberculichnus* is typified by *T. vagans*, a trace built by a series of almond-shaped hypichnial mounds, each individual mound strongly resembling *Lockeia siliquaria*. Although *Lockeia* usually is interpreted as a resting trace, the morphology of *Tuberculichnus* much more resembles that of *Lockeia* than that of *Protovirgularia*. In some ichnospecies of *Protovirgularia* such as *P. rugosa*, almond-shaped terminations occur. However, these almond-shaped, *Lockeia*-like elements are only subordinate morphologic features in *Protovirgularia*, which are clearly dominated by a chevron pattern (UCHMAN 1998). Since trace fossil taxonomy is based on the dominating morphology in a structure, forms known as *Tuberculichnus vagans* should be assigned to *Lockeia*. SEILACHER & SEILACHER (1994) designated "Muschelspur" in LINCK 1949b as holotype of *L. serialis*. However, there are neither specimens, illustrations, nor descriptions related to "Muschelspur" in LINCK 1949b and, thus, *L. serialis* is considered a *nomen nudum*.

Ichnogenus *Protovirgularia* MʻCOY, 1850

Type ichnospecies: *Protovirgularia dichotoma* MʻCOY, 1850: 272-273; by monotypy.

1948 undetermined fossil. – BARTRUM: 489, pl. 76 fig. 5-10.
1964 Trace fossil Type F. – BALLANCE: 492, fig. 24.
1969 *Radionereites* gen. nov. – GREGORY: 10.
1975 *Radionereites* GREGORY, 1969. – HÄNTZSCHEL: *W*99.
pt 1998 *Protovirgularia* MCCOY 1850. – UCHMAN: 163.

For additional synonyms see HAN & PICKERILL (1994) and UCHMAN (1998).

Diagnosis: Horizontal or subhorizontal cylindrical trace fossil, trapezoidal, almond-shaped or triangular in cross section, distinctly or indistinctly bilobate. Internal structure, if preserved, formed by successive pads of sediment that may be expressed as ribs on the exterior. Ribs arranged in chevron-shaped, biserial pattern along external or internal dorsal part. Occasionally with smooth mantle on exterior covering the structure and/or with oval mound-like terminations of the trace (UCHMAN 1998: 163).

Remarks: *Protovirgularia* is a much discussed ichnogenus (e.g., HAN & PICKERILL 1994, RINDSBERG 1994, UCHMAN 1998), and various ichnogenera, now considered junior synonyms of *Protovirgularia*, have been introduced so far. The latest detailed revision of *Protovirgularia* and its ichnospecies has been provided by UCHMAN (1998). His concept is followed here, except for the inclusion of *Tuberculichnus* KSIĄŻKIEWICZ, 1977 into *Protovirgularia* (see discussion on *Lockeia vagans*).

Both *Lockeia* and *Protovirgularia* certainly are mainly the work of bivalves, impressively shown by SEILACHER & SEILACHER (1994). Therefore a kind of relation of the both ichnogenera cannot be denied and the occurrence of almond-shaped elements in both ichnogenera corroborates this relation. However, there are also other progenitors known for structures named *Lockeia* and/or *Protovirgularia* (e.g., BROMLEY & ASGAARD 1979, SEILACHER & SEILACHER 1994, SCHLIRF et al. 2001). In addition, the taxonomy of trace fossils should be producer-independent and based on morphology instead.

Protovirgularia dichotoma M'COY, 1850

Fig. 26A-E

Diagnosis: *Protovirgularia* preserved as keel-like axis and paired, lateral, wedge-shaped short appendages or a series of invaginated calices tapering along their length (UCHMAN 1998: 163).

Material: Numerous specimens on one slab, PIW2002-I-27, *Acrodus*-*Corbula*-Horizont (*Acrodus*-*Corbula*-horizon; although the term horizon should not be applied to a series of beds, the traditional name is kept in order to avoid confusion), Grabfeld Fm, Middle Keuper, from the Schwanberg near Kitzingen, Lower Franconia, southern Germany.

Description: Horizontal to subhorizontal, cylindrical to flask-shaped in cross section (Fig. 26C). Made up of successive, inclined pads of sediment, laterally expressed as protuberances (Fig. 26A,B, E); with a median keel-like furrow (Fig. 26B). Occasionally with smooth mantle, surrounding the structures (Fig. 26D). Burrows 1-2cm long and 0.3-0.6cm wide. Preserved as fullreliefs and positive epireliefs.

Discussion: The presented material is an exceptional preservational variant of *Protovirgularia*, the trace fossils are preserved as fullreliefs or positive epireliefs, which makes an assignment to *Protovirgularia* slightly difficult at first glance. Most *Protovirgularia* are preserved as positive hyporeliefs or negative epireliefs. *Protovirgularia longespicata* is known as fullrelief structure (e.g., SEILACHER & SEILACHER 1994). The keel-like median part and the attached protrusions fit the

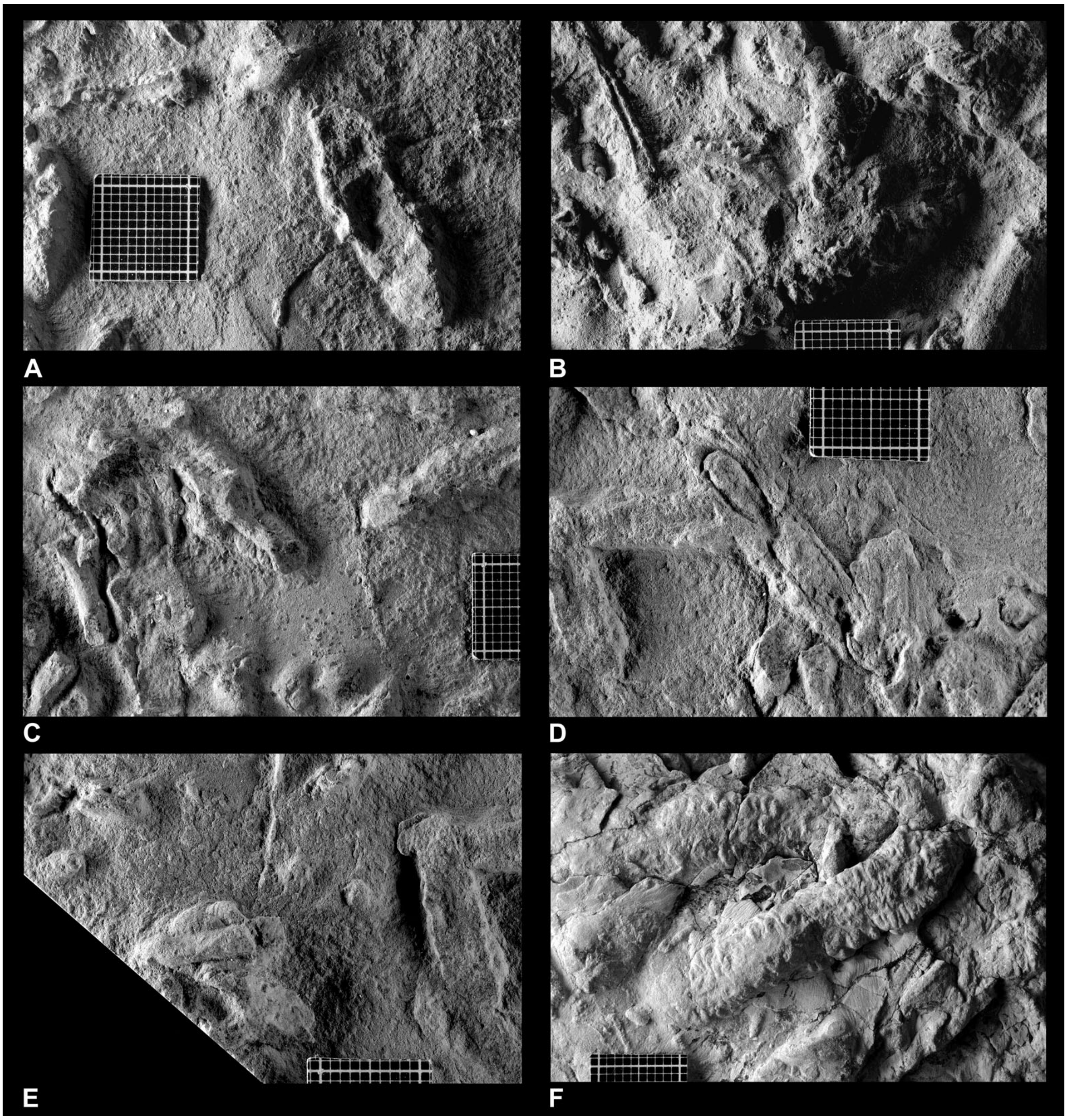


Figure 26: **A-E**. *Protovirgularia dichotoma* MʻCOY, 1850, fullreliefs, positive epireliefs, top view, *Acrodus-Corbula*-Horizont, Grabfeld Fm, Middle Keuper, Schwanberg near Kitzingen, Lower Franconia, southern Germany; PIW2002-I-27. **A**. Inclined pads of sediment appearing as lateral protuberances. **B**. Median, keel-like furrow. **C**. Flask-shaped cross-section; inclined, stacked pads of sediment appearing as lateral protuberances. **D**. Smooth mantle surounding stuctures. **E**. Inclined pads of sediment appearing as lateral protuberances. **F**. *Protovirgularia rugosa* (MILLER & DYER, 1878), positive hyporeliefs, bottom view. SMNS65495, Kieselsandstein, Hassberge Fm, Middle Keuper, Korber Kopf near Korb, Baden-Württemberg, southern Germany. Millimetre grids for scale.

diagnosis of *Protovirgularia* very well. The producer moved along a sand-mud interface, with the mud on top. The anchoring technique used by bivalves results in a horizontal and upward directed shift of sediment. Each individual sediment pad is the result of one anchoring step of the bivalve. The median keel-like furrow was produced by the proximal part of the foot of the bivalve. After weathering of the mud layer, some of the traces now appear as positive epireliefs (Fig. 26A-E).

Radionereites GREGORY, 1969 is also considered a junior synonym of *Protovirgularia*. The single elements of *Radionereites* clearly resemble the dichotomous, chevron-shaped pattern of *Protovirgularia*.

Protovirgularia rugosa (MILLER & DYER, 1878)

Not figured

Emended diagnosis: Commonly short *Protovirgularia* with closely spaced distinct chevron markings; terminated by smooth almond-shaped hypichnial mound, or cylindrical to subcylindrical slightly annulated hypichnial structure.

Discussion: The diagnosis by UCHMAN (1998) contains the name of a particular trace fossil (*Lockeia*) as description of morphological features occurring in *Protovirgularia rugosa*. Such formulations should be avoided. BERTLING et al. (in rev.) recommend the use of descriptive terms only. If a particular trace fossil, especially a very complex form, shows single elements, which could be attributed to a different ichnogenus if found separately, it should be avoided to use the particular ichnogenus name of the 'relative-form'. Such relations should rather be described in the description and discussed in the discussion. Due to the additional information provided and in order to avoid an ichnogenus name as descriptive term, the diagnosis is emended herein.

Protovirgularia cf. *rugosa* (MILLER & DYER, 1878)

Fig. 26F

Material: Three specimens on one slab, SMNS 65495, Kieselsandstein, Hassberge Fm, Middle Keuper, Korber Kopf near Korb, Baden-Württemberg, southern Germany.

Description: Straight, irregularly annulated, 2-4cm long, 0.7-1cm wide positive hyporeliefs.

Discussion: The material is assigned to *Protovirgularia* cf. *rugosa* because the almond-shaped (*Lockeia*) imprint and a truly chevron-shaped pattern is lacking. The specimens rather show an irregular imbrication. However, the general appearance resembles *P. rugosa*. Similar structures, also assigned to *P.* cf. *rugosa*, were reported by FÜRSICH (1998) from the soles of marine tempestites.

As other ichnospecies of *Protovirgularia*, the specimens are interpreted as locomotion traces of bivalves.

Ichnogenus *Bolonia* MEUNIER, 1886

Type ichnospecies: *Bolonia lata* MEUNIER, 1886, p. 567, pl. 15, fig. 8, by monotypy.

1886 *Equihenia.* – MEUNIER: 567.

Remarks: Although hitherto not known from Keuper beds, the taxonomy and ethology of *Bolonia* is discussed here, because *Bolonia* MEUNIER, 1886, frequently occurring in Jurassic marine sediments, has previously been assigned to different ichnogenera such as *Gyrochorte*, *Protovirgularia*, or *Scolicia* (e.g., MAUBEUGE 1965, 1970; FÜRSICH 1974c, 1998; SCHLIRF 2000). In a study of the Upper Jurassic trace fossils from the Boulonnais, SCHLIRF (2000) suggested to make *Bolonia* a valid ichnotaxon again. However, it was not clear then whether the type material collected by MEUNIER still existed. Subsequently, A. LAURIAT-RAGE from the Muséum National d'Histoire Naturelle in Paris communicated that all the collected material of STANISLAS MEUNIER is considered to be missing. Thus, a neotype could be designated and the trace fossil *Bolonia lata* MEUNIER, 1886 was reintroduced on a firm basis by SCHLIRF (2003a). In the following the differences between the above mentioned ichnotaxa and *Bolonia* are discussed.

Diagnosis: Horizontal to subhorizontal, non-branching, straight structures of variable diameter within a single specimen, occasionally tapering at the ends; bilobed, with median furrow; outline of cross-section trapezoidal to heart-shaped with elongate tip, somewhat similar to a gingko leaf. Trace fossil composed of biserial, subtriangular pads of sediment of inconstant thickness; pads inclined towards the bedding plane at an angle of about 30-45°. Top of trace fossil rarely shows an elliptical depression, which is slightly wider than the rest of the burrow, in respect to the long axis, and lacks distinct pads.

Material: Neotype, PIW1996-XI-4, Grès de la Crèche, *Gravesia gigas* Zone, Tithonian, Upper Jurassic, Le Portel, South of Boulogne sur Mer; PIW1996-XI-37 & 46, Grès de Châtillon, *Aulacostephanus eudoxus* Zone, Kimmeridgian, Upper Jurassic, Ambleteuse; Boulonnais, northern France. Besides specimens from the type locality, material from Jurassic deposits from Spain, France, and India has been investigated and the literature reviewed.

Discussion: The general outline of *Bolonia* may resemble that of *Protovirgularia* MʿCOY, 1850 (Fig. 30B), but, in contrast, *Bolonia* has a higher density of pads, a trapezoidal to gingko-leaf-like cross section, and is generally preserved as positive epirelief, although full-relief preservation is also known (see above), that makes it clearly distinguishable from *Protovirgularia*, which is commonly preserved as positive hyporelief and full relief (UCHMAN 1998 and references therein), and shows a more-or-less cylindrical cross section.

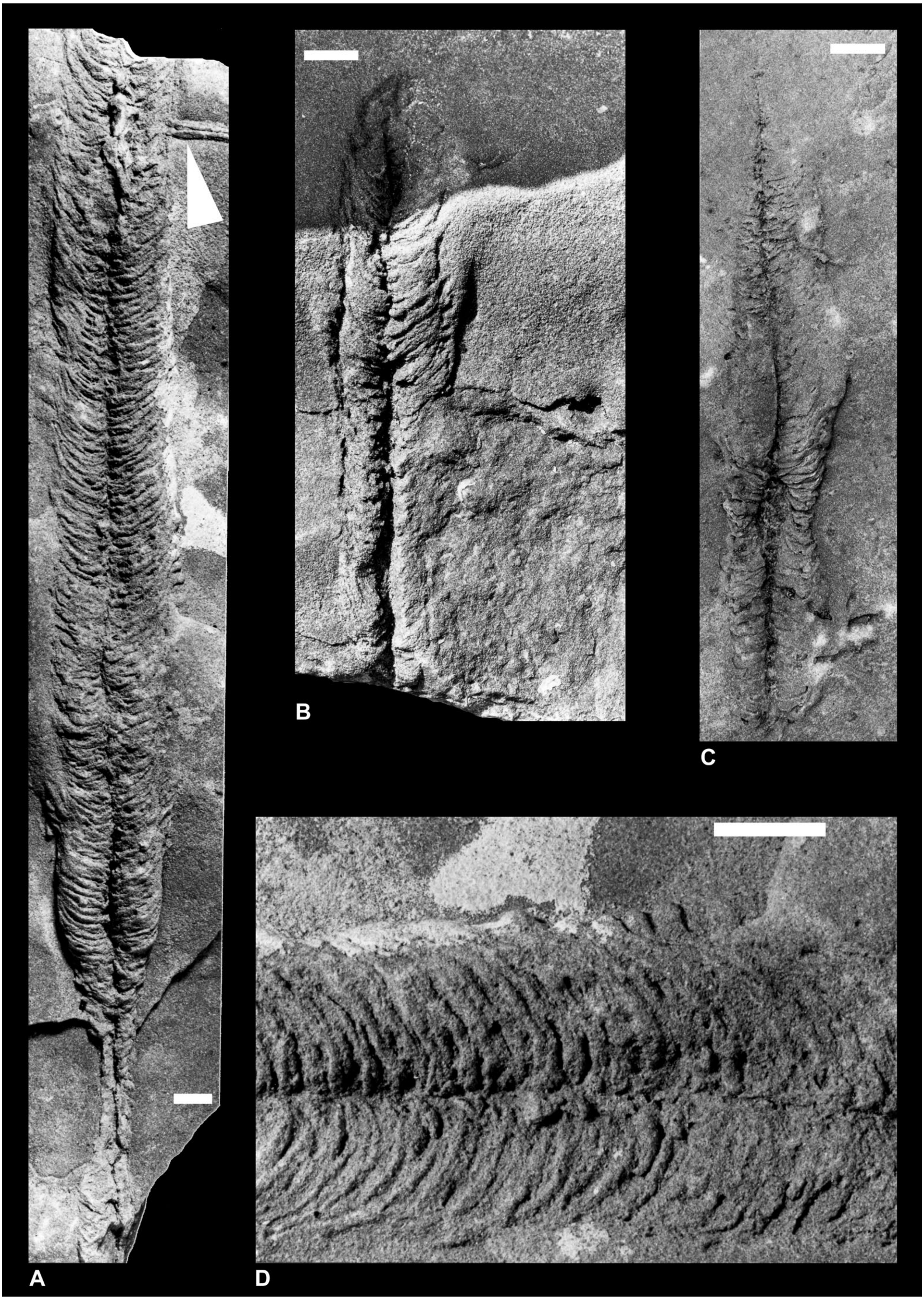


Figure 27: *Bolonia lata* Meunier, 1886. **A**. Neotype, PIW1996-XI-4; top view, positive epirelief, Grès de la Crèche, Le Portel; white arrow indicates the part where *B. lata* cross-cuts *Gyrochorte* isp. **B**. Field photograph; top view, positive epirelief, Grès de la Crèche, Le Portel. **C**. Field photograph, showing the rarely observed oval depression without distinct pads in the middle of the trace, top view, positive epirelief, Grès de Châtillon,

Ambleteuse. **D**. Detail of neotype, PIW1996-XI-4, top view, positive epirelief, Grès de la Crèche, Le Portel. **A-D**. Upper Jurassic, Boulonnais, northern France. Scale bars: 1cm.

In bedding plane preservation *Gyrochorte* HEER, 1865 is similar to *Bolonia*, especially as epichnial ridges. In *Gyrochorte* the pads are usually arranged in a zipper-like pattern and the ratio of the vertical extension compared to the diameter in true *Gyrochorte* is much higher than in *Bolonia*, what means *Gyrochorte* is more like a wall structure (HEINBERG 1973). Although size is not suitable as a sole ichnotaxobase, *Gyrochorte* is generally relatively small (maximum 1.5cm in width), whereas *Bolonia* is usually wider than 2cm (SCHLIRF 2000 and references therein).

Scolicia DE QUATREFAGES, 1849 is another structure to which *Bolonia* has been assigned, e.g., by FÜRSICH (1974c), BUCKMAN (1992), and with uncertainty by HÄNTZSCHEL (1975). After detailed revision of *Scolicia* by UCHMAN (1995) the ichnogenus is well understood and can clearly be distinguished from *Bolonia*. *Scolicia* (Fig. 30D) is characterized as a meandering, bilobate or trilobate burrow with two parallel strings of sediment along the lower side and a suboval outline of its cross-section, which clearly differentiates it from *Bolonia*.

Another similar trace fossil is *Bichordites* PLAZIAT & MAHMOUDI, 1988 (*emend.* UCHMAN, 1995). However, it is only a part of the complete structure of *Bichordites* that is similar to *Bolonia*: the interior, bilobed part that occasionally has a heart-shaped but predominantly oval outline in cross-section (PICKERILL et al. 1993: fig. 2). This burrow can be confused with *Bolonia* at first glance, but upon close examination differences among the two trace fossils can be observed. The inner part of *Bichordites* is rarely heart-shaped and in its upper part more often shows a ridge rather than a groove, which is typical of *Bolonia*. Although size alone is no valid ichnotaxobase, the interior part of *Bichordites* is consistently smaller (about 1cm in diameter) than that of *Bolonia* (about 2-3cm in diameter). In addition, so far none of the workers describing *Bolonia* has mentioned a surrounding structure or a halo of reworked sediment and/or an association of *Bolonia* with *'Laminites'*, which is a preservational variant of *Scolicia* (*sensu* UCHMAN 1995) and other trace fossils. On the slab with the neotype of *B. lata* (PIW1996XI-4), another trace, *Gyrochorte* isp., is cross-cut by *Bolonia*. If *Bolonia* were the inner part of *Bichordites*, there should be a backfill of reworked sediment surrounding *Bolonia* and hence the cross section of *Gyrochorte* isp. should not end at the border of *Bolonia* but at least some millimeters away (Fig. 27A). Since this is not the case, it is highly unlikely that *Bichordites* and *Bolonia* are synonyms. What is called *Bichordites* only is the inner well cemented part of spatangoid traces (see BROMLEY & ASGAARD 1975: 278-279).

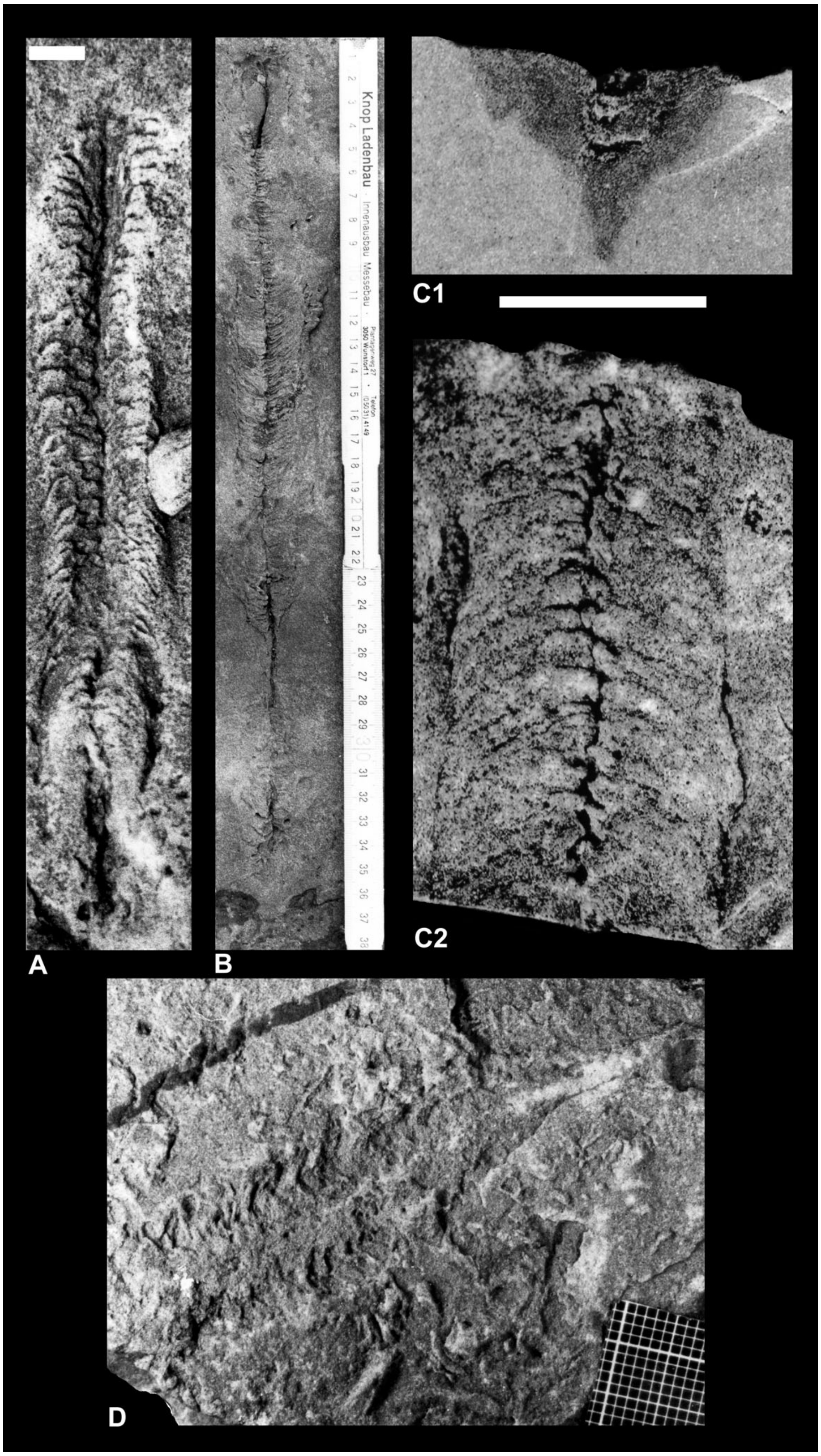


Figure 28: **A-C**. *Bolonia lata* MEUNIER, 1886. **A-B**. Field photographs, top view, positive epireliefs. **B**. Longest observed specimen. **C1**. Cross section, PIW1996-XI-46. **C2**. Top view of same specimen. **D**. *Bolonia* isp., PIW1996-XI-37, top view of a poorly preserved specimen. All Grès de Châtillon, Upper Jurassic, Ambleteuse, Boulonnais, northern France. **A, C**. Scale bars: 1cm. **D**. Millimetre grid for scale.

HAGADORN et al. (2000) introduced a new ichnospecies of *Taphrhelminthopsis*, namely '*T. nelsoni*' (quotas used by the author herein to show disagreement with the ichnogenus assignment) which shares some similarities with *Bolonia lata* at first sight. The lack of inclined pads resulting in a smooth surface of the trace, the U-shaped cross-section and the looping character of '*T. nelsoni*' are

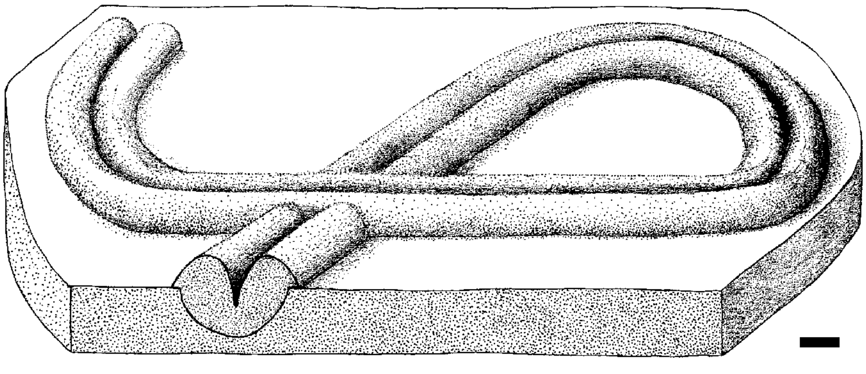


Figure 29: Reconstruction of '*Taphrhelminthopsis nelsoni*' HAGADORN et al., 2000. Full relief in positive bedding plane expression; reconstructed after data by HAGADORN et al. (2000). Scale bar:

considered as significant diagnostic criteria to separate '*T. nelsoni*' from *Bolonia* at the ichnogenus level. However, '*T. nelsoni*' should not be assigned to *Taphrhelminthopsis* due to the following reasons: 1) *Taphrhelminthopsis* only is a preservational variant of *Scolicia* and, thus, is synonymous with the latter (UCHMAN 1995, 1998). 2). If *Taphrhelminthopsis* were a valid ichnotaxon, it would be characterized by a bilobed groove on bedding planes, what means it builds a negative epirelief, whereas '*T. nelsoni*' clearly shows an opposite relief morphology, resulting in a bilobed positive epirelief (Fig. 29). Currently no ichnogenus exists to which '*T. nelsoni*' can be assigned without uncertainty. *Aulichnites* was supposed to be a bilobed, strongly curved positive epirelief structure. However, MÁNGANO et al. (2002) have shown that it is a preservational variant and younger synonym of *Psammichnites* and thus not available. Given the above reasons it can be stated that '*T. nelsoni*' does not belong to *Taphrhelminthopsis* but due to the lack of information on similar structures '*T. nelsoni*' cannot be assigned to a different or a new ichnogenus. To solve this problem, a revision of Cambrian *Taphrhelminthopsis* and similar structures is necessary (HAGADORN & SCHLIRF in prep.).

Finally, in his study of the "Bilobites", MEUNIER (1886) introduced not only *Bolonia lata*, but also another similar ichnospecies, *Equihenia rugosa*. The description for *Equihenia* is vague and the figure too poor to identify all details necessary for a proper assignment. However, the general morphology (width, arrangement of pads, epirelief preservation) makes it very likely that *Equihenia* and *Bolonia* are synonyms. In the absence of original type material, *Bolonia* is clearly to be preferred as the probable senior synonym of *Equihenia*.

Bolonia lata MEUNIER, 1886

Fig. 27A-D, 28A-C, 30A

1886 *Equihenia rugosa* STAN. MEUN. [sic]. – MEUNIER: 567, pl. 29 fig. 4.
* 1886 *Bolonia lata* MEUNIER: 567, pl. 30 fig. 8.
1955 *Bolonia lata* MEUNIER. – SEILACHER: fig. 5.44.
non 1956 *Crossochorda bureauana* (= *Bolonia lata*). – LESSERTISSEUR: 45, fig. 25F [= *Gyrochorte comosa*].
? 1965 *Gyrochorte vermicularis* HEER. – MAUBEUGE: 100, fig. 1.
? 1970 *Gyrochorte*. – MAUBEUGE: 471, fig. 1, 4-6.

? 1971 *Bolonia lata*. – CHAMBERLAIN: 244, pl. 29 fig. 5; fig. 4J.
non 1974 *Bolonia lata*. – HARY: 120, pl. 14 fig. 1-3 [= *Bichordites monastiriensis*].
1974c *Scolicia* sp. – FÜRSICH: 44, fig. 35a-c.
? 1976 *Scolicia*. – GARCÍA-RAMOS: pl. 5 fig. h.
?pt 1976 *Scolicia* DE QUATREFAGES 1849 [sic]. – GARCIA-RAMOS: 155.
non 1976 *Scolicia*. – GARCÍA-RAMOS: pl. 3 fig. c.
1976 *Scolicia*. – SEILACHER: fig. 2a.
? 1977 *Scolicia* sp. – CRIMES: pl. 7 fig. 1.
? 1979 *Bolonia lata* MEUNIER, 1886. – CAREY: 449, fig. 17A.
1986 *Crossopodia major* ichnosp. nov. – GHARE & KULKARNI: 47, pl. 3 fig. 1a-b.
1986 *Scolicia*. – SEILACHER: fig. 3.6b.
1990a *Scolicia* isp. – DAM: 141, fig. 5F.
1992 *Scolicia* ichnosp. – BUCKMAN: 233, fig. 13e.
1998 *Protovirgularia* cf. *dichotoma* MʻCOY. – FÜRSICH: pl. 47 fig. 4.
v, pt 1998 *Protovirgularia dichotoma* MʻCOY. – FÜRSICH: 264 [2nd paragraph only].
v 2000 *Protovirgularia* cf. *dichotoma* MʻCOY, 1850. – SCHLIRF: 179, fig. 30Aa, B-C; pl. 9 fig. 3-5.

Diagnosis: As for ichnogenus (because of monotypy).

Type material: PIW1996XI-4 (neotype), PIW1996XI-37, 46 (paratypes).

Description: Horizontal to subhorizontal, straight to slightly winding structures of inconstant diameter within a single specimen. Outline of cross-section heart-shaped (with elongate tip) to trapezoidal. Burrows composed of biserial pads of sediment of inconstant thickness (0.5-1.3mm); pads symmetrically arranged on either side of a median furrow. Individual pads curved and lunate in top view; all pads inclined to bedding plane at an acute angle (30-45°); pads of same material as host sediment. Burrow diameter 0.4-3.7cm in width and 0.7-1.8cm in height; maximum observed burrow length 36cm. Top surface rarely shows an oval depression, which is slightly wider than the rest of the burrow in respect to the long axis, and lacks distinct pads (Fig. 27C).

Discussion: The varying burrow diameter is interpreted as the result of undulatory movement of the trace maker in respect to the host medium. Upward or downward bending trace parts have never been observed. The oval depression, lacking distinct pads, is interpreted as a stop in the movement of the trace maker.

Bolonia is currently represented by one ichnospecies. It should be stated once again that the nomenclature of trace fossils is necessarily independent of possible producers as only behavioural patterns and their morphological results are suitable ichnotaxobases (e.g., SEILACHER 1953). However, in palaeoecological reconstruction the ethology of trace fossils is important although in many cases no final conclusion can be drawn since various organisms may produce identical traces.

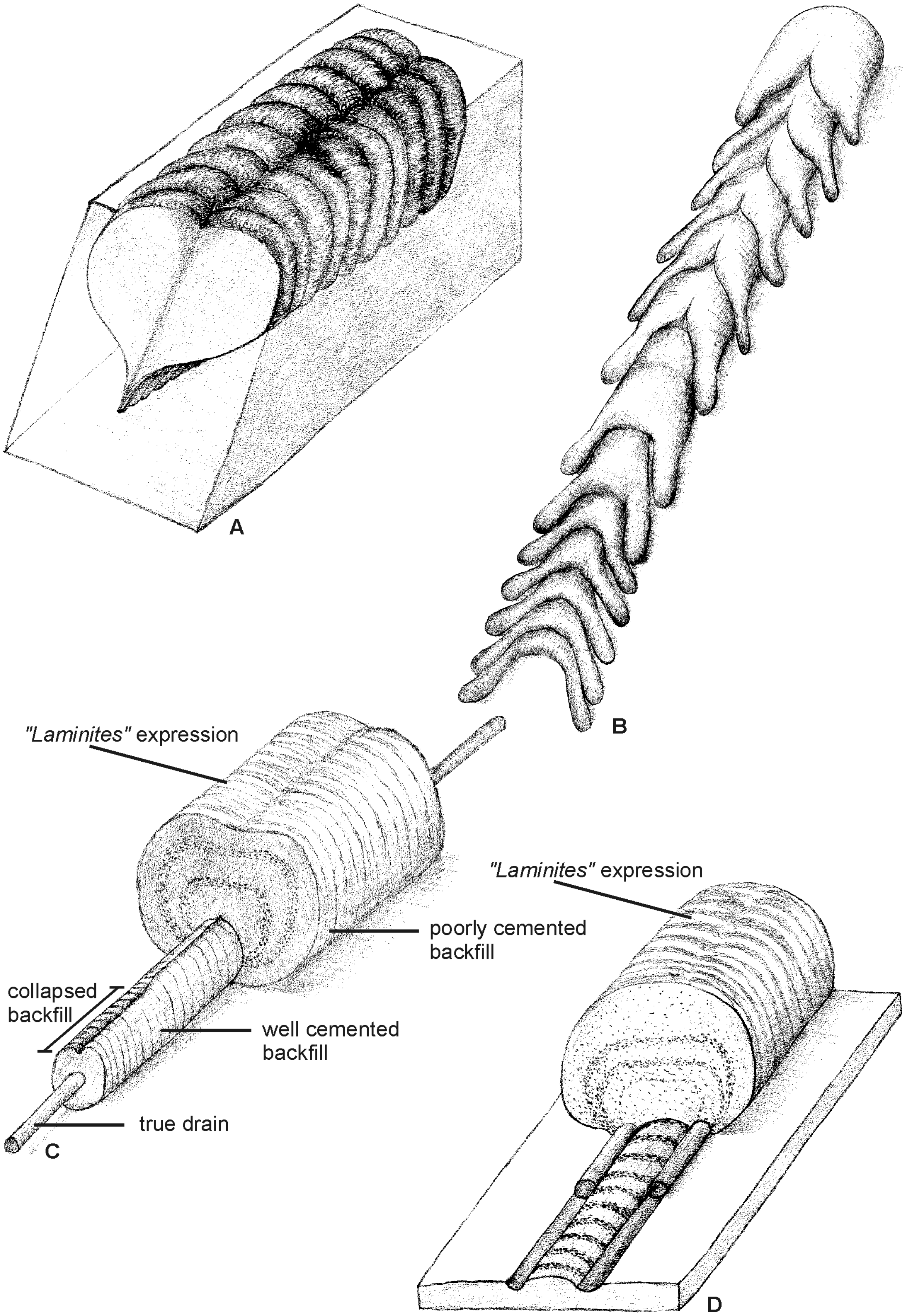


Figure 30: Reconstructions. **A**. *Bolonia lata*, full relief. **B**. *Protovirgularia* isp., positive hyporelief, compiled after figures in SEILACHER & SEILACHER (1994). **C**. *Bichordites monastiriensis*, full relief, the inner well cemented part, surrounding the true drain may resemble *Bolonia*; the median groove on top may form when the

true drain collapses; the median crest is a result of excessive cementation (pers. comm. R.G. BROMLEY). **D**. *Scolicia prisca,* full relief, after UCHMAN (1995). Not to scale.

Bolonia lata has been interpreted as a gastropod trail (e.g., FÜRSICH 1974c) or made by annelids or bivalves (summarized in HAN & PICKERILL 1994). Since spatangoid traces do have similar features as *B. lata* one should also discuss spatangoids as possible makers. However, spatangoids first occur in the Upper Jurassic, that means they cannot be responsible for Palaeozoic *Bolonia*. Additionally, a heart-shaped cross section seems highly unlikely in spatangoid traces. Only in the case of a trace collapse would one expect a heart-shaped cross section (pers. comm. R.G. BROMLEY 2001; Fig. 29C). Polychaetes such as the "sea mouse" *Aphrodite* might be possible producers. In present day oceans they live epifaunally or infaunally, and they have a wide range of environments where they occur: at a water depth between 1-2000m, on firm as well as in soft substrates. Due to the lack of faecal material within the burrows or other doubtless hints for feeding behaviour an interpretation as feeding burrow is problematic, although not excluded if one keeps in mind the morphological similarities to spatangoid traces. At the present stage of knowledge an interpretation of *B. lata* as a purely locomotive structure seems justified, as long as there are no features discovered to prove anything different.

There can be no doubt that *Bolonia lata* is an infaunal trace since its positive epirelief could hardly be made at the surface, and would be unlikely to be preserved in association with oscillatory ripples in any case. The size and general outline of the cross-section of *Bolonia* make the determination of a possible producer difficult.

The palaeoenvironment from which *Bolonia lata* has been reported so far is nearshore marine, influenced by storm waves.

SEILACHER & SEILACHER (1994) impressively showed that bivalves and scaphopods can be considered as possible producers of *Protovirgularia*. While crawling through the substrate, semi-infaunal bivalves often produce only an ichnotaxonomically ambiguous furrow in the upper part of the sediment, but this is not true for the resulting undertrace since it is produced in deeper, more cohesive sediment (SEILACHER & SEILACHER 1994). However, this cannot account for *Bolonia* because it is preserved as a positive epirelief, a feature that cannot be produced as an undertrace.

Protovirgularia as already mentioned is interpreted as a bivalve trace (SEILACHER & SEILACHER 1994; EKDALE & BROMLEY 2001); *Gyrochorte* is interpreted either as made by polychaete-like worms (HEINBERG 1973) or by arthropods (SCHLIRF 2000); *Scolicia* and *Bichordites* are explained as burrowing activities of infaunal spatangoid echinoids (UCHMAN 1995).

Ichnogenus *Gyrochorte* HEER, 1865

Type ichnospecies: *Gyrochorte comosa* HEER, 1865: 142, pl. 9 fig. 12; by subsequent designation (HÄNTZSCHEL, 1962: *W*196).

Diagnosis: Trace in epirelief preserved as plaited ridges with biserially arranged, obliquely aligned pads of sediment, separated by median furrow. Hyporelief shows smooth biserial grooves separated by median ridge. Course straight to strongly winding, direction changes sharply. Parts of the trace may intersect. Ridges and their grooves separated by a vertical distance (SCHLIRF 2000).

Gyrochorte comosa HEER, 1865

Fig. 31-32, 35

* 1865 *Gyrochorte comosa* HEER: 142, pl. 9 fig. 12.
? 2002 *Crossopodia maranhensis*. – FERNANDES et al.: 41, fig. 37-38 [probably wrong toponomy = upside down].
For additional synonyms see SCHLIRF (2000) and GIBERT & BENNER (2002).

Diagnosis: As for ichnogenus (because of monotypy).

Material: Several incomplete specimens on two slabs SMNS 65498-1, 2 from the Rhätsandstein, Exter Fm, Upper Keuper, near Nürtingen, Baden-Württemberg, southern Germany; several incomplete specimens on slab PIW-2215 from the Werksandstein, Würzburg Fm, Lower Keuper, Faulenberg, Würzburg, Lower Franconia, Bavaria, southern Germany; additional specimens PIW2002-I- from the Katrol Fm, Upper Jurassic, Jhura Dome, Kachchh, western India.

Description: Triassic specimens: Low, straight to slightly curved, bilobate burrows on bedding planes; burrows usually preserved as symmetrical plaits composed of biserially arranged pads of sediment with more-or-less distinct median furrow (in epirelief preservation). Pads with angle between 40 and 180° toward median furrow. Individual pads of sediment arranged opponing or alternating. If pads are not preserved, burrows appear as more-or-less smooth ridges (epirelief) or grooves (hyporelief) divided by a straight median furrow (epirelief) or crest (hyporelief) respectively. In hyporelief preservation the individual pads could not be observed. Burrows 3 to 4 mm wide and up to 2mm in height above bedding planes; entire burrow height unknown. Interpenetration of burrows could be observed. Preserved as positive epireliefs and negative hyporeliefs. Internal patterns of the burrows within the sediment only are vaguely visible.

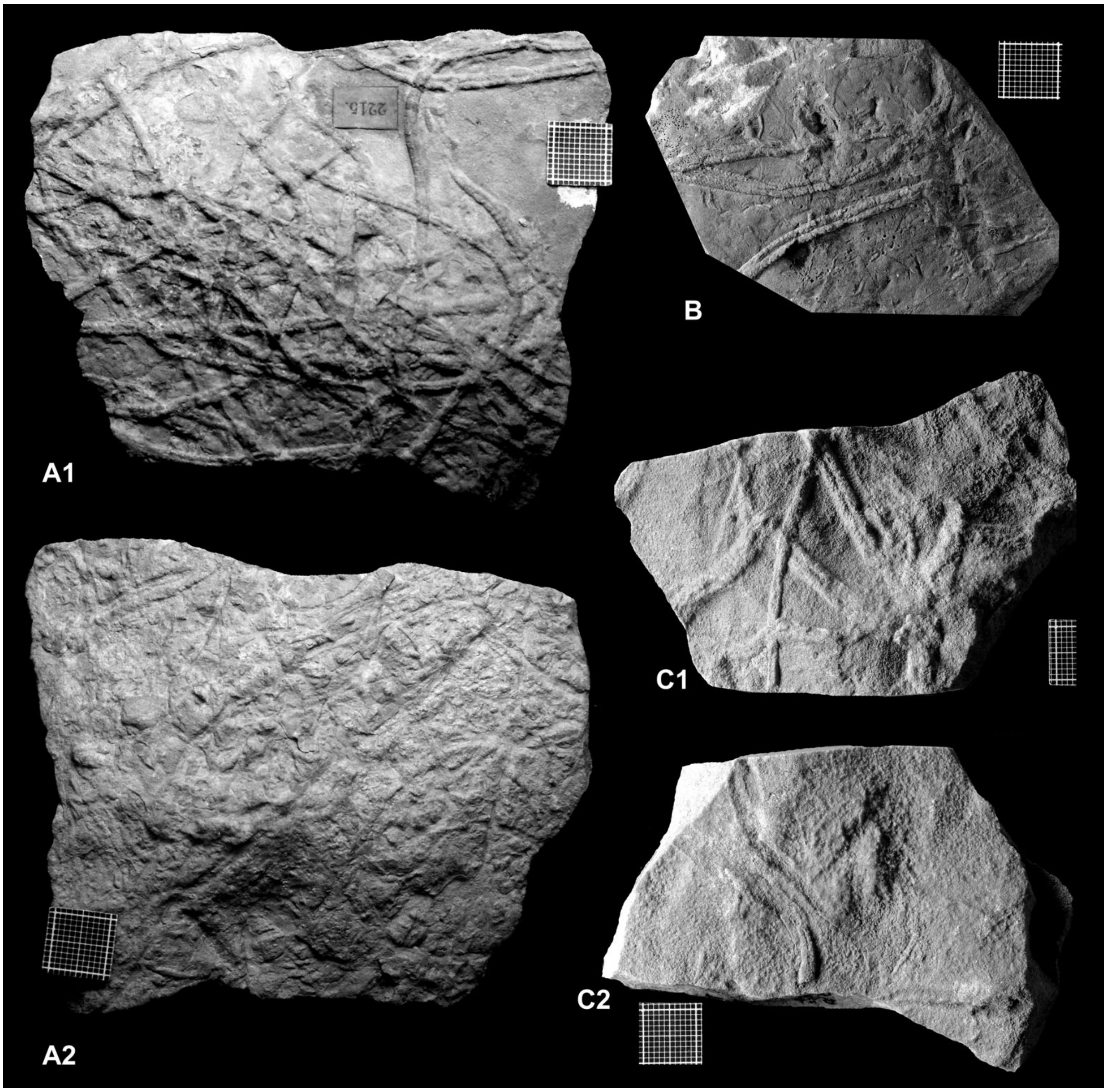


Figure 31: *Gyrochorte comosa* HEER, 1867. **A1**. PIW-2215, fullreliefs, top view. **A2**. Same, bottom view. Werksandstein, Würzburg Fm, Lower Keuper, Faulenberg, Würzburg, Lower Franconia, Bavaria, southern Germany. **B**. Fullreliefs, top view. **C1**. Fullreliefs, top view. **C2**. Same, bottom view. **B-C**. Rhätsandstein, Exter Fm, Upper Keuper, near Nürtingen, Baden-Württemberg, southern Germany. Millimetre grids for scale.

Jurassic specimens: Low, slightly sinuous to strongly winding, bilobate burrows on bedding planes; burrows usually preserved as symmetrical plaits composed of biserially arranged pads of sediment with more-or-less distinct median furrow. Pads with angle between 45 and 180° towards median furrow; individual pads of sediment arranged opponing; median furrow straight. If pads are not preserved, burrows appear as more-or-less smooth ridges divided by a straight median furrow. Burrows 3 to 9mm wide and up to 2mm in height above bedding planes; entire burrow height unknown. Interpenetration of burrows common. In some specimens a secondary successive branching may probably occur. Some specimens fan out into several parallel cylindrical structures (Fig. 32A) comparable to *Syringomorpha* of authors. Some specimens have a relatively wide median furrow and the pads are arranged in small separate groups (Fig. 32C). Hyporelief preservation and indistinct internal patterns of the burrows could be observed.

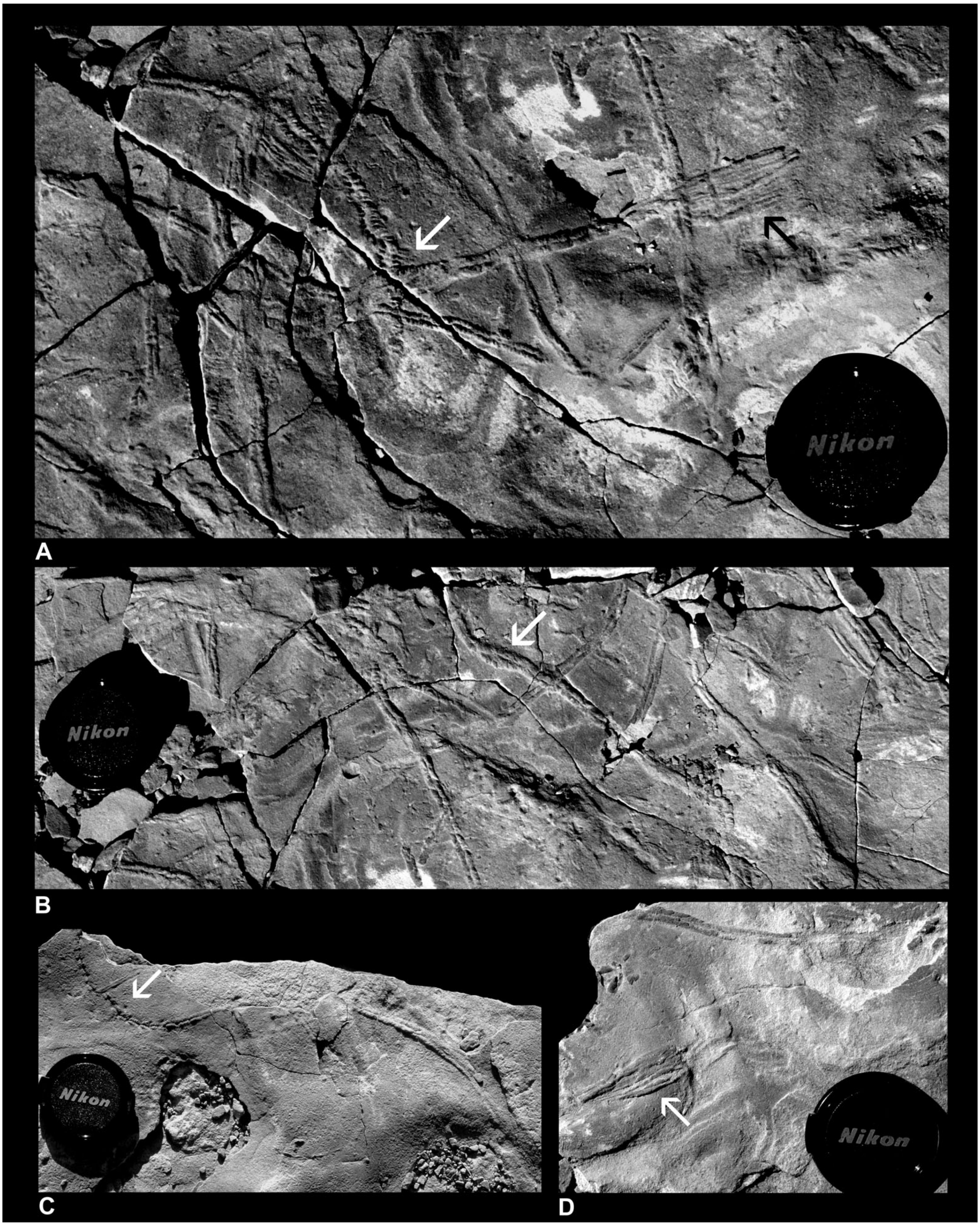


Figure 6: *Gyrochorte comosa* HEER, 1867, fullreliefs, top view, fiel photographs, Katrol Fm, Upper Jurassic, Jhura Dome, Kachchh, western India. **A**. Black arrow indicates *G. comosa* fanning out into several parallel cylindrical structures comparable to *Syringomorpha* of authors; white arrow indicates *G. comosa* fanning out into several short parallel cylindrical structures. **B**. Arrow indicates widening of burrow. **C**. Specimens with a relatively wide median furrow and the pads arranged in small separate groups (top left). **D**. Arrow indicates unidentified cylindrical structures associated with *G. comosa*. Lens caps 52mm across.

Discussion: The herein described material shows well-preserved details of the plaited epichnial nature of *Gyrochorte* and the corresponding hypichnial grooves. The Triassic specimens unfortunately are very short. For this reason no statements concerning course can be made. However, the material is well enough preserved to allow an exact assignment to *Gyrochorte comosa* because of the epichnial double ridges and corresponding hypichnial double grooves. Lately *Gyrochorte* was extensively discussed by POWELL (1992), SCHLIRF (2000), and GIBERT & BENNER (2002). SCHLIRF (2000) listed several abilities the progenitors of *Gyrochorte* must have in order to produce such structures. GIBERT & BENNER (2002) favour an annelid as possible producer without even discussing other possible progenitors such as arthropods. These authors assume an upward bent, worm-like animal moving through the sediment. The resulting trace fossil consists of a cylindrical structure at the bottom, topped by downward tangentially, obliquely arranged, spreiten-like structures, features never observed in *Gyrochorte* (Fig. 33). According to their reconstruction and the given direction of movement the anterior end of the progenitor crossed the sediment water interface, another assumption yet not supported by field observation. The assumption that the upper part of the proposed progenitor also was the anterior part, was made herein, because of the indicated direction of movement because a head down backward movement sounds even more unlikely. Although epichnial ridges are among the most characteristic features of *Gyrochorte*, the reconstruction by GIBERT & BENNER (2002) does not show epichnial plaited ridges. The epichnial ridges are indicative of an upward movement of sediment by the *Gyrochorte* progenitor. As already criticized by SCHLIRF (2000) the annelid body bauplan makes them unlikely producers of *Gyrochorte*. STANLEY & PICKERILL (1998) describe an intergradation of *Gyrochorte* and *Planolites*, and thus concluded a vermiform animal must have produced *Gyrochorte*. This is a very simplistic conclusion. The 'vermiform' nature of a trace fossil does not necessarily mean that its producer also had a vermiform body. In *Spongeliomopha* (*S.*) *suevica* very long 'vermiform' burrow parts can be observed and their producers are no vermiform animals but crustaceans, at least the majority of the modern ones. Additional material from the Katrol Formation (Upper Jurassic, Kachchh, India) shows very suprising variations of *Gyrochorte* specimens (Fig. 32). Some parts of *Gyrochorte* intergrade with *Syringomorpha*-like structures (Fig. 32A). In other parts *Gyrochorte* shows lateral displacement in curves (Fig. 32A), but not in the same manner as described by HALLAM (1970) and POWELL (1992) but building parallel strings of sediment. The material presented by HALLAM (1970) and POWELL (1992) shows features of *Gyrochorte* that are difficult to explain as being produced by a worm-like animal. The fan-like arrangement of short sediment strings at sharp bends of *Gyrochorte* make more sense when the progenitor was an animal with a more-or-less short and stiff body rather than a long and soft body.

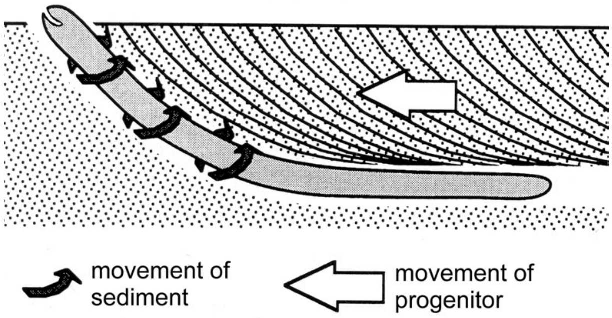


Figure 33: Assumed reconstruction of *Gyrochorte comosa*; redrawn after GIBERT & BENNER (2002). Several features in this reconstruction are not supported by observations, e.g., downward tangentially, obliquely arranged spreite-like structures; an open tunnel at the front and the bottom of the structure. In addition, the characteristic epichnial plates are missing. The mouth indicating the anterior part of the animal has been added herein (see text for discussion). Not to scale.

Currently *Gyrochorte* is monospecific, all other ichnospecies previously assigned to *Gyrochorte* remain doubtful except for *Gyrochorte comosa*. This is also supported by the investigations of UCHMAN (1998) and GIBERT & BENNER (2002). Nevertheless, a detailed restudy of all specimens hitherto assigned to *Gyrochorte* may reveal a different point of view, especially if one keeps in mind the morphological variety of the Jurassic specimens from India presented above.

To date no nonmarine *Gyrochorte* structures exists. The material from the Werksandstein (Würzburg Fm) can also be interpreted as marine, because the outcrop at the Faulenberg, Würzburg also bears other faunal elements (shark teeth) that support a marine origin (SANDBERGER 1890) for at least parts of the section.

Star-shaped and irregular, vermiform, slightly tapering structures with delicate protuberances

This form group basically is an ethological group based on complete and incomplete preservation of trace fossils produced by asteroids.

Ichnogenus *Heliophycus* MILLER & DYER, 1878

Type ichnospecies: *Heliophycus stelliforme* MILLER & DYER, 1878: 2, pl.2 fig. 3; by monotypy.

Emended diagnosis: Star-shaped structures with a varying number (> 3) of radially arranged, tapering arm-like structures originating from a central (proximal) circular to polygonal structure. Morphology of arm-like structures variable, from triangular to elongate triangular to vermiform cylindrical; ornamentation also variable, with fine chevron-shaped, transverse, or longitudinal, positive and negative relief elements, or transverse protuberances; arm-like structures may show overlapping appearing as branching (= false branching); overlaps usually occur at distal third of arm-like structures. Preserved as negative epirelief or positive hyporelief.

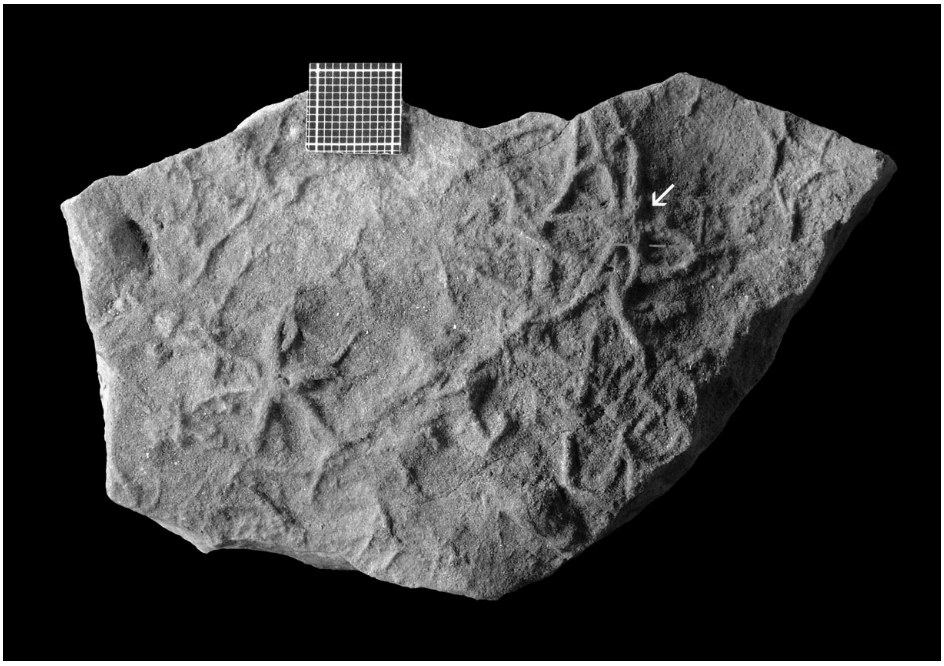


Figure 34: *Heliophycus* new ichnospecies, positive hyporeliefs; paratypes, SMNS 65494 Rhätsandstein, Exter Formation, Upper Keuper, Erlachsheim, Baden-Württemberg, southern Germany. Note star-shaped structures with a varying number (up to six) of radially arranged, tapering arm-like structures and a central polygonal structure (arrow); the ornamentation with fine, transverse protuberances, resulting from the imprints of ambulacra is only poorly visible; arms-like structures occasionally with overlaps appearing as branching (= false branching) at distal third. Millimetre grid for scale.

Discussion: The name *Asteriacites* SCHLOTHEIM, 1820 is invalid. Although HÄNTZSCHEL (1975) already recognized that the nomenclature of *Asteriacites* SCHLOTHEIM, 1820 was confused he retained the ichnogenus name, with an argument that is often used: “the ichnogenus name was a widely used and known name”.

SEILACHER (1953b) was the first to use *Asteriacites* after a very long time again. Between 1826 and 1938 only *Asterias lumbricalis* was used. Of course, *Asterias* was preoccupied and it was necessary to replace this ichnogenus name. However, while using or reassessing old names careful study of the type material is necessary to guarantee stability. Stability can only be achieved if the taxa are undoubtful. In the long run certain cuts in nomenclature will lead to lasting stability. However, it is usually very difficult to convince the scientific community of the emended use of a taxon. For instance, the *Cochlichnus* versus *Cymataulus* debate (RINDSBERG 1994; PICKERILL & NARBONNE 1995; STANLEY & PICKERILL 1998) is a very good example.

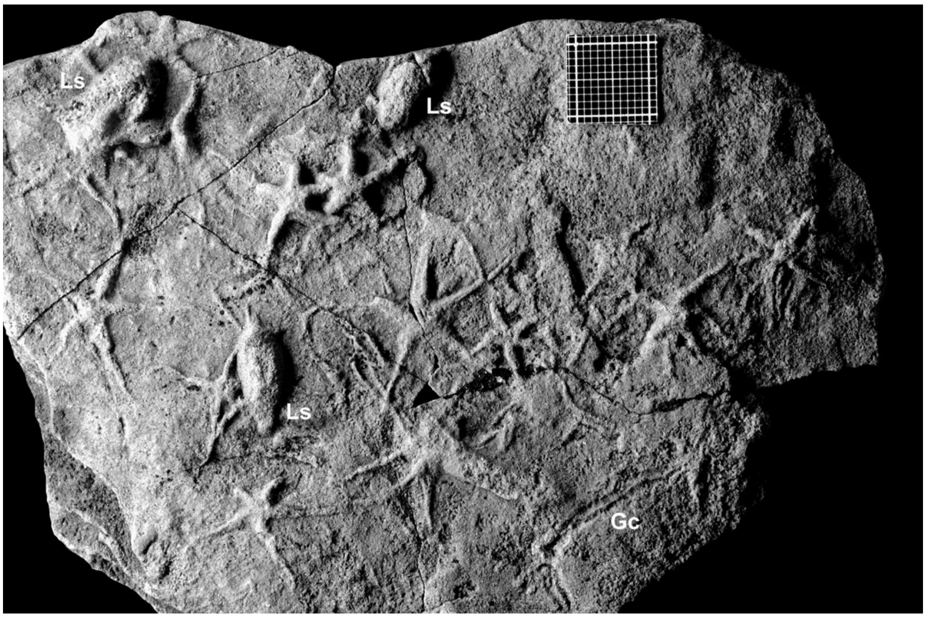


Figure 35: *Heliophycus* new ichnospecies, positive hyporeliefs; syntypes, SMNS 65493 Rhätsandstein, Exter Formation, Upper Keuper, Erlachsheim, Baden-Württemberg, southern Germany. Note the ornamentation with fine, transverse protuberances, resulting from the imprints of ambulacra in specimen in upper left corner (also see Fig. 37B for detail). Associated are *Lockeia siliquaria* [Ls] and *Gyrochorte comosa* [Gc]. Millimetre grid for scale.

There are strict rules to be followed if a name should be retained or re-introduced. Among all aspects to be fulfilled, a name that should be preserved must be valid. A fact not fulfilled in the case of *Asteriacites*. In his 'Petrefactenkunde', SCHLOTHEIM (1820) introduced various species of *Asteriacites*: *A. lumbricalis*, *A. ophiurus* and *A. pennatulatus* referring to previously published works by KNORR (1755) and LINCK (1733). Among these species, probably are trace fossils, foraminifera and echinoderms (crinoids and ophiuroids). This was mentioned by LOEBLICH & TAPPAN (1964), SPENCER & WRIGHT (1966) and RASMUSSEN & SIEVERTS-DORECK (1978). The material of SCHLOTHEIM's original collection, now housed in the Naturkundemuseum Berlin, has neither star-shaped nor any other trace fossils among it (pers. comm. C. NEUMANN 2004). Only an official opinion of the International Commission on Zoological Nomenclature (ICZN Article 78, 81) could retain the name in this case. This however, needs a detailed revision of all groups belonging to the taxa related to *Asteriacites* SCHLOTHEIM. Otherwise in the course of a revision another taxonomist may re-introduce the name for any of the taxa involved, e.g., a foraminifera or an asteroid.

For the trace fossil '*Asteriacites lumbricalis*' not even a type specimen exists. SEILACHER (1953b) designated a type ichnospecies for the ichnogenus but he neither designated a lectotype nor a neotype, and SCHLOTHEIM referred to an unidentifiable drawing, which makes *Asteriacites lumbricalis* a *nomen dubium*. In addition, SEILACHER (1953b) completely neglected the fact that SCHLOTHEIM (1820) introduced several species of *Asteriacites*, and he missed to discuss if one of the other species may also be a star shaped trace fossil. Moreover, in 1813 SCHLOTHEIM already published a genus called *Asteriatites* including several species, referring to the same illustrations as in 1820 for *Asteriacites*. Interestingly, HOLL (1843), and GIEBEL (1852), in his 'Deutschlands Petrefacten', do not use a single of SCHLOTHEIM's genera. It seems that already in 1842 and 1852 SCHLOTHEIM genera were considered dubious. The International Commission on Botanical Nomenclature decided to consider all genera introduced by SCHLOTHEIM (1820, 1822, 1823) as invalid, although they were used by botanists for more than 120 years by the time of their decision (see LANGER 1982), a wise decision that prevented a lot of confusion in botanical nomenclature.

OSGOOD (1970) refigured the type ichnospecies of *Heliophycus*, *H. stelliforme* and showed that the ichnogenus is clearly defined and type material exists. However, he placed *Heliophycus* in synonymy with *Asteriacites*, a decision not followed here. Given the above reasons a further use of *Asteriacites* SCHLOTHEIM, 1820 is not recommended. Instead the well-defined ichnogenus *Heliophycus* MILLER & DYER, 1878 should be used.

The diagnoses given by HÄNTZSCHEL (1975) and lately by WILSON & RIGBY (2000) for *Asteriacites*, a probable synonym of *Heliophycus*, contain information on possible producers and also relate descriptive terms of the trace fossil morphology to possible producers. Diagnoses should be free of interpretative data, because trace fossil taxonomy should be producer-independent. Although in the case of *Heliophycus* the possible producers apparently are well known, it is only the morphology of the resulting traces that counts for their identification. In the description and in the discussion interpretations may be used.

The terms 'branch' and 'branching' should be referred to true branches and true branching only. D'ALESSANDRO & BROMLEY (1987) refined the classification system of branching introduced by BROMLEY & FREY (1974). The major categories are true branching and false branching. Within true branching several modes of behaviour can lead to a ramification (Fig. 36). What appears to be branching in *Heliophycus* new ichnospecies is in fact the result of overlapping imprints of the arms of the progenitor and not branching *sensu stricto*. Recognition of different aspects of branching provides information on the behaviour of the progenitor, and thus, it allows a more precise definition of trace fossil names (KEIGHLEY & PICKERILL 1995).

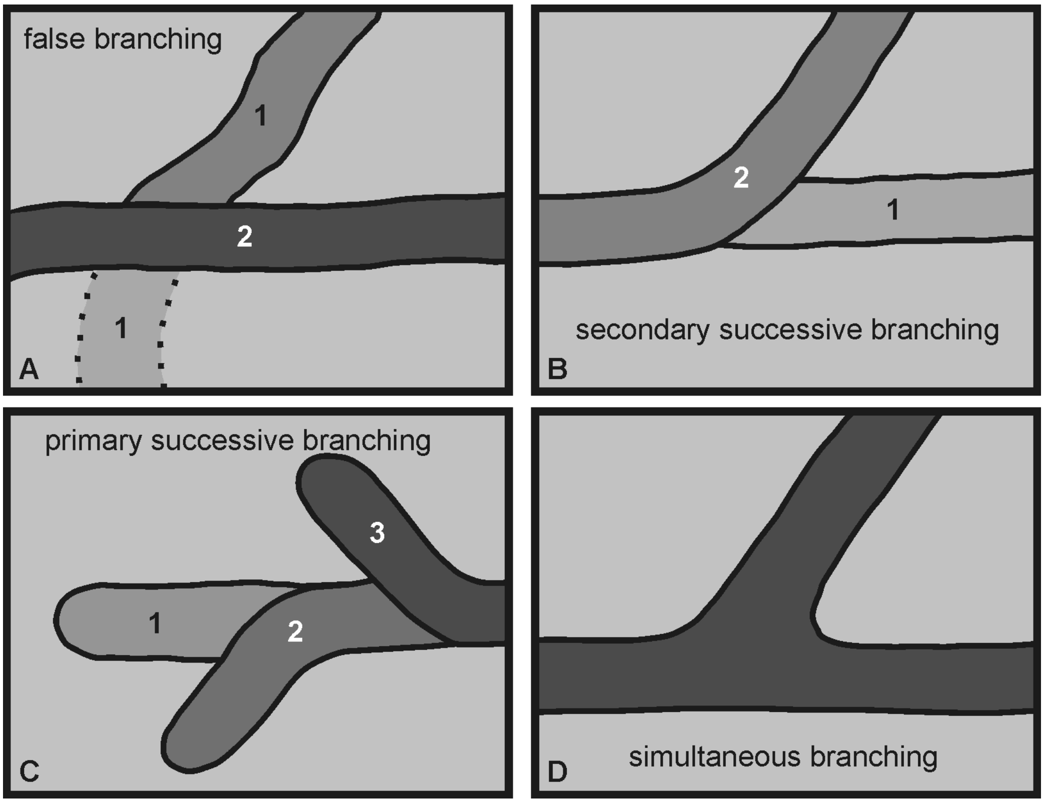


Figure 36: A-D. Styles of branching in burrows. **A**. False branching: by accidental intersection of burrow 2 through 1, and incomplete preservation; often observed in *Planolites*. **B**. Secondary successive branching: an unbranched burrow 2 enters and follows an earlier fill 1 (or later deviates from it); often observed in *Taenidium* and *Scoyenia*. **C**. Primary successive branching: an unbranched burrow produces a cumulative structure by probing (e.g. *Treptichnus*). **D**. Simultaneous branching: permanently open burrows in which the branches were simulatenously open (e.g. *Spongeliomorpha*). Modified after D'ALESSANDRO & BROMLEY (1987).

Heliophycus new ichnospecies

Fig. 34-35, 37

? 1820 *Asteriacites lumbricalis.* – SCHLOTHEIM: 324 [*nomen dubium*].

?pt 1953b *Asteriacites lumbricalis* SCHLOTHEIM. – SEILACHER: 94, fig. 2-3; pl. 7-9 [the references in the synonymy list are doubtful except for the ones indicated as *videt*, these figures and plates most likely all belong to the proposed new ichnospecies].

1970 *Asteriacites lumbricalis.* – OSGOOD: 312.

1990 *A. lumbricalis* VON SCHLOTHEIM, 1820. – MIKULÁŠ: 134.

1990 *Asteriacites lumbricalis*. – MIKULÁŠ: fig. 2.

non 1992b *Asteriacites lumbricalis* VON SCHLOTHEIM, 1820. – MIKULÁŠ: 35, pl. 10 fig. 1, pl. 12 fig. 3-4, pl. 14 fig.4 [= *Heliophycus stelliforme*].

1999 *Asteriacites lumbricalis.* – MÁNGANO et al.: 19, fig. 3A-I, 4A-D, 5A-D.

2004 *Asteriacites lumbricalis.* – BELL: fig. 3-8.

Diagnosis: Star-like structure with distinct central, circular to polygonal disc from which narrow, vermiform, slightly tapering arm-like structures evolve; delicate, ideally bisymmetrically arranged, polygonal to round, positive or negative protuberances occur along the arm-like structures; arm-like structures themselves may overlap and appear dichotomously or multi-branched in the terminal third of their length.

Material: Two slabs, SMNS 65493 (syntypes), SMNS 65494 (paratypes), Rhätsandstein, Exter Formation, Upper Keuper, Erlachsheim, Baden-Württemberg, southwest Germany.

Derivatio nominis:

Description: Star-shaped positive hyporelief structures with a varying number (3-5) of radially arranged, tapering arm-like structures originating from a central polygonal structure (disc). Arms are elongate triangular to vermiform cylindrical; ornamentation with fine, transverse protuberances, resulting from the imprints of ambulacra; arms occasionally with overlaps appearing as branching at distal third of arms.

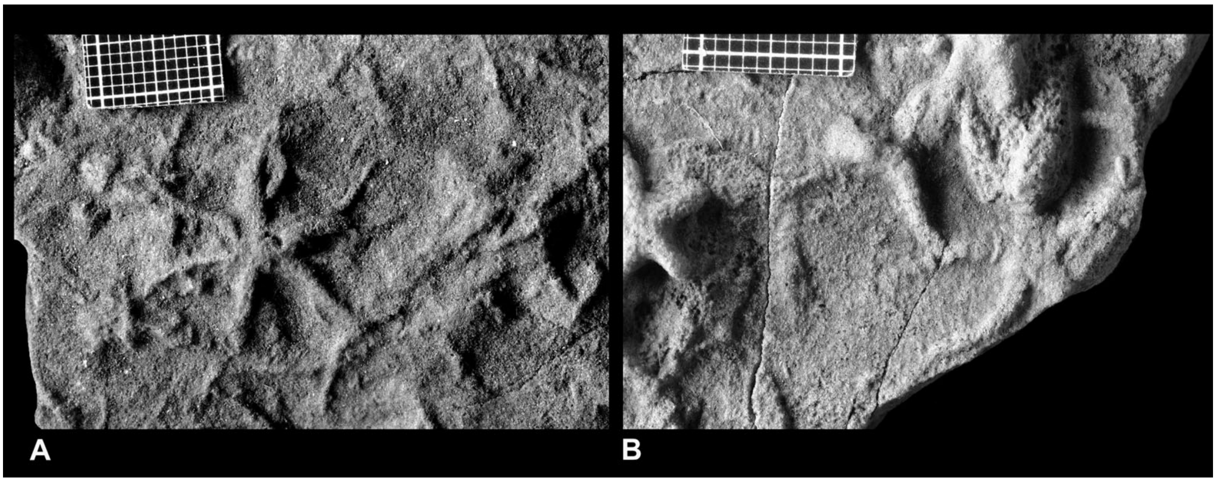


Figure 37: A-B. *Heliophycus* new ichnospecies, positive hyporeliefs. **A**. Detail of SMNS 65494. **B**. Detail of SMNS 65493. Note transverse protuberances, resulting from the imprints of ambulacra. Millimetre grids for scale.

Discussion: The synonymy suggests that *Asteriacites lumbricalis* SCHLOTHEIM is, in fact, synonymous with *Heliophycus* new ichnospecies However, it is only our current understanding of *Asteriacites* that makes it likely. Due to the lack of type material this cannot be proved. As already shown by many other examples (e.g., *Skolithos*, *Monocraterion*, '*Ophiomorpha*', *Sabellarifex*, etc.), very often our understanding is incorrect if the type material is consulted, and type material is the only fact that counts. Nomenclatural stability is very important, however, it should not be an objection for changes. As already written in the *Spongeliomorpha* chapter, stability is stability on the long run. By the time BROMLEY (1967) studied the trace fossils of the British Chalk common believe was that the Chalk was barren of trace fossils. All tubular structures were interpreted as dissolved sponges or sponge remains (e.g., BROMLEY 1967), a view that has drastically changed ever since. Morphologically *Heliophycus* can be distinguished from *H. stelliforme* chiefly by having thinner arm imprints. Occasionally a central disk can be observed.

If a central disk structure occurs the traces most probably are produced by ophiuroids (e.g., MIKULÁŠ 1990; MÁNGANO et al. 1999). *Heliophycus* without such a central disk are better explained as being produced by asteroids (BELL 2004).

THÜRACH (1888, 1889) already mentioned irregularly star-shaped ridges in Keuper sandstones associated with worm-like burrows. Unfortunately he did not figure any of these finds. However, the localities and stratigraphical positions from which he described these structures lead to the conclusion that in most of the cases he found poorly preserved desiccation or synaeresis cracks rather than star-shaped trace fossils. Only the finds from the '*Acrodus* Bed' (*Acrodus* Bank of German authors) and the '*Corbula* Bed' (*Corbula* Bank of German authors) were made in environments in which asteroid or ophiuroid trace fossils potentially may occur.

The origin and the palaeoecologic significance of *Heliophycus* (*Asteriacites* in their papers) are extensively discussed by MIKULÁŠ (1992a), MÁNGANO et al. (1999) and BELL (2004) and are not repeated here in detail.

Ichnogenus *Biformites* LINCK, 1949b

Type ichnospecies: *Biformites insolitus* LINCK, 1949b: 44, pl. 4 fig. 1-2; by original designation.

**v*	1949b	*Biformites* n.g. LINCK: 44.
v	1962	*Biformites* LINCK, 1949. – HÄNTZSCHEL: *W*186.
v	1965	*Biformites* LINCK, 1949. – HÄNTZSCHEL: 16.
non	1970	*Biformites*, LINCK, 1949 [sic]. – CHIPLONKAR & BADVE: 8 [= *Protovirgularia*].
non	1971	*Biformites* LINCK, 1949. – CHAMBERLAIN: 233 [= not identifiable].
v	1975	*Biformites* LINCK, 1949. – HÄNTZSCHEL: *W*46.
non	1985	*Biformites* LINCK, 1949. – MILLER & KNOX: 83 [= *Protovirgularia*].
non	1994	*Walcottia* MILLER & DYER, 1878. – RINDSBERG: 56 [= *Protovirgularia*].
non	1994	*Protovirgularia.* – SEILACHER & SEILACHER: 10.
non	1998	*Biformites* LINCK 1949. – BUCKMAN et al.: 87 [= most likely some kind of *Spongeliomorpha* (*Ophiomorpha*) like burrow].
?	2002	*Biformites* LINCK, 1949. – FERNANDES et al.: 173.

Diagnosis: Narrow, vermiform, slightly tapering, horizontal, straight to curved structures with delicate, ideally bisymmetrically arranged, perpendicular elongate, or polygonal to round, positive or negative protuberances. Preserved as positive hyporeliefs.

Discussion: RINDSBERG (1994) placed *Biformites* in synonymy with *Walcottia*, which is a younger synonym of *Protovirgularia* (UCHMAN 1998). SEILACHER & SEILACHER (1994) put *Biformites* in synonymy with *Protovirgularia* with reservations only. Both synonymisations are not followed here because of distinct morphological differences between the two ichnogenera. *Protovigularia* is a plaited burrow consisting of obliquely arranged pads of sediment (see discussions of *Bolonia*, *Gyrochorte* and *Protovirgularia*). As can be seen in Fig. 38-40, *Biformites*, by contrast, is not a burrow *sensu stricto*, but represents impressions of body parts of the producer. The perpendicular ornamentations are no sediment pads but are the result of impressions.

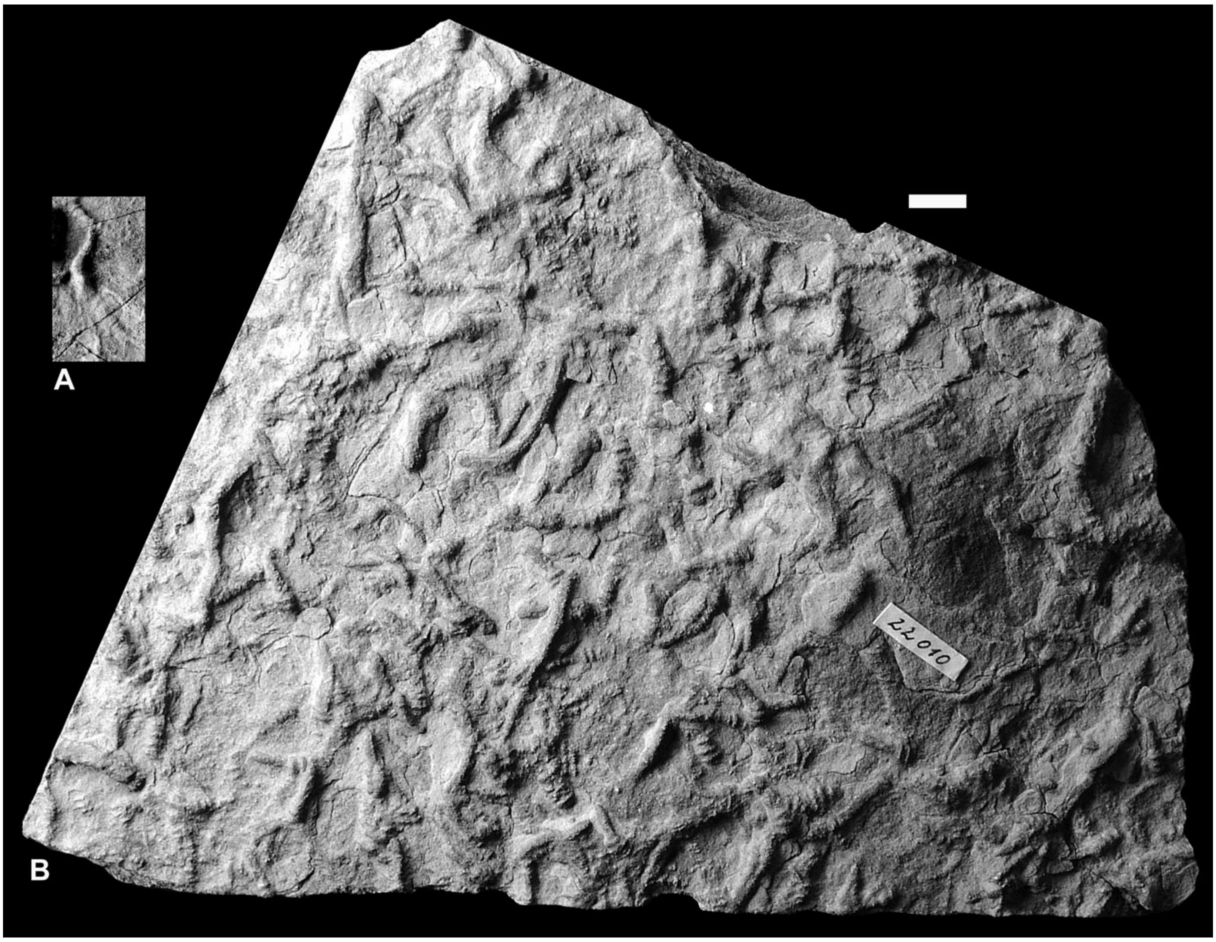


Figure 38: **A**. Arm imprint in *Heliophycus* new ichnospecies; positive hyporelief, SMNS 65493. The figure is given in exactly the same magnification as figure B to express the similarities between both structures. **B**. *Biformites insolitus* LINCK, 1949b, positive hyporeliefs, syntypes SMNS 22010, Upper Schilfsandstein, Stuttgart Fm, Middle Keuper, Maulbronn, Baden-Württemberg, southern Germany. Original of LINCK 1949b, pl. 4 fig. 1-2. Note similarites in ornamentation pattern between **A** and **B** (also see Fig. 37). Scale bar: 1cm.

Biformites insolitus LINCK, 1949b

Fig. 38-40

**v*	1949b	*Biformites insolitus* n.g. n.sp. LINCK: 44, pl. 4 fig. 1-2.
v	1955	*Biformites insolitus* LINCK. – SEILACHER: fig. 5.34.
v	1962	*B. insolitus.* – HÄNTZSCHEL: *W*186, fig. 114A-B.
v	1965	*B. insolitus* LINCK 1949. – HÄNTZSCHEL: 16.
non	1970	*Biformites* cf. *insolitus* LINCK. – CHIPLONKAR & BADVE: 8, pl. 3 fig. 2, 2A [= *Protovirgularia rugosa*].
non	1971	*Biformites insolitus* LINCK. – CHAMBERLAIN: 234, fig. 7K, L, O; pl. 31 fig. 14, 16-18 [= not identifiable].
v	1975	*Biformites insolitus.* – HÄNTZSCHEL: *W*46, fig. 29.3a-b.
non	1994	*Walcottia rugosa*, *Biformites* aspect. – RINDSBERG: 57, pl. 16 fig. A [= *Protovirgularia rugosa*].
non	1998	*Biformites* ichnosp. – BUCKMAN et al.: 87, fig. 2, 3b [= most likely *Spongeliomorpha* (*Ophiomorpha*) isp.].
v	2001	*Protovirgularia rugosa* (MILLER & DYER). – SCHLIRF et al.: 95, tab. 1.

Diagnosis: As for ichnogenus (because of monotypy).

Material: Syntypes on slab, SMNS 22010, Upper Schilfsandstein, Stuttgart Fm, Middle Keuper, Maulbronn, Baden-Württemberg, southern Germany.

Description: Narrow (1.5-4mm wide), short (5-24mm long), vermiform, slightly tapering, horizontal, straight to curved structures, with delicate, bisymmetrically arranged, or perpendicular elongate, or polygonal to round, positive or negative protuberances (Fig. 40B-E); cross-section subquadrangular U-shaped (Fig. 39A-C). Preserved as positive hyporelief. Overlaps of individual imprints very common.

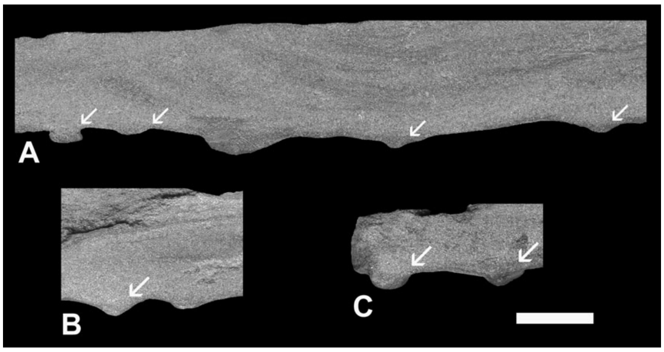


Figure 39: A-C. *Biformites insolitus* LINCK, 1949b, SMNS 22010, Upper Schilfsandstein, Stuttgart Fm, Middle Keuper, Maulbronn, Baden-Württemberg, southern Germany; polished cross-sections, side view. Arrows indicate semireliefs produced by the imprint of arms. The cross-sections show that *Biformites* has an open upper part, thus it is no burrow but an imprint. Scale bar: 1 cm.

Discussion: Judging from the figures presented by HÄNTZSCHEL (1975), based on the originals of LINCK (1949b), some authors concluded that *Biformites insolitus* was a younger synonym of *Protovirgularia dichotoma* (e.g., RINDSBERG 1994; SEILACHER & SEILACHER 1994; SCHLIRF et al. 2001). However, a re-study of the type material suggests that *Biformites insolitus* indeed is a separate ichnogenus and ichnospecies. The bioglyphs are delicate, and due to the small size of the trace fossils, often are difficult to identify. However, upon close examination, the structures revealed a bisymmetrical arrangement of perpendicular, elongate, positive protuberances, which can be interpreted as imprints of the ambulacrals of an asterozoan, probably an ophiuroid. Unfortunately no central disc, typical of ophiuroid traces, could be observed. However, *Ophioichnus aysenensis* BELL, 2004 also does not show the imprint of the central disc but only the imprints of the arms. In *Ophioichnus*, the arm imprints are generally hook-shaped, and it is interpreted as locomotion trace of ophiuroids (BELL 2004). In analogy to *Ophioichnus*, *Biformites insolitus* is also interpreted as locomotion trace of ophiuroids. The varying external morphology of *B. insolitus* is interpreted as a result of imprint depth and the kind of movement performed by the progenitor. If the progenitor pressed its arms deeply into the sediment and removed them again with a push movement, the chances that the details of the ambulacrals are preserved are high. If the arms were removed with a pull movement the imprints are blurred and the result is a more-or-less smooth exterior morphology. Some bioglyphs of the arm imprints of *Heliophycus* new ichnospecies are strikingly similar to the bioglyphs of *B. insolitus* (Fig. 36, 38). The cross sections of *B. insolitus* show that the structures are imprints and no burrows *sensu stricto* because the upper part of each imprint is open. LINCK (1949b) stated that *B. insolitus* is frequently branching. However, this is not true branching but overlap of imprints. If the progenitor pressed one arm into the sediment more than once it appears as branching but is in fact only an overlapping of multiple imprints.

The new interpretation of *Biformites insolitus* of course has serious consequences for the interpretation of the palaeoenvironment in which the traces were produced. The Schilfsandstein complex is interpreted as deposits of a large fluvial system (WURSTER 1964; DITTRICH 1989), reaching from Fennoscandia in the north to the coast of the Tethys in the south (GEYER 2002). However, signs that at least parts of the Schilfsandstein were formed in marine or marginal marine environments are given (e.g., KOZUR & KANNEGIESSER 1972; HELING & BAYER 1982; GEYER & GWINNER 1986; GEYER 1989, 1990; MADER 1995). Glauconite, believed to form exclusively under fully marine conditions (ODIN & MATTER 1981), can be found in the Schilfsandstein complex as allochthonous (see GEYER 2002 for discussion) as well as autochthonous mineral deposits (own observations). Especially the supposed autochthonous glauconite is a strong argument in favour of at least short termed temporary marine incursion, and the huge amounts of allochthonous glauconite in the Schilfsandstein complex do also raise questions (GEYER 2002). Unfortunately no animal body fossils could be found in association with the trace fossils that support marine influences in this part of the Schilfsandstein but also no that can disproove the assumptions. The preservational potential of calcite skeleton elements in siliciclastic deposits is very low. *Kouphichnium*, a xiphosuran trackway, can also be found in the Schilfsandstein (see below), and may give hints for temporary marine incursions during the deposition of the Schilfsandstein. Plant remains, common in the Schilfsandstein, however, clearly indicate a provenance from a terrestrial environment (summarized in GEYER 2002).

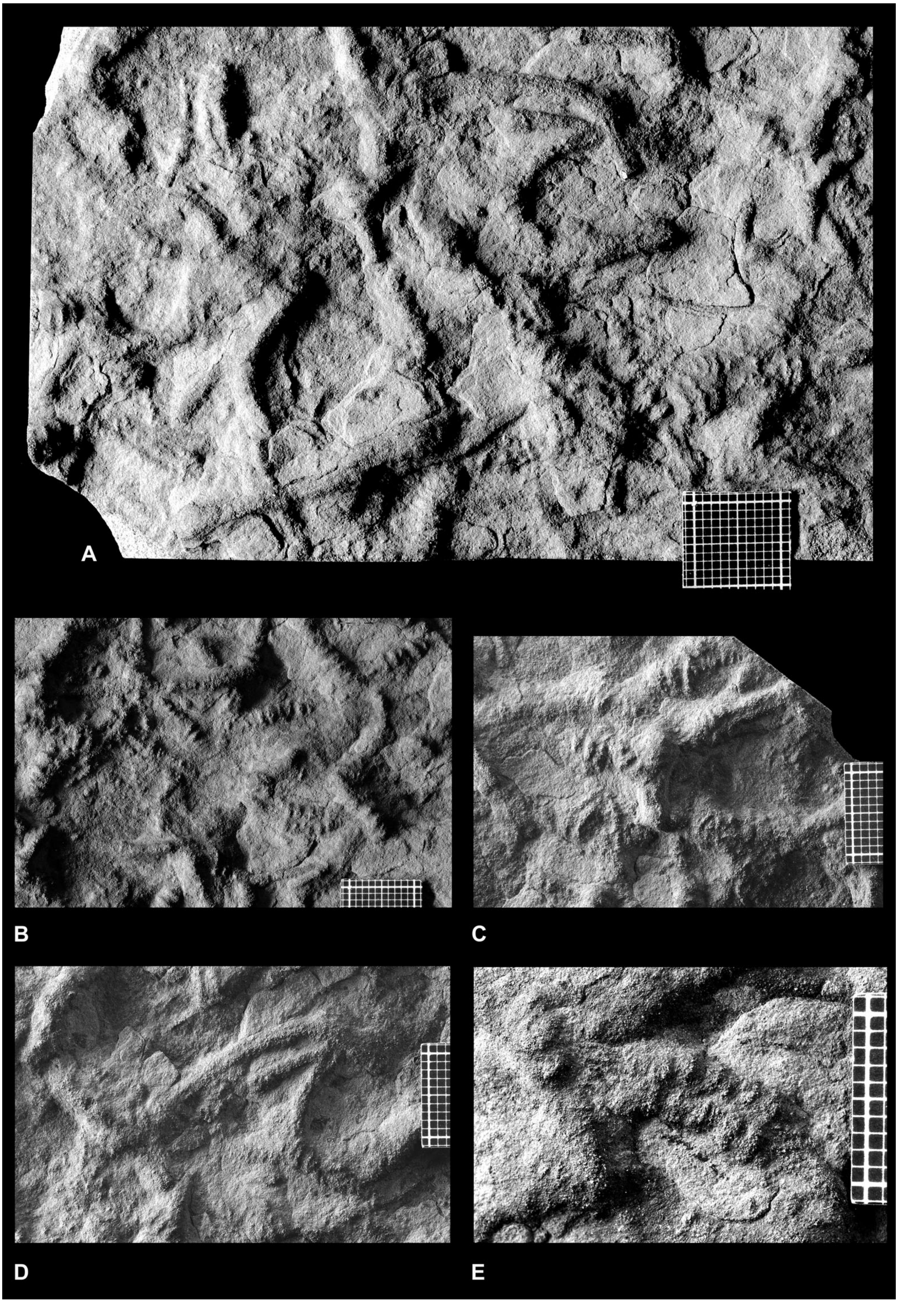


Figure 40: **A-E**. Variuos patterns of ornamentation of *Biformites insolitus* LINCK, 1949b. Positive hyporeliefs, syntypes, SMNS 22010, Upper Schilfsandstein, Stuttgart Fm, Middle Keuper, Maulbronn, Baden-Württemberg, southern Germany. **B, C, E**. Details of ambulacrals preserved due to deep impression and push removal of arms. **D**. Blurred ornamentation due to pull movement of arms. Millimetre grids for scale.

Simple, vertical U-shaped and Y-shaped forms, and irregular vertical structures with associated mounds

This form-group includes simple U-shaped burrows such as *Arenicolites*, Y-shaped structures such as *Solemyatuba*, and the irregular, vertically oriented proposed new Ichnogenus 2.

Ichnogenus *Arenicolites* SALTER, 1857

Type ichnospecies: *Arenicola carbonaria* BINNEY, 1852: 192; by subsequent designation (RICHTER 1924: 137).

Diagnosis: Vertical U-tubes without spreite (after FÜRSICH 1974c).

Arenicolites isp.

Fig. 41

pt 1976 cf. *Cylindricum* sp. LINCK 1949. – POLLARD & LOVELL: 219, fig. 6g, pl. 1 fig. a4-5, b4-5 [*non* fig. 6a-f + h-i; pl. 1 fig. a1-3 + 6, fig. b1-3 + 6 , fig. c = *Skolithos* isp.].

Material: Two specimens on PIW1998VIII-86; Hassberge Fm; Vetter quarry at Schönbachsmühle.

Description: Poorly preserved, irregular U-shaped, cylindrical structure. Fill massive, finer than host rock. Host rock medium grained, yellowish to pinkish sandstone; fill greenish fine-grained to medium-grained sandstone with high clay content. Tube diameter: 9-10mm; burrow length: 55mm; maximum width of U-limbs: 55mm.

Discussion: Due to poor preservation and asymmetry of the structure, an exact assignment is not possible. The burrow diameter is similar to the specimens of *Skolithos* isp. A, also occurring in this bed. This and the poorly developed U-shape makes the same producer very likely. It seems that the *Arenicolites* structures, only found in two specimens on this slab, are forms of exceptional behaviour. The rare occurrence and the asymmetric U-shape seem best explained as a 'mistake' of the producer rather than particular recurring behaviour. For this reason, no further detailed discussion on the behavioural pattern of these structures is given. Similar forms were described by POLLARD & LOVELL (1976). Their material also co-occurs with *Skolithos* isp. and shares the same size range as undoubtful *Skolithos* isp. and consequently was assigned to *Skolithos* isp. by them (= *Cylindricum* in their paper).

BROMLEY & ASGAARD (1979) described *Arenicolites* isp. from nonmarine environments and interpreted the structures as produced by annelids, and pointed out the similarities of their material to the burrows of tubificid oligochaetes from recent freshwater muds described by REINECK (1974). However, the structures presented by REINECK (1974: pl. 3 fig. 11) show a much stronger boxwork pattern than the Triassic material of BROMLEY & ASGAARD (1979). In recent shallow lakeshore sediments tubificid oligochaetes are very important bioturbators and are very abundant in water depth of up to 60m. Tubificid oligochaetes prefer fine-grained nutrient rich sediments (REINECK 1974). *Arenicolites* ranges in age from Ealy Cambrian (NARBONNE et al. 1987) to Holocene (CHAMBERLAIN 1978).

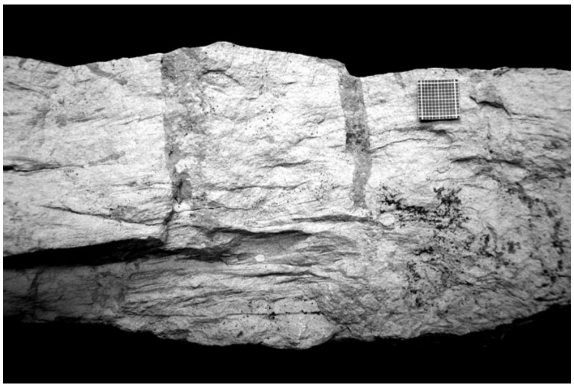


Figure 41: *Arenicolites* isp., PIW2002-I-29, fullrelief, side view, Coburger Sandstein, Hassberge Fm., Vetter quarry at Schön-bachsmühle. Millimetre grid for scale.

Ichnogenus new Ichnogenus 2

Type ichnospecies*:* *Arenicolites franconicus* TRUSHEIM, 1934: 412, pl. XIII fig. 1-2.

Diagnosis*:* Irregularly winding, vertical to oblique, unbranched, short tubular structures; wall smooth without lining; circular in cross-section; associated with a small, epichnial mound next to opening of tubular structure; distal termination of tubular structure built by a small, oval to spherical chamber.

Derivatio nominis*:* After FERDINAND TRUSHEIM, professor for geology, in honour of his work on Franconian geology, and *ίχνος* (ichnos) = Greek for trace.

Remarks*:* While reviewing the invertebrate trace fossils of the Keuper from the southern Germanic Basin, related forms from other localities and/or stratigraphic levels were also studied. In the course of the studies of Franconian *Arenicolites*, the type material of *Arenicolites franconicus* TRUSHEIM, 1934 was re-visited and re-evaluated.

new Ichnogenus 2 *franconicus* (TRUSHEIM, 1934)

Fig. 42-46

v	1934	*Arenicolites franconicus.* – TRUSHEIM: 412, pl. 13 fig. 1-2.
non	1974	*Arenicolites franconicus* TRUSHEIM. – HARY: 114, pl. 10 fig. 2 [= indet].

Diagnosis*:* As for ichnogenus (because of monotypy).

Material*:* Numerous specimens on four slabs, PIW2002-I-1, 2, 3, from Dicke Bank, Upper Muschelkalk 1, Zeil am Main, Lower Franconia, Bavaria, southern Germany.

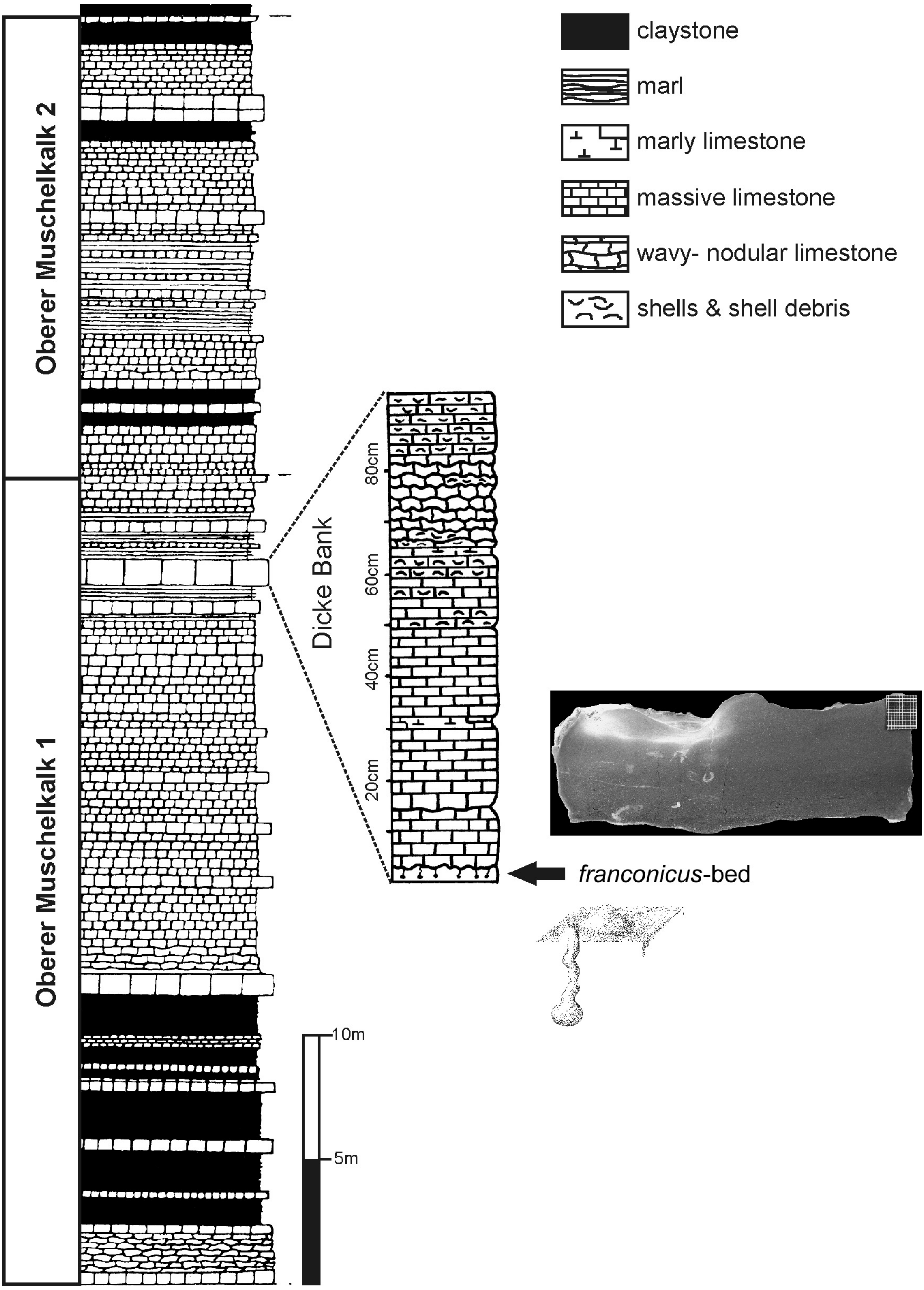


Figure 42: Lithostratigraphic log of the upper Middle Triassic of the Germanic Basin (Upper Muschelkalk 1 & 2) with a detailed log of the so-called "Dicke Bank" ('thick bed', the base of which is formed by the "*Franconicus*-Platte" = '*Franconicus*-slab') near Würzburg, Bavaria, southern Germany. Black arrow indicates the position of new Ichnogenus 2 *franconicus*. Millimetre grid for scale in photograph; reconstruction drawing of new Ichnogenus 2 not to scale. Logs modified after TRUSHEIM 1934; HOFFMANN 1967; GEYER 2002.

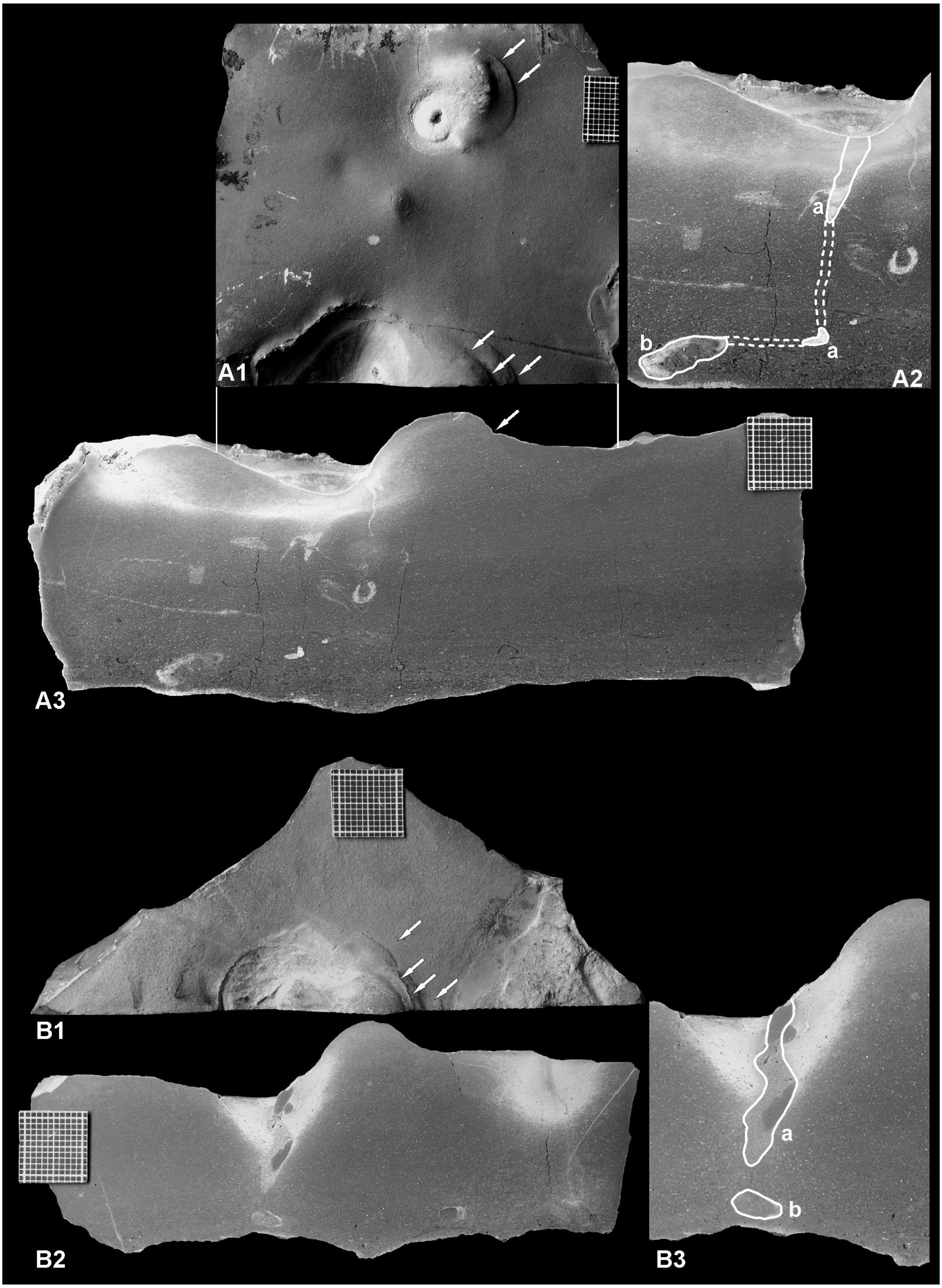


Figure 43: *franconicus.* **A1**. Top view of PIW2002-I-1a, paratypes. Note narrow burrow opening and close epichnial mound (top); white arrows indicate terraces probably formed during mound building. As with any sediment mound the slopes become instable when a certain angle is reached or when the mound becomes too high. If this is the case mounds tend to collapse; a result of such collapses are terraces. **A2**. Detail of **A3** with the irregular tubular structure (a) and the terminal chamber (b) highlighted by white continuous lines; dashed lines indicate supposed course of burrow. **A3**. side view of **A1** in exactly same position; note that terraces (indicated by white arrows) are much more difficult to identify in side view. **B1**. Top view of PIW2002-I-2a, paratypes. **B2**. Side view of **B1**. **B3**. Detail of **B2** with the irregular tubular structure (a) and the terminal chamber (b) highlighted by white continuous lines. Extreme light colour of limestone due to etching with hydrochlorid acid to enhance contrast between burrows and host sediment; the colour differences reflect different calcite/clay content. Millimetre grids for scale.

Description*:* Short, max. 6cm, thin, max. 0.2cm, irregularly winding, unbranched, tubular structures associated with epichnial mounds, 0.2-2cm high, diameter at base, 1-6cm, angle of slope dominantly 10º-30º with a maximum of 60º; some mounds show terraces; burrow fill massive; no wall-lining observed; tubular structures terminate at small, ovoid to spherical chambers, max. 1cm in diameter; burrow tops frequently with funnel-shaped openings, 0.5-4cm in diameter, 0.3-2cm deep, angle of slope 30º-65º.

Discussion*:* The material was first described by TRUSHEIM (1934) and introduced as a new ichnospecies of *Arenicolites* because of its supposed U-shape morphology and its apparent similarity to modern burrows of *Arenicola marina*. However, cross-sections of type material show no U-shape morphology but reveal a very irregular vertical to oblique oriented tubular structure that terminates in an oval or bulbous chamber. In contrast to *Arenicola*-burrows, the corresponding conical mound is not located directly above the burrow opening but next to it (Fig. 43-45). This was not observed by TRUSHEIM. The entire morphology of new Ichnogenus 2 is distinctly different from other known vertical tubular structures, especially from *Skolithos* (see ALPERT 1974, 1975; SCHLIRF & UCHMAN in press). Many specimens show a funnel-shaped top. However, this funnel is not considered to be of ichnotaxonomic importance since the formation of these funnels cannot be reconstructed unequivocally. Funnel-shaped tops of vertical to oblique oriented tubular structures may form due to collapse, by currents, or may be actively built by the producer. However, a final conclusion is impossible in this case, and thus the funnel structures are not considered a valid ichnotaxobase (Fig. 7). For a detailed discussion on ichnotaxobases in simple vertical and horizontal tubular burrows see SCHLIRF & UCHMAN (in press).

By contrast, the epichnial conical mounds associated with the tubular burrows are considered valid ichnotaxobases. Their preservational potential is generally very low, but if present they should not be neglected. Epichnial conical mounds located next to burrow openings obviously are the result of behaviour, and an abiogenic formation can be excluded. As the mounds are located next to the opening they possibly represent faecal material of the progenitor, or are excavated material from the burrowing activity, or are a mixture of both. Thin sections do not show any lithological differences of mound material to material of the host matrix; faecal pellets could not be identified (Fig. 43-45). Interestingly, no discontinuity between the base of the mounds and the bedding plane was observed. The excavated material building the mounds and the sea floor sediment must have been soft enough to allow a

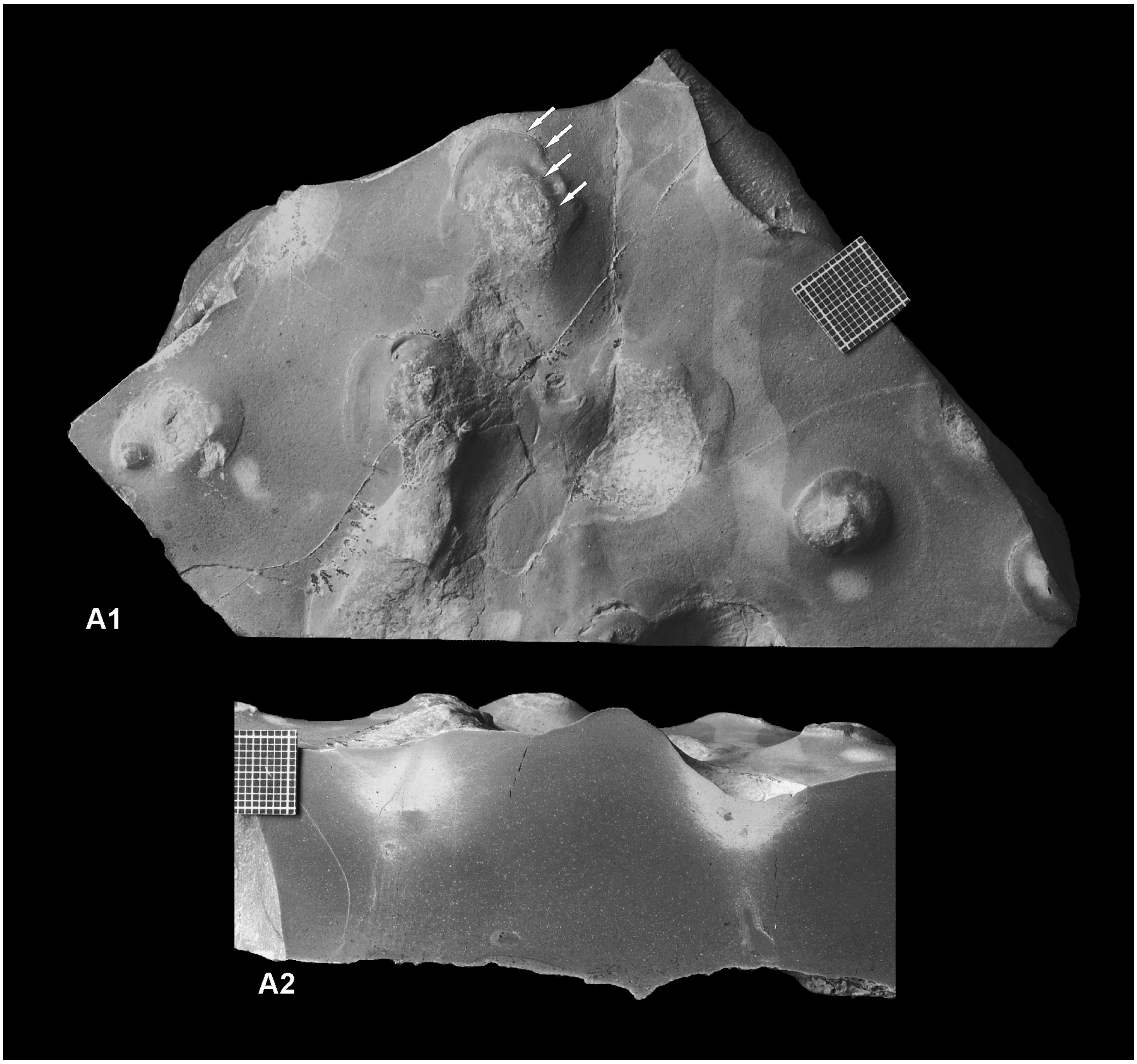


Figure 44: New Ichnogenus 2 *franconicus.* **A1**. Top view of PIW2002-I-2b, paratypes; white arrows indicate terraces. **A2**. side view of **A1** in exactly same position. Millimetre grids for scale.

‘melting together’. On the other hand, the sediment must have been cohesive enough to allow the formation of mounds with terraces. The observed terraces in the mounds are interpreted as being formed due to excavation. They may reflect discontinuous mound building or may have formed during a continuous mound building. As with any sediment mound the slopes become instable when a certain angle is reached or when the mound becomes too high. If this is the case mounds tend to collapse. As a result of such collapses the terraces have formed. The observed maximum slope angle of 60° suggests a subaquatic formation of the mounds. Only subaqueous sediment mounds can support such steep angles. The fact that the burrows are associated with a funnel and a mound structure indicates a biogenic origin and excludes weathering effects.

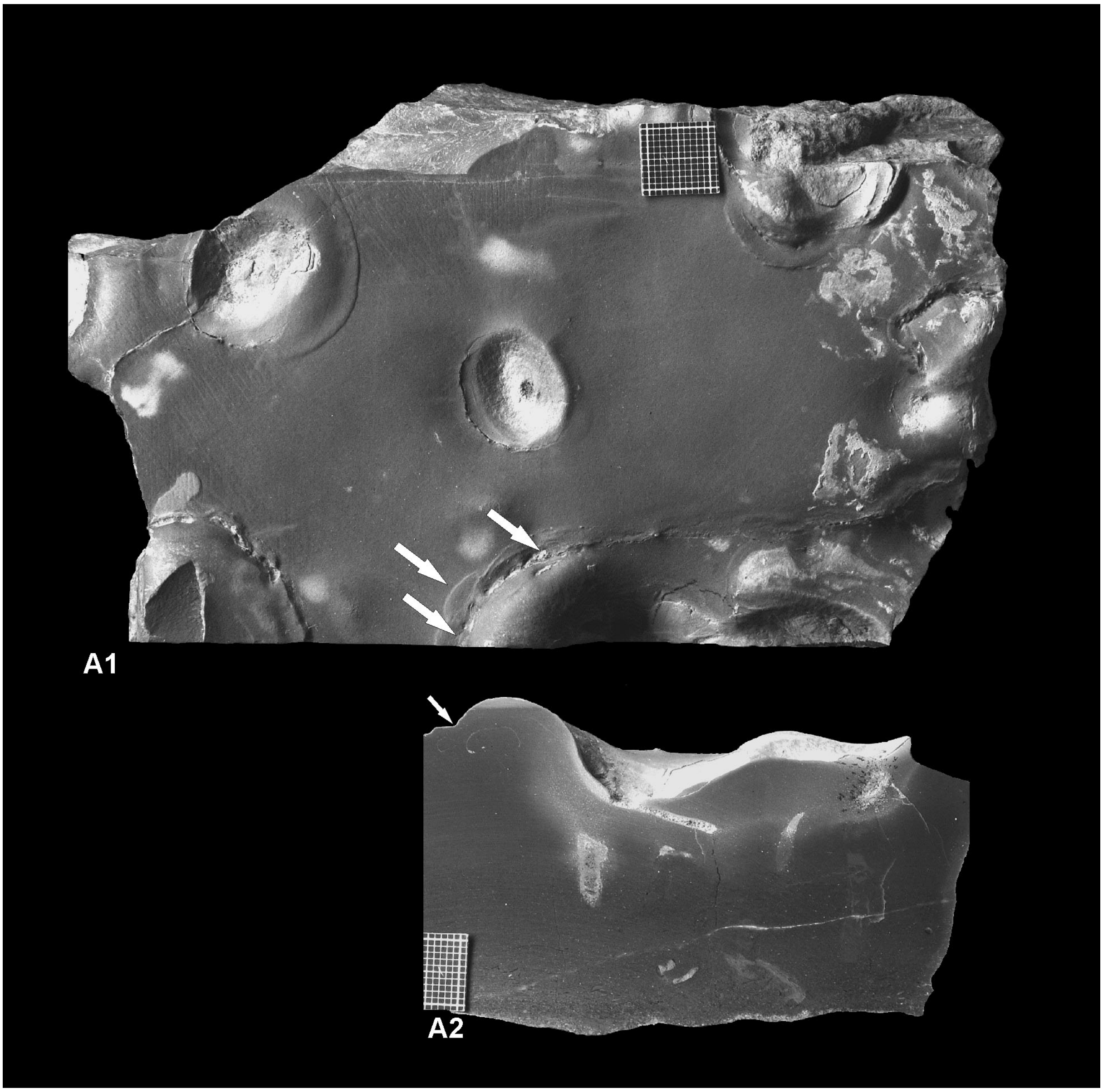


Figure 45: New Ichnogenus 2 *franconicus.* **A1**. Top view of PIW2002-I-1b, paratypes. **A2**. Side view of **A1** in exactly same position. White arrows indicate terraces. Millimetre grids for scale.

Epichnial mounds are only rarely reported from the marine realm. RIETH (1931) reported epichnial mounds associated with *Arenicolites* from Rhaetic sandy deposits in southern Germany. The only true epichnial mound-shaped trace fossil hitherto known is *Chomatichnus* DONALDSON & SIMPSON, 1962. *Chomatichnus* is a small conical mound with a centrally located vertical tubular burrow; the mounds are made up of faecal castings (DONALDSON & SIMPSON 1962). SCHLIRF et al. (2001) assigned a report by GEYER (1987) of an undetermined conical trace fossil from the *Modiola* bed (Grabfeld Fm, Middle Keuper) to *Chomatichnus* with restrictions only because of the lack of faecal material in the mound.

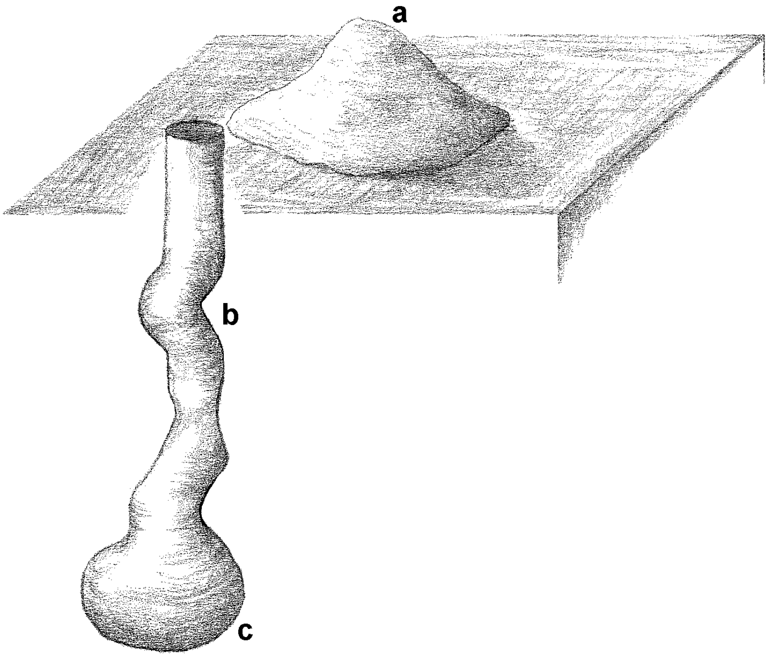


Figure 46: Reconstruction of *Trusheimichnus franconicus* with the epichnial mound (a) situated close to the funnel-shaped burrow opening; irregular course of the tubular structure (b) and the terminal chamber (c). Not to scale.

The newly proposed ichnogenus is common in the Middle Triassic (‘*Franconicus*-Platte’ at the base of ‘Dicke Bank’, Upper Muschelkalk 1, upper Middle Triassic) of the Germanic Basin. The horizons bearing new Ichnogenus 2 *franconicus* are long known as ‘*Franconicus*-Platte’ (‘*Franconicus*-slab’) of German authors and are locally of stratigraphic use. The newly proposed ichnogenus name was chosen in masculine gender to maintain the gender of the ichnospecies *T. franconicus* in order to avoid confusion.

Any small marine arthropod could be a possible producer of new Ichnogenus 2. Unfortunately, a more precise statement is impossible because no morphological features (e.g., faecal pellets, scratch ornaments etc.) have been observed, which reveal details of the body morphology of the progenitor. Due to the fact that the burrows are very irregular and the terminal chamber is quite small, a non-vermiform producer seems more likely than a vermiform one. Most burrows of vermiform animals tend to be elongate and may be branching but usually consist of relatively long regular burrow parts (e.g., the burrows of *Lanice*, *Arenicolites*, *Heteromastus* etc.). Due to the small size, little sediment of the host bed is disturbed. This and a predominantly vertical orientation make a suspension-feeding mode of life of the progenitor likely. The amount of reworked sediment seems too small for an effective deposit-feeding. The deposits bearing the trace fossils are normal graded, dark grey mudstones to wakestones, with erosive base, best interpreted as distal tempestites. The stratigraphic occurrence of new Ichnogenus 2 is upper Middle Triassic (‘*Franconicus*-Platte’, Upper Muschelkalk 1) (TRUSHEIM 1934).

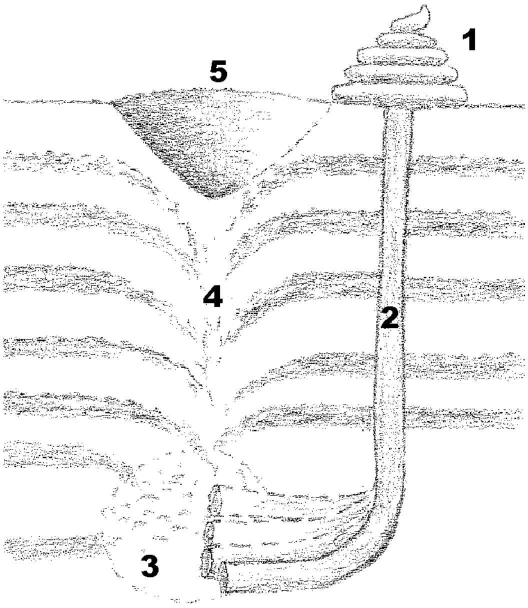


Figure 47: Sketch of a structure produced by *Arenicola* spp. (after SCHÄFER 1962). 1, faecal castings; 2, J-shaped tubular burrow; 3, mottled area due to feeding action (removal of sediment); 4, destroyed sedimentary structures as a result of collapse in direction of the cavity produced by feeding behaviour; 5, funnel-shaped collapse structure on sea-floor. While feeding *Arenicola marina* removes sediment, the so formed cavity is usually immediately filled with collapsed sediment from above; as a result, funnel-shaped collapse structures frequently can be observed on the sea floor. From all the observed structures only 1 & 2 qualify as trace fossils if fossilized. 3 is an area with indistinct mottling, thus no truly recurrent morphological entity, which can be called bioturbated. 4 & 5 are unambiguously structures related to behaviour but are just passive physical reactions of the sediment and are neither bioturbation nor trace fossils.

Ichnogenus *Solemyatuba* SEILACHER, 1990b

Type ichnospecies: *Solemyatuba ypsilon* SEILACHER, 1990b: 307, fig. 5; by subsequent designation herein.

Emended diagnosis: Vertical, U- to Y-shaped structure made up of a U-tube, with smooth wall and elliptical cross-section, whose longer diameter is always in plane of the U. Occasionally a vertical to steeply oblique, blind extension tube descending from the base of the U is present.

Discussion: Yet no type ichnospecies has been designated for *Solemyatuba*. Since all ichnogenera should have type ichnospecies this is done here. *Solemyatuba ypsilon* is proposed as type ichnospecies, since only this ichnospecies shows the typical Y-shaped morphology. *S. subcompressa* (EICHWALD, 1856) is characterized by lacking a lower extension tube (SEILACHER 1990b). This results in a U-shaped pattern. U-shaped trace fossils are usually assigned to *Arenicolites*. SEILACHER (1990b) pointed out that *Solemyatuba* differs from *Arenicolites* in having a semicircular shape, rather than a typical U-shape with upward directed parallel limbs, and having an elliptically flattened cross-section in the plane of the U. Upon close examination the figures provided by SEILACHER (1990b: fig. 5) do not reveal a semicircular shape but rather a true U-shape. The elliptical cross-section may be very difficult to ascertain in every specimen. Only future will show if the distinction criteria mentioned above justify a separation at the ichnogeneric level. RIETH (1931) provided the first descriptions of *Solemyatuba ypsilon* from Rhaetic deposits near Nürtingen, Baden-Württemberg. However, he erroneously interpreted them as borings.

Solemyatuba ypsilon clearly shows an overall Y-shaped morphology due to the lower extension tube, and thus can easily be identified and distinguished from other trace fossils. *Psilonichnus* FÜRSICH, 1981 also has a Y-shaped morphology, but the tubes have a circular cross-section, the ratio of the tube diameter to the diameter of the U is higher. *Polykladichnus* FÜRSICH, 1981 by contrast, shows single to multiple upward directed Y- to U-shaped branching and has a much higher depth to width ratio. BROMLEY & GOLDRING (1992) and GOLDRING et al. (2002) describe bow-form burrows as *Glyphichnus* and *Cylindrichnus*. They argue that their material should not be assigned to *Arenicolites* because it does not show a complete U-shaped morphology with parallel limbs opening at the surface. Rather it shows a cateniform, limb-free vertex morphology. The structures are filled either passively (*Glyphichnus*) or semi-actively (*Cylindrichnus*). Semi-active filling is assumed because the fill material was most likely transported passively into the open burrow but due to burrow maintenance action of the progenitor, this material was pushed aside and finally resulted in a concentrically laminated fill. At first sight such structures may be confused with *Solemyatuba*, however, *Solemyatuba* shows a more true U-shaped nature than the bow-form burrows.

The original diagnosis provided by SEILACHER (1990b) contains assumptions on possible behaviour and progenitors of the trace fossil. Such information should be avoided in a diagnosis, thus it is emended.

Solemyatuba ypsilon SEILACHER, 1990b

Fig. 48

	1931	U förmige Bohrröhren. – RIETH: fig. 1, 2, 4.
*	1990b	*Solemyatuba ypsilon* n. ichnog., n. ichnosp. – SEILACHER: 307.
	1990b	*Solemya tuba ypsilon* n. ichnog., n. ichnosp [sic]. – SEILACHER: fig. 5.
	2001	*Solemyotuba ypsilon* SEILACHER [sic]. – SCHLIRF et al: 96, tab. 1.

Emended diagnosis: Y-shaped structure made up of semicircular U-tube with smooth wall and elliptical cross-section, whose longer diameter is always in plane of the U. Essentially with a lower extension tube.

Material: Specimens GIPT-1682-1, 2, 3, 4 from the collection of the Geologisch-Paläontologisches Institut Tübingen, Rhätsandstein, Exter Fm, Olgahain quarry, Bebenhausen near Tübingen, Baden-Württemberg, southern Germany [not seen].

Discussion: SEILACHER's (1990b) original diagnosis did not consider the orientation of the structure, and is thus emended. Unfortunately, due to a print error the figure showing the holotype of *Solemyatuba* is erroneously assigned to a non-existing bivalve subspecies ('*Solemya tuba ypsilon*'). However, since SEILACHER (1990b) correctly introduced the new name, and there can be no doubt that the error is a type error, the ichnogenus and the ichnospecies introduced by SEILACHER (1990b) remain avilable.

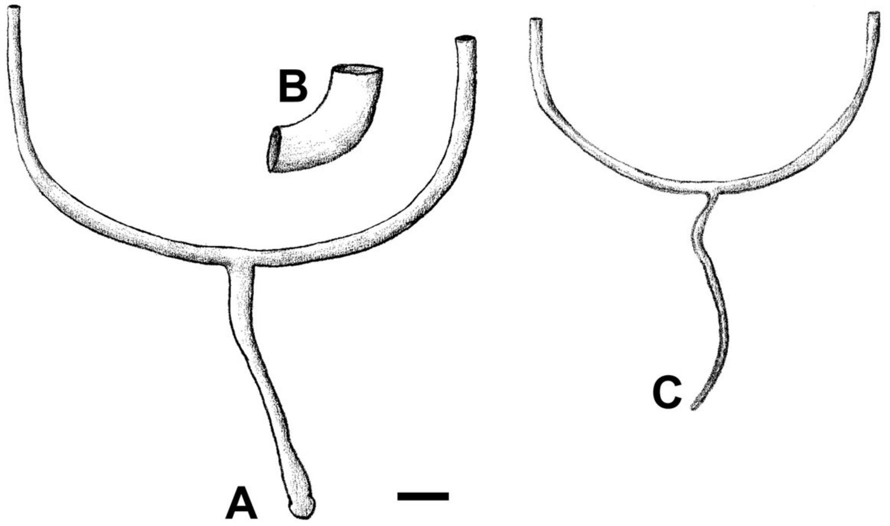


Figure 48: Reconstructions of paratypes of *Solemyatuba ypsilon,* redrawn after fig. 5A-B of SEILACHER (1990b). **A** & **C**. Complete specimens. **B**. Enlarged tube segment with elliptical cross-section. Scale bar: 1cm.

Simple and complex, vertically oriented tubular structures

This form-group includes straight and curved, vertical to sub-vertical burrows such as *Skolithos*, multiple upward branched forms such as *Polykladichnus,* and epichnial mound and funnel structures such as *Monocraterion*, *Mammilichnis*, *Arenituba*, and *Chomatichnus*.

Ichnogenus *Polykladichnus* FÜRSICH, 1981

Type ichnospecies: *Polykladichnus irregularis* FÜRSICH, 1981: 3, fig. 2, pl. 3 fig. 1-4; by monotypy.

Emended diagnosis: Lined or unlined, vertical to steeply oblique tubes with single or multiple Y- or U-shaped, upward branched bifurcation and slight enlargement at junctions; tubes usually connecting to the bedding surface.

Ichnogenera and ichnospecies belonging to *Polykladichnus*:

p 1890 *Scolithus* [sic]. – DAWSON: 602, only left specimen of fig. 8 [= *Polykladichnus aragonensis*; *non* fig. 7 and right specimen of fig. 8 = *Skolithos linearis*].
v, p 1937 *Sabellarifex eifliensis* (RUD. RICHTER, 1920). – DAHMER: 535 [only branched specimens = *Polykladichnus aragonensis*; *non* unbranched specimens = *Skolithos linearis*].
v, p 1938 *Sabellarifex eifliensis* (RUD. RICHTER, 1920). – DAHMER: 72 [only branched specimens = *Polykladichnus aragonensis*; *non* unbranched specimens = *Skolithos linearis*].
?p 1939 *Sabellarifex eifliensis* (RUD. RICHTER). – DAHMER: 357 [only branched specimens = *Polykladichnus aragonensis*; *non* unbranched specimens = *Skolithos linearis*].
p 1955 *Tigillites* (= *Scolithus*) [sic]. – LESSERTISSEUR: 60, fig. 34F [only branched specimens; *non* unbranched specimens = *Skolithos linearis*].
v, p 1962 *Sabellarifex* RUDOLF RICHTER, 1921. – HÄNTZSCHEL: *W*214 [only unbranched specimens = *Skolithos linearis*; *non* branched specimens = *Polykladichnus aragonensis*].
v, p 1962 *S. eifliensis*. – HÄNTZSCHEL: *W*215, fig. 132.1a-b [only unbranched specimens = *Skolithos linearis*; *non* branched specimens = *Polykladichnus aragonensis*].
v, p 1975 *Sabellarifex* RICHTER, 1921. – HÄNTZSCHEL: *W*102 [only branched specimens = *Polykladichnus aragonensis*; *non* unbranched specimens = *Skolithos linearis*].
v, p 1975 *S. eifliensis*. – HÄNTZSCHEL: *W*102, fig. 64,5 [only branched specimens = *Polykladichnus aragonensis*; *non* unbranched specimens = *Skolithos linearis*].
? 1977 probable cerianthid anemone dwelling structure. – CURRAN & FREY: 143, pl. 1 fig. e.
p 1979 *Arenicolites* sp. – BROMLEY & ASGAARD: 43, fig. 3A-C, 4 [only branched forms = *Polykladichnus aragonenis*; U-shaped forms = *Arenicolites* isp.; slightly curving, unbranched forms = *Skolithos linearis*].
1981 *Polykladichnus* gen. nov. – FÜRSICH: 155.
* 1981 *Polykladichnus irregularis* sp. nov. – FÜRSICH: 155, pl. 3 fig. 1-4, fig. 2.
1986 *Polykladichnus* ichnosp. – D'ALESSANDRO & BROMLEY: 82 [= *Polykladichnus aragonensis*].
1988 *Polykladichnus irregularis* FÜRSICH. – PEMBERTON & JONES: 499, fig. 7.1, 7.3, 7.5.
1988 *Polykladichnus*. – POLLARD: 340, fig. 2e.
1989 *Polykladichnus*. – JONES & PEMBERTON: 345.
1990 *Polykladichnus* isp. – BROMLEY: 208, fig. 11.15, 11.16a.
1991 *Arborichnus* new ichnogen. – EKDALE & LEWIS: 264, fig. 3-4.
1992 ?*Polykladichnus* isp. – D'ALESSANDRO et al.: 501, fig. 12.
? 1992 ?*Polykladichnus* isp. – MELCHOR & POIRÉ: 246, fig. 2c.
1994 *Polykladichnus*. – WEISSBROD et al.: 69.
1995 *Polykladichnus irregularis* FÜRSICH. – PORĘBSKI: 38, fig. 25.
1996 *Polykladichnus*. – BROMLEY: 233, fig. 10.16, 10.17a.
1996 *Polykladichnus*. – ZHANG et al.: 134.
? 1997 *Polykladichnus irregularis* (FÜRSICH 1981) [sic]. – WEISSBROD & SNEH: 90; fig. 13.
? 1998 *Polykladichnus irregularis* FÜRSICH 1981. – WEISSBROD & BARTHEL: 160.
? 1998 *Polykladichnus irregularis*. – WEISSBROD & BARTHEL: fig. 3.1-3.7, 3.9.
? 1996 *Polykladichnus*. – WROBLEWSKI: 1091.

2000 *Polykladichnus irregularis* FÜRSICH. – ACEÑOLAZA & ACEÑOLAZA: 218, pl. 4 fig. B.
2000 *Polykladichnus irregularis* FÜRSICH. – LECH et al.: 154, fig. 5a-a'.
v 2000 *Polykladichnus aragonensis* n. isp. – UCHMAN & ÁLVARO: 214, fig. 6A-E.
v 2001 cf. *Polykladichnus* isp. – SCHLIRF et al.: 73, fig. 4A.
v, p 2002 *Sabellarifex eifliensis* RICHTER, 1921 [sic]. – SCHLIRF et al.: 48, pl. 2 fig. 1-2 [only branched specimens = *Polykladichnus aragonensis*; *non* unbranched specimens = *Skolithos linearis*].

Remarks: The author is aware that a synonymy should compare genera only to genera, not to species, but this is often done, and is so often useful (e.g., KEIGHLEY & PICKERILL 1994; UCHMAN 1995, 1998). The diagnosis given by SCHLIRF et al. (2001) is corrected here to consider multiple branching in *Polykladichnus*.

Discussion: *Polykladichnus* is a well-defined and generally well-understood ichnogenus and is hardly ever confused with other ichnogenera. Only *Sabellarifex* seems to be confused with *Polykladichnus* as shown in the above list. However, this is clearly the result of overseeing the branching pattern in some specimens among the studied material.

Arborichnus sparsus EKDALE & LEWIS (1991) from Quaternary fan delta deposits of New Zealand is synonymous with *Polykladichnus irregularis*.

Polykladichnus aragonensis UCHMAN & ÁLVARO, 2000

Fig. 49-53, 57

Diagnosis: Unlined, vertical to steeply oblique tubes with single or multiple Y- or U-shaped bifurcation and slight enlargement at junctions. Tubes usually connecting to the bedding surface (after UCHMAN & ÁLVARO 2000).

Material: PIW1998VIII-36, Coburger Sandstein, Hassberge Fm, Middle Keuper, Schleifsteinwerke quarry near Eltmann, Lower Franconia, Bavaria, southern Germany; PIW2002VI-1, 2, 3, 4, SMF collection Richter XVI 1a-f, Taunus quartzite, Lower Devonian, Rossel, west of Rüdesheim, Hesse, Germany; numerous field observations. Only the branched specimens on the various slabs are assigned to *Polykladichnus aragonensis*; co-occurring unbranched forms on the slabs are assigned to *Skolithos linearis*. See list above for more details.

Description: Unlined, vertical to steeply oblique, straight to slightly curved, Y-shaped and U-shaped upward branched tubular structures with slight enlargements at junctions; diameter of single tube 1-2mm; length of entire structures up to 7cm. Burrow fill generally finer than host sediment. Preserved as full-relief.

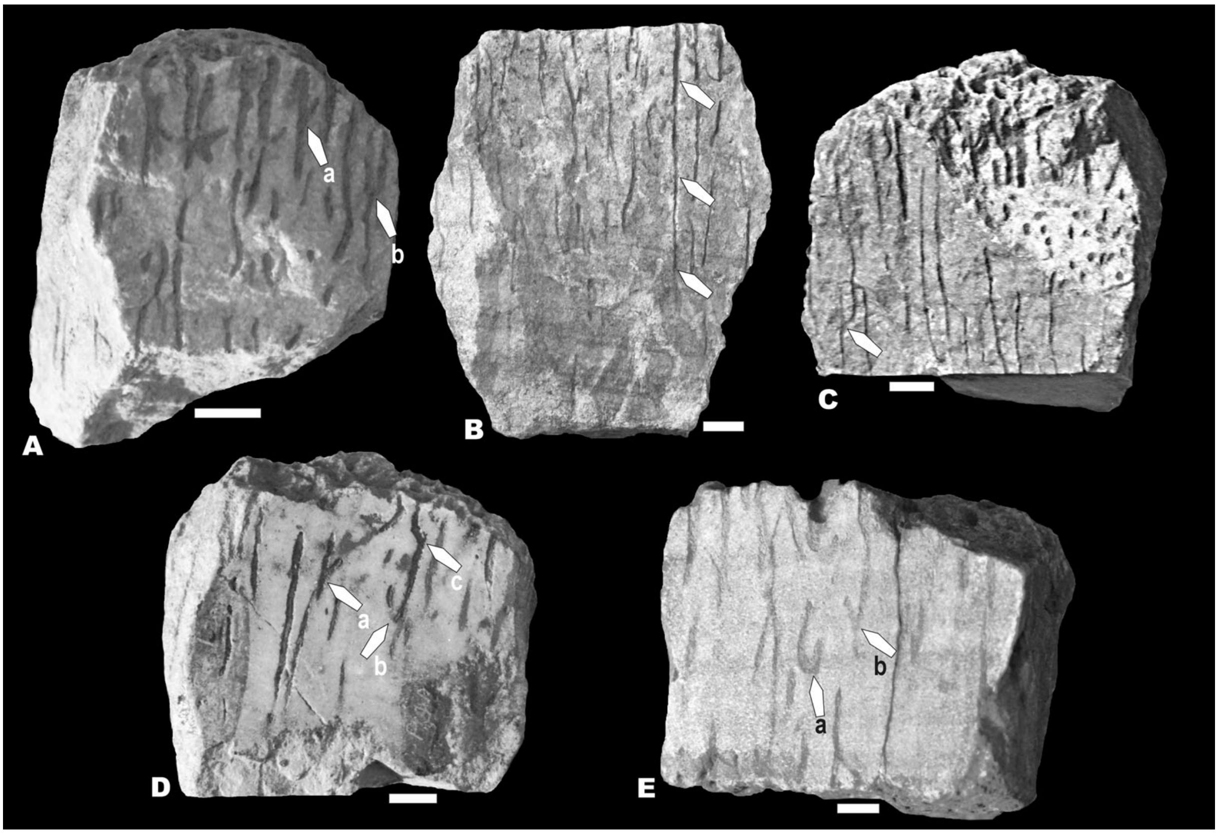


Figure 49: **A**. Y-shaped branching pattern of *Polykladichnus aragonensis* (a); U-shaped branching pattern of *P. aragonensis* (b); both side view, full relief (SEN Richter XVI 1e). **B**. Lectoptype of *Sabellarifex eifliensis* (= *Skolithos linearis*) indicated by three white arrows (SEN Richter XVI 1d). **C**. truly branched *P. aragonensis* indicated by white arrow; side view, full relief; original of RICHTER (1920: fig. 1; SEN Richter XVI 1a). **D**. cross-over of two specimens (a); true branching of *P. aragonensis* (b&c); side view, full relief; original of Richter (1920: fig. 1; SEN Richter XVI 1a). **E**. U-shaped branching pattern of *P. aragonensis* indicated by white arrow (a) and Y-shaped branching pattern of *P. aragonensis* indicated by white arrow (b); side view, fullreliefs (SEN Richter XVI 1f). Scale bars: 1cm.

Discussion: Currently two ichnospecies of *Polykladichnus* are known: *P. irregularis* FÜRSICH, 1981 (with wall-lining) and *P. aragonensis* UCHMAN & ÁLVARO, 2000 (unlined). The two forms are distinguished by the presence/absence of a wall-lining. As discussed below, a wall-lining is considered an ichnotaxobase at the ichnospecific level in vertically oriented tubular burrows.

Arenicolites isp. in BROMLEY & ASGAARD (1979: fig. 3-4), displays a similar pattern, but is slightly thinner and shows a much higher burrow density. However, among their specimens of *Arenicolites* isp. are obvious U-shaped burrows. These trace fossils were interpreted by BROMLEY & ASGAARD (1979) as produced by annelids and referred to burrows of tubificid oligochaetes illustrated by REINECK (1974: pl. 3 fig. 11). However, morphological similarities between them are doubtful.

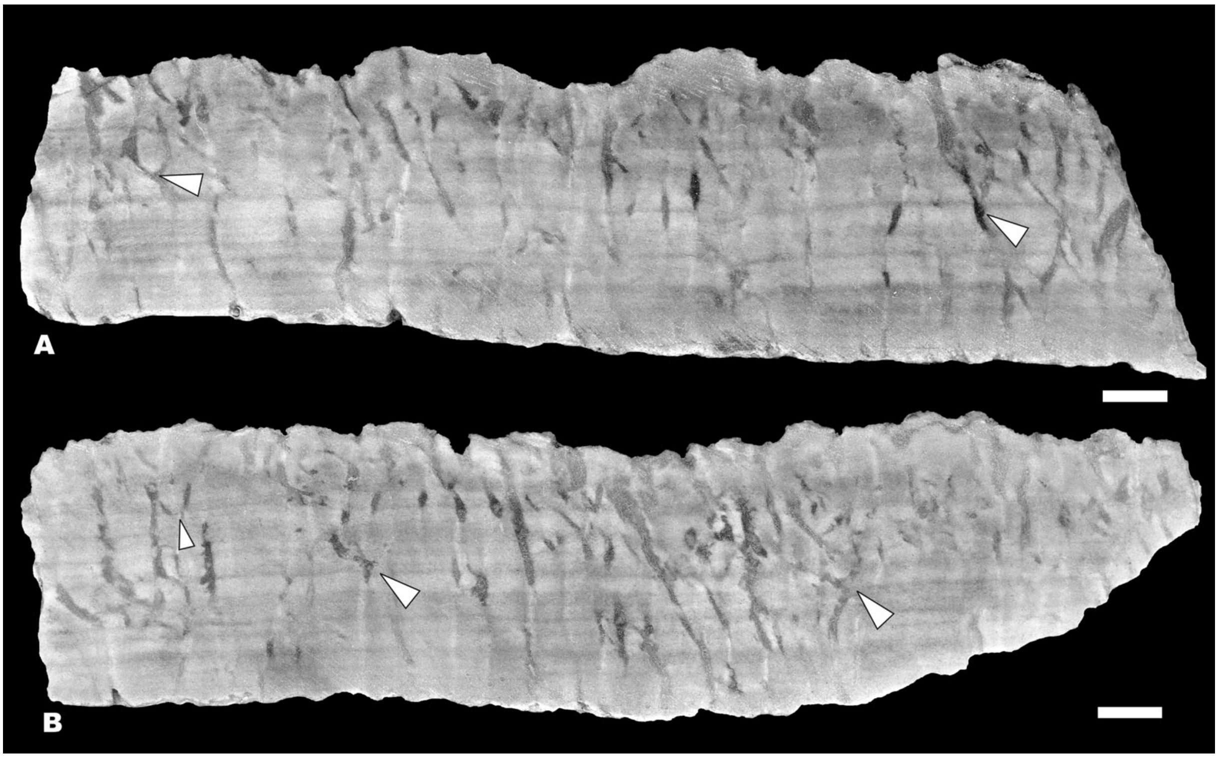


Figure 50: A-B. Numerous *Skolithos linearis* and *Polykladichnus aragonensis* on polished slabs. **A**. PIW2002VI-3. **B**. PIW2002VI-4, Lower Devonian Taunus Quartzite, near Rüdesheim, Hesse, Germany. Arrows indicate junctions of *P. aragonensis*. Burrow density increases toward top of sandstone bed, interpreted as a result of frequent upward directed branching. Both side view, fullreliefs. Scale bars: 1cm.

Polykladichnus aragonensis ranges from Devonian (e.g., RICHTER 1920, 1921; SCHLIRF et al. 2002) to Pleistocene (D'ALESSANDRO et al. 1992) marine deposits to Upper Triassic (e.g., SCHLIRF et al. 2001) and Miocene (UCHMAN & ÁLVARO, 2000) nonmarine deposits.

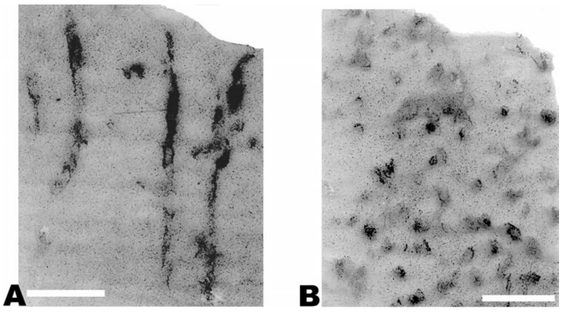


Figure 51: Thin sections of *Polykladichnus aragonensis* and *Skolithos linearis* from the Lower Devonian Taunus Quartzite near Rüdesheim, Germany. **A**, PIW2002VI-1, side view. **B**, PIW2002VI-2, top view; both fullreliefs. Scale bars: 1cm.

Polykladichnus occurs in marine and nonmarine environments. However, in contrast to *Skolithos,* marine occurrences clearly dominate over nonmarine occurrences. So far, only two reports of nonmarine *Polykladichnus* are known (UCHMAN & ÁLVARO 2000; SCHLIRF et al. 2001). UCHMAN & ÁLVARO (2000) introduced a new ichnospecies of *Polykladichnus* namely *P. aragonensis*. This form differs from *P. irregularis* by having a wall-lining (see discussion below).

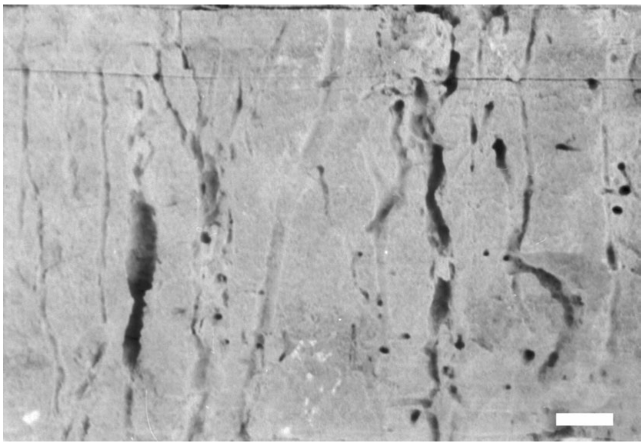


Figure 52: Field photograph of *Polykladichnus aragonensis* (paratype) from the Miocene of the Teruel Basin near Terrer (Zaragoza), Spain. Fullreliefs, side view. Scale bar: 1 cm.

The form reported by SCHLIRF et al. (2001) was only assigned with reservation to *Polykladichnus* but is here assigned to *P. aragonensis*. BROMLEY & ASGAARD (1979) described high-density *Arenicolites* from their terrestrial suite, some specimens of which strongly resemble *Polykladichnus*.

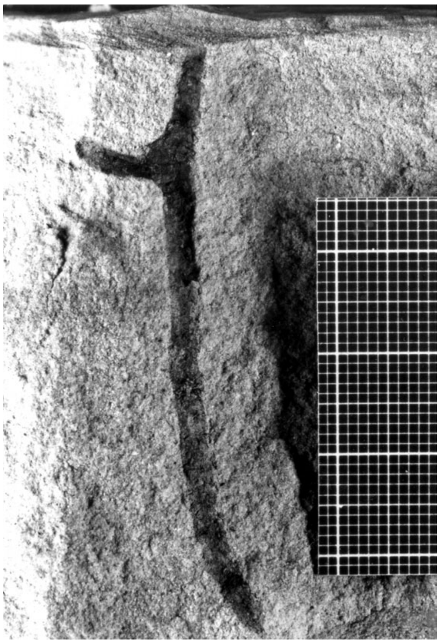


Figure 53: *Polykladichichnus aragonensis*, PIW1998-VIII-36, Coburger Sandstein, Hassberge Fm, Middle Keuper, Schleifsteinwerke quarry near Eltmann, Lower Franconia, Bavaria, southern Germany. Note slight enlargement at point of bifurcation . Fullrelief, lateral view. Millimetre grid for scale.

As possible producers for marine *Polykladichnus,* polychaetes are relevant candidates and cerianthid anemones. FREY (1970) described traces of recent actinian and cerianthid anemones. The actinian anemones produce simple, vertical, non-branching tubular traces without any stabilization; FREY (1970) reported that these structures were readily destroyed while digging them free for studies. The cerianthid *Cerianteopsis americanus* builds Y-branched, vertical tubes with a mucus-stabilised wall-lining (Fig. 54). The anemones incorporate sand grains, shell debris and mucilaginous cnidae (shed nematocysts) in their burrow wall-lining (FREY 1970). Of course those cnidae have no fossilisation potential but the mucus-stabilised wall increases the general fossilisation potential. FÜRSICH (1981) stated that the recent polychaete *Heteromastus filiformis* builds similar structures that look like *Polykladichnus*. However, according to studies by SCHÄFER (1962) and HOWARD & FREY (1975) the

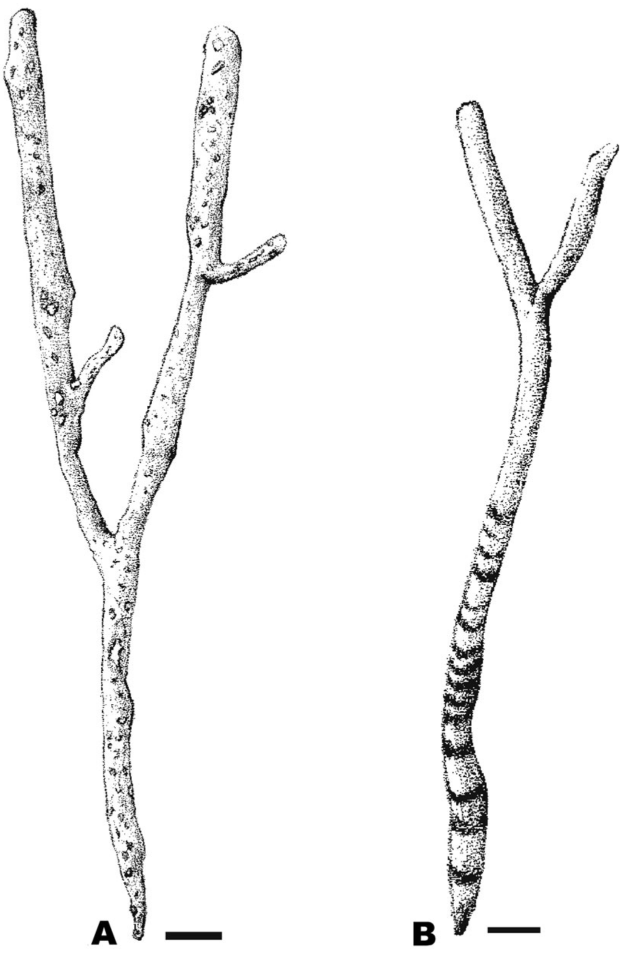


Figure 54: **A**. Sketch of burrow of the anemone *Ceriantheopsis americanus* with upward directed Y-shaped branching. Function of secondary small Y-shaped branches is unknown (after FREY 1970). **B**. Sketch of probable cerianthid anemone dwelling structure with meniscate fill in the lower part (after CURRAN & FREY 1977). Scale bars: 1cm.

structures built by *H. filiformis* generally are more complex (Fig. 55B) than *Polykladichnus*. Studies of some Georgia estuaries by HOWARD & FREY (1975) and DÖRJES & HOWARD (1975) showed that recent polychaetes do play a very important role in these environments and that they build a wide range of vertically oriented tubular burrows. The probable cerianthid burrow of CURRAN & FREY (1977) shows meniscate backfill in the lower part of the structure (Fig. 54), a feature not uncommon in cerianthid burrows (SCHÄFER 1962; Fig. 56).

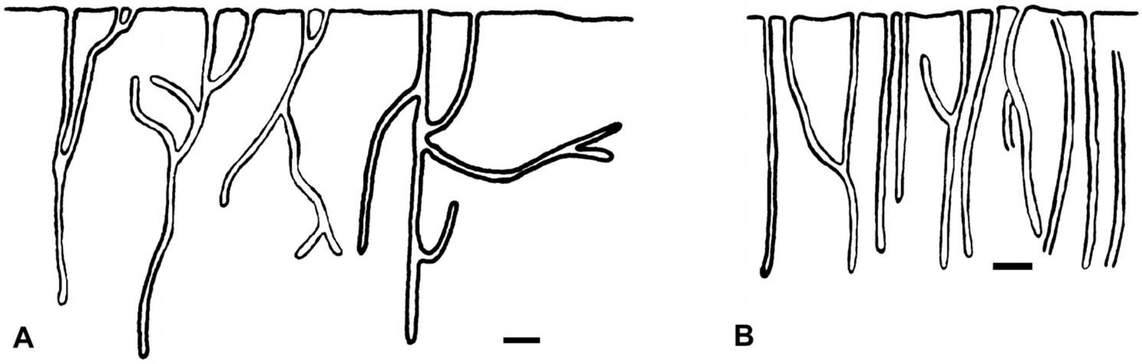


Figure 55: **A**. Sketch of multiple branching burrows of the polychaete *Heteromastus filiformis*. Note the frequent downward directed Y-shaped branching (right specimens) and the generally very complex nature of the

burrows. Slight enlargements at junctions can be seen in all specimens (after SCHÄFER 1962; HOWARD & FREY 1975). **B**. Sketch of simple vertical (*Skolithos linearis* if fossil) and upward Y-shaped branching burrows (*Polykladichnus aragonensis* if fossil) of the polychaetes *Magelona* and *Scolecolepides* (after HOWARD & FREY 1975). Scale bars: 1cm.

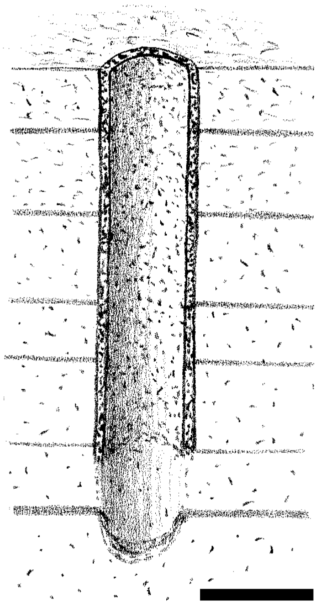


Figure 56: A. Sketch of a burrow made by the anemone *Cerianthus* spp. Burrow wall with distinct wall-lining, stabilised with mucus, sand grains, shell debris and cnidae. The lowermost ends of cerianthid burrows often show meniscate sediment fillings and lack a wall-lining (after SCHÄFER 1962).

The polychaetes *Magelona*, and *Scolecolepides* also build simple vertical burrows which, if fossilised, would be named *Skolithos*; as well as simple, upward directed Y-shaped branching structures, named *Polykladichnus* if found fossilised (HOWARD & FREY 1975, Fig. 55B). The nonmarine *Polykladichnus* are certainly built by other organisms than the marine examples. UCHMAN & ÁLVARO (2000) assumed insects or insect larvae as possible producers. This opinion was also supported by SCHLIRF et al. (2001). However, concerning an insect origin of *Polykladichnus* the following facts should be mentioned. Insect traces typically have chambered structures or cells. Branching tunnel systems are known among insects but if they show Y-shaped branching it usually is an inverted Y and the tunnels usually terminate at cells. Horizontal branching structures are also known, but again the tunnels end at cells. Today bees, beetles, ants or termites are possible tracemakers of such structures (pers. comm. GENISE, Trelev). One of the few examples of truly Y-shaped branching traces made by a staphylinid beetle (*Bledius*) were reported by LARSEN (1936) and RATCLIFFE & FAGERSTROM (1980). Vertical U-shaped structures are typical of subaqueous and not common of terrestrial environments (pers. comm. GENISE, Trelev).

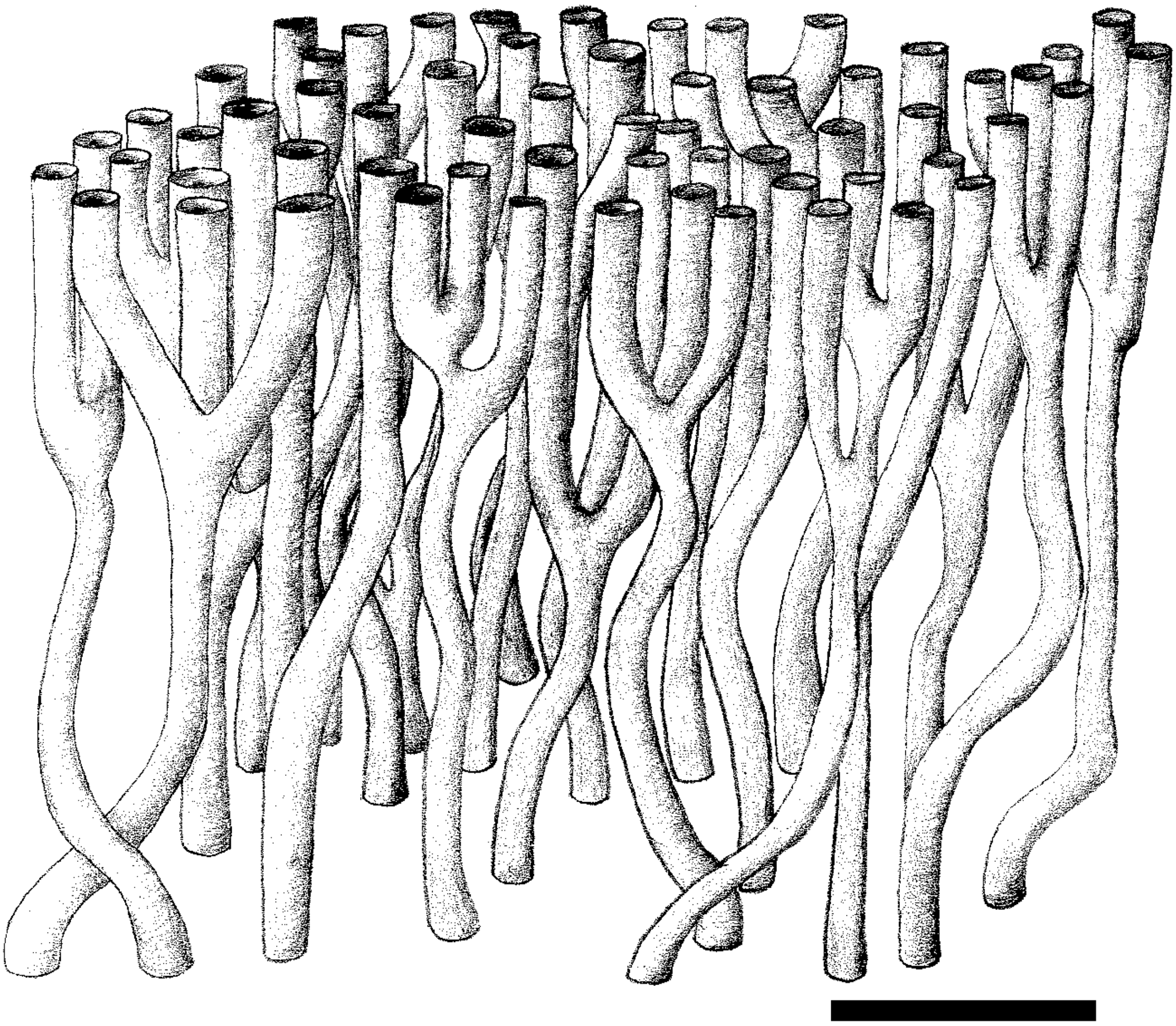


Figure 57: Idealised sketch of *Polykladichnus aragonensis*. Burrows show upward directed U-shaped and Y-shaped single or multiple branching and slight enlargements at junctions. Note the increase of burrow density toward top due to branching. Scale bar: 1 cm.

Ichnogenus *Skolithos* HALDEMAN, 1840

Type ichnospecies: *Fucoides* ?(*Skolithos*) *linearis* HALDEMAN, 1840: 3; by subsequent designation (HALL 1847).

Diagnosis: Unbranched, vertical to steeply inclined, straight to slightly curved, cylindrical to subcylindrical, lined or unlined structures with or without funnel-shaped top. Wall distinct or indistinct, smooth to rough, some specimens annulated; fill massive; burrow diameter in some individuals slightly inconstant (SCHLIRF 2000).

Synonyms: For further ichnogeneric synonyms see ALPERT (1974), except for *Monocraterion*. *Monocraterion*, commonly put in synonymy with *Skolithos*, is discussed below. Only those references that deal with *Sabellarifex* (=*Skolithos*) or morphologically related forms are provided. The classification of ichnospecies of *Skolithos,* follows ALPERT (1974), FILLION & PICKERILL (1990) and SCHLIRF (2000).

1845 *Tubifex antiquus*. – PLIENINGER: 159, pl.2 fig. 5 [= *Skolithos* cf. *magnus*].
1850 *Tigillites*, MARIE ROUAULT. – ROUAULT: 740.
1850 *Tigillites Dufrenoyi*, MARIE ROUAULT. – ROUAULT: 741 [= *Skolithos ingens*].
non 1890 *Sabellarites* gen. nov. – DAWSON: 605, fig. 11-12 [= not determinable].
1908 *Tigillites vertebralis* FR. [sic]. – FRITSCH: 18, pl. 5 fig. 7-8 [= *Skolithos linearis*].
v, p 1920 *Sabellarites eifliensis.* – RUD. RICHTER: 226, fig. 1, 3, 4 [only unbranched specimens = *Skolithos linearis*; *non* branched specimens = *Polykladichnus aragonensis*].
v, p 1921 *Sabellarifex eifliensis.* – RUD. RICHTER: 50 [only unbranched specimens; branched specimens = *Polykladichnus aragonensis*].
? 1929 *Sabellarifex eifliensis* RICHTER. – WOLF: 10.
1931 *Sabellarifex molassica* n. sp. – GÖTZ: 429, pl. 3 fig. 4a-b.
1931 *Scolithus* HALDEMAN, 1840 [sic]. – WESTERGÅRD: 14.
1931 *Scolithus linearis* HALDEMAN, 1840 [sic]. – WESTERGÅRD: pl. 7-9, pl. 10 fig. 1a-c.
1931 *Scolithus linearis* HALDEMAN, 1840 [sic]. – WESTERGÅRD: pl. 7-9, pl. 10 fig. 1a-c.
? 1932 gerade oder schwach gebogene, unverzweigte Gebilde. – WEYLAND & BUDDE: 262, fig. 8 [= most likely *Skolithos* isp.].
? 1932 gerade oder schwach gebogene, unverzweigte Gebilde. – WEYLAND & BUDDE: 262, fig. 8 [= most likely *Skolithos* isp.].
v, p 1935 *Sabellarifex eifliensis.* – ABEL: 467, fig. 391.4a-b [only unbranched specimens = *Skolithos linearis*; branched specimens = *Polykladichnus aragonensis*].
1935 *Scolithus linearis* [sic]. – ABEL: 468, fig. 392
1935 Ausfüllungen von senkrecht im Sande verlaufenden Wurmröhren. – ABEL: 468, fig. 393 [= *Skolithos annulatus*].
v, p 1937 *Sabellarifex eifliensis* (RUD. RICHTER, 1920) [sic]. – DAHMER: 535 [only the unbranched specimens = *Skolithos linearis*; branched specimens = *Polykladichnus aragonensis*].
v, p 1938 *Sabellarifex eifliensis* (RUD. RICHTER, 1920) [sic]. – DAHMER: 72 [only unbranched specimens = *Skolithos linearis*; branched specimens = *Polykladichnus aragonensis*].
p 1938 *Tigillites vertebralis.* – BOUČEK: 245, pl. 17 fig. 2 [= *Skolithos linearis*; *non* pl. 17 fig. 1; pl. 18 fig. 1-3, fig. 1 = *Pragichnus fascis*].
? 1938 Tigillitenmündungen. – BOUČEK: 253, pl. 19 fig. 1 [= most likely *Skolithos linearis*].
? 1938 Tigillitenöffnungen. – BOUČEK: 253, pl. 19 fig. 2 [= most likely *Skolithos linearis*].
? 1938 Tigilliten-Fraßgänge. – BOUČEK: 253, pl. 19 fig. 3 [= most likely *Skolithos linearis*].
? 1938 Trichter um die Mündungen. – BOUČEK: 253, pl. 19 fig. 4 [= most likely *Skolithos linearis*].
?p 1939 *Sabellarifex eifliensis* (RUD. RICHTER). – DAHMER: 357 [only unbranched specimens = *Skolithos linearis*; branched specimens = *Polykladichnus aragonensis*].
? 1940 *Sabellarifex tassiliensis* n. f. – DESIO: 72, pl. 9 fig. 2a-d; [= most likely *Skolithos linearis*].
? 1940 *Sabellarifex parvus* n. f. – DESIO: 74, pl. 9 fig. 1 [= most likely *Skolithos linearis*].
? 1955 *Sabellarifex.* – LESSERTISSEUR: 60, fig. 34C.
1955 cf. *Scolithus* [sic]. – LESSERTISSEUR: 60, pl. 21 fig. 8, fig. 34D [= *Skolithos annulatus*].
p 1955 *Tigillites* (= *Scolithus*) [sic]. – LESSERTISSEUR: 60, fig. 34F [only unbranched specimens = *Skolithos*; branched specimens = *Polykladichnus aragonensis*].
1958 *Skolithos woodi.* – HOWELL: 17, pl. 1 fig. 1, pl. 2 fig. 2 [=*Skolithos linearis*].
?p 1958 *Skolithos woodi.* – HOWELL: 17, pl. 2 fig. 1 [maybe branched forms among specimens; unbranched forms = *Skolithos linearis*].
v, p 1962 *Sabellarifex* RUDOLF RICHTER, 1921. – HÄNTZSCHEL: *W*214 [only unbranched specimens = *Skolithos linearis*; *non* branched specimens = *Polykladichnus aragonensis*].

v, p 1962 *S. eifliensis*. – HÄNTZSCHEL: *W*215, fig. 132.1a-b [only unbranched specimens = *Skolithos linearis*; *non* branched specimens = *Polykladichnus aragonensis*].
?p 1962 *Skolithos*?. – HECKER: 457, pl. 2 fig. 3, 5 [clearly unbranched forms = *Skolithos linearis;* branched forms possibly present as well].
1962 *Skolithos*?. – HECKER: 457, pl. 2 fig. 6 [= *Skolithos linearis*].
? 1962 röhrenförmige Wurmbauten. – HUCKRIEDE et al.: fig. 2 [= indet].
? 1962 *Sabellarifex* Typ. – HUCKRIEDE et al.: 24 [= indet].
1963 *Sabellarifex dufrenoyi* (ROUAULT). – BENDER: 253, pl. 13 fig. 1 [= *Skolithos annulatus*].
1968 *Sabellarifex dufrenoyi* (ROUAULT). – BENDER: 55, pl. 1 fig. 4 [= *Skolithos annulatus*].
non 1970 *Sabellarifex*. – SELLEY: 484, pl. 1, fig. e-f [= ?*Rosselia socialis*].
v, p 1975 *Sabellarifex* RICHTER, 1921. – HÄNTZSCHEL: *W*102 [only unbranched specimens = *Skolithos linearis*; *non* branched specimens = *Polykladichnus aragonensis*].
v, p 1975 *S. eifliensis*. – HÄNTZSCHEL: *W*102, fig. 64,5 [only unbranched specimens = *Skolithos linearis*; *non* branched specimens = *Polykladichnus aragonensis*].
non 1987 *Pragichnus* n. ichnogen. – CHLUPÁČ: 255.
non 1987 *Pragichnus fascis* n. ichnosp. CHLUPAC: 255, pl.2 figs 1-5, pl. 3 fig. 1-3, fig. 4.
p 1993 *Skolithos verticalis* (HALLE, 1843) [sic]. – MIKULÁŠ: 106; [only the reference to BOUČEK, 1938: pl. 17 fig. 2; *non* the reference to BOUČEK, 1938 pl. 17. fig. 1, pl. 18 fig. 1-3 = *Pragichnus fascis*].
? 1993 *Skolithos verticalis* (HALLE, 1843) [sic]. – MIKULÁŠ: 106; [the reference to BOUČEK, 1938: pl. 19 fig. 1-4 = most likely *Skolithos linearis*].
1998 *Sabellarifex* RUDOLF RICHTER. – DE: 166, fig. 3D [= *Skolithos* isp. with a funnel]
v p 2002 *Sabellarifex eifliensis* RICHTER, 1921 [sic]. – SCHLIRF et al.: 48, pl. 2 fig. 1-2; [only unbranched specimens = *Skolithos linearis*; *non* branched specimens = *Polykladichnus aragonensis*].
2003 *Skolithos musicalis* isp. n. – SCHALLREUTER & HINZ-SCHALLREUTER: 38, fig. 3-4 [= *Skolithos linearis*].
2003 *Skolithos tibia* isp. n. – SCHALLREUTER & HINZ-SCHALLREUTER: 38, fig. 1 [= *Skolithos linearis*].

Remarks: HOWELL (1943) choose a U-shaped burrow as neotype, a rather unfortunate choice, which certainly affects the stability of the use of *Skolithos*. In order to correct this mistake and guarantee stability in the further use of *Skolithos* the International Commission of Zoological Nomenclature must be called upon to use its plenary power (ICZN 1999 Art. 82) to set aside the neotype designated by HOWELL (1943).

Although being one of the most cited ichnogenera (e.g., RINDSBERG 2001), *Skolithos* also is in urgent need of a detailed ichnospecific revision. This attempt, however, is well beyond the scope of this study, which focuses on the taxonomic differences among *Skolithos*, *Sabellarifex* (=*Skolithos*) and *Polykladichnus* as well as a review of *Monocraterion*.

If further used, although strictly not recommended, concerning the nomenclature of *Sabellarifex* the following remarks should be kept in mind. In 1920, RICHTER introduced *Sabellarites,* later he realized that the name was already preoccupied and he consequently renamed *Sabellarites* RICHTER, 1920 in *Sabellarifex* RICHTER, 1921. The single ichnospecies belonging to *Sabellarifex* must be cited as: *Sabellarifex eifliensis* (RICHTER, 1920). Although the replacement name (*nomen novum*) was introduced by RICHTER himself in 1921, the first available ichnospecies was *Sabellarites eifliensis* RICHTER, 1920. In case of a replacement name the new name receives its own author and date, thus the previously introduced ichnospecies must be cited with the author in parentheses and the date of publication of the ichnospecies (ICZN Articles 22A.3, 51.3, 60.3).

Original diagnosis (RICHTER 1920: 226)**:** 'Wir nennen dementsprechend diese scolithen-ähnlichen, senkrechten, unverzweigten und rasenartig in sandigen Gesteinen vereinigten Pfeifen, die sich von *Scolithus* [sic] durch geringere Geradlinigkeit unterscheiden: *Sabellarites eifliensis* n.g, n.sp.' (Accordingly we call these *scolith*-like, vertical, unbranched, and turf-like united pipes in sandy rocks that differ from *Scolithus* [sic] in being less rectilinear: *Sabellarites eifliensis* n.g, n.sp.).

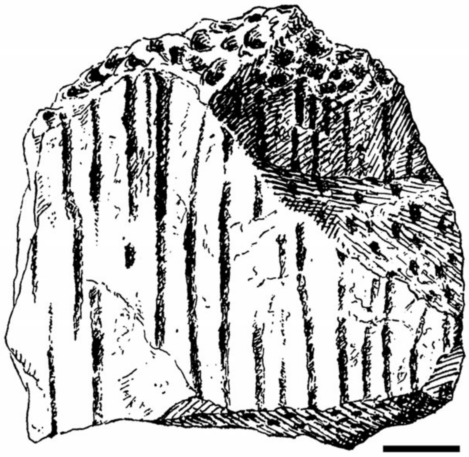


Figure 58: Sketch of *Polykladichnus* and *Skolithos* by RICHTER (1920: fig. 1; SEN Richter XVI 1a). Fig. 49C shows the specimen that was model for this sketch. In the drawing the burrow density on top appears higher than it actually is in the specimen. Scale bar: 1cm.

Discussion: Neither RICHTER (1920, 1921) nor subsequent authors designated a unique holotype or lectotype for *Sabellarifex*. Thus, according to the ICZN the entire original collection and all specimens to which RICHTER (1920) referred are to be considered a type series and all individual specimens are syntypes (Art. 72.1.1, 73.2).

RICHTER (1920, 1921) particularly stressed the fact that the new ichnotaxon *Sabellarifex eifliensis* is unbranched. In addition, RICHTER (1921) understood the assignment of his material to *Sabellarifex eifliensis* only of temporary use, and he pointed out that he hoped that *Sabellarifex* would disappear in favour of *Skolithos* after doing his heuristic duty (RICHTER 1921: 50 'Dieser letztere Begriff [*Sabellarites*] sollte also nur vorläufige Bedeutung haben und nach Erfüllung seiner heuristischen Aufgabe zu Gunsten von *Scolithus* [sic] wieder verschwinden'). RICHTER (1920, 1921) considered *Sabellarifex* to differ from *Skolithos* chiefly on the basis of *Sabellarifex* being curved and *Skolithos* being straight, but subsequent authors mostly agree that a continuum exists between straight and curved, unbranched vertical tubes, thus there is no need for the separate name *Sabellarifex* (e.g., WESTERGÅRD 1931). RICHTER noticed some apparently branched forms among his specimens but considered them to be crossovers of individual burrows. A restudy of the type material in the collection of the Senckenbergmuseum in Frankfurt Main revealed that the type series includes unbranched forms, crossovers, and truly branched forms. Thus, there are two different ichnogenera within the type material: simple, unbranched, vertical, tubular burrows (generally referred to *Skolithos* HALDEMAN, 1840) and Y- or U-shaped branched, vertical, tubular burrows (generally referred to *Polykladichnus* FÜRSICH, 1981). The question now is, with which of these ichnotaxa *Sabellarifex* competes for synonymy.

Biologically, the type material of *Sabellarifex* is a population of trace fossils that displays variation. Still, no biologic population is equivalent to a trace fossil 'population'. Even a monospecific population of bivalves can produce diverse lebensspuren (e.g., *Lockeia*, *Protovirgularia*). If considered as a population, *Sabellarifex* would be diagnosed to include branched as well as unbranched forms. However, this would lead to an unacceptable taxonomic situation in which *Skolithos*, *Sabellarifex*, and *Polykladichnus* could not be separated rigorously, and thus would have to be synonymised. From a purely nomenclatural point of view this is fine, however, impractical. Of course one should always consider as many facts as possible and include as much biological background as possible when naming trace fossils but one also has to consider the resulting practicability. In addition, following the preamble of the ICZN a taxonomist is asked to promote stability and universality in the scientific names of animals.

The dilemma with *Sabellarifex* now is that bifurcation at first glance appears to be of low significance in the studied type material of *Sabellarifex* because the 'population' of *Sabellarifex* specimens clearly includes similar forms with and without branching. There are two possible reasons for the formation of both the forms. A) There were only branched forms but due to preservation artefacts only a certain amount of specimens shows the branching pattern. It cannot be excluded that the upper, branched part was removed by erosion, converting branched forms to unbranched forms. Presence or absence of funnel-shaped tops in *Skolithos* has been explained in a similar way (HALLAM & SWETT, 1966). However, since this can neither be proved nor disproved the following reason is favoured here. B) Although it appears that the type series is a single population there may have been two different behavioural patterns behind the branched and unbranched forms analogous to *Lockeia* (bivalve resting trace) and *Protovirgularia* (bivalve locomotion trace). Polychaete species are also known to produce different traces for various purposes, however, the resulting burrow variety cannot be explained by population variability (RONAN 1977). The geologic record of separately occurring forms supports this point of view. In the vast majority of published descriptions of *Skolithos*, scarcely any specimens, among thousands, show bifurcation. For this reason, the bifurcation pattern in the described material is considered to be an ichnotaxobase of a high level of significance. Some authors (e.g., RICHTER 1920; ALPERT 1974; FILLION & PICKERILL 1990) described prismatic cross-sections of vertically oriented tubular burrows. Although, it cannot be excluded that the one or the other polygonal cross-sections may result from burrow activity, this morphological feature generally results from high burrow density and thus is not suitable as an ichnotaxobase (Fig. 59).

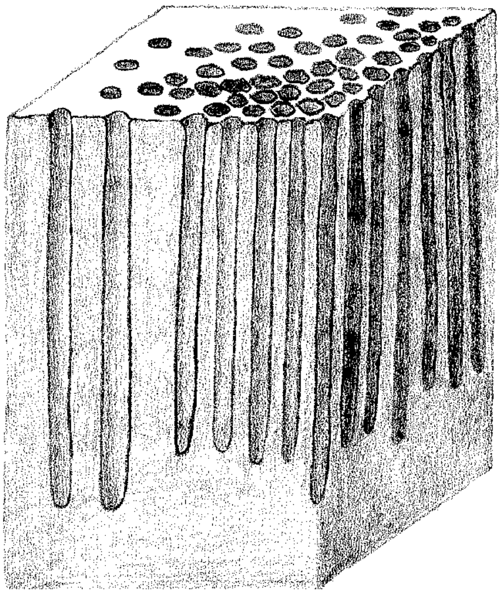


Figure 59: Sketch of *Skolithos linearis*, occurring in various densities; resulting in a circular cross-section of the burrows when loosely packed, and in a polygonal cross-section when densely packed. Not to scale.

Keeping in mind RICHTER's (1920, 1921) original descriptions, as well as the exhortation of the preamble of the ICZN to maintain stability in taxonomy, the following conclusion is drawn: A lectotype for *Sabellarifex* that unambiguously puts it in synonymy with *Skolithos* is hereby designated.

Lectotype: *Sabellarites eifliensis* Sammlung RICHTER XVI, 1c, indicated by white arrows on the specimen and Fig. 49B in this paper.

Discussion: Given the above reasons *Sabellarifex* RICHTER, 1921 is considered to be a junior synonym of *Skolithos* HALDEMAN, 1840. Further use of *Sabellarifex* is not recommended. *Polykladichnus* FÜRSICH, 1981, a well established and well documented ichnogenus, remains valid and its further use is explicitly recommended.

As can be seen by the number of synonyms, the name *Sabellarifex* has been infrequently used by authors, apparently because most researchers could not pragmatically differentiate *Skolithos* and *Sabellarifex*. *Tigillites* ROUAULT, 1850 is taken into consideration because some authors previously discussed similarities among *Skolithos*, *Sabellarifex* and *Tigillites*. *Tigillites* ROUAULT, 1850 is considered to be synonymous with *Skolithos*. The description made by ROUAULT (1850) is very simple and unfortunately no material is figured but since the general morphology of *Skolithos* also is simple there can be no doubt in an assignment of *Tigillites* to *Skolithos*.

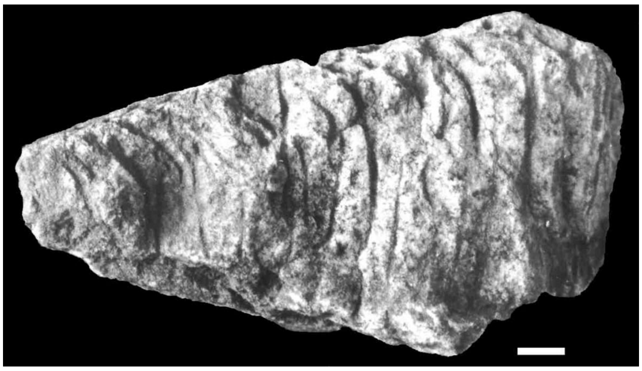


Figure 60: *Skolithos linearis* and *Polykladichnus aragonensis* with bent burrow tops resulting from tectonic deformation. Upper Devonian Taunus quartzite; all side view, fullreliefs; original of RICHTER (1920: fig. 4; SEN Richter XVI 1b). Scale bar: 1cm.

ALPERT (1974) came to the same conclusion, however, he hesitated to synonymise *Tigillites vertebralis* FRITSCH, 1908 with *Skolithos* because of probable downward-directed branching. In his original description FRITSCH (1908) did not mention branching, nor do his figured specimens show branching. The specimens described and figured by BOUČEK (1938: fig.1, pl. 17 fig. 2, pl. 18 fig. 1-4), however, do indeed show a downward-directed branching pattern. The specimens figured by BOUČEK (1938: pl. 19 fig. 1-4) are difficult to assign because only bedding surfaces are shown. CHLUPÁČ (1987) reviewed the material of FRITSCH (1908) and BOUČEK (1938) and re-identified the specimens as two different ichnogenera. Simple, unbranched forms were assigned to *Skolithos* HALDEMAN and downward-branched forms to a new ichnogenus, *Pragichnus* CHLUPÁČ, 1987. CHLUPÁČ (1987) synonymised the unbranched form of *Tigillites vertebralis* FRITSCH (1908) with *Skolithos linearis* HALDEMAN because he found that the annulated surface of *T. vertebralis* was a weathering artefact. In general, MIKULÁŠ (1993) followed CHLUPÁČ (1987) in considering the unbranched material of BOUČEK (1938) to be *Skolithos*, but he assigned all figured specimens of BOUČEK (1938) to *Skolithos verticalis*, and thus partly included *Pragichnus* by mistake (see BOUČEK, 1938 in the synonymy above for details). WOLF (1929) reported *Sabellarifex eifliensis* RICHTER from Devonian rocks of the Harz Mountains in Germany, but provided no figured material or discussion. Since the material comes from a similar facies and age to the original material of RICHTER (1920, 1921), it is very likely that the forms of WOLF (1929) belong in part to *Polykladichnus* and in part to *Skolithos*. In her work on fossil serpulids, GÖTZ (1931) also introduced a new ichnospecies of *Sabellarifex*, *S. molassica*. GÖTZ (1931) stated that the specimens show a slight and sudden increase of burrow diameter (1-2.5 mm per 3-4 cm length) in the uppermost quarter to third. Most of the specimens are slightly bent towards the top, all in the same direction. This feature made her think that the specimens belong to *Sabellarifex* because she considered this as evidence that the structures were built like sabellariid reefs, with bending due to currents. The specimen comes from the Alpine Molasse, where folding is very common (at least in the so-called “Faltenmolasse” or folded Molasse); thus, in analogy to the specimen shown in Fig. 60 the bending is best explained as a result of folding. WESTERGÅRD (1931) could not make out any differences that would justify a separation of *Sabellarifex* and *Skolithos* because he found all transitional forms from strictly straight to slightly curving in one bed. ABEL[1] (1935) refigured the original drawings of RICHTER (1920), which are undoubtedly *Skolithos* and *Polykladichnus*. In addition, he also reported *Skolithus linearis* [sic] (his fig. 392) and an annulated form "Ausfüllungen von senkrecht im Sande verlaufenden Wurmröhren", 'fillings of vertically running worm-tubes in sand' (his fig. 392) from questionable Upper Cretaceous sandstones in northern Saudi Arabia, which is assigned to *Skolithos annulatus* because of its clearly annulated exterior. DAHMER (1937, 1938, 1939) never figured any specimens of his material. While restudying the material collected by him for his 1937 and 1938 papers it was discovered that his material contains two different forms, branched and unbranched forms. His 1939 material was not seen but it is most likely synonymous with *Polykladichnus* and *Skolithos*, since his description stated that this material is similar to the specimens described in previous papers (DAHMER 1937, 1938). The two ichnospecies, *Sabellarifex tassiliensis* and *S. parvus,* introduced by DESIO (1940) do not show any significant differences with previously named ichnospecies of *Skolithos*. *Sabellarifex tassiliensis* is synonymous with *Skolithos linearis* because the structures are smooth, simple, slightly curved, vertically oriented tubular burrows with a wall-lining. DESIO (1940) introduced a new species because his material shows a lower burrow density than classical Cambrian piperock *Skolithos* and is less strictly rectilinear. DESIO (1940) made some curious synonymisations that are unacceptable from a nomenclatural point of view. Because of morphological similarities he put the ichnogenus *Skolithos* in synonymy with the ichnospecies '*Sabellarifex dufrenoyi* ROU.', which, however, in this combination did not exist at that time, and was not formally introduced as such by DESIO (1940). If anything, it would be *Tigillites dufrenoyi* ROUAULT but synonymisation of an ichnospecies with an ichnogenus is not in line with general nomenclatural and taxonomic practice.

LESSERTISSEUR (1955) refigured previously published material of RICHTER (1920, 1921), WESTERGÅRD (1931), WEYLAND & BUDDE (1932) and ABEL (1935), and concluded that *Skolithos* and *Tigillites* are synonymous. The refigured material of WEYLAND & BUDDE (1932) is difficult to

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[1] As an anecdote it might be mentioned that ABEL's (1935) locality description is somewhat confusing. He wrote that the discovery was made near the 'Hedschasbahn' ('Hejaz railway', built under the Turkish government with the help of German engineers before WW1). In the figure captions, he wrote that the sample comes from the 'Kreidesandstein von Aula Pascha südlich von Tibuk' ('the Cretaceous sandstone of/from Aula Pascha south of Tibuk'), which is an unfortunate German formulation, a misspelling and, in addition, the name 'Aula Pascha' was not written in capitals and can thus be mistaken for an Arabian locality (although, it is the name of a German engineer and military officer called KARL AULER PASCHA). The locality south of Tibuk does not exist. Research in old and new literature has shown that the name of the place must be "Tabuk", sometimes also spelled "Tebuk". Tabuk was a railway station of the former Hejaz railway and is located in the North of today's Saudi Arabia. The Cretaceous age of the sandstone is wrong according to finds of associated fauna (e.g., PICARD 1942) and more likely is of Cambrian age.

assign since only a bedding surface is shown, and thus it cannot be determined whether the specimens are branched; because the authors did not mention branching, their material is assigned to *Skolithos* with restrictions. HOWELL (1958) described *Skolithos woodi* from Upper Cambrian rocks. ALPERT (1974) considered *Skolithos woodi* WHITFIELD to be synonymous with *Skolithos verticalis*. The figured specimens of HOWELL (1958) are more-or-less straight and slightly oblique. Two specimens (HOWELL 1958: pl. 2 fig 1) do seem to branch but it cannot be excluded that it is a crossover effect. For this reason they are put it in synonymy with restrictions only but if they branch then they certainly belong to *Polykladichnus*. HECKER (1962) also reported questionable *Skolithos* but unfortunately did not describe any details of his material. According to the figures presented some specimens (HECKER 1962: pl. 2 fig. 3 & 5) may belong to *Polykladichnus* but as in many other cases the final decision remains open.

BENDER (1963, 1968) described *Sabellarifex dufrenoyi* from Ordovician sandstones in Jordan. He discussed the stratigraphic range of the trace fossils and put *Tigillites dufrenoyi* ROUAULT in synonymy with *Sabellarifex dufrenoyi* (ROUAULT), but did not discuss why he gave priority to the younger generic synonym and named his material *Sabellarifex dufrenoyi* (ROUAULT). BENDER (1963) also stated that HUCKRIEDE et al. (1962) found *Sabellarifex* in the Bathonian of central Iran. However, HUCKRIEDE et al. (1962) only report tubular worm-burrows from Precambrian rocks and suggest that these worm burrows can only be walled worm burrows of the *Sabellarifex* type. Unfortunately the figure of HUCKRIEDE et al. (1962) does not allow an assignment. OSGOOD (1970) discussed similarities of *Skolithos* and *Sabellarifex* and referred to WESTERGÅRD (1931) who could not differentiate the ichnotaxa; OSGOOD (1970) made no final decision and left everything open. SELLEY (1970) reported *Sabellarifex* from lower Palaeozoic rocks in Jordan; this material, however, is better assigned to *Rosselia socialis* because of its distinct, concentric lamination and the half-spindle-shaped morphology. HÄNTZSCHEL (1962, 1975) refigured previously published material of RICHTER (1920, 1921), thus, his material unambiguously belongs to *Polykladichnus* and to *Skolithos*. HÄNTZSCHEL (1975) recommended that *Sabellarifex dufrenoyi* in BENDER (1963) should be named *Tigillites dufrenoyi* because of its distinct annulation. HÄNTZSCHEL (1975) suggested that such annulated forms should be named *Tigillites*. This view is not supported here and *Tigillites* is considered a synonym of *Skolithos*. DE (1998) described *Sabellarifex* from early Cambrian deposits in the Himalayas. The material was assigned to *Sabellarifex* because of being less straight and less crowded than *Skolithos*. According to DE the burrows are simple unbranched forms with a funnel-shaped burrow top. As discussed below funnel-shaped openings are not considered a valid ichnotaxobase and the burrows are best assigned to *Skolithos* isp. Since only a top view of the structures is provided by DE (1998) a more detailed assignment is not possible. SCHLIRF et al. (2002) stated that the type material of *Sabellarifex eifliensis* contains branched forms, and emended the diagnosis for *Sabellarifex*. They did not review the ichnogenus, but did remark that the branching pattern of some specimens among the type material would have taxonomic consequences for the further use of *Sabellarifex*. SCHALLREUTER & HINZ-SCHALLREUTER (2003) introduced two new ichnospecies of *Skolithos*, *S. musicalis* and *S. tibia*. Fortunately the figures are of good quality, which allows an assignment of the presented material. As a consequence of the given arguments both new ichnospecies are considered to be subjective junior synonyms of *Skolithos linearis*.

Skolithos isp. A

Fig. 61A-D

Material: Numerous specimens on slabs PIW1998VIII-32-35, PIW2002-I-28, Vetter quarry at Schönbachsmühle, PIW1998VIII-39-46, Schleifsteinwerke quarry, PIW1998VIII-51, 54-55, 82, 86, Natursteinwerke quarry, near Dörflis, numerous field observations. All from Coburger Sandstein, Hassberge Fm, Middle Keuper, Lower Franconia, Bavaria, southern Germany.

Description: Cylindrical, vertical, slightly curved, rarely straight, unlined burrows, with or without smooth or indistinctly striated external burrow surface and hemispherical terminations. Burrow length 65-90mm, burrow diameter 9-10mm; burrow fill predominantly massive and identical with overlying sediment. In a few specimens, local isolated convex-down, menisci are observed. Positive hyporeliefs of hemispherical, strongly elevated knobs, covered with indistinct striae, occur occasionally. Burrows are relatively isolated and appear predominantly as circular projections on the tops of bedding planes.

Discussion: The isolated menisci probably resulted from gradual filling of the burrow and its later compaction. Hemispherical, sculptured terminations of *Skolithos* were also described by BROMLEY & ASGAARD (1979).

Relatively large vertical shafts such as the forms from the Haßberge, were previously described as *Cylindricum grande* LINCK, 1961 (see Tab. 1). The ichnogenus *Cylindricum* was partly included in *Skolithos* by ALPERT (1974). This is followed here, except for the forms discussed under new Ichnogenus 1.

Skolithos predominantly occurs in various shallow-marine environments from the Late Precambrian to the Recent (FILLION & PICKERILL 1990) and is generally regarded as feeding and dwelling burrow of annelids or phoronids (ALPERT 1974). Occasionally, *Skolithos* has been reported from non-marine environments (e.g., BROMLEY & ASGAARD 1979). In these cases, it may have originated from burrowing activities of insects or spiders and can be interpreted as dwellings or shelters (RATCLIFFE & FAGERSTROM 1980).

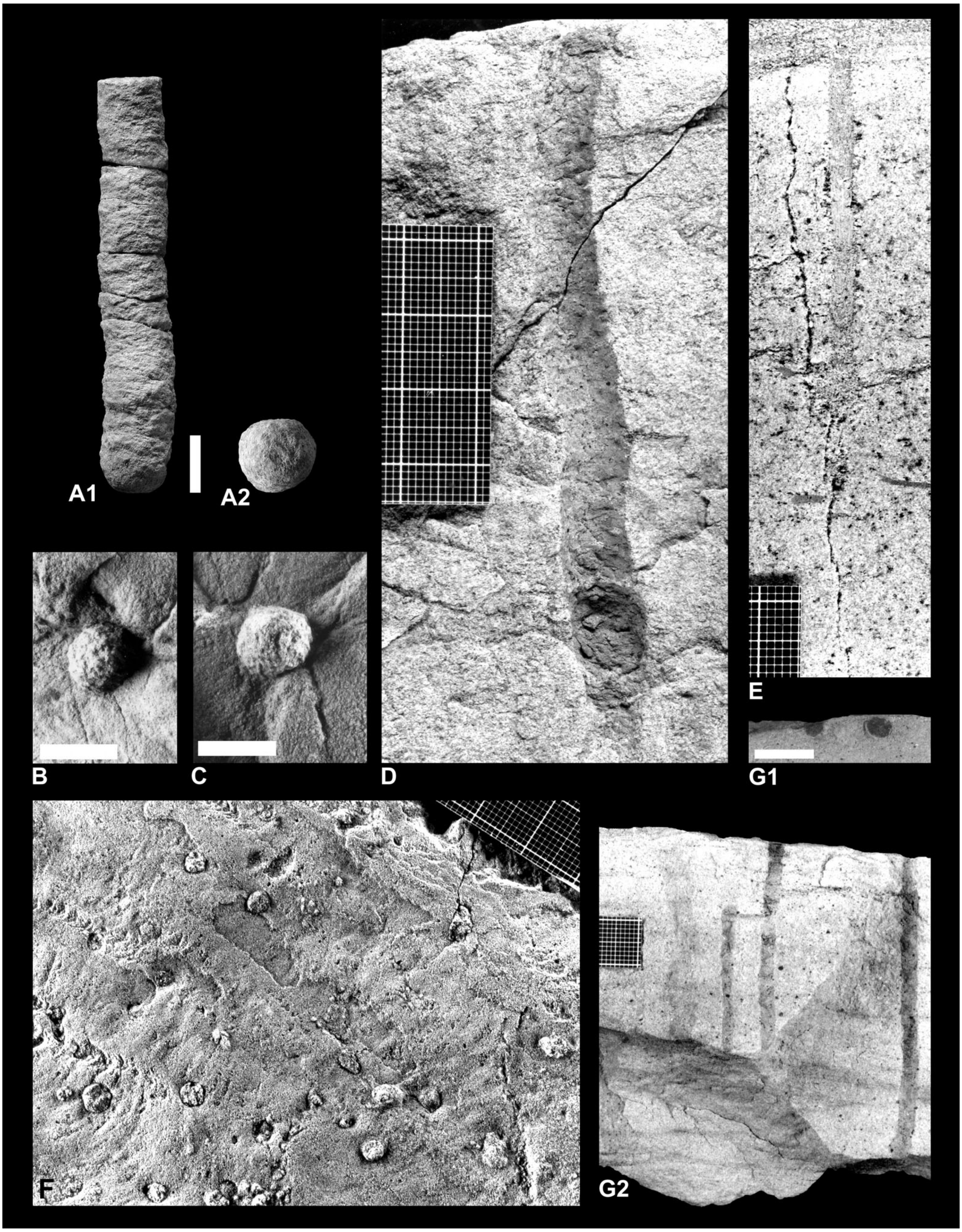

Figure 61: **A-D**. *Skolithos* isp. A. **A**. Fullrelief. **A1**. Lateral view. **A2**. Bottom view; Vetter quarry at Schönbachsmühle; PIW2002-I-28. **B-C**. Sculptured terminations of *Skolithos* isp. A. Positive hyporelief, basal view; Natursteinwerk quarry near Dörflis; PIW1998-VIII-86. **D**. *Skolithos* isp. A, fullrelief, lateral view, Vetter quarry at Schönbachsmühle; PIW1998-VIII-32. **E-G:** *Skolithos* isp. B. **E**. Fullrelief, lateral view, Schleifsteinwerke quarry near Eltmann; PIW1998VIII-41. **F**. Epirelief, top view; Natursteinwerk quarry; natural size; PIW1998VIII-26. **G**. Fullrelief, Schleifsteinwerke quarry near Eltmann; PIW1998VIII-42. **G1**. Top view. **G2**. Lateral view. **A-C, G1**: Scale bar: 1cm. **D-F, G2**. All Coburger Sandstein, Hassberge Fm, Middle Triassic. Millimetre grids for scale.

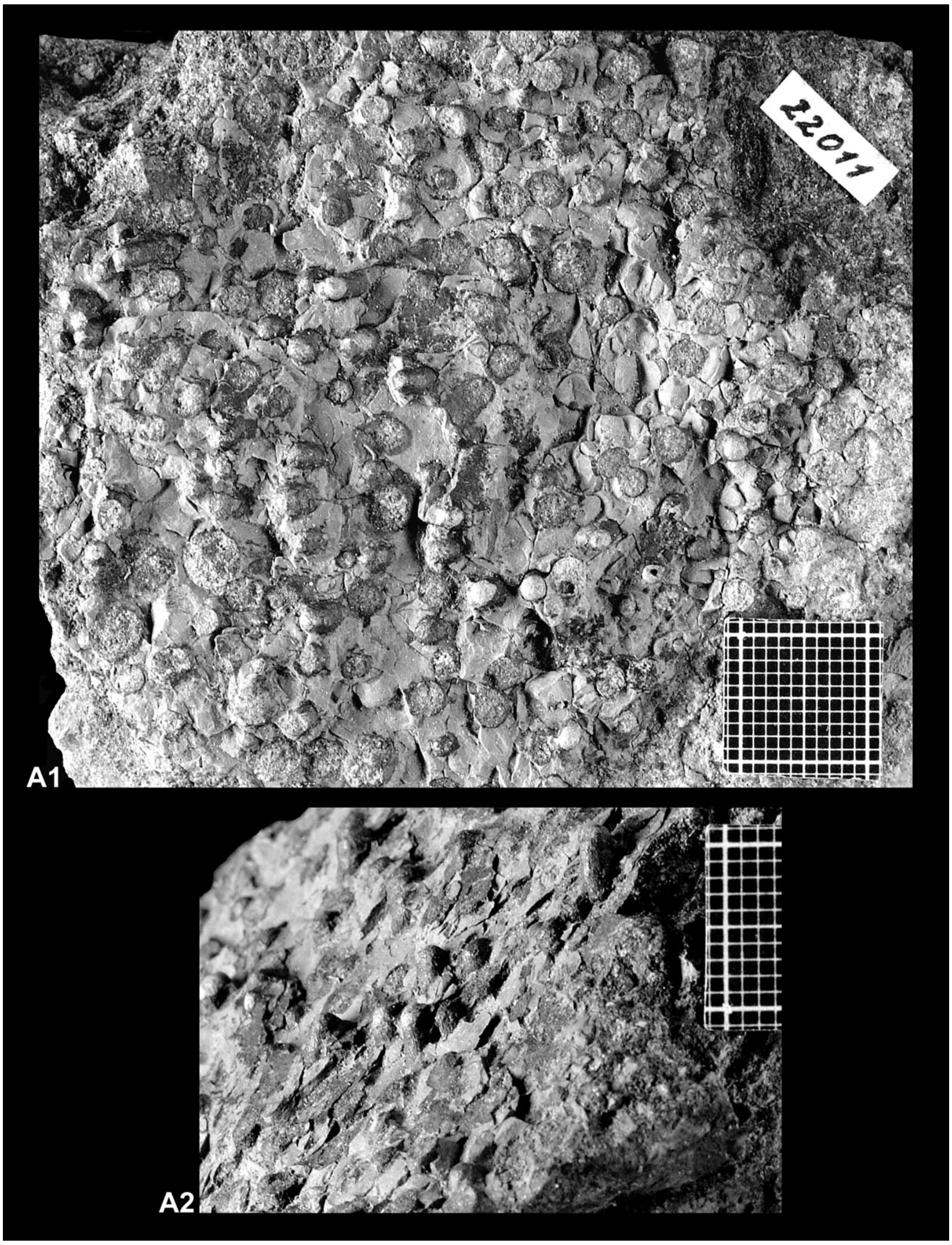

Figure 62: Short, eroded *Skolithos* isp. B with hemispherical terminations, fullreliefs, SMNS 22011, Lower Schilfsandstein, Stuttgart Fm, Middle Keuper, Stockheim, Baden-Württemberg, southern Germany. Holoype of *Cylindricum gregarium* Linck, 1949b: pl. 1 fig. 1. No diagnostic features exist that justify a separate Ichnogenus and ichnospecies. **A1**. Bottom view. **A2**. Oblique bottom view to show hemispherical terminations. Millimetre grids for scale.

Skolithos isp. B

Fig. 61E-G, 62

Material: PIW1998VIII-26, 31, Vetter quarry at Schönbachsmühle, PIW1998VIII-38, 40-43, Schleifsteinwerke quarry near Eltmann, PIW1998VIII-47-53, 57-64, 83-85, Natursteinwerke quarry near Dörflis; Coburger Sandstein, Hassberge Fm, Middle Keuper, Lower Franconia, Bavaria, southern Germany.

Description: Vertical, cylindrical, slightly curved, rarely straight, thinly lined or unlined burrows; length 19-50mm, width 3-4mm. Lower terminations rounded. Burrow fill massive, similar or different to host rock. These trace fossils are commonly observed only as circular projections on bedding planes or parting surfaces.

Discussion: *Skolithos* isp. B occurs together with cf. *Polykladichnus aragonensis*. It corresponds in size and associated trace fossils to *Skolithos* isp. B from the "terrestrial suite" in BROMLEY & ASGAARD (1979). However, whereas their *Arenicolites* isp. is like cf. *Polykladichnus aragonensis*, *Skolithos* isp. B is interpreted as an insect burrow.

Skolithos is an extremely facies-crossing trace fossil and the sole occurrence of *Skolithos* does not indicate any particular environment. The same is also true of *Planolites*. The main reason for this facies-crossing habit most likely is the simple nature of these structures; *Planolites* and *Skolithos* are among the simplest of trace fossils. Since their general morphology is so simple and apparently easy to detect, even poorly preserved material often is assigned to *Planolites* or *Skolithos*. In addition, building simple tubular structures serves many purposes and thus is a generalised way of constructing burrows. A detailed revision of all known occurrences of *Skolithos* may reveal a different picture, but this is beyond the scope of this study. Hitherto *Skolithos* has mostly been reported from various marine environments from the late Neoproterozoic to recent (FILLION & PICKERILL 1990) and also from nonmarine environments (e.g., BROMLEY & ASGAARD 1979; GIERLOWSKI-KORDESCH 1991; SCHLIRF et al. 2001). It ranges in size from very thin (1-2mm in diameter) to thick (up to 30mm; Fig. 63A) and from short (few centimetres length) to very long (up to 200cm length; Fig. 63B-C).

In marine environments *Skolithos* is interpreted as a domichnion made by phoronids or annelids (e.g., FÜRSICH 1974c). In terrestrial environments *Skolithos* may be built by insects (SMITH & HEIN 1971, BOWN 1982) or spiders and can be interpreted as dwellings or shelters (RATCLIFFE & FAGERSTROM 1980). The reported sculptured terminations of some of the larger forms of *Skolithos* (e.g., BROMLEY & ASGAARD 1979; SCHLIRF et al. 2001; Fig. 61B-C) are hitherto only known from nonmarine forms. Whether this may be a diagnostic feature for all nonmarine forms needs further investigation.

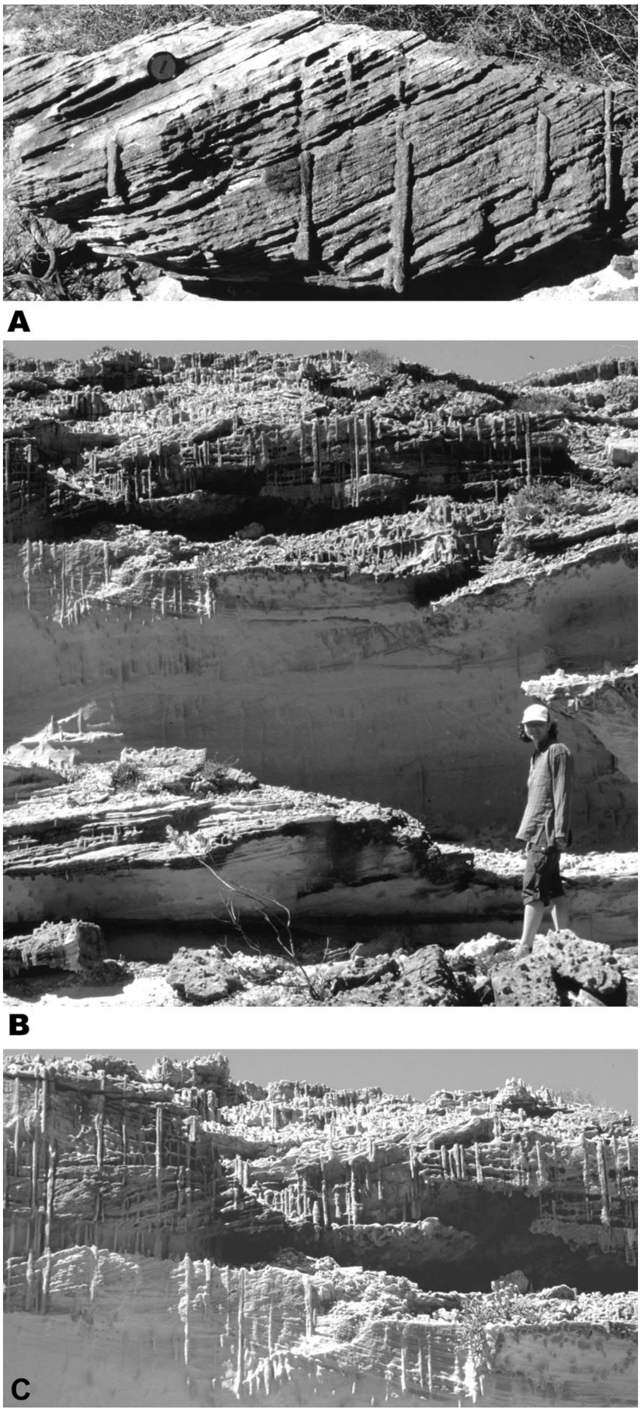

Figure 63: **A**. Diagenetically superimposed *Skolithos linearis* in cross-bedded marine sandstones. Burrow diameter can extend up to 3cm. Field photograph, Tumblagooda sandstone, Ordovician, Kalbarri National Park, near Kalbarri, Western Australia. Lens cap diameter: 72mm. **B**. Very long, diagenetically superimposed *Skolithos linearis* in trough cross-bedded marine sandstones. Single specimens can be traced over a distance of more than 200cm. Field photograph, coastal outcrop, Tumblagooda sandstone, Kalbarri National Park, near Kalbarri, Western Australia, Australia. Person (160cm) for scale. **C**. Detail of B.

Ichnogenus *Monocraterion* TORELL, 1870

Type ichnospecies: *Monocraterion tentaculatum* TORELL, 1870: 13, by monotypy.

Emended diagnosis: Funnel-shaped negative epirelief with a raised knob on the floor of the funnel; this knob is continuous with a short, vertical, centrally located tubular structure. Essentially with numerous small, horizontal, slightly curving, rarely branching, occasionally lined, tubular, full-relief structures with smooth outer surface going out from the raised knob.

Discussion: So far no detailed diagnosis based on the type material has been provided since the original description by TORELL (1870). For this reason an emended diagnosis is presented.

Monocraterion tentaculatum TORELL, 1870

Fig. 64

* 1870 *Monocraterion tentaculatum* n.g. et sp. TORELL: 13.
? 1891 *Monocraterion magnificum* n. sp. – MATTHEW: 161, pl. 26.
non 1977 *Monocraterion* sp. – CRIMES et al.: 120, fig. 7, Pl. 6 fig. f.
p, non 1984 *Monocraterion tentaculatum* TORELL, 1869 [sic] and *Skolithos linearis* (HALDEMAN, 1840). – HEINBERG & BIRKELUND: 363, fig. 4H, 7A-B.
non 1990 *Monocraterion tentaculatum* TORELL, 1870. – DAM: 134, fig. 9B-D.
non 1993 *Monocraterion* TORELL. – BARTHOLOMÄUS: 316; pl. 3 fig. 1-3; pl. 4 fig.3; [= *Skolithos linearis* with funnel-shaped top].
p? 1997 *Monocraterion tentaculatum* TORELL, 1870. – JENSEN: 38, fig. 38, 39A, 40A; [only specimen with radiating tubes in fig. 38 and fig. 39A, which is the lectotype = *Monocraterion tentaculatum*].

Emended diagnosis: As for ichnogenus because of monotypy.

Occurrence: Hitherto, undoubtful *Monocraterion tentaculatum* has been found only in the Lower Cambrian Mickwitzia sandstone, Sweden. The material is deposited in the collection of the Swedish Geological Survey SGU Type 5364. The material is figured in JENSEN 1997: text-figs 38 (only specimen with radiating tubes), 39A = lectotype. Fig. 64 shows the lectotype and a sketch of it. An additional specimen is housed in the collection of the Swedish Museum of Natural History in Stockholm (RM X3309).

Discussion: The taxonomy of *Monocraterion* and *Skolithos* is the subject of a long taxonomic debate that goes largely back to material figured by WESTERGÅRD (1931). Actually, WESTERGÅRD (1931) did not figure original type material of TORELL (1870) but what he thought TORELL might have had in mind when speaking of *Monocraterion*. As it happened, among the trace fossils from the Mickwitzia sandstone only a few specimens are funnel-shaped and only one specimen with 'tentacles' could be found. Ever since the publication of WESTERGÅRD (1931) many authors believed that his figured material was *Monocraterion*, although WESTERGÅRD (1931) frequently stated that he saw his material only tentatively as what *Monocraterion* may be. Nevertheless, HÄNTZSCHEL (1975) refigured WESETRGÅRD'S material in the *Treatise* and thus added to the confusion about *Monocraterion*. The type ichnospecies (formally not existing at TORELL'S time, but the only assigned ichnospecies) *M. tentaculatum* does bear tentacular structures associated with the funnel as indicated by the name. However, this fact was widely neglected, most probably because the forms with 'tentacle structures' are very rare. MATTHEW (1891) reported large *Monocraterion magnificum* with tentacle-like structures. If these structures belong to *Monocraterion* is questionable (Jensen 1997). NATHORST (1881) already questioned whether these 'tentacles' in TORELL'S description are true tentacles; he believed they are better explained as faecal strings comparable to those of *Arenicola marina*: one more example of how important type material is for the understanding of trace fossils as well as body fossils.

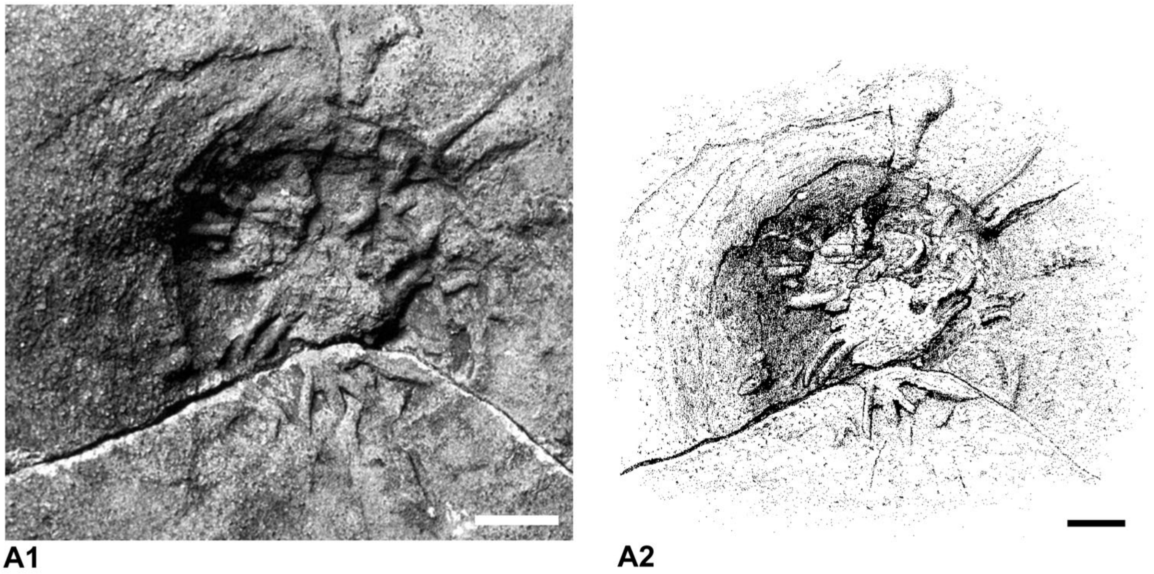

Figure 64: A1. Lectotype of *Monocraterion tentacultum* (taken from JENSEN 1997: fig. 39A). Sketch of lectotype. Note small, massive, full relief structures within funnel-shaped depression. The origin of these fullrelief structures is dubious and secondary burrowing cannot be excluded. Top view; large structure: negative epirelief; small structures: full reliefs. Scale bars: 1cm. See also Fig. 65.

Since type material still exists and the taxonomy of *Monocraterion* is anything but clear, and in addition, the name *Monocraterion* is used for various structures by various authors, JENSEN's (1997) figures and descriptions become very important. Hitherto simple, vertical tubular structures with a funnel-shaped top (e.g., WESTERGÅRD 1931; CRIMES et al. 1977) were considered to be *Monocraterion*, but also concentrically laminated conical structures have been assigned to *Monocraterion* (e.g., SELLEY 1970). Only in the case of a well established name can type material be considered irrelevant and disregarded in order to guarantee stability and universality in the use of names (ICZN Art. 81). This is definitely not the case with *Monocraterion*, thus the only thing that counts is the lectotype designated by JENSEN (1997). The refigured type material of *Monocraterion* TORELL in JENSEN (1997) is of technically high quality but no less dubious.

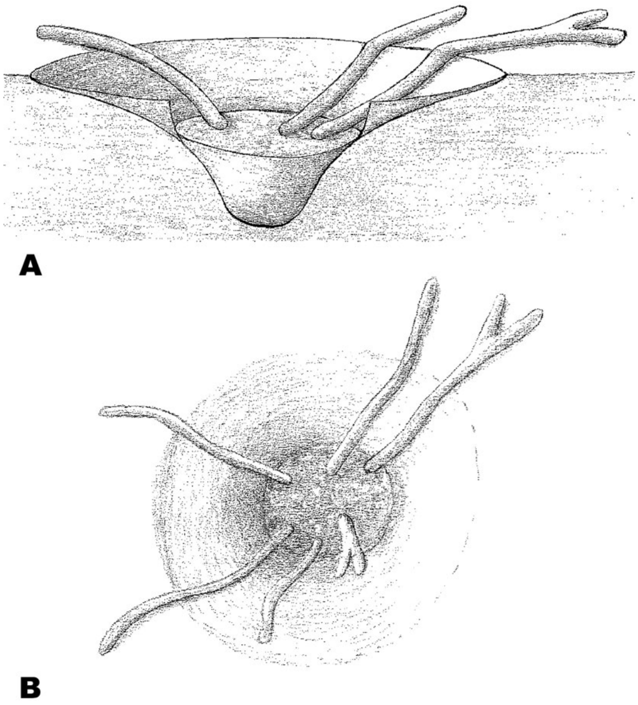

Figure 65: Idealized sketch of *Monocraterion tentaculatum* with additional 'tentacle' structures **A**. Side view. **B**. Top view. Not to scale.

With his designation JENSEN (1997) once and for all defined *Monocraterion* as a funnel-shaped negative epireliefs with a raised knob at the floor of the funnel, with additional horizontally oriented tubular structures. Whether this was a good choice or not is irrelevant. The lectotype clearly shows some additional horizontally oriented tubular structures from which the ichnospecies name *M. tentaculatum* resulted (JENSEN 1997: fig 38, 39A; Fig. 64). However, the relation of the funnel and the horizontal structures is very difficult to explain. *Monocraterion* is interpreted as an originally open burrow, a view supported by JENSEN (1997). He also interpreted the small horizontal tubular structures as permanent structures, possibly used for excursions of the tracemaker. JENSEN (1997) considered the central knob as the top expression of a vertical tube. When and how the surrounding funnel has formed is a matter for speculation. JENSEN (1997) suggested that the radial elements were dug in sediment that occupied the position of what is now the funnel. The radiating structures were filled with sediment before the surrounding sediment was eroded, this view is not supported here. If *Monocraterion* were a permanent dwelling structure, the funnel-shaped structure should not be filled with sediment during the lifetime of the producer, since the animal was living within it. However, the type material clearly shows a raised knob and small, tubular full-relief structures going through the entire funnel-shaped structure. JENSEN (1997) even observed a distinct wall-lining in some of these structures.

Figure 66: *Arenicola* castings drifted over several decimetres by a slight current of well-water at a beach section near Ambleteuse, northern France. If found fossilised the structures would be identified as *Planolites*, despite not being burrows. The castings may drift over a short distance because they are stabilised by mucus. Scale bar: 1cm.

How could these full-relief structures have formed if the burrow were open that is unfilled? There are only two plausible explanations how these full-relief structures have formed. 1) The burrow, including the funnel, was filled with sediment after it was no longer used by the *Monocraterion* maker. Another organism moved through the funnel and left an additional trace behind. Hence the structures were the result of secondary burrowing and *Monocraterion tentaculatum* is a composite trace fossil. 2) As already proposed by NATHORST (1881) the 'tentacles' are faecal castings. The preservation potential of excrements like those of *Arenicola marina* is extremely low, but *Arenicola* castings may be quite stable and even be transported by low-energy currents. A mucous lining or high mucus content of the excrements may stabilise them. Fig. 66 shows an example from a beach in the Boulonnais near Ambleteuse where a small but continuous flow of well-water transported *Arenicola* castings over a distance of several decimetres. As already stated, the preservation potential of such structures is nearly zero but only nearly zero after all. The fact that the structure described by TORELL was never found again may support the exceptionality of this find. The slab with the lectotype, is only a few centimetres thick and probably shows only the upper part of a much larger structure whose nature is unknown (JENSEN 1997). Incompleteness disqualifies a specimen as lectotype for an ichnospecies and in this case a type ichnospecies. Unfortunately incomplete type specimens are no exception and a lot of work has do be done in future to achieve stability in trace fossil nomenclature and taxonomy. As shown by JENSEN (1997) additional funnel-shaped trace fossils occur on the slab that bears the lectotype but non show the tentacle structures. WESTERGÅRD (1931) and JENSEN (1997) state that in the beds of the Mickwitzia sandstone frequently funnel-shaped burrow tops can be observed, but non showing tentacle structures. In addition, it should be mentioned that funnel-shaped tops of

WESTERGÅRD'S (1931) material have a width of only 10-15mm, rarely 20mm, whereas the lectotype and the paratypes are 30-40mm wide. Size alone is no suitable ichnotaxobase, but in the case of *Monocraterion* and *Skolithos* with funnel-shaped top this is not the only distinction criterion and should not be dismissed.

Figure 67: *Rosselia socialis*, NWI Sammlung Galadé, no number, from the type locality Rossel, near Rüdesheim, Hesse, Germany, Taunus quartzite, Lower Devonian. *Rosselia* clearly differs from *Monocraterion* by having a concentric lining. When preserved in its entirety *Rosselia* has a spindle-shaped morphology. The half-spindle shape is the result of erosion. Scale bar: 1cm.

It seems obvious that whatever *Monocraterion* may be it has little in common with *Skolithos*. Authors considering a funnel-shaped top in *Skolithos*-like structures as taxonomically important and wanting to distinguish such structures at the ichnogeneric level (although strictly not recommended) should be aware that the name *Monocraterion* is inappropriate for this use. Although the figures of the type material of *Monocraterion* in JENSEN (1997) are of good quality the above discussion underscores that the taxonomic status of this structure remains doubtful. *Monocraterion* is based on a unique, probably composite trace fossil and its use is best confined to the type material only. *Arenituba* STANLEY & PICKERILL, 1995 seems to be very similar to *Monocraterion* but in contrast to the latter is much more frequently found. *Arenituba* was previously named *Micatuba* by CHAMBERLAIN (1971) and received a replacement name by STANLEY & PICKERILL (1995; see additional discussion on *Arenituba* below). Similarities between *Monocraterion* and *Rosselia* are only given in very poorly preserved material. *Rosselia socialis* DAHMER (Fig. 67) is a large spindle-shaped structure with a central or excentric inner tube with massive filling surrounded by thin, more-or-less concentric layers of sediment. Restudy of the type material (SCHLIRF et al. 2002, NARA 2004) and additional detailed studies by NARA (e.g., 2002) show that *Rosselia* is best explained as a trace fossil caused by pushing sediment aside rather than a sediment-feeding structure. The striae on the exterior of some *Rosselia* are tension cracks caused by sediment pushed aside, rather than scratch ornaments in the usual sense (OSGOOD, 1970).

The value of ichnotaxobases in simple vertical burrows

Ichnotaxonomy often seems, and certainly often truly is, difficult to understand and even arbitrary. For this reason it is important to present the process how certain potential ichnotaxobases are evaluated. A comprehensive and uniform approach on how to deal with ichnotaxonomy and nomenclature of trace fossils, is given by BERTLING et al. (2004, in rev.), and their suggestions are strictly followed here. One of their main conclusions is that ichnotaxobases should be uniformly used within groups, though the value of an ichnotaxobase may differ between groups. This follows the intent of FÜRSICH (1974a, b), who encouraged the use of ethologically based significant and accessory features as ichnotaxobases. In both cases an ichnotaxonomist must evaluate which ichnotaxobases are important. However, in order to be as objective as possible a substantial effort to gain biological background information is needed. In the following section, such an evaluation process is discussed.

Aside from the different value of ichnotaxobases between different groups, there is a number of features that should never serve as ichnotaxobases. Examples such as the paper by SCHALLREUTER & HINZ-SCHALLREUTER (2003)[2] clearly show the necessity of having well defined ichnotaxonomic guidelines. In their diagnosis of *S. musicalis* they give measurements of tube size and distance between tubes as well as data such as sedimentary structures between tubes and the amount of tubes seen in side view per cm and top view per cm^2. All of these are unsuitable ichnotaxobases. Even though the host sediment is always important in ichnology, the sedimentary structures of the host sediment are certainly not a feature to be mentioned in the diagnosis. In general one should only

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[2] The figures of *S. musicalis* show a distinct wall-lining, a feature that is neither mentioned by the authors in their diagnosis nor in their discussion of *S. musicalis*. A few lines later in the same manuscript, wall-lining is used as a criterion to differentiate their second new ichnospecies, *S. tibia*, a rather strange conclusion. Morphological details are generally missing besides the statement that the new ichnospecies are tubes. The diagnosis does not state how the tubes are oriented, whether they are straight or curved, what the cross section looks like, all of which are features of taxonomic importance. In their definition for *S. musicalis* they state that the tubes may touch each other, yet in their discussion they state that the new species can be distinguished from *S.* aff. *linearis* because in *S.* aff. *linearis* the tubes are closer. Besides the fact that the distance between two tubes does not matter at all, the question arises how tubes can be even closer than touching each other. As stratum typicum the authors give Lower Cambrian, something absolutely unacceptable. An entire subsystem such as the Lower Cambrian can certainly not serve as type stratum, for instance this would also include igneous rocks as a possible source, strange! The second new ichnospecies *S. tibia* is defined by size of the tubes, the distance between tubes and the existence of a wall-lining, again all other morphological features are missing. In addition to the facts mentioned above, erratic blocks of such small sizes are not suitable for studies presented. One the few generally accepted ichnological principles are that ichnotaxonomy of invertebrate trace fossils is absolutely producer independent and size alone is no ichnotaxobase (e.g., BERTLING et al. in rev.). The latest version of the ICZN should also be consulted before writing papers dealing with nomenclature. A statement such as "…sollte man in diesem Falle die Regeln nicht zu streng auslegen…" SCHALLREUTER & HINZ-SCHALLREUTER (2003: 35) '… in this case one should not adhere too strictly to the rules…' is as such unacceptable. There are exceptions in the rules of the ICZN, however, in order to correct a mistake there are again clear rules how to proceed but certainly not by not too strictly adhering to the rules. Another obscure statement in SCHALLREUTER & HINZ-SCHALLREUTER (2003: 42) is that *Asabellarifex* KLÄHN, 1932 is a *nomen nudum* because no type species had been assigned, which is simply wrong, because before 2000 no type ichnospecies were necessary for ichnotaxa (ICZN 1999 Art. 13.3.3). Besides these nomenclatural weaknesses the authors also seem to have problems in using the correct ichnological terms. Frequently they use borings and burrows synonymous, which however are fundamentally different types of trace fossils.

consider the morphological features of a trace fossil that reflect biological activity, and moreover that have a reasonable preservation potential (BERTLING et al. in rev.). Such features include the funnel-shaped upper parts of *Diplocraterion* or *Skolithos*. These funnels may be rapidly eroded or even created abiogenically by currents, and hence are unsuitable ichnotaxobases (FÜRSICH 1974b; Fig. 47).

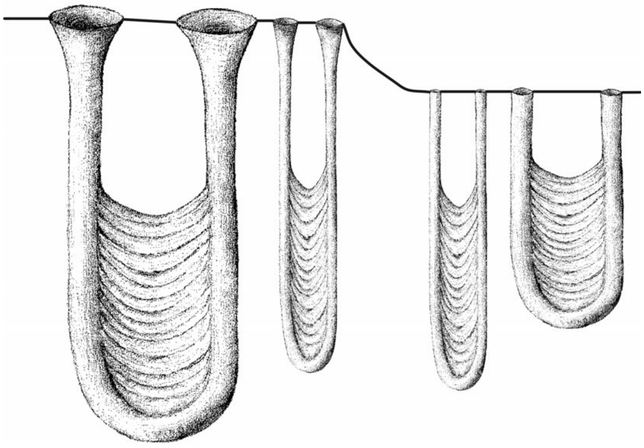


Figure 68: Sketch of funnel-shaped burrow tops in *Diplocraterion parallelum,* and how lack of funnels arises due to erosion.

Wall-linings in horizontally oriented burrows may be of different value than in vertically oriented burrows. Vertical, tubular burrows, with or without wall-lining, are usually permanently inhabited by their producers; exceptions include escape structures, which however can be distinguished by special characteristics (Fig. 69). A wall-lining may be the result of stabilizing the burrow wall (burrow construction action) as an intentional reaction of the producer to inadequate sediment cohesion, to stabilise the burrow wall. Another reason for building a wall-lining may be in-falling sediment into the open burrow. In this case the producer presses sediment particles into the wall, creating a lining (burrow maintenance action). In either case, stabilisation of the burrow is the result. This is a very interesting aspect of wall-linings. Whether the primary intention of the trace maker was tidying up the burrow or stabilisation, the result is a more stabilised structure. In addition, such stabilisation also improves the ability of the progenitor to move within the burrow (SCHÄFER, 1962). However, this must be considered as accessory behaviour of only minor taxonomic importance. Nevertheless, a detailed study of all simple, vertically oriented trace fossils may reveal that it is useful and justified to differentiate various ichnospecies using the existence or absence of a wall-lining. Such a detailed study, however, is beyond the scope of this study.

In the case of *Polykladichnus aragonensis* (unlined) and *P. irregularis* (lined) the presence of a wall-lining distinguishes the two ichnospecies. In the case of horizontal tubular burrows, such as *Planolites* and *Palaeophycus*, the situation is different. Among other features, *Planolites* is distinguished from *Palaeophycus* at the ichnogeneric level by absence or presence of a wall-lining (PEMBERTON & FREY, 1982; KEIGHLEY & PICKERILL, 1995). At first sight this seems to be inconsistent. However, in the case of *Planolites* and *Palaeophycus* the existence of a wall-lining reflects behaviour at a high level of significance. *Planolites* (unlined) is interpreted as an impermanent locomotion and/or feeding structure (pascichnion and/or fodinichnion), thus there is no need of stabilising the burrow wall, even if the substrate was unstable. In contrast, *Palaeophycus* (with wall-lining) is a permanently open burrow of a possible deposit-feeder, suspension-feeder, or predator (fodinichnion or domichnion). For this reason the wall-lining is interpreted as being essential for keeping the burrow permanently open and thus of a high level of significance. In addition, *Planolites* has an active filling and *Palaeophycus* is passively filled. This example clearly shows the problematic and imponderable aspects of ichnotaxonomy, and why the ethologic background is highly important in understanding the value of ichnotaxobases.

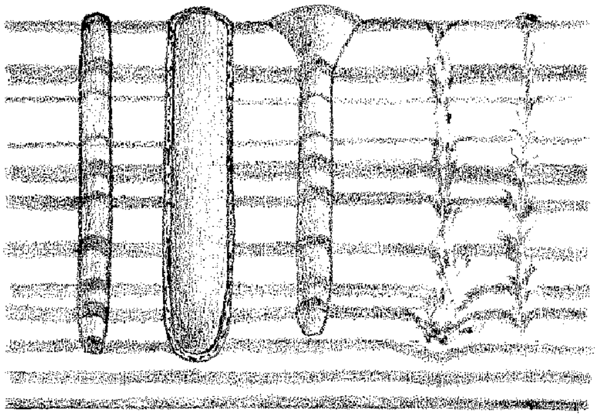


Figure 69: Sketch of simple vertical, lined and unlined, permanently inhabited burrows (left three specimens); burrow margins are distinct; when left by their progenitors such burrows will be filled by sediment. Right two specimens show escape structures; note indistinct nature of structures with no distinct wall identifiable. Not to scale.

Burrow cross-sections may be important ichnotaxobases, but they must be used with care. Most oval cross-sections are nothing but the result of compaction of formerly circular cross-sections, at least in horizontal structures. In vertical structures this is different, since usually compaction acts in the vertical plane, although horizontal deformation is very common during folding (Fig. 60). Fortunately such kinds of deformation are usually easily detected and should hardly be confused with biogenically produced morphologies.

Another factor is burrow density (Fig. 59). RICHTER (1920) considered the burrow density of *Sabellarifex* as an important criterion, which is why he compared his fossil material with the recent domichnia of the "sand coral" polychaete *Sabellaria*. FENTON & FENTON (1934) pointed out that straightness of worm tubes is partly a function of crowding. Unless it can be proved that burrow density has a clear behavioural reason, it is recommended not to consider burrow density in ichnotaxonomy. The frequently described contacts of many specimens of *Skolithos*, resulting in a polygonal cross-section of the tubes, must not be considered as an ichnotaxobase (e.g., ALPERT 1974). So far, no one has been able to demonstrate a behavioural reason behind high burrow density in *Skolithos*. Thus the polygonal cross-sections are to be interpreted analogous to deformed brachiopods in high-density occurrences, or any other deformation resulting from contacts.

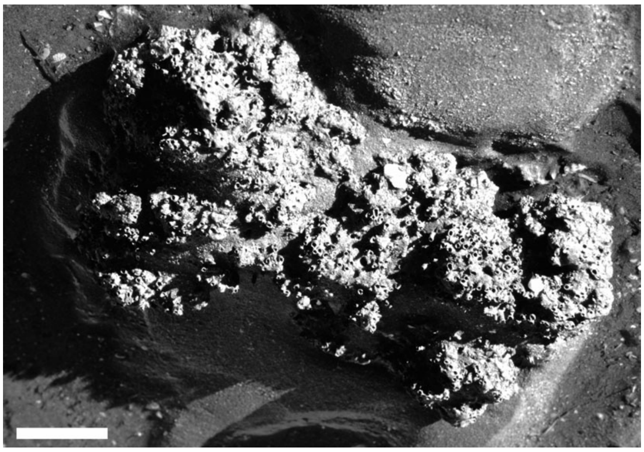


Figure 70: Field photograph of a Recent sabellariid mini-reef structure in a tidal flat near Cossack, Western Australia. Scale bar: 5cm.

EKDALE & LEWIS (1993) suggested the basal substrate on which *Skolithos*/*Sabellarifex* structures grow as an ichnotaxobase, since modern sabellariids build agglutinated tubes solely on primary or secondary hard-grounds. Their rationale was that if the base of a piperock were a hardground then the piperock could have been built by sabellariids and thus would be an aedificichnion (built above the ground; Fig. 70) whereas *Skolithos* piperocks are the result of burrowing activity. This is a fundamental difference and certainly deserves ichnotaxonomic distinction, but where criteria are lacking to recognise such forms they simply cannot be distinguished. The pure existence of a hardground at the base of a piperock does not necessarily indicate sabellariid activity. For this reason, the suggestion made by EKDALE & LEWIS (1993) is not supported here, though the presence of a primary or secondary hard-ground at the base of a piperock should lead to a closer examination of all morphological details.

Substrate as such should never be chosen as an ichnotaxobase except for general differentiation of borings and 'burrows' (hard-ground and/or wood-ground vs. soft and/or firm-ground) (BERTLING et al. in rev.). If substrate were chosen as an ichnotaxobase one would certainly open a Pandora's Box, resulting in a plethora of names based only on host sediment differences. According to SCHÄFER (1949, 1962) and EKDALE & LEWIS (1993) sabellariid reefs do show distinct morphological features. The walls of the tubes are built of single to double layers of sand grains. The walls constructed by the sabellariid *Phragmatopoma lapidosa* are built of imbricated grains and have a tough, smooth interior organic lining. No host sediment exists between the tubes (KIRTLEY & TANNER 1968). The base of a sabellariid reef often shows horizontal, interwoven tubular structures, something not known from *Skolithos*. The cause for horizontal growth in sabellariid reefs is unknown but it frequently occurs. Since true sabellariid reef structures are aedificichnia they can only be preserved if they are buried by sediment, a fact that should also leave distinct sedimentological features that differentiate sabellariid reefs from *Skolithos* burrows. To sum up, there should be enough morphological features to distinguish between sabellariid reefs and *Skolithos* piperocks (EKDALE & LEWIS 1993).

Ichnogenus *Arenituba* STANLEY & PICKERILL, 1995

Type ichnospecies: *Micatuba verso* CHAMBERLAIN, 1971: 238, pl. 29 fig.9; by monotypy.

Currently recognized ichnospecies belonging to *Arenituba*:
Arenituba verso (CHAMBERLAIN, 1971).

Figure 71: Holotype of *Arenituba verso* (from CHAMBERLAIN, 1971: pl. 29 fig. 9).

Discussion: In 1995, STANLEY and PICKERILL replaced a preoccupied name of a trace fossil, *Micatuba* CHAMBERLAIN, 1971, which was a homonym of *Micatuba* AVNIMELECH, 1952. In general their nomenclatural act was correct. However, the authorship of the replacement name was chosen incorrectly. In the case of a replacement name the new name (*nomen novum*) receives its own author and date (ICZN 1985 Art. 60c). Relevant at the time of publication was the 1985 version of the ICZN. Although the authors have correctly cited Article 60c and even repeated it by word they incorrectly chose CHAMBERLAIN as the author of the new name *Arenituba*. To correct this error it his herewith stated that the authorship must be as given above.

While performing nomenclatural acts, one should not only follow the rules of the ICZN but also take care of the correct use of terms. In their taxonomic note, STANLEY & PICKERILL (1995) incorrectly stated that the name *Micatuba* was unavailable because of preoccupation (*homonymy*). However, the name was available but invalid in the case of CHAMBERLAIN'S homonym (ICZN 1985 Art. 10g; ICZN 1999 Art. 10.6). The authors also stated that *Micatuba paganzoi* ACEÑOLAZA, 1978 was more likely a trace fossil composed of intersecting trace fossils such as *Planolites* or *Palaeophycus* and thus was best considered a *nomen oblitum* (forgotten name), a term that is inapplicable here. If the observation of STANLEY & PICKERILL (1995) was correct, the name proposed by ACEÑOLAZA was a subjective junior synonym. If their opinion concerning *Planolites* or *Palaeophycus* was wrong and the specimen is unidentifiable, then it was a *nomen dubium* (name of unknown or doubtful application). Since the misuse of nomenclatural terms is very common a list with explanations of the most frequently used nomenclatural and taxonomic terms in zoological publications is given in Appendix III.

Ichnogenus *Chomatichnus* DONALDSON & SIMPSON, 1962

Type ichnospecies: *Chomatichnus wegberensis* DONALDSON & SIMPSON, 1962: 78; by original designation.

Diagnosis: Small conical mounds, consisting of faecal castings, connected with a central, vertical tubular structure (after Häntzschel 1975).

cf. *Chomatichnus* isp.

Fig. 72

1987 ichnog. et ichnosp. incert. – GEYER: 299, fig. 8.20-8.22, fig. 9.
2001 *Chomatichnus* isp. – SCHLIRF et al.: 96, tab.1.

Material: SMF 44080, SMF 44081, SMF 44082; *Modiola*-Bank, Grabfeld Fm, Middle Keuper, Oberscheinfeld-Ost, Franconia, Bavaria, southern Germany.

Description: Positive epichnial ring surrounding a straight, unlined, vertical tubular structure. The ring is made up of coarser sediment particles than the surrounding sediment. The ring structure gradually intergrades with the host sediment by lateral grain size reduction. In cross section several layers of coarse sediment in the ring structure can be identified.

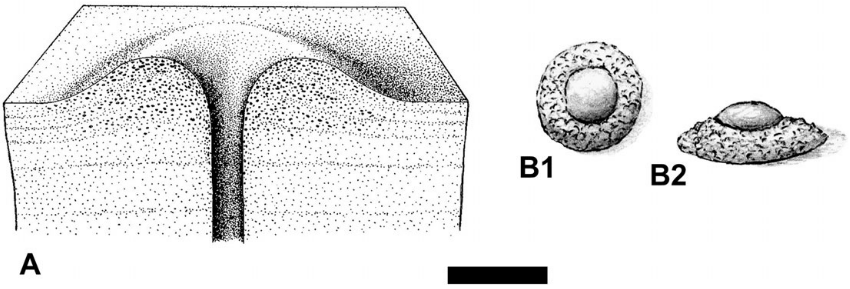


Figure 72: **A**. Reconstruction of cf. *Chomatichnus* isp., fullrelief, *Modiola*-bed, Grabfeld Fm, Middle Keuper, Oberscheinfeld-Ost, Franconia, Bavaria, southern Germany. **B**. Reconstruction of *Mammilichnis aggeris*, positive hyporelief. **B1**. Bottom view. **B2**. Lateral view, upside down.Scale bar 1cm.

Discussion: These structures were first described by GEYER (1987). He compared the structures with *Laevicyclus* QUENSTEDT, 1879 and concluded that they differ from it by lacking concentric rings, which are typical of *Laevicyclus*. He also compared the structures with *Mammilichnis aggeris* CHAMBERLAIN, 1971. At first glance *Mammilichnis* (Fig. 72B) is slightly similar to the trace fossils from the *Modiola*-bed, however, there is a fundamental difference between them; *Mammilichnis* is a positive hyporelief. The structures are best assigned to cf. *Chomatichnus* isp. *Chomatichnus* is a conical mound made up of faecal castings, connected with a central, vertical tubular structure. Since no faecal material could be observed the assignment to *Chomatichnus* is made with restrictions only.

The material may be explained as domichnion of a suspension-feeder in analogy to *Skolithos*. The various layers of coarse sediment make a longer use of the structure by its progenitor likely (GEYER 1987). Suggestions on the phylogenetic background of the possible producer are difficult. Due to the fact that the vertical tubular structure is straight any vermiform animal seems likely as a producer.

Spreite structures

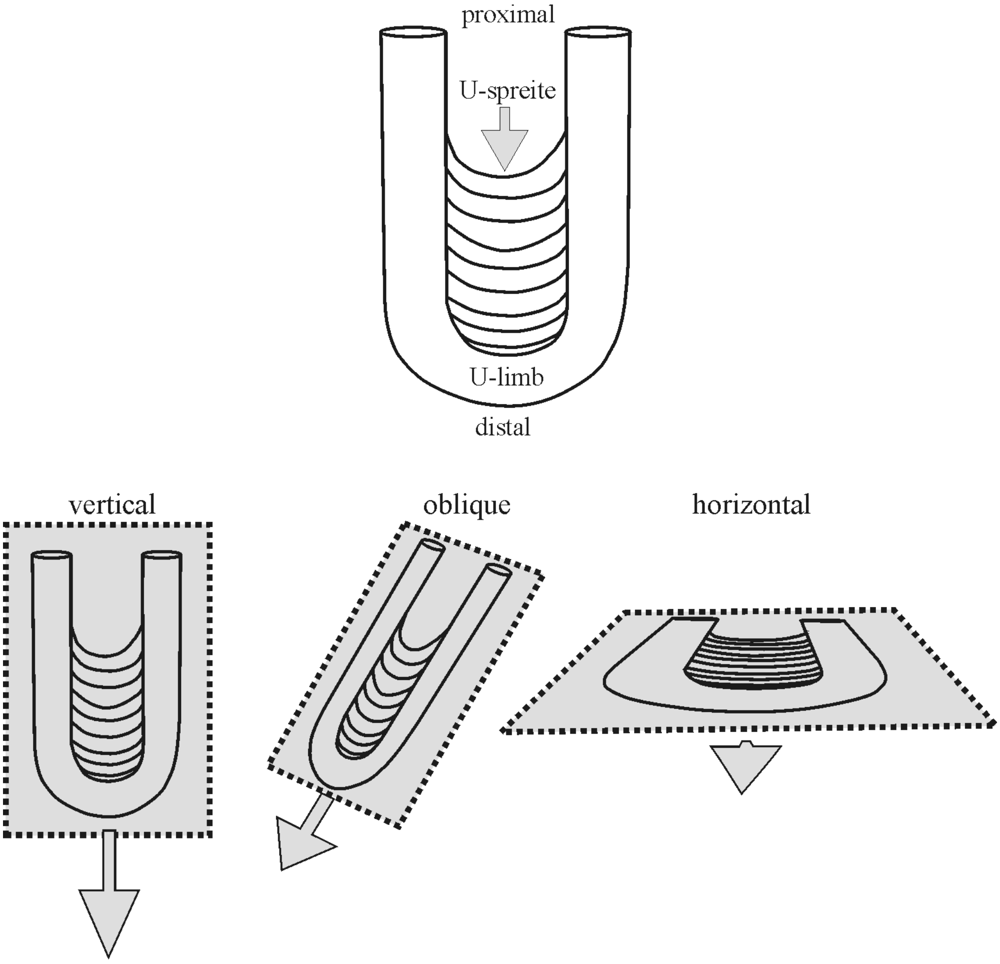
These structures are characterized by spreite which from through displacement of a limb. This group includes horizontal, inclined, or vertical U-shaped, or composed U- or J-shaped spreite burrows such as *Diplocraterion*, *Ilmenichnus*, *Rhizocorallium* and *Zoophycos*. In addition, wall-like structures such as *Teichichnus* belong to this group.

Ichnogenus *Diplocraterion* TORELL, 1870

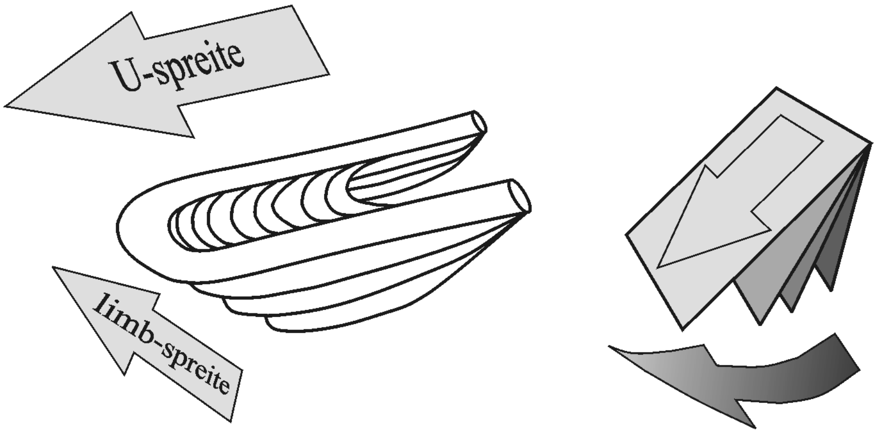
Type ichnospecies: *Diplocraterion parallelum* TORELL, 1870: 13; by subsequent designation (RICHTER 1926: 213).

Emended diagnosis: Vertical to oblique, U-shaped, single-spreite burrows; spreite may be unidirectional or bidirectional, continuous or discontinuous. Limbs unlined and smooth, or with bioglyphs, sometimes with heavy lining. Limbs either parallel or diverging upward or downward; top of limbs sometimes with funnel shaped opening.

Discussion: An emendation of the diagnosis was necessary because the previous diagnosis did not consider lining, bioglyphs, and burrow openings. In addition, oblique U-shaped, single-spreite structures are suggested to belong to *Diplocraterion* rather than to *Rhizocorallium* (for the terminology of U-shaped spreite burrows see Fig. 73). It is an inconsistency in trace fossil taxonomy that horizontal unilobed, U-shaped structures and multilobed structures are assigned to *Rhizocorallium* together with oblique forms whereas vertical forms belong to a different ichnogenus. Morphologically and ethologically *Diplocraterion parallelum* (vertical) and many *Rhizocorallium jenense* (oblique) have much more in common than *Rh. jenense* and '*Rh. irregulare*' (quotas are used because of existing synonymy with *Ilmenichnus devonicus*; see below). Thus, vertical and oblique forms should be placed in one ichnogenus, namely *Diplocraterion* (see below). In general, all U-shaped spreite structures are in need of a detailed revision, especially the type material of all their ichnospecies. If heavily lined vertical U-shaped structures should be assigned to *Diplocraterion* or kept as a separate ichnogenus needs further investigations. Following the commonly used SOT classification concept a separation at the ichnogeneric level would be appropriate. If one follows the new SOT classification concept presented herein, a separation at the ichnosubgeneric level would be appropriate. However, a final decision can only be made after a detailed analysis of all ichnospecies belonging to vertical U-shaped spreite structures. U-shaped spreite burrows seem to be well-defined and understood, but like in many other cases our understanding turns out to be very poor if it comes to close examination of type material. A classification scheme for a trace fossil genus should be consistent and the morphological aspects taken into account for the classification should be valued. FÜRSICH's (1974a) observations on the various forms of *Rhizocorallium* contributed tremendously to our understanding of this group of trace fossils. Thirty years later, however, an even more rigorous use of FÜRSICH's classification concept leads to some refinements in the classification of U-shaped spreite burrows (Fig. 74). *Rhizocorallium jenense* specimens from the type locality of this ichnospecies is difficult to explain in ethological terms. An interpretation as a mixture of a suspension- and deposit-feeder strategies seems plausible. Horizontal, unilobed or multilobed, U-shaped spreite structures are best assigned to an ichnogenus different from *Rhizocorallium*.



spreite only between U-limbs (U-spreite) ==> ‘single-spreite’



spreite between U-limbs (U-spreite) and through retrusive shift of U-limbs (limb-spreite) ==> 'double spreite'

Figure 73: Terminology of U-shaped spreite trace fossils.

HECKER (1980) already pointed out the inconsistencies in the classification scheme of *Rhizocorallium* and *Diplocraterion*. Although widely neglected, his ichnospecies *Rh. devonicum* is and always was valid and available. The description and the figures provided by HECKER (1930) fulfil the demands of the Code. Thus, *Rh. irregulare* clearly is a younger synonym of *Rh. devonicum*. Pointing out that *Rh. devonicum* was a deposit-feeder structure and *Rh. jenense* was a suspension-feeder structure, HECKER (1980) introduced a new ichnogenus, namely *Ilmenichnus*, for horizontal U-shaped spreite structures. This is a suggestion absolutely consistent with FÜRSICH's classification scheme. HECKER's (1980) suggestion is followed here and *Ilmenichnus devonicus* (HECKER, 1930) is used in favour of *Rhizocorallium irregulare* MAYER, 1954. *Glossifungites saxicava* ŁOMNICKI, 1886 is a simple, oblique, U-shaped single-spreite structure as shown by UCHMAN et al. (2000). An oblique or a vertical orientation in simple U-shaped spreite structures is considered an accessory feature because both structures may be convincingly explained as suspension-feeder structures. As a consequence *Diplocraterion* TORELL, 1870 is considered an older synonym of *Glossifungites* ŁOMNICKI, 1886. However, the different orientation should be used to distinguish ichnospecies. As a result, vertical, U-shaped, single-spreite structures should be assigned to *Diplocraterion parallelum* and similar structures with an oblique orientation should be assigned to *Diplocraterion saxicavum*. Material from the type locality clearly reveals that *Rhizocorallium jenense* is a U-shaped double-spreite structure. This means that several U-shaped spreite structures are shifted vertically, which results in an overall wedge-shaped structure. Thus, *Rh. jenense* has a U-spreite and so-called limb-spreite. This distinguishes *Rh. jenense* from other U-shaped spreite structures and makes them an intermediate form; intermediate from a morphological and ethological point of view. The morphology of *Rh. jenense* combines vertical and oblique growth. The resulting amount of reworked sediment is very high compared to *Diplocraterion* but not as high as in *Ilmenichnus*. Thus, *Rh. jenense* is interpreted as a result of a mixture of deposit- and sediment-feeding and kept as a separate ichnogenus and ichnospecies. A combination of deposit- and sediment-feeding behaviour is known from recent fossorial decapod crustaceans (EKDALE 1992) so that such behaviour is plausible.

The resulting classification scheme unites simple, U-shaped, single-spreite structures with a vertical or oblique orientation under *Diplocraterion* (suspension-feeder). Wedge-shaped, double spreite structures remain under *Rhizocorallium* (mixed deposit- and suspension feeder), and horizontal structures are assigned to *Ilmenichnus* (deposit-feeder) (Fig. 74).

Diplocraterion occurs from Lower Cambrian (NARBONNE et al. 1987) to the Miocene (FLEMING 1973). Pleistocene reports of U-shaped equilibrium structures by D'ALESSANDRO & BROMLEY (1986) may be attributed to *Diplocraterion* (FILLION & PICKERILL 1990).

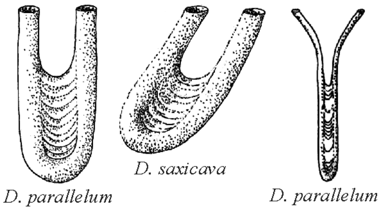
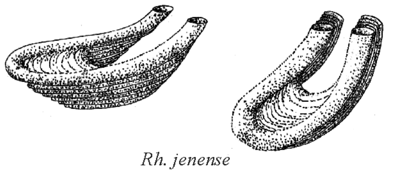
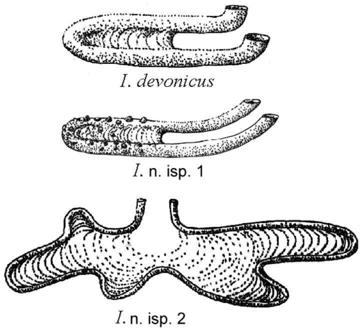
Diplocraterion	*Rhizocorallium*	*Ilmenichnus*
		
suspension-feeder	mixed deposit-suspension-feeder	deposit-feeder
single spreite, vertical to oblique	double spreite, oblique to almost horizontal	single- to multi-lobed, dominantly U-spreite, subordinate limb-spreite, horizontal

Figure 74: Classification scheme of, and feeding habits represented by the various U-shaped spreite trace fossils.

Diplocraterion parallelum TORELL, 1870

Fig. 68, 74-76

Emended diagnosis: Vertical, U-shaped, single-spreite burrows; spreite may be unidirectional or bidirectional, generally continuous, rarely discontinuous. Limbs unlined and smooth, or with bioglyphs (longitudinal or transverse ridges and grooves). Limbs either parallel, or diverging upward or downward; top of limbs sometimes with funnel shaped opening.

Material: One slab with numerous specimens, SMNS 65497, Rhätsandstein, Exter Fm, Upper Keuper, Steinberg near Nürtingen, Baden-Württemberg, southern Germany.

Description: Numerous short, densely packed, vertical to slightly oblique, generally truncated, incomplete, U-shaped spreite burrows, with distinct longitudinal to transverse, criss-crossing, fine ridges and grooves. The structures can be divided into two size classes with a width of the U of: 5-14mm or 32-41mm. The entire length of the structures remains unknown since the tops, especially of the larger forms all are truncated. The trace fossils all show a distinct iron mineralisation. The slab is made up of a fine to medium-grained, moderately sorted, rounded to subrounded, greyish to brownish quartz sandstone.

Discussion: The burrows are all likely to be truncated. However, the co-occurrence of small and relatively large (wide) structures needs further explanation. If all burrows would have been truncated by one erosional event, the smaller ones would have been very long in comparison to their width. It therefore seems more likely that the large forms represent an earlier ‘population’ which was truncated, and the smaller forms were built at a later stage and – if at all – were cut in a second erosion event. The erosion surface of the slab bearing the *Diplocraterion* is mineralised and now has a ferritic crust. The trace fossils also show a ferritic mineralisation. The surface may well be interpreted as an omission surface. By the time the trace fossils were formed the sediment must have been sufficently cohesive to allow the preservation of scratch ornaments.

U-shaped spreite burrows are very common in strata with omission surfaces or surfaces indicating environmental changes (FÜRSICH et al. 1981; SAVRDA 1995; BROMLEY & UCHMAN 2003; SCHLIRF 2003b). Grooves and ridges on the limbs of *Diplocraterion* are usually interpreted as scratch ornaments and make arthropods very likely as progenitors (FÜRSICH 1974b, c). *Diplocraterion parallelum* and *Rhizocorallium jenense* are thought to be very similar. According to general assumption they only differ in orientation. However, as shown below, material from the type locality reveals that *Rhizocorallium jenense* seems to be more complex than *Diplocraterion parallelum* although type material for the latter is lacking. The specimens presented by WESTERGÅRD (1931) and JENSEN (1997), and the observations of these authors on material from the type locality leaves no doubt that *Diplocraterion* is a U-shaped, single-spreite burrow (“one dimensional”). Of course a trace fossil can never be one-dimensional so that the term in this case is understood as the direction of a vector parallel to the long axis of the U-limbs (Fig. 73). Besides growth and orientation in one dimension, *D. parallelum* also does not show a distal increase of the width of the U-limbs.

Specimens of *Diplocraterion parallelum* dominantly have a protrusive spreite; if it was an equilibrium structure this was a response to erosion. Observations on Recent burrows made by *Corophium volutator* (very similar to *Diplocraterion*) in semi-firm and firm, muddy intertidal and salt marsh deposits supports this assumption. In the following a short description of the observations by DASHTGARD & GINGRAS (2004) is given. If the burrows were passively trapped with sediment the resulting structures were similar to *D. parallelum* with protrusive and retrusive spreite. If the burrows were truncated by erosion the resulting structures are similar to protrusive *D. parallelum*. In semi-firm substrates dominated by deposition, the resulting burrows show retrusive spreite. In all environments a multiple subsequent occupation of one burrow by several *Corophium* could be observed. If the progenitor outgrows an existing burrow, *Corophium* builds a larger burrow around the old one. This may result in a sort of nested *Arenicolites* (DASHTGARD & GINGRAS 2004).

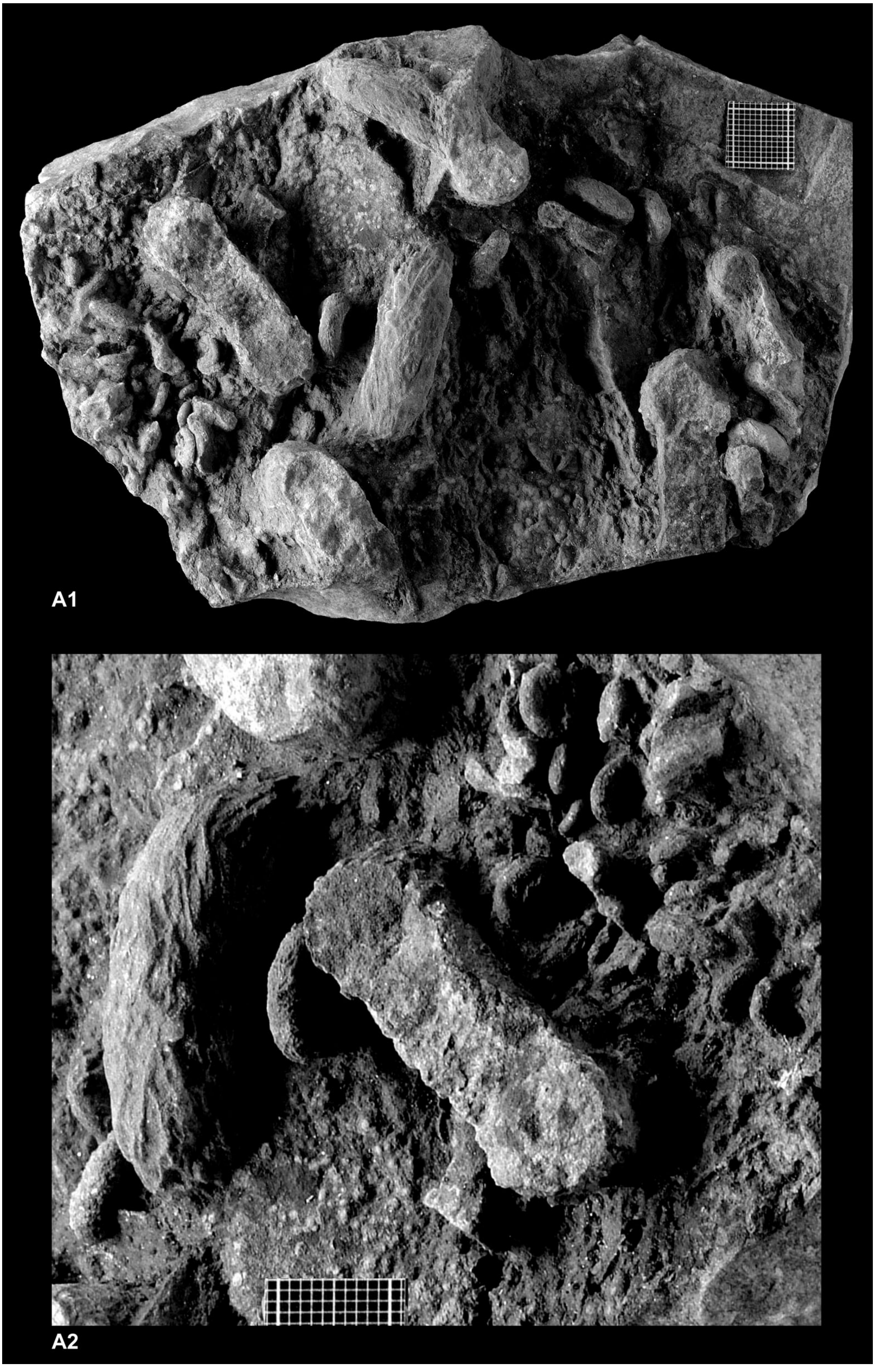

A1
A2

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Figure 75: *Diplocraterion parallelum*. Torell, 1870, SMNS 65497, fullreliefs, Rhätsandstein, Exter Fm, Upper Keuper, Steinberg near Nürtingen, Baden-Württemberg, southern Germany. Note well-preserved scratch ornaments. **A1**. Bottom view. **A2**. Detail of A1. Millimetre grids for scale.

In general, *Diplocraterion* are best explained as domichnia/equilibrichnia of a suspension-feeder, most likely arthropods (crustaceans) or annelids (FÜRSICH 1974b, c; SCHLIRF 2003b).

Diplocraterion saxicavum (ŁOMNICKI, 1886)

Fig. 74,76

* 1886 “*Glossifungites*” *saxicava* n. sp. ŁOMNICKI: 99, pl. 3 fig. 64a-b.
1985 *Rhizocorallium* sp. – WALTHER et al.: 102, fig. 1-3, pl. 1 fig. 1-6, pl. 2 fig. 1-6.
2000 “*Glossifungites saxicava*” ŁOMNICKI (= *Rhizocorallium jenense* ZENKER). – UCHMAN et al.: 183, fig. 3-5.

Diagnosis: Steeply oblique, U-shaped, single-spreite burrows; spreite unidirectional, continuous or discontinuous. Limbs parallel, unlined and smooth or with bioglyphs; top of limbs sometimes with funnel shaped opening.

Discussion: The assignment of *Glossifungites saxicava* ŁOMNICKI, 1886 to *Diplocraterion* is a logical consequence of a reorganisation of U-shaped spreite burrows. As discussed above it is an ichnotaxonomic inconsistency that vertical U-shaped spreite burrows were kept separately at the ichnogeneric level from oblique forms whereas oblique and horizontal forms were kept in one ichnogenus although being fundamentally different in the reflected behavioural pattern. However, it is this behavioural pattern, which should form the base for considering the ichnotaxonomic value of morphological features (FÜRSICH 1974b,c). As discussed in detail in the SOT chapter, scratch ornaments are not considered highly a significant ichnotaxobase and should be chosen as diagnostic at the ichnospecific level only.

Ichnogenus *Ilmenichnus* HECKER, 1980

Type ichnospecies: *Rhizocorallium devonicum* HECKER, 1930: 156, pl. 16 fig. 1; by original designation.

Probable synonym: *Myelophycus* ULRICH, 1904

Emended diagnosis: Unlined, horizontal to slightly oblique, straight to sinuous or plan spiral, unilobed to multilobed U-shaped spreite structures; subordinate retrusive limb-spreite may occur; ratio of limb to limb-spreite < 1 to 2; exterior smooth, with longitudinal to transverse grooves and ridges and maybe with additional pustules on the upper surface. Burrow fill massive or with a low to high ovoid pellet content. Diameter of U-limb frequently enlarged towards distal burrow part.

Remarks: The diagnosis was emended to include information on wall-lining and bioglyphs. *Myelophycus* ULRICH, a probable older synonym of *Ilmenichnus* was discussed by MCCANN & PICKERILL (1988). They put *Myelophycus* in synonymy with *Scolicia*, a decision not followed here. According to RINDSBERG (pers. comm.), *Myelophycus* is a bedding plane parallel U-shaped spreite structure. However, the type material (hosted in black shales) only shows very indistinct limbs and no terminal burrow part. In addition, the spreite between the limbs are very faint. Thus, *Myelophycus* is considered a *nomen dubium*, its and further use is not recommended.

A unique find, which shows the close relation of the progenitors of SOT and *Ilmenichnus* comes from the Middle Triassic of the Germanic Basin. The specimen shows *Ilmenichnus* attached to *Spongeliomorpha* (Fig. 77).

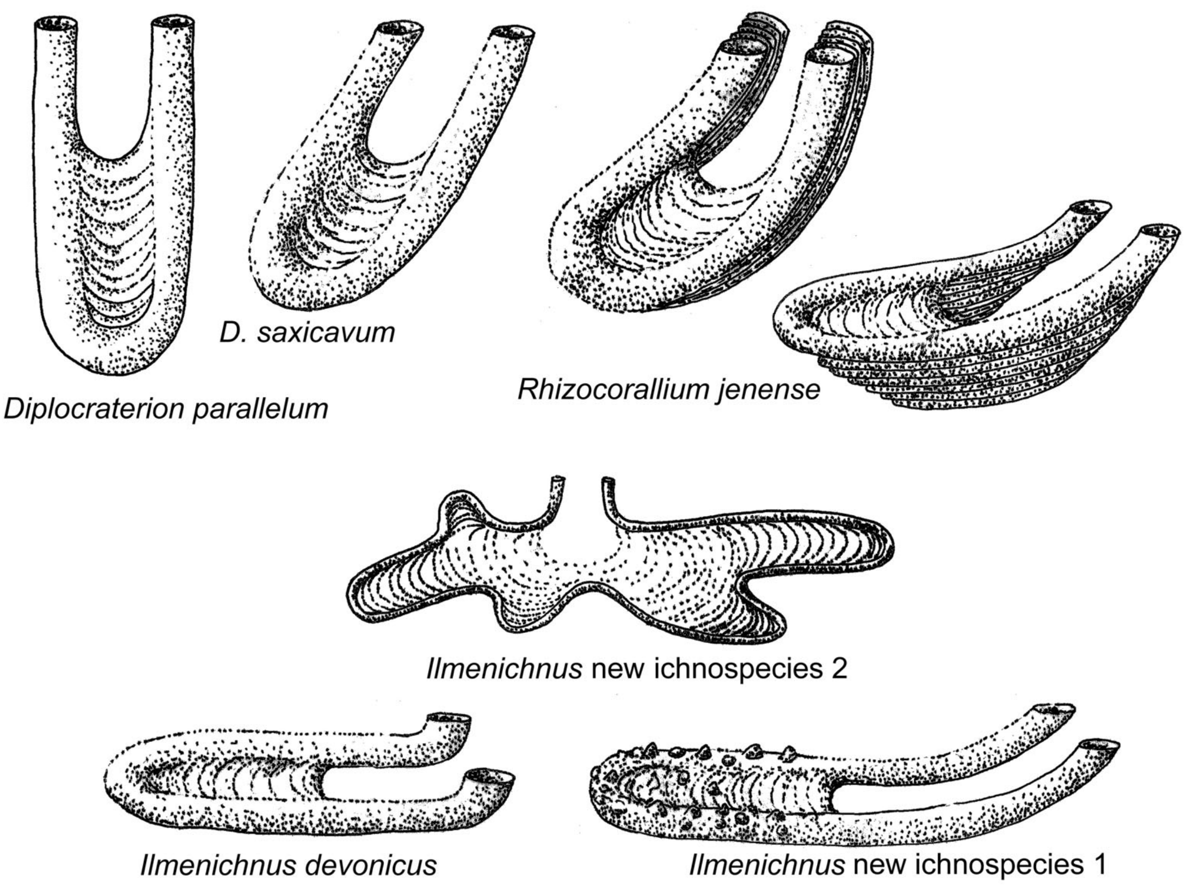

Figure 76: Reconstructions of various U-shaped spreite trace fossils. Not to scale.

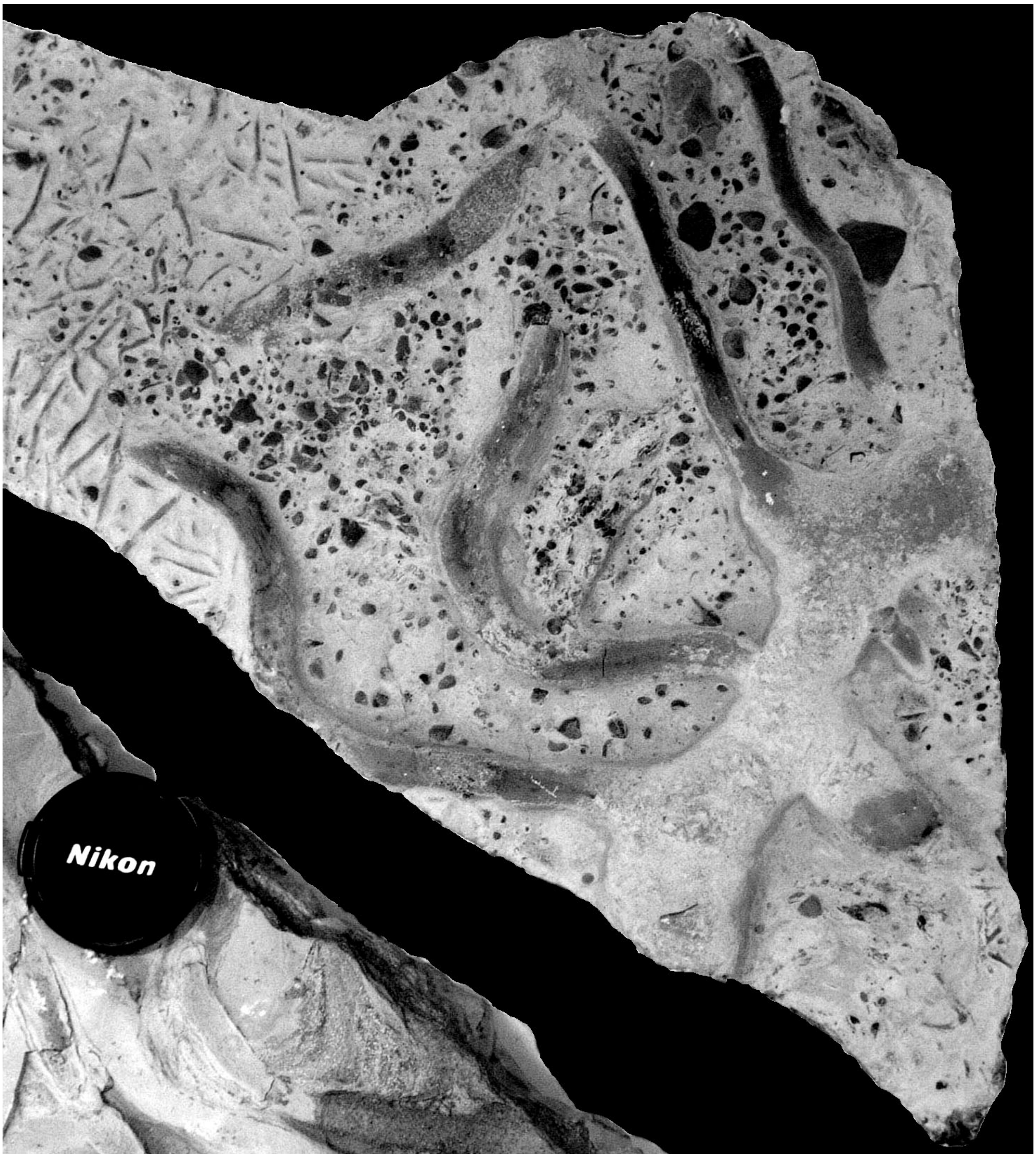

Figure 77: *Ilmenichnus* new ichnospecies 2 attached to *Spongeliomorpha* (*S.*) cf. *suevica*; picture taken in the exhibition hall of the Muschelkalkmuseum, Ingelfingen. Unfortunately, the spreite are very faint and thus poorly visible in the picture; the shell debris slightly traces the spreite; the general burrow morphology and the size is the same as of better preserved specimens from the same bed. Note gradual decrease of burrow diameter from *Spongeliomorpha* part to *Ilmenichnus* part. Positive hyporelief, bottom view. Lens cap 52mm in diameter.

Ilmenichnus new ichnospecies 1

Fig. 76, 78-81

Diagnosis: More-or-less straight, horizontal to slightly oblique, unlined, unilobed U-shaped spreite burrows, with protrusive U-spreite and subordinate retrusive limb-spreite; ratio of limb to limb-spreite < 1 to 2. Surface with longitudinal and/or transverse, fine ridges and grooves. Upper surface with pustules of irregular shape. Fill with ovoid pellets. Diameter of U-limb frequently enlarged towards distal burrow part.

Derivatio nominis:

Material: Holotype SMNS-L204h, paratypes SMNS-L204, SMNS-L204a-g, i-k, *orbicularis*-Schichten, Lower Muschelkalk, Middle Triassic, old quarry in Tiefental-Elm, near Königslutter, Lower Saxony.

Description: More-or-less straight, dominantly horizontal, subordinately slightly oblique, unlined, unilobed U-shaped spreite burrows, with protrusive U-spreite and a subordinate retrusive limb spreite. Surface with longitudinal and/or transverse, fine ridges and grooves. Upper surface with irregularly shaped pustules. Burrows filled with ovoid pellets. One specimen (SMNS L204b) has a true side branch emerging from the limb, with enlargements at the point of branching (Fig. 80).

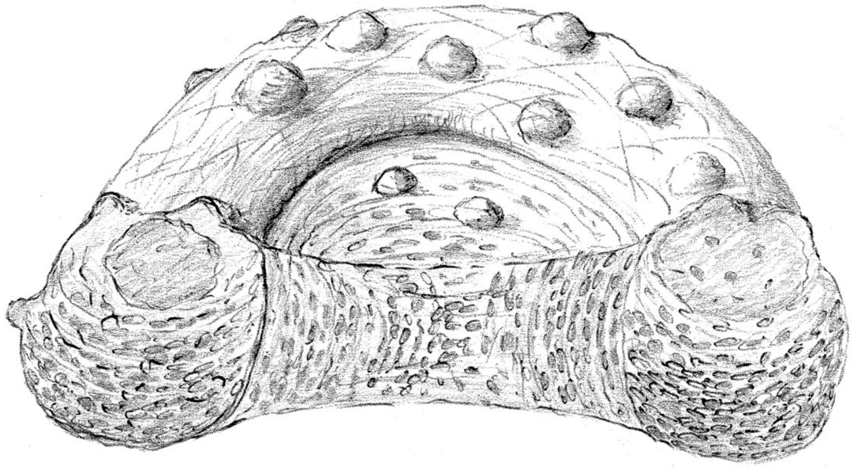

Figure 78: Reconstruction drawing with cross-section of *Ilmenichnus* new ichnospecies 1. U-limbs and spreite filled with ovoid pellets. Not to scale.

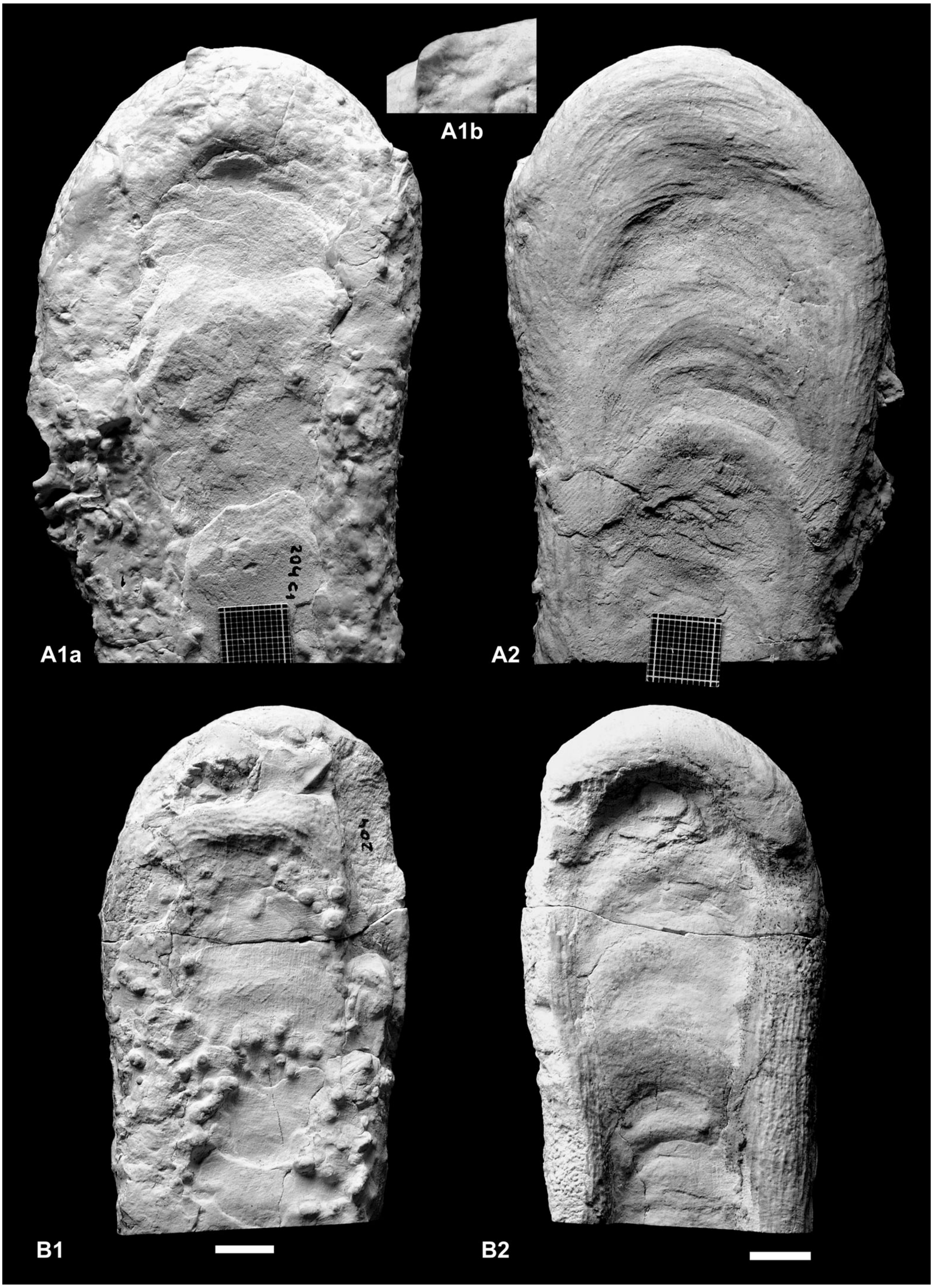

Figure 79: A-B. *Ilmenichnus* new ichnospecies 1; fullreliefs. **A**. Paratype. **A1a**. Pustulous upper surface of burrow; secondary burrowing at left U-limb visible; burrows widening towards the distal part. **A1b**. Detail of A1a showing ideally preserved pustule; top view. **A1c**. Various growth stages through distal and slight retrusive shift of U-limbs; scratch ornaments characteristically well-preserved on sole of burrow, but without pustules; bottom view; SMNS L204c1; millimetre grid for scale. **B1**. Holotype. Pustules define former distal U-limb; top view. **B2**. Pelletal fill of limb in lower left corner visible; bottom view; SMNS L204h; scale bars: 1cm.

Figure 80: Paratype of *Ilmenichnus* new ichnospecies 1, paratype, full relief; SMNS L204b. **A1**. Burrow widening towards distal part; pustules on upper surface; top view. **A2**. Bottom view. Scale bars: 1cm. **A3**. Detail showing side branch. Note enlargement at point of branching. Millimetre grid for scale.

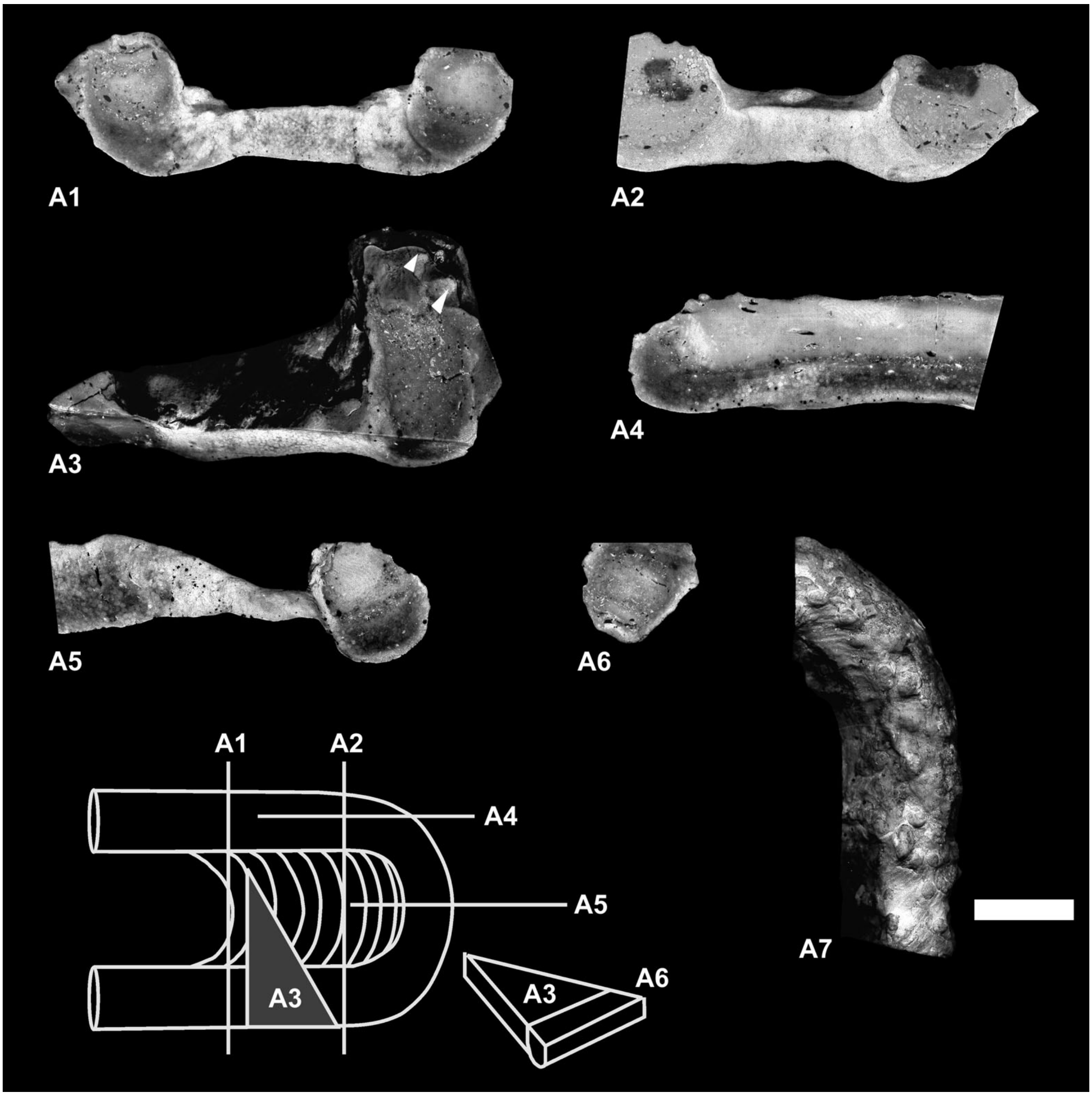

Figure 81: Paratype of *Ilmenichnus* new ichnospecies 1; full relief, SMNS L204f. **A1-A6**. Polished cross-sections; sketch in lower left corner indicates position of cross-sections. A3. Serial section through a large pustule that shows pelletal fill (white arrows). A4-A5. Retrusive shift of U-limbs resulting in subordinate secondary limb-spreite; note that ratio of open U-limb to spreite is < 1:2. Ovoid pellets can be seen in all cross-sections. **A7**. Pustules on upper surface. Scale bar: 1cm.

Discussion: The pustules are interpreted as small cavities made by the progenitor for unknown reasons. The pustules seem to be diagenetically overprinted. A purely abiogenic (diagenetic) formation of the pustules seems unlikely since the cavities were filled with the same sediment as the limbs (Fig. 81). In small specimens the pustules are small whereas in large specimens the pustules are larger. In addition, other trace fossils co-occurring with *Ilmenichnus* new ichnospecies 1 in the same beds do not show such features. The pustules are restricted to the upper surface of the U-shaped structures; they occur on the limbs as well as on the U-spreite. Moreover, the pustulous exterior is known from various localities in the Muschelkalk (Middle Triassic) (pers. comm. HANS HAGDORN, Ingelfingen). Yet, this feature is only known from Muschelkalk specimens. The observed side branch obviously is an exception and not considered relevant for the ichnotaxonomy of *Ilmenichnus* new ichnospecies 1. However, such features show that sometimes the usual program of the progenitor fails. From an ichnotaxonomical point of view such observations are not relevant because only the recurring pattern in trace fossils should be considered (see BERTLING et al. in rev.). From an ethological point of view such observations should be taken into account because they may reveal important information on the progenitor. In this case the pattern of branching is similar to that of other crustacean burrows since an enlargement of the burrow at the point of bifurcation can be observed. It suggests that the burrow was formed by an animal with a short and stiff (or not very flexible) body. A soft animal could have curved without the need of widening a burrow because its body would have been flexible enough to allow bending. Of course, other features, long well-known from *Ilmenichnus* support crustaceans as possible progenitors (see FÜRSICH 1974a for further details *Ilmenichnus* = *Rhizocorallium irregulare* in his paper). *Ilmenichnus* is interpreted as a deposit-feeding structure.

Ilmenichnus devonicus (HECKER, 1930)

Fig. 74, 76

? 1904 *Myelophycus curvatum* n.g. n. sp. – ULRICH: 145, pl. 13 fig. 2; [incomplete specimen, spreite difficult to recognize].
* 1930 *Rhizocorallium devonicum* nov. sp. – HECKER: 156, pl. 16 fig. 1-2.
non 1940 *Rhizocorallium praecursor* nov. spec. – HUNDT: 3, fig. 1; [= abiogenic sedimentary structures].
1954a *Rhizocorallium jurense* n. sp. – MAYER: 25, fig. 1.
1954b *Rhizocorallium irregulare* n. sp. – MAYER: 82, pl. 2-3.
1974a *Rhizocorallium irregulare* MAYER, 1954. – FÜRSICH: 24, fig. 1, 2 [*Rh. irregulare*].
? 1988 *Scolicia plana.* – MCCANN & PICKERILL: 341.
pt 1997 *Rhizocorallium jenense.* – JENSEN: 78, fig. 40a, 52; [*non* fig. 6A-B = *Rhizocorallium jenense*].
pt 1997 *Rhizocorallium jenense.* – JENSEN: fig. 65A; [only horizontal oriented forms = *Rh. jenense*].
pt 1997 *Zoophycos* isp. – JENSEN: 97, fig. 65C.
? 1997 *Zoophycos* isp. – JENSEN: fig. 65B, D.
1998 *Rhizocorallium irregulare* MAYER. – SCHWEIGERT: 5, pl. 1.
v 2000 *Rhizocorallium irregulare* MAYER, 1954. – SCHLIRF: 169, fig. 23, pl. 9 fig. 8, pl. 10 fig. 1-3.
v 2003b *Rhizocorallium irregulare.* – SCHLIRF: 133.
For further synonyms see SCHLIRF (2000).

Emended diagnosis: Unlined, horizontal, straight to sinuous or plan spiral, unilobed U-shaped spreite structures, with protrusive U-spreite and subordinate retrusive limb-spreite; ratio of limb to limb-spreite < 1 to 2. Exterior smooth, or with longitudinal to transverse grooves and ridges. Burrow fill massive or with a low to high ovoid pellet content.

Material: Numerous field observations.

Description: Unilobed horizontal to slightly oblique U-shaped structures with distinct grooves and ridges on the exterior. Pellet fill common.

Discussion: The terms "unilobed" or "multilobed" are preferred instead of "bifurcating" or "branching", respectively. "Bifurcation" should be used for tubular structures, which truly branch (see Fig. 36). The diagnosis was emended to include information about the exterior of the burrows. In addition, the new classification scheme of U-shaped spreite structures presented herein makes an emendation of the diagnosis necessary because hitherto unilobed and multilobed forms of *Ilmenichnus* were not kept separate. The holotype of *Ilmenichnus devonicus* (HECKER, 1930) is a unilobed form.

Ilmenichnus new ichnospecies 2

Fig. 77, 82-83

? 1876 *Rhizocorallium commune* n. sp. – SCHMID: 14; [= *nomen dubium*].

Figure 82: Multilobed pattern of *Ilmenichnus* new ichnospecies 2; positive epirelief, paratype, PIW-D6286, Trochitenkalk 4, Upper Muschelkalk, top view. Scale bar: 10cm.

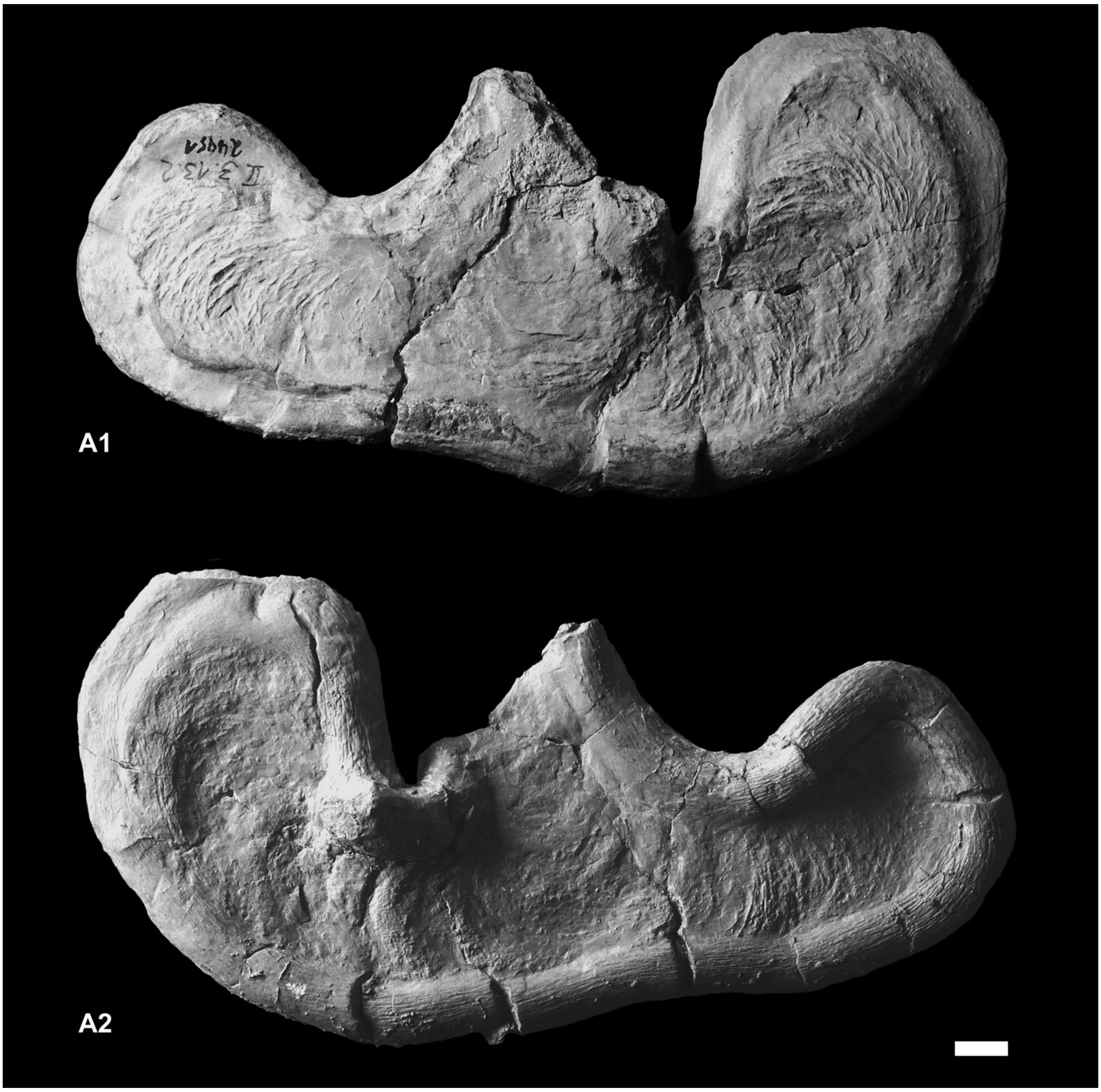

Figure 83: A1-A2. Multilobed pattern of *Ilmenichnus* new ichnospecies 2 fullrelief, holotype, SMNS 24451. **A1**. Note distinct scratch ornaments in spreite section; top view. **A2**. Outer limb with distinct longitudinal scratch ornaments; bottom view. Scale bar: 1cm.

Diagnosis: Unlined, horizontal to slightly oblique, multilobate spreite structures; spreite between a lobe-forming tubular limb. Exterior smooth or with longitudinal to transverse grooves and ridges. Burrow fill massive, or with a low to high ovoid pellet content.

Material: Holotype, SMNS 24451, Trochitenkalk 4, Upper Muschelkalk, Ehrmann quarry at Neckarrems, Baden-Württemberg, southern Germany (collected by URLICHS 1978).

Description: Unlined, horizontal to slightly oblique, multilobate spreite structures. The spreite are located between a distinct outer tubular limb that forms the lobes. Exterior of entire burrow may be smooth, or with longitudinal to transverse grooves and ridges. Burrow fill massive, or with a low to high ovoid pellet content.

Discussion: Multilobed forms should be kept separate from unilobed forms because of covering an extended area, thus exploiting the sediment in a more efficient way than unilobed forms. This is in analogy to simple feeding structures and meandering forms, which also show an enhanced surface exploitation. SCHMID (1876) introduced *Rhizocorallium comune*, which was considered by some workers to be a multilobed form. However, the original description is not diagnostic, no material was figured, and no type material collected. Thus, *Rh. comune* SCHMID, 1876 is considered a *nomen dubium*.

Multilobed forms most likely have a unilobed initial stage. This means, that initial stages represent specimens of *Ilmenichnus devonicus*. At first glance this sounds puzzling, however, it is consistent with other classification schemes. A name can only be given to an existing structure and not to something it might end up with. For instance, if the initial stage of a crustacean burrow system was a simple vertical tubular burrow and found fossilised, it should be named *Skolithos* and not *Spongeliomorpha.* If it is found connected with a predominantly horizontal network, than of course it is part of a larger structure and should be named *Spongeliomorpha* (*S.*) *suevica.* A separate almond-shaped impression is *Lockeia*; if found connected with a row of chevrons, it is part of *Protovirgularia*.

Ichnogenus *Rhizocorallium* ZENKER, 1836

Type ichnospecies: *Rhizocorallium jenense* ZENKER, 1836: 219; by monotypy.

Emended diagnosis: Wedge-shaped, double-spreite burrows, built up of U-limbs, oblique to parallel towards bedding plane; width of U constant or distally increasing; limbs distinct. Exterior smooth, or with longitudinal or transverse ridges and grooves.

Discussion: *Rhizocorallium* as well as *Diplocraterion* lack type material. The type-ichnospecies, *Rhizocorallium jenense*, has no type material. Fortunately, the horizon from which ZENKER (1836) described *Rhizocorallium* is well known (MÜLLER 1959), and, thus, neotype material can be designated. One slab from this horizon bearing tens of specimens of *Rh. jenense* was studied. Unlike in many other cases the material from the type locality showed that *Rhizocorallium* is in fact what it is commonly assumed to be. It is a U-shaped spreite burrow with scratch ornaments on the limbs. However, is not a single U-shaped spreite burrow but a package of such. As discussed in the section dealing with the SOT group, the value of scratch ornaments as an ichnotaxobase is low and should be used at the ichnospecific level only. The specimens from the type locality vary in oblique orientation from straight to bending (Fig. 84). All specimens are short. The most interesting feature of the material is that almost all specimens are built by several U-limbs varying in size. This means that the U-limbs grew continuously of in one direction, which resulted in a single, protrusive U-shaped spreite burrow plus an additional shift of the construction direction in another dimension. The final result was a package of protrusive U-shaped spreite burrows. The arrangement of the single, protrusive U-burrows can either be retrusive or rarely protrusive, finally resulting in a wedge-shaped complex burrow system. No fan-like arrangement exists. As shown in Fig. 73, there are various possibilities for constructing U-shaped three-dimensional complex burrow systems.

Trochospiral forms (*Rhizocorallium uliarense* FIRTION, 1958) should be kept in a separate ichnogenus. The behavioural pattern and the resulting general morphology are so unique that these forms should not be assigned to *Rhizocorallium*. However, in order to guarantee a correct taxonomic assignment to an existing or a new ichnogenus, the type material of *Rh. uliarense* should be re-visited, which was beyond the scope of this study.

Rhizocorallium jenense ZENKER, 1836

Fig. 72, 76, 84-85

Emended diagnosis: More-or-less straight to bent, short, protrusive U-shaped, double-spreite structures, commonly oblique to bedding plane with a vertically retrusive component (limb-spreite); ratio of limb to limb-spreite > 1 to 2; overall morphology of resulting structure is wedge-shaped; exterior may be covered with short, parallel longitudinal or criss-crossing ridges and grooves.

Material: Several specimens on one slab from the type locality (collection M. HAUTMANN, Würzburg).

Description: More-or-less straight to bent, short (length: 1-3cm; width: 0.7-1.7cm), protrusive U-shaped, double-spreite structures; commonly arranged oblique to bedding plane, with a vertically retrusive component (limb-spreite). The width of the U generally increases from proximal to distal by a factor of 1.3; overall morphology of resulting structure is wedge-shaped.

Discussion: The specimens from the type locality not only have one growth direction from proximal to distal, building the U-shaped protrusive spreite, but also do have an additional shift of the U-shaped spreite structures towards the top of bedding planes. This results in retrusive limb-spreite and finally in a wedge-shaped, double-spreite structure (Fig. 73). The first U-shaped spreite structure often shows a slight bend in the proximal part. The trace fossils are arranged at an acute angle with the horizontal. This distinguishes *Rhizocorallium jenense* from *Diplocraterion saxicava*, which only has one growth direction at an obtuse angle with the horizontal.

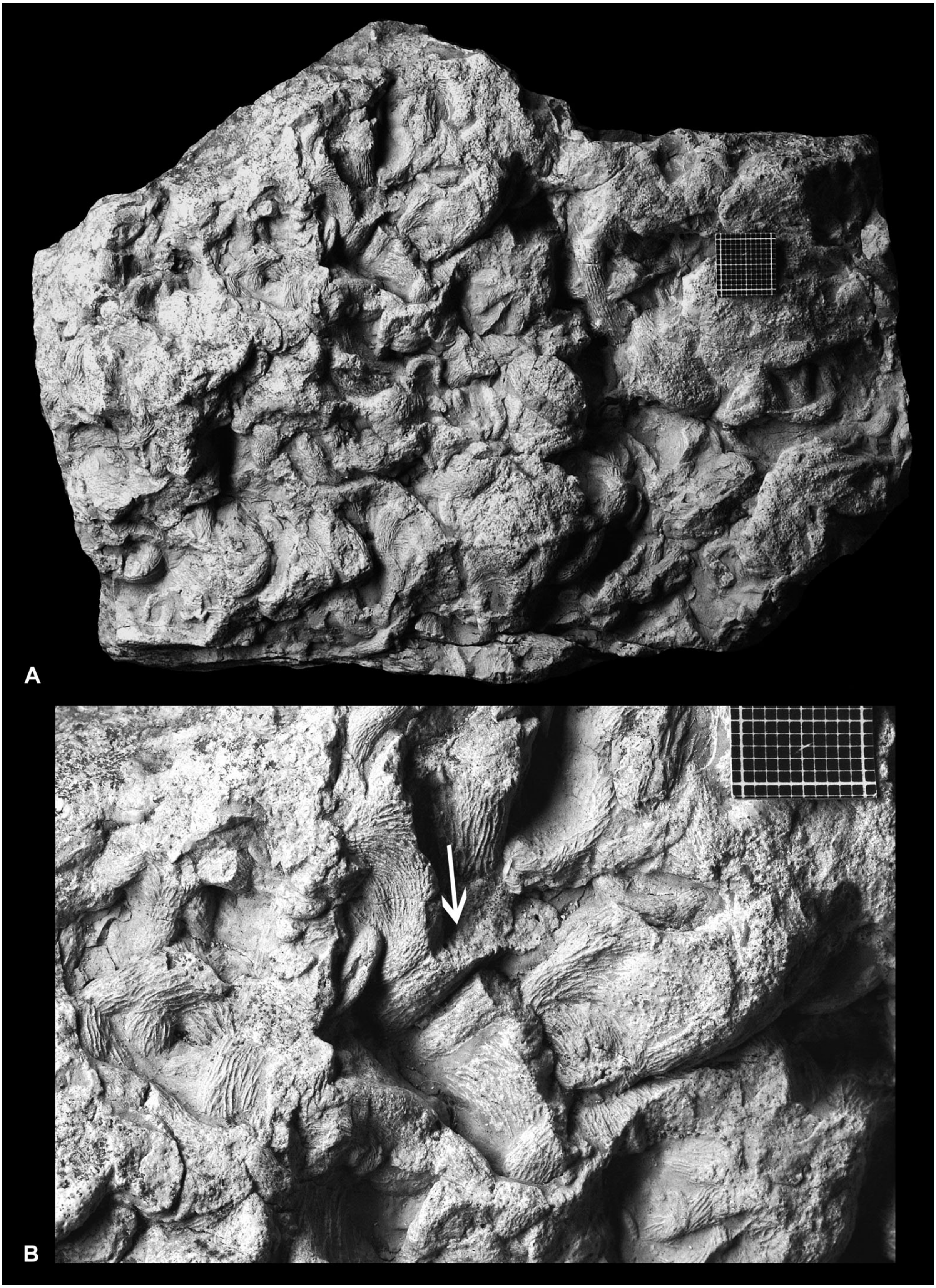

Figure 84: A-B. *Rhizocorallium jenense*; fullrelief; bottom view. Specimens on a slab from the type locality, collection M. HAUTMANN. **A**. View of entire slab; note high degree of bioturbation. **B**. Detail showing distinct scratch ornaments in spreite and limb sections. White arrow indicates very thick limb-spreite. Millimetre grids for scale.

Figure 85: Detail of Fig. 84A. Dense bioturbation by *Rhizocorallium jenense*. Millimetre grid for scale

Ichnogenus *Teichichnus* SEILACHER, 1955

Type ichnospecies: *Teichichnus rectus* SEILACHER, 1955: 378, pl. 24 fig. 1; by monotypy.

Emended diagnosis: Long, straight, sinuous to zigzag-shaped, unbranched or branched, wall-like spreite structures, formed by vertical displacement of horizontal or oblique, erect to undulose tubes without wall-lining, resulting in a unilobed (gutter-shaped) or bilobate (double gutter-shaped) spreite in frontal view. Bioglyphs may be present.

Remarks: Since a new ichnospecies is assigned to *Teichichnus*, the existing diagnosis of the ichnogenus has to be emended in order to give all possible information on morphological details of the ichnogenus.

Teichichnus new ichnospecies

Fig. 86-88, 89A-E

Diagnosis: Unbranched, straight or slightly sinuous *Teichichnus*, with dominantly retrusive, bilobate (double gutter-shaped) spreite and bioglyphs.

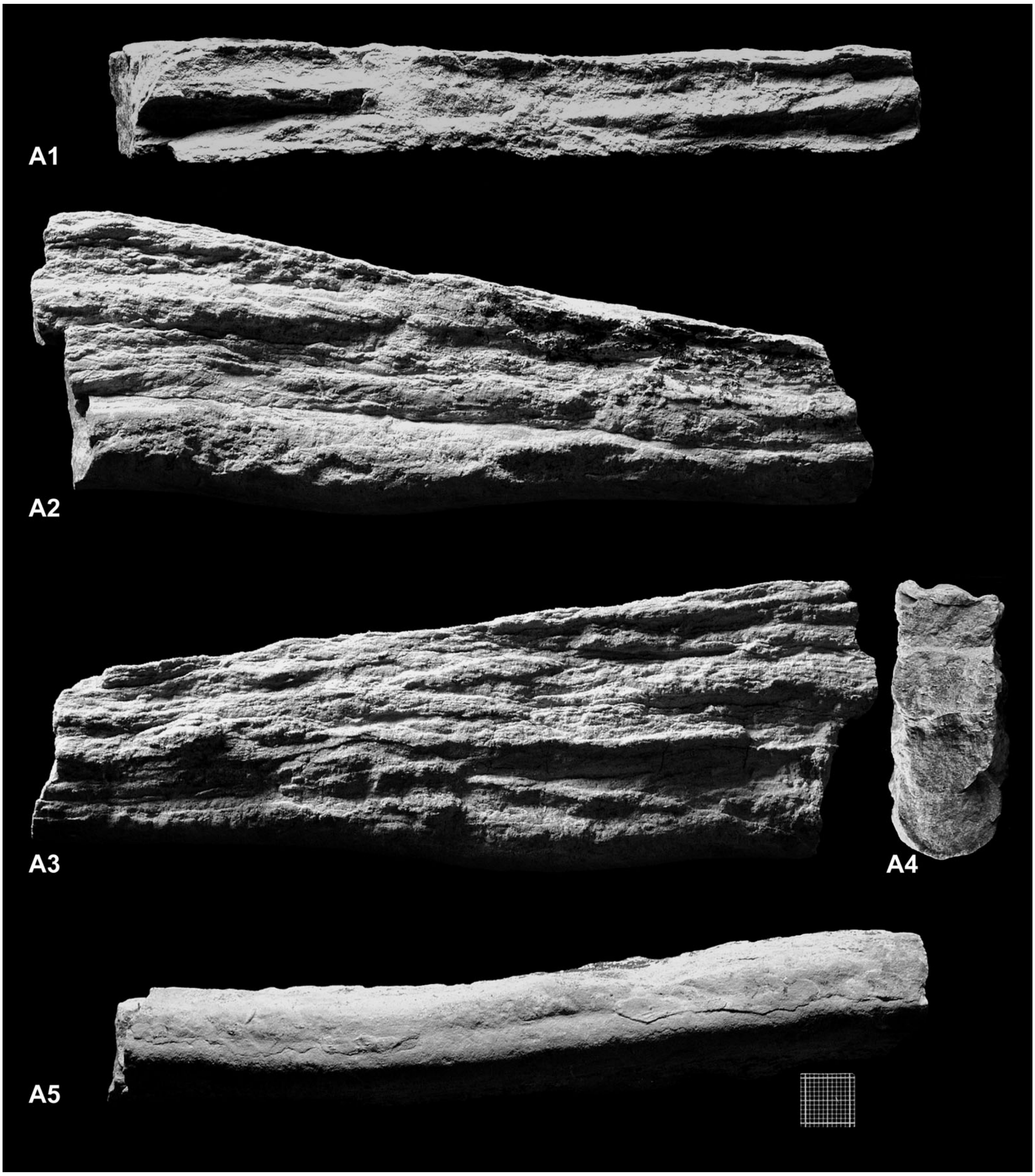

Figure 86: *Teichichnus* new ichnospecies; holotype, fullrelief, PIW2002-I-26, *Paradoxissimus* Silt, Äleklinta, Middle Cambrian, Öland, Sweden. **A1**. Double gutter-shape, top view. **A2-A3**. Wall-like spreite, side view. **A4**. Retrusive spreite, frontal view. **A5**. Bilobed pattern of premier lamina, bottom view. Millimetre grid for scale.

Material: Holotype: PIW2002-I-26 from the *Paradoxissimus* Silt at Äleklinta, Middle Cambrian, Öland, Sweden. Paratypes: PIW2002-I-25; Öl.1292, Öl.1293 (figured in MARTINSSON 1965: fig. 27 A, B), all *Paradoxissimus* Silt, Äleklinta, Middle Cambrian, Öland; SMNS 65492, Rhätsandstein, Exter Fm, Upper Keuper, Nürtingen, Baden-Württemberg, southern Germany (collected by E. KOCH 1896).

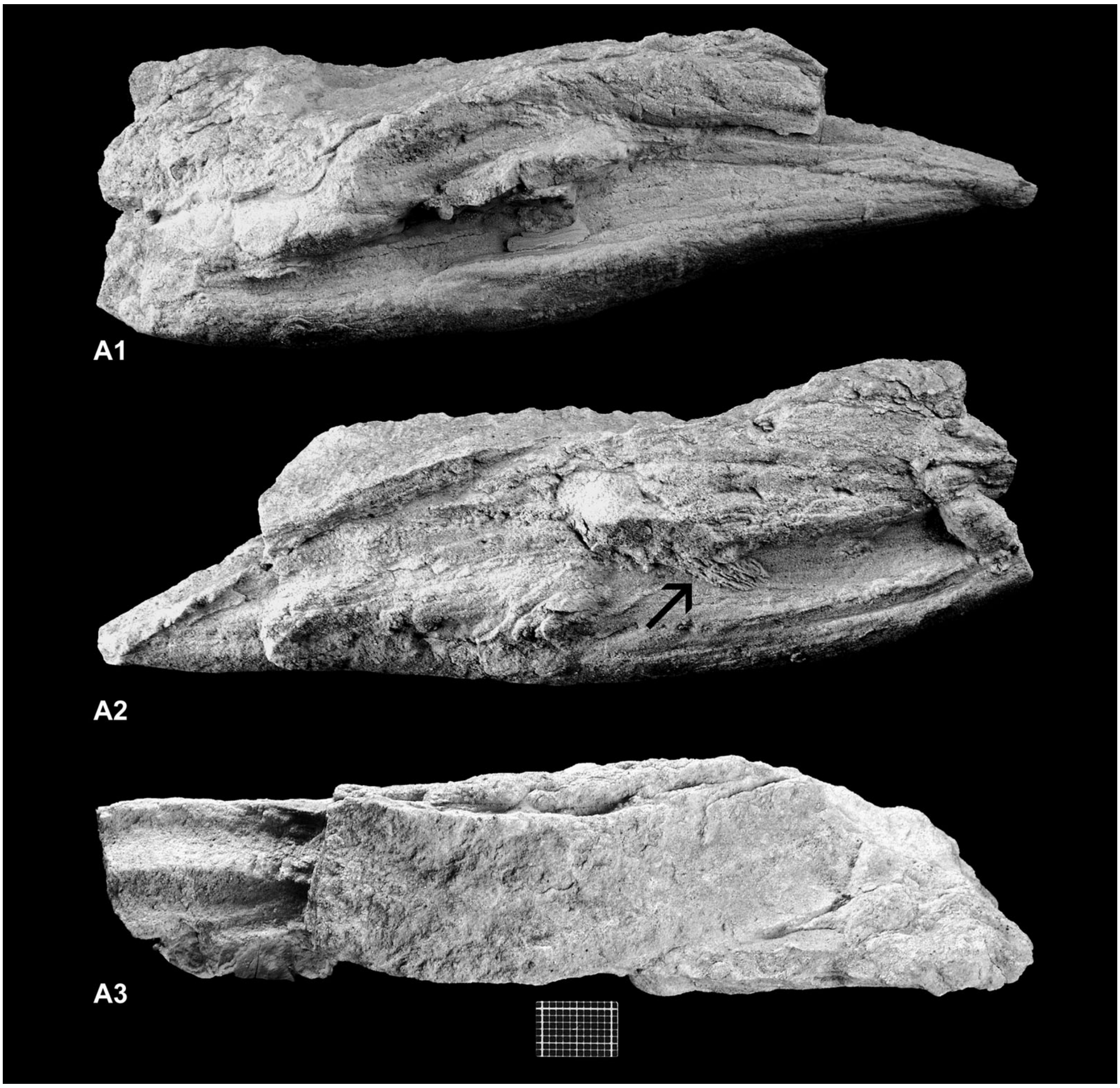

Figure 87: *Teichichnus* new ichnospecies. paratype, fullrelief, PIW2002-I-25, *Paradoxissimus* Silt, Äleklinta, Middle Cambrian, Öland, Sweden. **A1-A2**. Wall-like spreite, side view. **A2**. Black arrow indicates distinct scratch ornaments. **A3**. Bilobed pattern, top view. Millimetre grid for scale.

Derivatio nominis:

Description: Horizontal to slightly inclined, straight to slightly winding, unbranched burrows. Burrows consist of bilobate (double-gutter shaped), convex-down lamina, forming wall-like structures. Lamina are predominantly arranged retrusive, occasionally protrusive arranged lamina can be observed. Terminal burrow tube only rarely preserved; seldom with strongly upward bending terminal tubes. In lateral view: parallel, more-or-less horizontal to undulose lamina forming a spreite structure, ideally topped by a tube. In frontal view: frequently slight lateral displacement of lamina can be observed. Tube diameter 0.9-2.5cm; width of single lamina identical; height 2.8-12cm; maximum

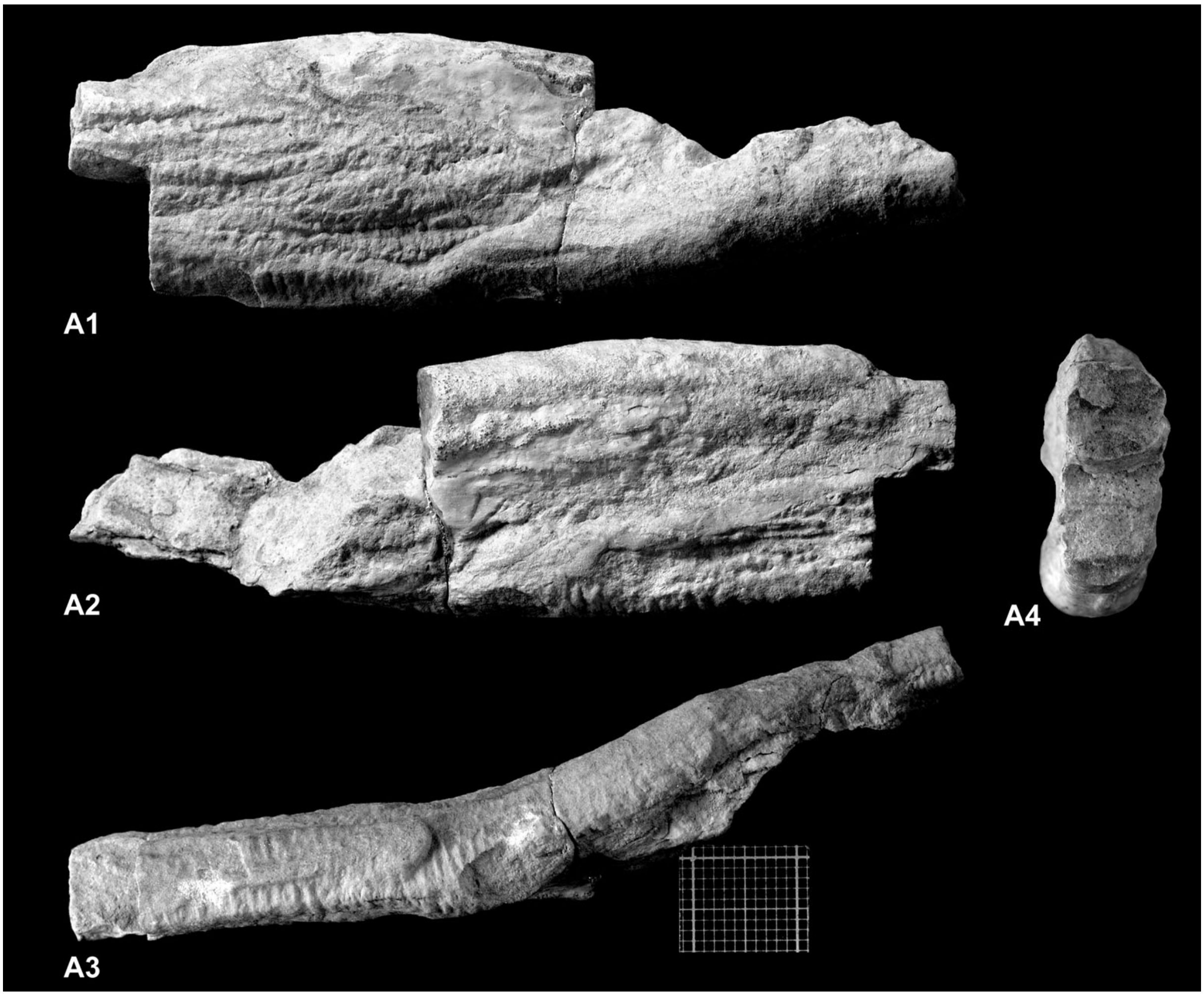

Figure 88: *Teichichnus* new ichnospecies; paratype, fullrelief, SMNS 65492, Rhätsandstein, Exter Fm, Upper Keuper, near Nürtingen, Baden-Württemberg, southern Germany. **A1-A2**. Wall-like spreite; note distinct scratch ornaments, side view. **A3**. Initial lamina with median ridge and perpendicular to oblique scratch ornaments; bottom view. **A4**. Retrusive spreite; frontal view. Millimetre grid for scale.

observed length 135cm, common length 15-40cm. Thickness of individual lamina varies from 0.05-0.9cm. The material from Äleklinta mostly has smooth burrow walls or lamina, respectively, but some specimens show well-preserved bioglyphs in form of oblique to

perpendicular (orientation towards long axis of burrow) scratch ornaments (on the exterior visible as ridges); occasionally longitudinal scratch ornaments can be observed. The scratch ornament pattern strongly resembles that observed in cruzianids and rusophycids. One specimen (PIW2002-I-25) also shows scratch ornaments on the wall (Fig. 87). The material from Nürtingen has a median hypichnial ridge on the bottom of the basal lamina and additional perpendicular to slightly oblique ridges, which can also be observed in lateral view on the wall structure (Fig. 88).

Discussion: The new ichnospecies of *Teichichnus* differs from other *Teichichnus* structures in having a double gutter-shaped morphology of the lamina forming the spreite. Such forms are long known (e.g., MARTINSSON 1965) but this distinctive form of *Teichichnus* remained unnamed. SEILACHER

(1955) mentioned various forms of *Teichichnus* and found it surprising that no one had named these forms, but himself did not formally introduce them. The general appearance (a wall-like morphology, formed by a multiple repetition of straight to slightly curving lamina) clearly represents *Teichichnus*. The ornamentation in the specimens presented by MARTINSSON (1965: fig. 27 A & B) and additional specimens collected from the same locality (Fig. 87) show the bilobed pattern and occasional scratch ornaments produced by appendages. These structures strongly resemble the morphology of patterns known from *Cruziana* and makes trilobites or other arthropods very likely as progenitors of the Cambrian representatives of *Teichichnus* new ichnospecies. The material from the Upper Triassic also shows ornamentation (Fig. 88), which can be explained as being produced by arthropods. The size of the Triassic material is distinctively smaller than that of Cambrian age, but since the general morphology is the same and as repeatedly pointed out by several authors size is no suitable ichnotaxobase, the entire material is assigned to *Teichichnus* new ichnospecies.

Especially the size discussion questions the usefulness of *Teichichnus pescaderoensis* STANTON & DODD, 1984. This material is larger than other known specimens of *Teichichnus*, but this should not justify a separation. Unfortunately, no real holotype exists. Because of the nature of the host sediments and the trace fossils, no complete specimen was collected. Instead, the authors designated two sediment samples as the holotype. Type material by its nature must resemble the morphology of what it stands for, or in the case of a DNA sequence, must permit an equivocal identification. Sediment samples, even though representing the burrow fill and the border zone of the burrow and the host sediment, are not indicative of one particular trace fossil and thus do not qualify as a holotype. Nevertheless, the introduction of a new ichnospecies of *Teichichnus* by STANTON & DODD (1984) remains formally valid since a holotype for a trace fossil is only necessary since the latest edition of the ICZN (1999). In addition, the formal validity, the question remains open if there are only size criteria that distinguish *T. pescaderoensis* from other known ichnospecies of *Teichichnus*. The authors primarily refer to size differences. They also state that after having examined all Neogene outcrops at the Pacific coast of California and southern Oregon, *T. pescaderoensis* was only found at two localities. They assumed that this fact would also justify the introduction of a new ichnospecies for these forms; a statement that is highly questionable since neither geographic nor stratigraphic distributions of trace fossils qualify as ichnotaxobases. However, such information is of great importance. Detailed measurements of material in the outcrops and a subsequent verification of these data with other known representatives of *Teichichnus* may reveal differences other than size. As long as this has not been shown and no morphological differences between *T. rectus* and *T. pescaderoensis* can be found, it is considered a junior synonym of *T. rectus* and its further use is not recommended.

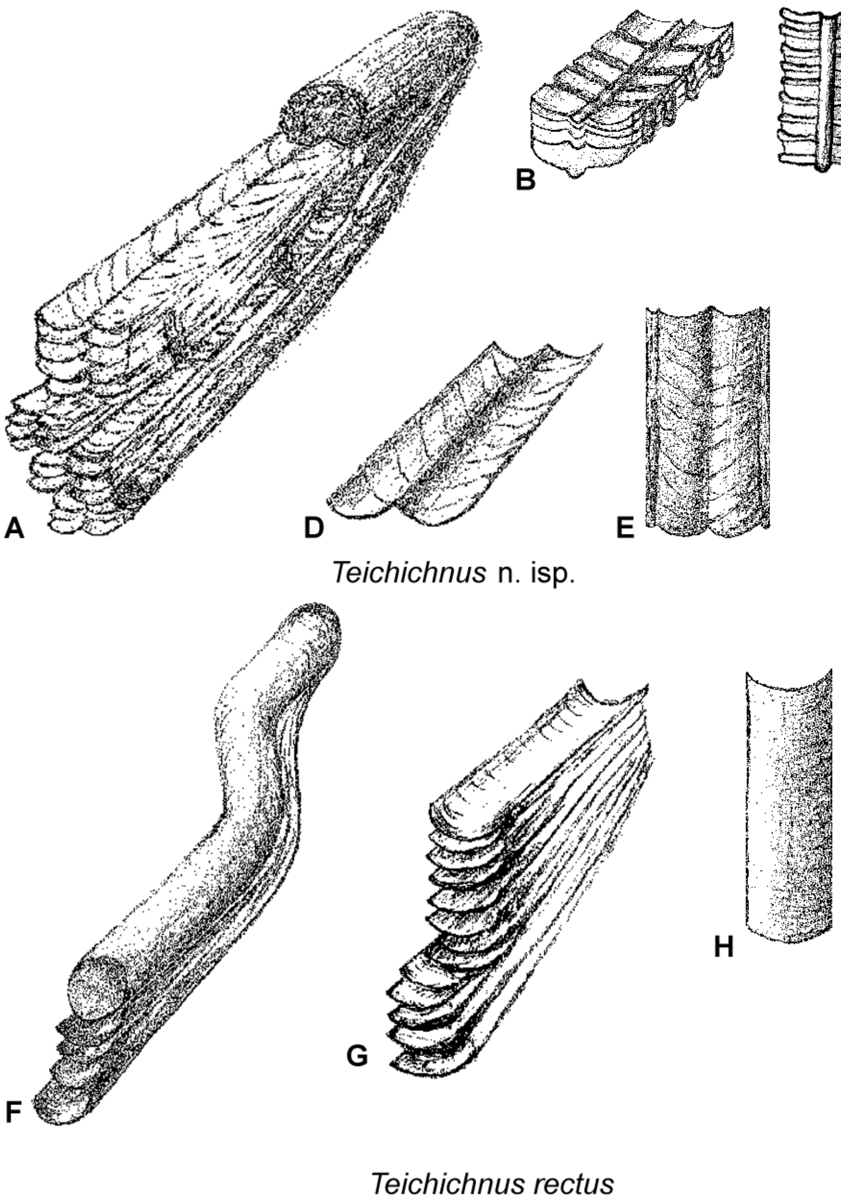

Figure 89: **A-E**. *Teichichnus* new ichnospecies. **A**. Reconstruction of the Cambrian form. **B**. Stacking pattern of lamina in the Triassic form. **C-D**. Form of lamina which built the spreite; bottom view. **D**. Double gutter lamina characterisitic of the Cambrian form; top view. **E**. Idealized sketch of lamina of the Cambrian form; bottom view. **F-H**. *Teichichnus rectus*. **F**. Reconstruction of *T. rectus*. **G**. Gutter-shape of individual lamina, characteristic of *T. rectus*. **H**. Single gutter-shaped lamina seen from below. **A-H**. Not to scale.

The ratio of spreite-wall to terminal tube has been discussed in the literature (e.g. Legg 1985; Jensen 1997, Schlirf 2000). Certainly, this is a very important feature of *Teichichnus*, and ‘true’ *Teichichnus* should have a high ratio of wall versus terminal tube. That means that a *Teichichnus* in its original sense as introduced by Seilacher (1955) must show these wall structures. There are intergradations from *Spongeliomorpha* to *Teichichnus* (e.g. Schlirf, 2000), and sometimes the ratio of wall to tube might be high as well. However, the general burrow morphology of *Spongeliomorpha* remains different from *Teichichnus* and the teichichnid burrow parts are only subordinate. In addition, a

Teichichnus '*in statu nascendi*' may also show a low wall to terminal tube ratio and could still be identified as a 'true' *Teichichnus*. This seems to be a very subjective decision but nature (and especially behaviour) is more complex than one morphometric ratio can express. There are always intergradations and in trace fossil taxonomy the entire concept represented by a burrow or burrow system, respectively, is what counts.

Additional detailed discussions on *Teichichnus* are given by BUCKMAN (1996), JENSEN (1997), and SCHLIRF (2000), the latter also providing a detailed synonymy of *Teichichnus rectus*.

The work of arthropods

Various burrows, tracks, and trackways with a bilobate morphology or bisymmetrical arrangement of tracks belong to this group such as *Arthrophycus*, *Cruziana*, *Rusophycus*, having a more-or-less bilobate morphology, and *Kouphichnium* and *Tasmanadia*, which are bisymmetrical trackways.

Ichnogenus *Arthrophycus* HALL, 1852 emend. RINDSBERG & MARTIN (2003)

Type ichnospecies: *Arthrophycus harlani* (CONRAD, 1838); by subsequent designation by HALL, 1852: 4.

1937 *Steigerwaldichnium.* – KUHN: 366.
1937 *Steigerwaldichnites* n. g. – KUHN: 368 [= *nomen nudum*].
1975 *Steigerwaldichnium* KUHN, 1937. – HÄNTZSCHEL: *W*111.

Remarks: According to RINDSBERG & MARTIN (2003) *A. harlani* is the type ichnospecies of *Arthrophycus*. *Arthrophycus harlani* (CONRAD, 1838), however, is an objective junior synonym of *A. brongniartii* (HARLAN, 1832), which is a subjective older synonym of *A. linearis* SEILACHER, 2000. For a detailed discussion on the type ichnospecies see (RINDSBERG & MARTIN 2003).

Diagnosis: Subhorizontal to oblique, straight to curved, bilaterally symmetrical burrows with fill arranged in an imbricate series of spoon-like pads; cross-section subquadrangular; burrows simple, sparsely branched, or densely branched in an overlapping, fan-like pattern; lower half part of burrow sheathed by outer zone of closely spaced pads of sediment; lower surface of burrow with closely spaced transverse ridges, commonly with median groove (RINDSBERG & MARTIN 2003: 211).

Discussion: RINDSBERG & MARTIN (2003) state that probably all post-Palaeozoic material assigned *Arthrophycus* does not belong to this ichnogenus. The Triassic forms presented here are very similar to *Arthrophycus alleghaniensis* in general pattern, in cross-section, and in external ornamentation. Thus, from a morphological point of view there is no objection for assigning the material to *Arthrophycus*.

Arthrophycus is interpreted in two fundamentally different ways. SEILACHER (2000) interpreted *Arthrophycus* as a worm burrow following the strip mining technique, whereas RINDSBERG & MARTIN (2003) favour an arthropod progenitor. As it is often the case in palaeontology, a definite answer remains open. SEILACHER (2000) showed similarities between various ichnospecies of *Arthrophycus* and the relation of *Arthrophycus* to *Daedalus* and *Phycodes*. RINDSBERG & MARTIN (2003), re-studying the type material of *Arthrophycus harlani*, *A. brongniartii*, *A. alleghaniensis*, and associated ichnofaunas, also showed intergradational forms of *Arthrophycus* and other ichnotaxa, such as *Phycodes flabellum* and *Rusophycus*. Especially their intergradational forms to *Rusophycus* make an arthropod progenitor likely.

The view of RINDSBERG & MARTIN (2003) that *Arthrophycus* was made by arthropods is followed here because the interpretation of the type ichnospecies seems plausible. However, some arguments given by SEILACHER (2000) in favour of a worm progenitor are supported by his material, which, however, is not the type material. SEILACHER's assignment of his material to *Arthrophycus* thus is questionable. To which ichnogenus it belongs needs further investigation. However, a clarification of this problem is beyond the scope of this study.

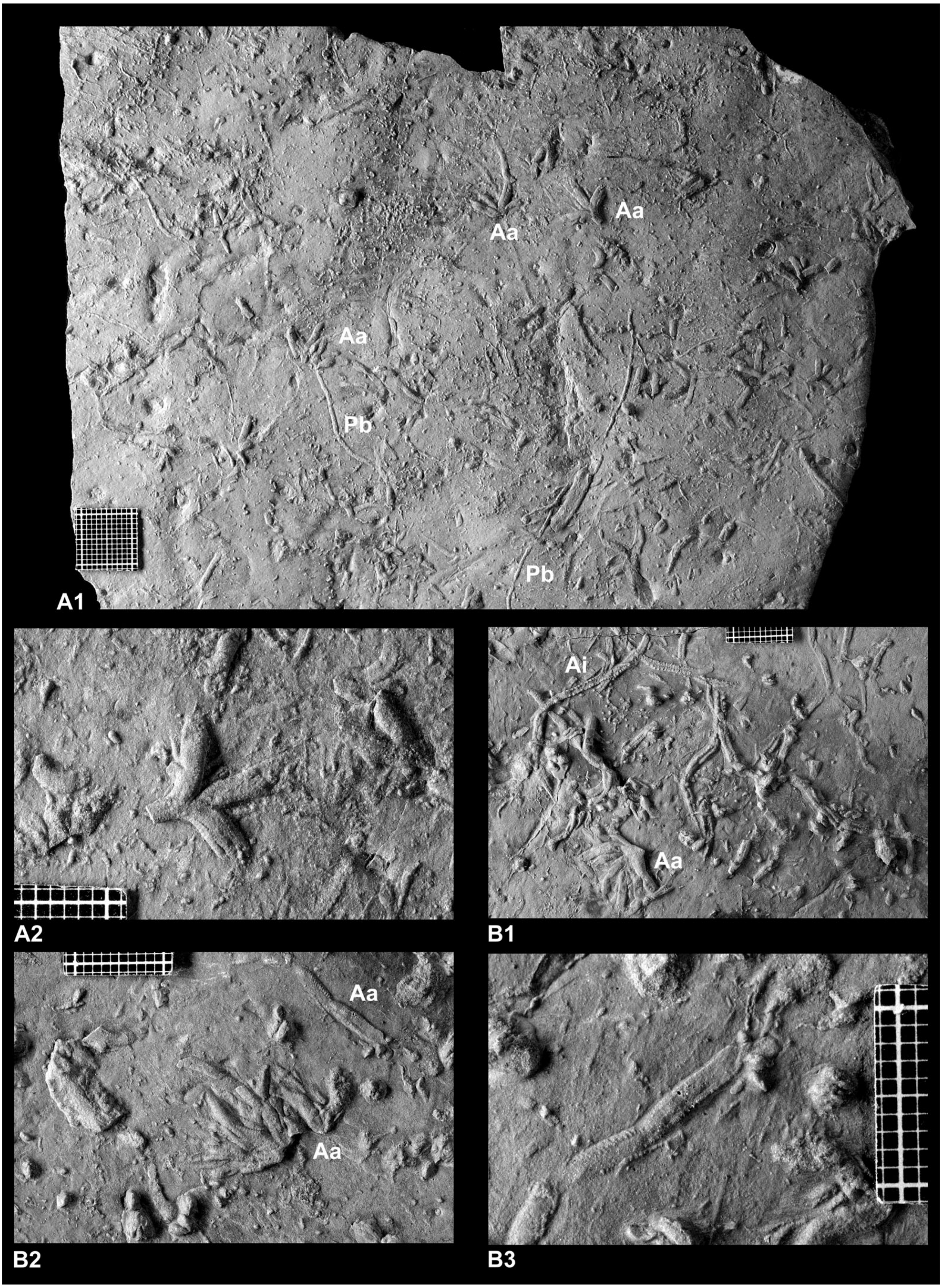

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Figure 90: A1. Aa = *Arthrophycus alleghaniensis* (HARLAN, 1831), Pb = *Planolites beverleyensis* (BILLINGS, 1862), SMNS 65490, Öhringen-Unterohrn, Kleinknecht quarry, Estherienschichten, Erfurt Fm, Lower Keuper. **A2**. Detail of **A1**, showing the fan-like arrangement of individual burrow parts. **B1-3**. SMNS65491 from Weißenburg, Kers quarry, Estherienschichten, Erfurt Fm, Lower Keuper. Aa = *Arthrophycus alleghaniensis* (HARLAN, 1831), Ai = *Arthrophycus* isp. B1: Fan-like arrangement of individual burrow parts characteristic of *Arthrophycus alleghaniensis,* and straight forms. **B2**. Detail of **B1**, showing fan-like form. **B3**. Detail of **B1**, with fine perpendicular to oblique scratch ornaments. All positive hypichnia; all Baden-Württemberg, southern Germany. Millimetre grids for scale.

Arthrophycus alleghaniensis (HARLAN, 1831)

Fig. 90A1-2, B1-3, 91B-D

* 1831 *Fucoides Alleghaniensis* HARLAN: 289, pl. 15 fig. 1-3.
2003 *Arthrophycus alleghaniensis* (HARLAN, 1831). – RINDSBERG & MARTIN: 212, fig. 4C-D, 12A, 13A-B.
For further synonyms see RINDSBERG & MARTIN (2003).

Diagnosis: *Arthrophycus* with sparse to extensive, palmately branched burrows; galleries straight to gently curved, generally with subquadrangular cross section, branching at acute angle, self-penetrating; internal structure expressed on lower surface as nearly transverse sculpture; lower surface with median groove in some specimens (RINDSBERG & MARTIN 2003: 213).

Material: Numerous specimens on slab SMNS 65490 from Öhringen-Unterohrn, Kleinknecht quarry, Estherienschichten, Erfurt Fm, Lower Keuper; SMNS 65491 from Weißenburg, Kers quarry, Estherienschichten, Erfurt Fm, Lower Keuper. SMNS 65495, SMNS 65496, Kieselsandstein, Hassberge Fm, Middle Keuper km3s, Korber Kopf near Korb; SMNS 22014, Sternenfels, uppermost Schilfsandstein, Stuttgart Fm, Middle Keuper. All from Baden-Württemberg, southern Germany.

Description: Small, fan-like arranged, or straight to slightly curved, horizontal, multiple branched, or unbranched burrows with subquadrangular cross-section; individual burrows 1.5-2.5mm wide; angle of branching dominantly acute; surface smooth, with fine perpendicular to oblique ornaments (annulated), or with distinct double rows of hemispherical protuberances; cross-overs common; burrows preserved as positive hyporeliefs. The structures occur in a fine-grained, greyish to greenish silt- to claystone.

Arthrophycus alleghaniensis specimens occur together with cf. *Arthrophycus* isp., minute *Planolites beverleyensis*, small *Rusophycus* cf. *carbonarius* and *Protovirgularia rugosa*.

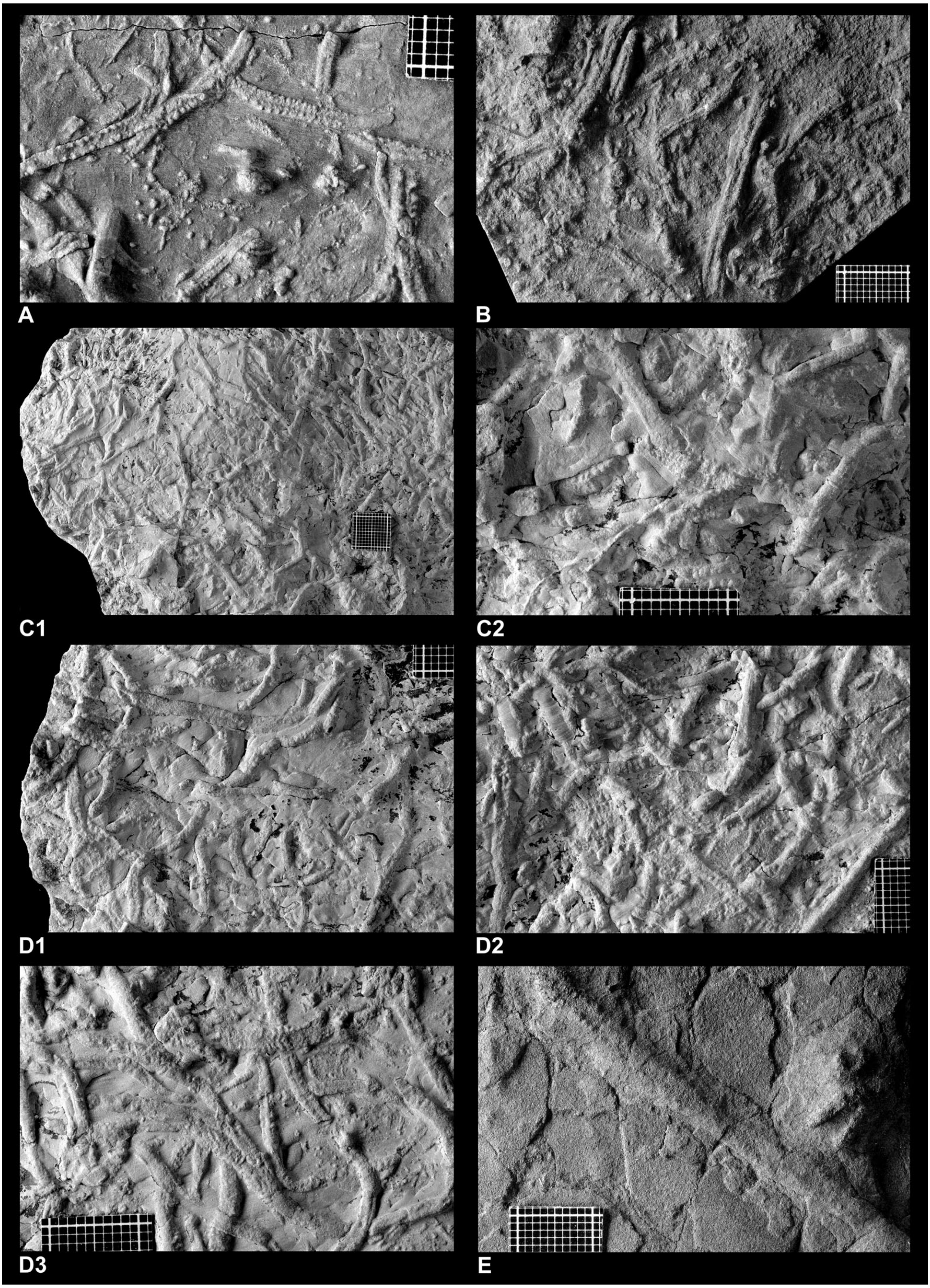


Figure 91: **A**. *Arthrophycus* isp. Note hemispherical protuberances. SMNS 65490, Öhringen-Unterohrn, Kleinknecht quarry, Estherienschichten, Erfurt Fm, Lower Keuper. **B**. *Arthrophycus alleghaniensis* (HARLAN, 1831). SMNS 22014, Sternenfels, uppermost Schilfsandstein, Stuttgart Fm, Middle Keuper. **C1-2**. *Arthrophycus alleghaniensis* (HARLAN, 1831), SMNS 65495, Kieselsandstein, Hassberge Fm, Middle Keuper km3s, Korber Kopf near Korb. **C2**. Detail of **C1**, showing straight form with perpendicular to oblique striation. **D1-3**. *Arthrophycus alleghaniensis* (HARLAN, 1831). **D2**. Detail of **D1**, straight to slightly curved forms, with fine

perpendicular to oblique scratch ornaments. **D3**. Detail of **D1**, staright to slightly curved forms, with fine perpendicular to oblique scratch ornaments. **E.** *Arthrophycus* isp. SMNS 22015, Schilfsandstein, Stuttgart Fm, Middle Keuper, Stuttgart. Note hemispherical protuberances. All positive hypichnia; all Baden-Württemberg, southern Germany. Millimetre grids for scale.

Figure 92: Cf. *Unionites* sp. on top of slab SMNS 65490, Öhringen-Unterohrn, quarry Kleinknecht, Estherienschichten, Erfurt Fm, Lower Keuper. Baden-Württemberg, southern Germany. Millimetre grid for scale.

Discussion: The studied specimens are small representatives of *Arthrophycus alleghaniensis*. In addition, the sediments bearing *A. alleghaniensis* were deposited in hyposaline environment as indicated by co-occurring bivalves cf. *Unionites* isp. (GEYER et al. in press; Fig. 92). These facts make the finds unique. However, it shows once more that even complex morphologies may be produced by different groups of organisms. The morphology of a trace fossil largely depends on the behaviour of the progenitor, it shows that various organisms from phylogenetically different groups may develop a similar way to exploit sediments. Of course, trace fossils also reflect the producers' body morphology. *Arthrophycus alleghaniensis* from the Keuper is interpreted as feeding structure of small arthropods. The perpendicular to oblique striations are interpreted as scratch ornaments, made by the appendages of arthropods. The double rows of hemispherical impressions are interpreted as imrprints of appendages. The different morphologies created by the appendages may be a result of different behaviour. The perpendicular to oblique striations depict the movements of the appendages from lateral towards the median of the structures. This can be explained as bringing sediment below the body during search for food. The hemispherical imprints are the result of locomotion. The size of the co-occurring trace fossils, especially *Arthrophycus* isp. and *Rusophycus* cf. *carbonarius*, support this interpretation. All these trace fossils were most likely made by small arthropods. RINDSBERG & MARTIN (2003) also report co-occurrence and intergradation of *A. alleghaniensis* with *Rusophycus* in marine Silurian deposits.

Arthrophycus isp.

Fig. 90B1, 91E, 93

pt 1937 *Steigerwaldichnium heimi* n.g. n.sp. – KUHN: 366, fig. 2a [*non* 2b = not determinable].

Material: Numerous specimens on slab SMNS 65490 from Öhringen-Unterohrn, Kleinknecht quarry, Estherienschichten, Erfurt Fm, Lower Keuper; SMNS 65491 from Weißenburg, Kers quarry, Estherienschichten, Erfurt Fm, Lower Keuper. SMNS 22015, Stuttgart, Schilfsandstein, Stuttgart Fm, Middle Keuper. All from Baden-Württemberg, southern Germany. PIW2002-I-12, Werksandstein, Würzburg Fm, Lower Keuper, outcrops between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

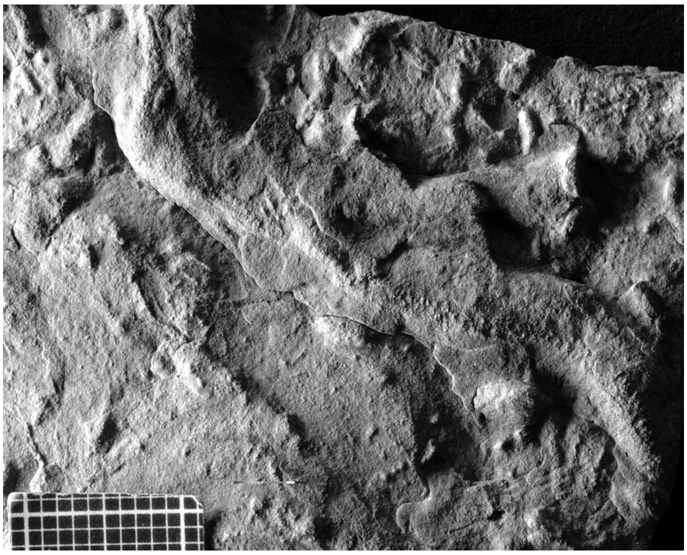


Figure 93: Hypichnial preservation of *Arthrophycus* isp. Note indistinct double row of hemispherical protuberances. PIW2002-I-12, Werksandstein, Würzburg Fm, Lower Keuper, outcrops between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany. Millimetre grid for scale.

Description: Small, unbranched, straight to slightly curved, horizontal to undulose burrows with subquadrangular cross-section; individual burrows 1.5-4mm wide; maximum length of individual burrow 90mm; surface smooth, or laterally with fine but distinct, positive, hemispherical ornaments; burrows preserved as positive hyporeliefs. The material from the Estherienschichten occurs in a fine-grained, greyish to greenish silt- to claystone. The structures from the Schilfsandstein occur in a red medium- to fine-grained sandstone, and those from the Werksandstein are preserved in a greenish silty claystone.

Discussion: The burrows from the Estherienschichten occur on the same slabs as *Arthrophycus alleghaniensis* and their size is similar to that of *A. alleghaniensis*. The typical annulation of *Arthrophycus* could not be observed. Although the structures are not connected to *A. alleghaniensis*, the similarities of the general morphology and the bioglyphs as well as the size justify an assigment to *Arthrophycus* but preservation does not allow a precise taxonomic distinction. *Arthrophycus* isp. is interpreted as a result of a combination of feeding and locomotion made by the same progenitors as *A. alleghaniensis* from the same beds (see above).

The additional material shows double rows of indistinct hemispherical protuberances. The general morphology is similar to the material from the Estherienschichten, and is thus also assigned to *Arthrophycus*.

Ichnogenus *Cruziana* D'ORBIGNY, 1842

Type ichnospecies: *Cruziana* rugosa D'ORBIGNY, 1842; by subsequent designation (MILLER 1889: 115).

Diagnosis: Elongated, band-like, bilobate or, rarely, unilobate furrows or burrows covered by herringbone-shaped or transverse ridges; with or without two outer smooth or longitudinally striated zones outside the V-markings; with or without lateral ridges and/or wisp-like markings if preserved on bedding soles (FILLION & PICKERILL 1990).

Discussion: *Cruziana* was synonymised with *Rusophycus* (SEILACHER 1970), but this view did not find general acceptance (see FILLION & PICKERILL 1990 for discussion). BROMLEY & ASGAARD (1979) included *Isopodichnus* BORNEMANN, 1889 in *Cruziana*. This was not accepted by HAKES (1985), POLLARD (1985), and SEILACHER (1985). However, there is obviously no significant morphological difference between *Isopodichnus* and *Cruziana* that would allow a separation of these ichnogenera consistent with several ichnological procedures (see FILLION & PICKERILL 1990 for further discussion). The fact that in contrast to Palaeozoic forms Mesozoic and Cenozoic *Cruziana* specimens cannot have been produced by trilobites is no objection for a synonymisation because the possible producers of trace fossils are generally regarded as irrelevant for ichnotaxonomy.

Cruziana pascens SCHLIRF & UCHMAN, 2001

Fig. 94, 95

Diagnosis: Straight to meandering, sometimes rotating, undulose *Cruziana* with fine striation, perpendicular or slightly oblique with respect to main axis of each double row; rows tend to be parallel (SCHLIRF et al. 2001).

Material: Holotype PIW1998-VIII-12C, paratypes PIW1998-VIII-11D-H, PIW1998-VIII-29, numerous field observations. Coburger Sandstein, Hassberge Fm, Vetter quarry, Lower Franconia, Bavaria, southern Germany.

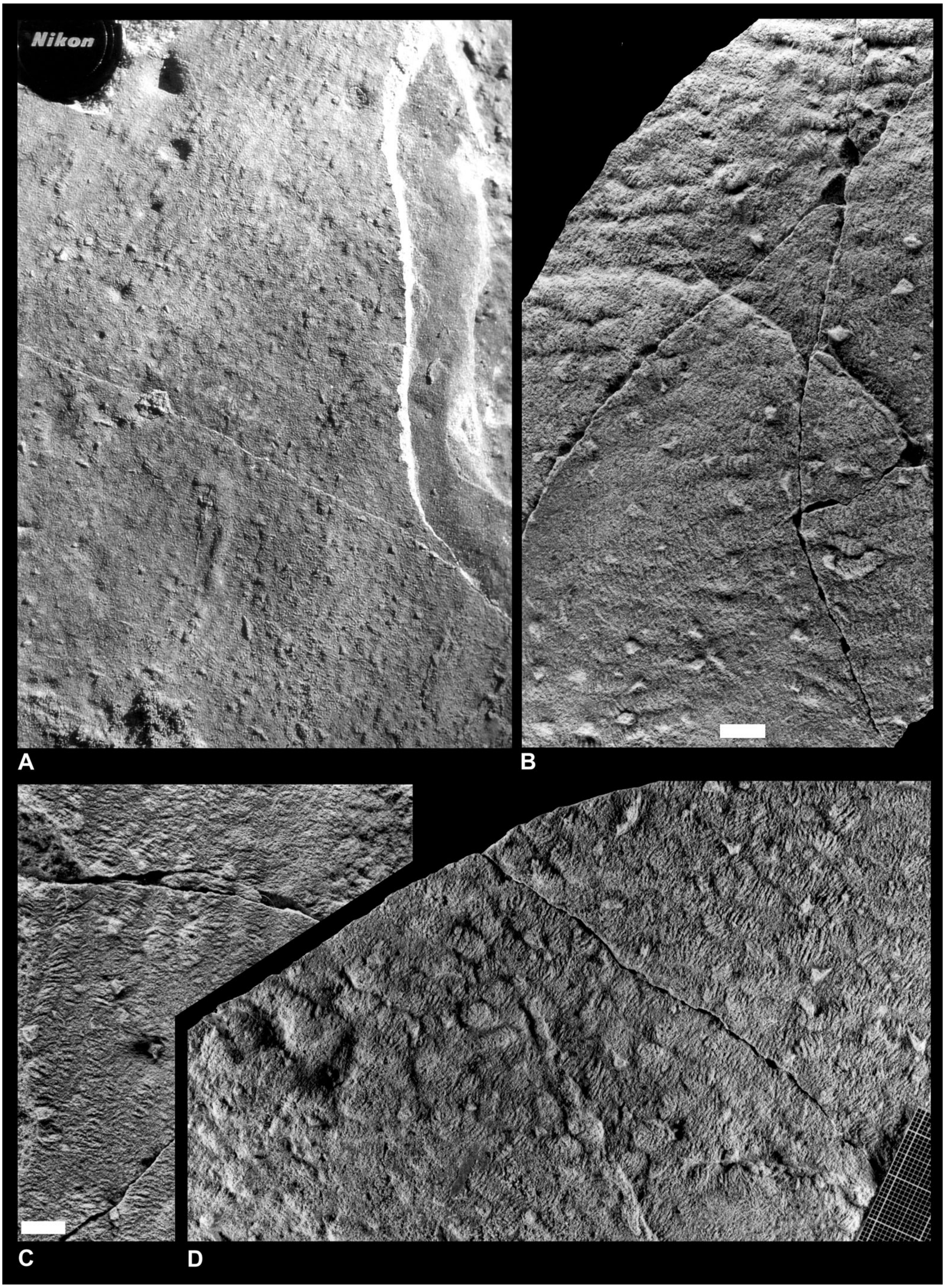


Figure 94: **A-D:** *Cruziana pascens* SCHLIRF & UCHMAN, 2001. **A**. Positive hyporelief, basal view; field photograph. **B**. Detail of holotype, PIW1998-VIII-12B. In addition, small triangular structures can be identified; positive hyporelief, basal view. **C**. Detail of holotype, PIW1998-VIII-12F. Positive hyporelief, basal view. **D**. Detail of holotype, PIW1998-VIII-12C. In addition, small triangular structures can be identified; positive hyporelief, basal view. All Coburger Sandstein, Hassberge Fm, Vetter quarry at Schönbachsmühle. Lens cap 52mm across; scale bars: 1cm; millimetre grid for scale in D.

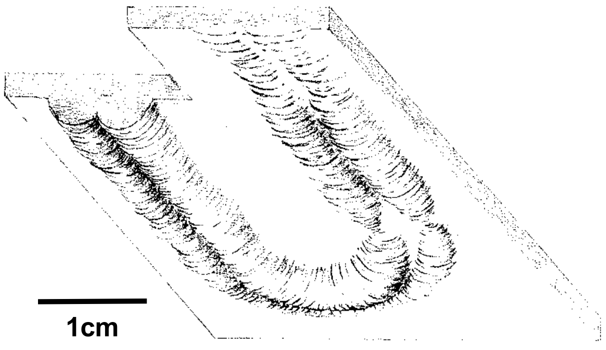


Figure 95: Sketch of hypichnial preservation of a curved segment and undulose pattern of *Cruziana pascens*.

Description: Hypichnial, straight to meandering, sometimes rotating, undulose double rows of fine striae, perpendicular or slightly oblique with respect to main axis of a single row. Width of double row 10-14mm. Number of striae: 15 per centimetre. Rows tend to be parallel and occur in high density.

Discussion: *Cruziana pascens* differs from all other known *Cruziana* ichnospecies by showing a meandering and/or rotating pattern. *Diplichnites triassicus* (LINCK 1943) displays much shorter striae, which are commonly preserved as small knobs only (POLLARD 1985; MACHALSKI & MACHALSKA 1994). Similar forms are described under the ichnogenus *Acripes* MATTHEW 1910, which is still used by some authors for non-marine arthropod traces (see GŁUSZEK 1995 for discussion). However, there are no significant differences between these ichnotaxa that would justify a separation at the ichnogeneric level (HÄNTZSCHEL 1965, 1975).

There is a transition of *Cruziana pascens* to *C. problematica* and to *Rusophycus carbonarius*, and the three taxa can be referred to the same tracemaker supposed to be notostracan crustaceans. The behaviour reflected by *Cruziana pascens* represents an efficient way of exploiting a surface for food. Possibly, notostracans penetrated a thin veneer of sand to reach the top of an underlying mudstone, and the overlying sand immediately covered the fine scratche ornaments produced in the mudstone (SEILACHER 1970). An origin as surface trail, as proposed by CRIMES (1975), seems unlikely because the preservational potential of surface traces in the studied environment is very low. However, an origin as undertrack seems also possible (SEILACHER 1994).

Cruziana pascens specimens together with *C. problematica* and *Rusophycus carbonarius* occur on the soles of slabs from pointbar deposits of a meandering river. Apparently, the nutrient content was very high in these deposits to allow a meandering mode of sediment exploitation.

It should be mentioned that the notostracan *Triops cancriformis*, the animal species with the longest range in earth history, was found in the same formation in Bavaria (TRUSHEIM 1937; also see 'probable *Triops* resting trace').

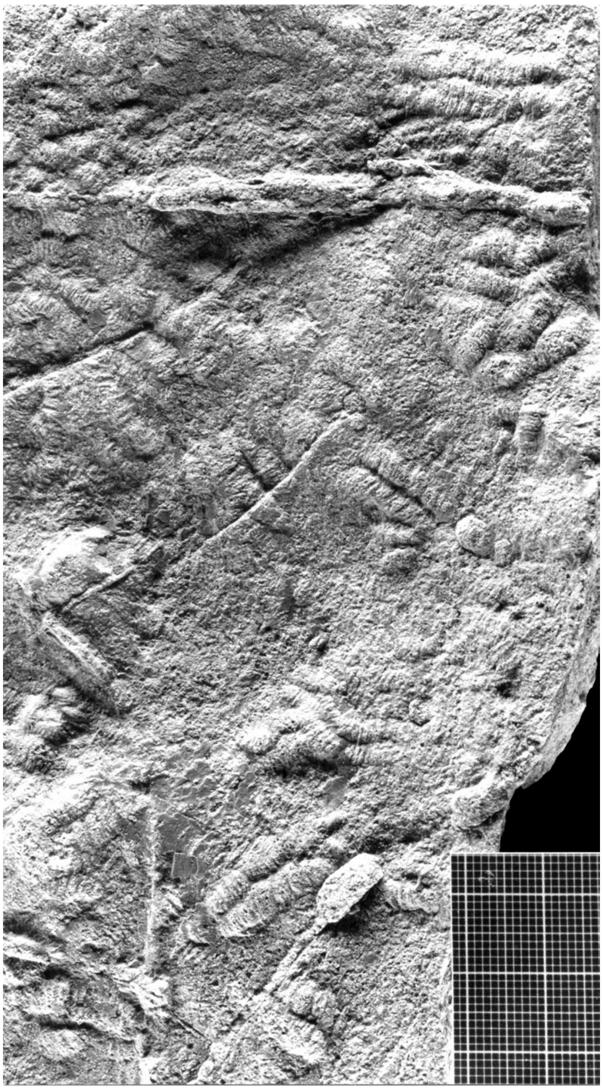


Figure 96: *Cruziana problematica* (SCHINDEWOLF, 1921). Positive hyporelief, basal view; PIW1998-VIII-11A. Coburger Sandstein, Hassberge Fm, Vetter quarry. Millimetre grid for scale.

Cruziana problematica (SCHINDEWOLF, 1921)

Fig. 96

pt 1937 *Isopodichnus moenanus* n. sp. – KUHN: 364, fig. 1 [only long double rows; *non* short coffee-bean shaped = *Rusophycus carbonarius*].

Diagnosis: Straight to curved, relatively small *Cruziana* showing faint, transverse striae which can reach the margin of the trace in shallow specimens or terminate before reaching the margin in deep specimens (SCHLIRF et al. 2001).

Material: PIW1998-VIII-11A- B, 15, Coburger Sandstein, Hassberge Fm, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Straight to winding, hypichnial, flat double-ridges, 8-10mm wide and up to 35mm long, covered with perpendicular fine striae; ridges divided by a distinct median furrow.

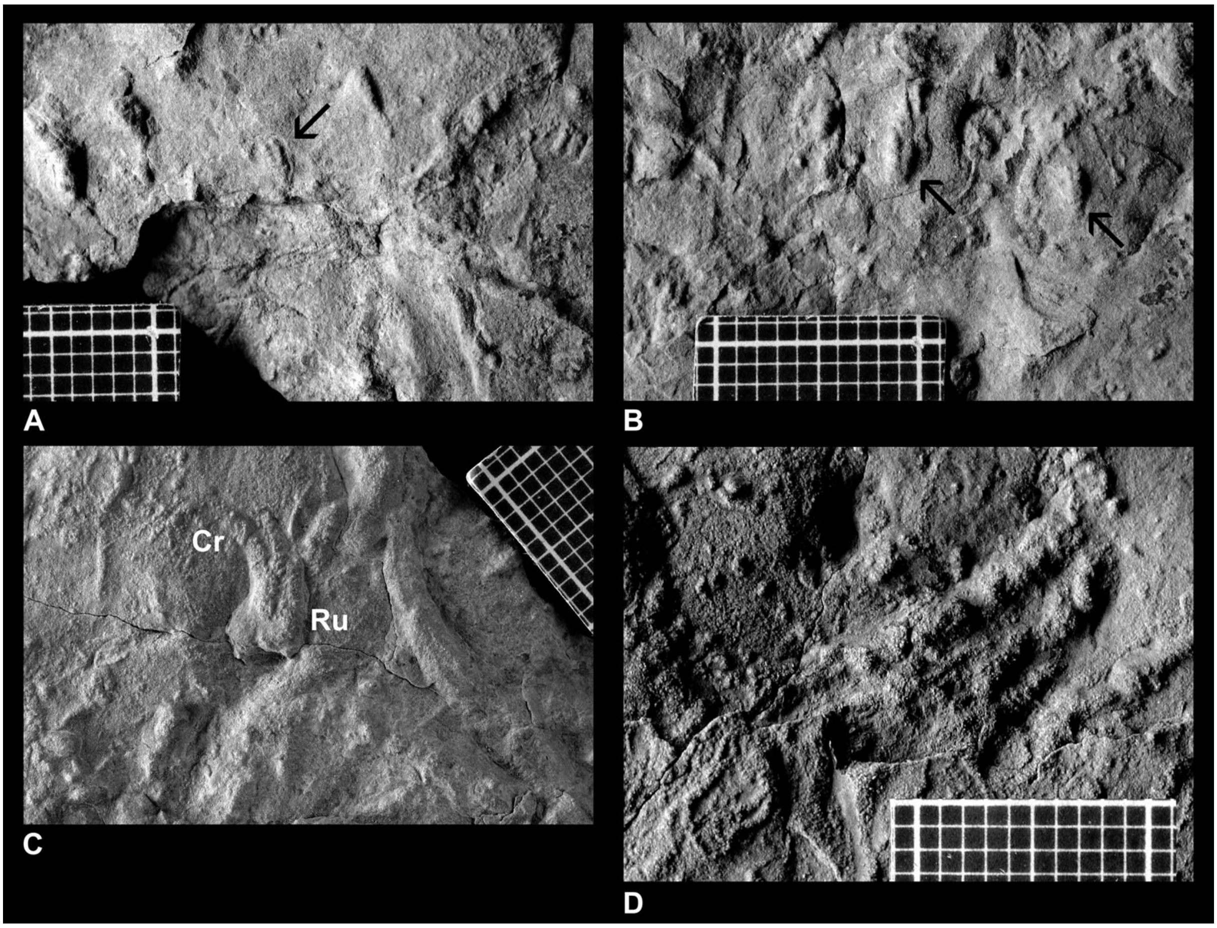


Figure 97: **A-B**. *Rusophycus* cf. *carbonarius*, positive hyporeliefs. **A**. PIW2002-I-5. **B**. PIW2002-I-5. **C**. Ru = *Rusophycus* cf. *carbonarius* grading into Cr = *Cruziana* cf. *problematica*, PIW2002-I-8. **D**. *Cruziana* cf. *problematica*, PIW2002-I-14. All Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany. Millimetre grids for scale.

Discussion: This trace fossil commonly passes into *Rusophycus carbonarius*. Triassic *Cruziana problematica* is regarded as the trace of notostracan crustaceans (POLLARD 1985 and references therein).

In their diagnosis of *C. problematica* FILLION & PICKERILL (1990) indicated that it is less than 7mm wide. Nevertheless, POLLARD (1985: fig. 4), who measured this ichnotaxon in different collections, observed larger forms. For this reason, a strict size limit is excluded from the diagnosis.

Cruziana cf. *problematica* (SCHINDEWOLF, 1921)

Fig. 97C, D

Material: PIW2002-I-8, 14, Werksandstein, Würzburg Fm, Lower Keuper, outcrops between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

Description: Minute, short, bilobate, positive hyporeliefs with very fine, oblique to perpendicular scratch ornaments. Length 6mm, width 2mm. One specimen emerges from *Rusophycus* cf. *carbonarius* (Fig. 97C).

Discussion: These minute forms are assigned to *Cruziana* cf. *problematica* because of their very small size and indistinct scratch ornaments. Due to the small size the scratch ornaments are barely visible.

These structures occur in greenish grey claystones to siltstones that are interpreted as overbank deposits. In analogy to *Rusophycus* cf. *carbonarius* described below, conchostracans or other small arthropods may have produced this trace fossil. Due to the minute size no details except for the size are detectable that help to identifying the progenitors.

Ichnogenus *Rusophycus* HALL, 1852

Type ichnospecies: *Fucoides biloba* VANUXEM, 1842: 79, fig. 11.1; see discussion below.

Diagnosis: Short, bilobate, rarely multilobate traces. Lobes predominantly bilaterally symmetrical. Convex forms (hypichnia) with a distinct median furrow; concave forms (epichnia) with median ridge. Outline ovate to coffee-bean-shaped; with oblique to transverse or longitudinal striae in various arrangements, or almost smooth (SCHLIRF et al. 2001).

Discussion: FILLION & PICKERILL (1990) and KEIGHLEY & PICKERILL (1996) stated that the type ichnospecies of *Rusophycus* is *Rusophycus clavatus* HALL, 1852, by subsequent designation by MILLER (1889: p. 138). FILLION & PICKERILL (1990) pointed out the problem of *R. clavatus* being the type ichnospecies (not formally mandatory for ichnogenera at the time of their publications). According to FILLION & PICKERILL (1990) *R. clavatus* is better assigned to *Cruziana* than to *Rusophycus*. This would make *Rusophycus* a junior synonym of *Cruziana*. For this reason FILLION & PICKERILL (1990) and subsequently KEIGHLEY & PICKERILL (1996) stated that *Fucoides biloba* was better chosen as type ichnospecies by the ICZN through the use of its plenary power. Many authors already considered *Fucoides biloba* VANUXEM (1842: 79) as type ichnospecies of *Rusophycus* (e.g., OSGOOD 1970; HÄNTZSCHEL 1975; OSGOOD & DENNEN 1975; ALPERT 1976). HÄNTZSCHEL (1975) was not entirely certain about the original designation of *Fucoides biloba* as type ichnospecies, and thus put it in quotation marks. Unfortunately, he did not comment on his decision. In order to avoid confusion, the view of HÄNTZSCHEL (1975) is followed here. To weed out this nomenclatural jungle, a call of the ICZN for an official opinion on this case should be made before the next edition of the Treatise will be published.

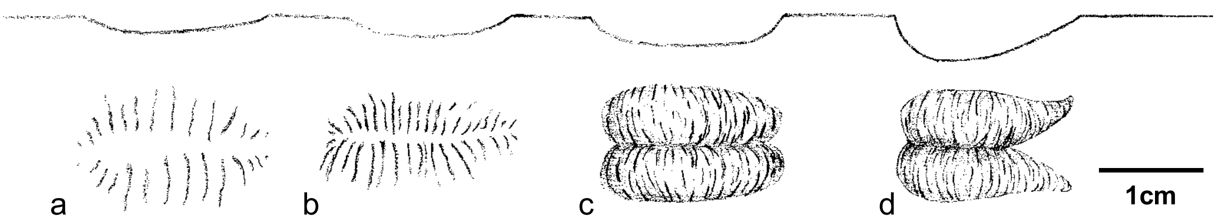


Figure 98: Sketches of preservational variants of *Rusophycus carbonarius* as a result of burrow depth. Upper line depicts vertical section at sediment surface, lower part indicates resulting hypichnial preservation. **A:** Very flat burrowing activity resulting in a wide gap between the two lobes and poorly defined coffee-bean-shape with scratches of different length resulting in a poorly defined burrow outline. **B:** Slightly deeper burrow resulting in a narrower gap, a better defined coffee-bean-shape and burrow outline. **C:** Deep burrow with both ends similar in shape, resulting in a well defined coffee-bean-shape with smooth burrow outline. **D:** Very deep burrow with steep posterior part and flat anterior part, resulting in a chevron-shaped posterior part; outline well defined.

Apart from obvious *Rusophycus* specimens, there are transitional forms to *Cruziana* which show a length to width ratio of about 2 to 1. This ratio has been recommended by KEIGHLEY & PICKERILL (1996) as the diagnostic criterion to distinguish *Cruziana* from *Rusophycus*. However, transitional forms do not display evidence of a distinct downward directed digging (SEILACHER 1970) typical of *Rusophycus*, which should be considered as one of the most diagnostic features of *Rusophycus*, expressed in the coffee-bean shape. This and the presence of a more complex form than just bilobate grooves (see *Rusophycus versans*) made an emendation of the diagnosis necessary.

During the Palaeozoic, *Rusophycus* was apparently predominantly produced by trilobites (see OSGOOD 1970 and RINDSBERG 1994 for discussion). PRATT (1993) noted a “rusophyciform” Cruziana from Lower Cambrian sandstones of Ellesmere Island, Antarctica, Canada. As PRATT discussed, some of the specimens preserved the imprints of the anterior part of a carapace, indicating that the progenitors had a bivalved carapace and therefore were not trilobites. Lately, HAGADORN & HOLLINGSWORTH (2004) presented extraordinarily well preserved Early Cambrian *Rusophycus marginatus* from the Wood Canyon Formation of Nevada-California that show soft tissue impressions of their progenitors. The observed distinctive sub-cephalic soft-tissue impressions and a lack of natant hypostome impressions imply a nontrilobite origin of the trace fossils. The observed features rather are consistent with crustacean-like arthropods from other Cambrian finds (HAGADORN & HOLLINGSWORTH 2004). Such observations corroborate the necessity of an absolute producer independent trace fossil nomenclature and taxonomy. A trilobite origin can be excluded for Mesozoic to Cenozoic specimens of *Cruziana* and *Rusophycus*.

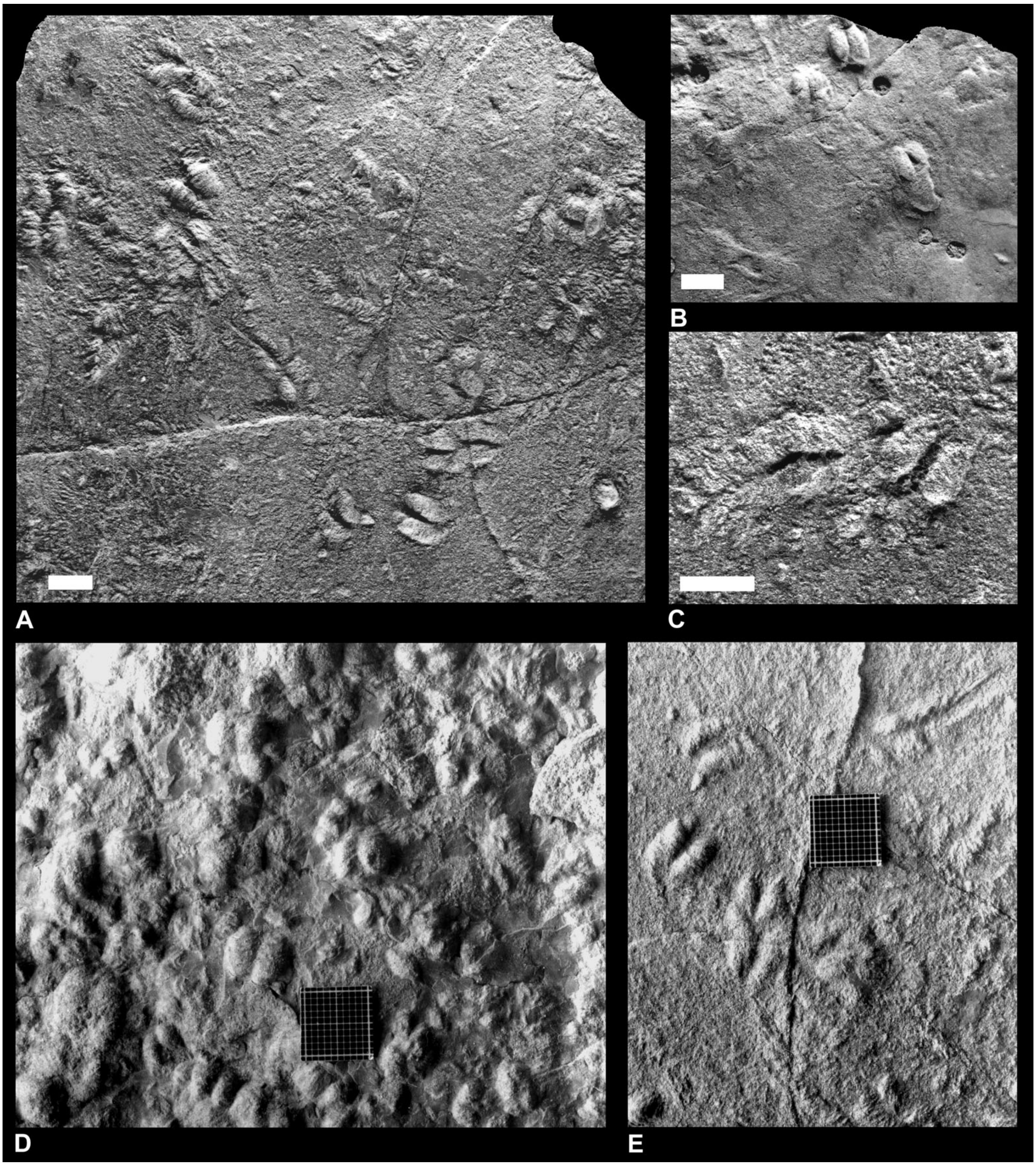


Figure 99: A-E. *Rusophycus carbonarius* DAWSON, 1864. Positive hyporelief, basal view; **A**. PIW1998-VIII-1. **B**. PIW1998-VIII-81. **C**. PIW1998-VIII-1. **D**. PIW1998-VIII-7. **E**. PIW1998-VIII-1. All Coburger Sandstein, Hassberge Fm, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany. Scale bars: 1cm; millimetre grids for scale in D-E.

Rusophycus carbonarius DAWSON, 1864

Fig. 98-99

*	1864	*Rusophycus carbonarius* DAWSON: 364, fig. 3.
pt	1937	*Isopodichnus moenanus* n. sp. – KUHN: 364, fig. 1 [only coffee-bean shaped specimens; *non* long double rows = *Cruziana problematica*].
v	1942	*Isopodichnus eutendorfensis*. – LINCK: 240, fig. 8.
	1954	*Cruziana didyma* SALTER. – FÜRST: 113, pl. 8.

pt 1979 *Cruziana problematica* (SCHINDEWOLF, 1921). – BROMLEY & ASGAARD: 66, fig. 16A.
pt 1979 *Rusophycus eutendorfensis* (LINCK 1942). – BROMLEY & ASGAARD: 64, fig. 17A, B [? fig. 17C, E].
non 1979 *Rusophycus eutendorfensis* (LINCK 1942). – BROMLEY & ASGAARD: 17D, F, 20A.
1990 *Rusophycus eutendorfensis* (LINCK, 1942). – FILLION & PICKERILL: 55, pl. 13 fig. 11.
pt 1990 *Isopodichnus eutendorfensis.* – DEBRIETTE & GAND: 23, text-fig. 4, pl. 1 fig. A, B.
pt 1996 *Rusophycus carbonarius* (DAWSON, 1864) [sic]. – KEIGHLEY & PICKERILL: 278, fig. 1A, pt. fig. 1B-C.
1996 *Rusophycus eutendorfensis* (LINCK 1942). – KEIGHLEY & PICKERILL: 279, fig. 1G.

Diagnosis: Small, coffee-bean-shaped form, with transverse to oblique, generally fine striation; lobes parallel or slightly gaping (SCHLIRF et al. 2001).

Material: PIW1998-VIII-1A-B, 7A-B, 9, 11A-B, 25, 81, 82, 85, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Variably oriented, hypichnial, bilobate mounds, 5-15mm across, and 6-15mm long, with a distributional maximum of 10-12mm. Lobes separated by median furrow, commonly wider and deeper towards anterior end where lobes are splayed. Lobes predominantly smooth, rarely covered with fine oblique striae. Overlaps common in dense occurrences (e.g., PIW1998-VIII-7). Intergradation with *Cruziana problematica* common.

This trace fossil co-occurs with *Cruziana problematica, Skolithos* isp. B, and *Planolites* isp.

Discussion: KEIGHLEY & PICKERILL (1996) revised *Rusophycus carbonarius* (DAWSON) and separated it from *R. eutendorfensis* sensu FILLION & PICKERILL (1990) (see discussion of *R. eutendorfensis*) based on the lateral range of the striation. They regarded the striation in *R. carbonarius* as not extending beyond the margins of the lobes in contrast to *R. eutendorfensis*, in which the striation extends beyond the margins. However, the range of striation can be interpreted as a result of minor differences in the behaviour of the tracemaker as well as a preservational artefact. In shallower burrows, the striae can be produced easily beyond the margin of the main part of the burrow. By contrast, in deeper burrows appendages of the tracemaker are too short for the production of striae extending beyond the main burrow (Fig. 98). Moreover, the lectotype of *R. eutendorfensis* selected by FILLION & PICKERILL (1990) and discussed by KEIGHLEY & PICKERILL (1996) does not belong to *R. eutendorfensis* (see discussion above). These facts allowed an emendation of the diagnosis of *R. carbonarius* DAWSON by SCHLIRF et al. (2001). However, for final conclusions, the type material of *R. carbonarius* (the location of which is currently unknown) should be redescribed, since neither the illustration by DAWSON (1864: fig. 3) nor his description present enough data for a precise characterisation.

Rusophycus carbonarius was discussed by Bromley & Asgaard (1979) (= *R. eutendorfensis* in their article) who regarded their Triassic material as cubichnia of notostracans. This interpretation is also probable for the present material. Bromley & Asgaard (1979) mentioned that Palaeozoic forms related to trilobites show a comparable behavioural pattern. However, the forms described herein do not display a distinct change of direction in the striation as was described by Bromley & Asgaard (1979).

Rusophycus cf. *carbonarius* Dawson, 1864

Fig. 97A-C

Material: PIW2002-I-5, 8, Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

Description: Minute, bilobed, coffee-bean-shaped, positive hyporeliefs with very fine, oblique scratch ornaments. Length 2-4mm, width 1-2mm. Single specimen (PIW2002-I-8; Fig. 97C), grading into *Cruziana* cf. *problematica*.

Discussion: These minute forms are assigned to *Rusophycus* cf. *carbonarius* because of their small size and poorly developed scratch ornaments. Due to the small size, the scratch ornaments are barely visible. Small sized *Cruziana* and/or *Rusophycus* were often ascribed to *Isopodichnus*, a junior synonym of *Cruziana* (see Keighley & Pickerill 1996 for a detailed discussion). The view of Keighley & Pickerill (1996) that *Isopodichnus* should not be kept separate from *Cruziana* because of arbitrary size divisions is followed here. Pollard (1985) described very small *Rusophycus* and *Cruziana* specimens (termed *Isopodichnus* in his article) from the Triassic of Britain and Germany.

The trace fossil occurs in greenish grey claystones to siltstones that are interpreted as overbank deposits. As possible producers of these structures conchostracans or other small arthropods are plausible. Due to the minute size, no details except the size information are detectable that could help to identify the progenitors.

Rusophycus eutendorfensis (Linck, 1942)

Fig. 100

v, pt 1942 *Isopodichnus* sp. – Linck: 234, fig. 1-2.
**v* 1942 *Isopodichnus eutendorfensis* n. sp. – Linck: 238, fig. 5 [vertically oriented specimen at the centre of the slab below the coin].
v, pt 1942 *Isopodichnus eutendorfensis* n. sp. – Linck: 238, fig. 5.
v, ? 1942 *Isopodichnus eutendorfensis* n. sp. – Linck: 239, fig. 7.

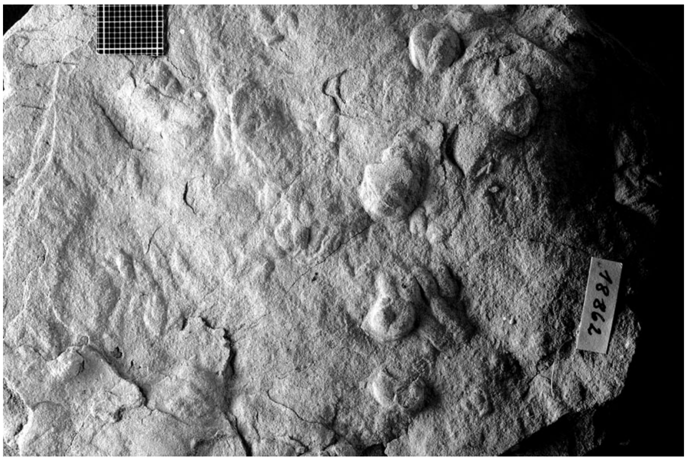


Figure 100: *Rusophycus eutendorfensis* LINCK, 1942. SMNS 18862, uppermost Schilfsandstein, Stuttgart Fm, Middle Keuper, Mühlbach, Baden-Württemberg, southern Germany. Millimetre grid for scale.

Diagnosis: Small, predominantly smooth, coffee-bean-shaped forms with longitudinal striation along lobes; lobes either parallel or diverging at one end. Occasionally with perpendicular to transverse striation (SCHLIRF et al. 2001).

Material: SMNS 18862, uppermost Schilfsandstein, Stuttgart Fm, Middle Keuper, Mühlbach, Baden-Württemberg, southern Germany.

Discussion: LINCK (1942) pointed out in his original description of *Rusophycus eutendorfensis* (=*Isopodichnus eutendorfensis* in his LINCK's article) that the most important feature and morphological difference to other *Rusophycus* known so far was the fact that *R. eutendorfensis* is predominantly smooth, elongated, diverging at one end, and shows distinct longitudinal furrows along the lobes, "...vor allem aber zeigen manche der gestreckteren, klaffenden Buckel auf den Lateralwülsten flache Längsrinnen, wie sie bei noch keinem anderen *Isopodichnus*-Vorkommen beobachtet wurden" (LINCK 1942: 238). He also described a flat, perpendicularly to obliquely striated form under the same name (LINCK 1942: 240, fig. 8), but as a form transitional to *Cruziana* (= "Kriechspur" in LINCK 1942). Unfortunately, this transitional form was selected by FILLION & PICKERILL (1990) as the lectotype of *R. eutendorfensis* despite the description given by LINCK. This treatment does not accord to the rules of ICZN (Article 74). Other authors regarded *R. eutendorfensis* as the perpendicularly to obliquely striated form (BROMLEY & ASGAARD 1979; DEBRIETTE & GAND 1990; KEIGHLEY & PICKERILL 1996). According to the original descriptions and illustrations by LINCK (1942), the longitudinally striated forms are the only representatives of *R. eutendorfensis*. Hence, a new lectotype has been designated by SCHLIRF et al. (2001). We do not have to worry about a confusion of *R. eutendorfensis* with *R. didymus* (SALTER) as discussed by FILLION & PICKERILL (1990: 55) because the longitudinal striation in *R. eutendorfensis* is a characteristic feature unknown from *R. didymus*.

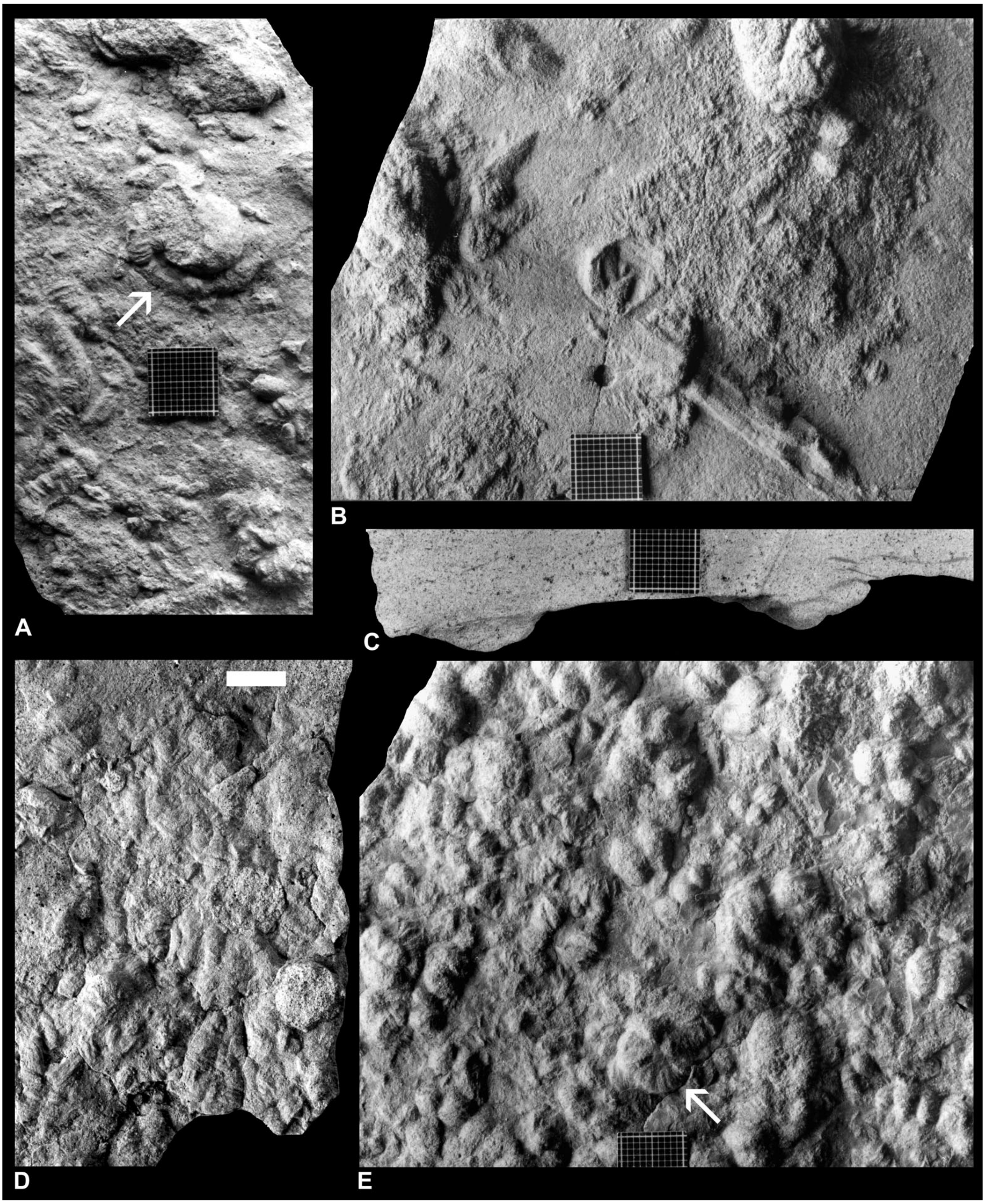


Figure 101: A-E. *Rusophycus versans* SCHLIRF & UCHMAN, 2001. **A**. Arrow indicates trace segment caused by rotating movement of the tracemaker; positive hyporelief, basal view; topotype, PIW1998-VIII-9. **B**. Positive hyporelief, basal view; holotype, PIW1998-VIII-18. **C**. Full relief, lateral view; holotype, PIW1998-VIII-18. **D**. Positive hyporelief, basal view; topotype, PIW1998-VIII-10. **E**. Arrow indicates trace segment caused by rotating movement of the tracemaker; positive hyporelief, basal view; topotype, PIW1998-VIII-8. All Coburger Sandstein, Hassberge Fm, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany. Millimetre grids for scale, scale bar: 1cm in D.

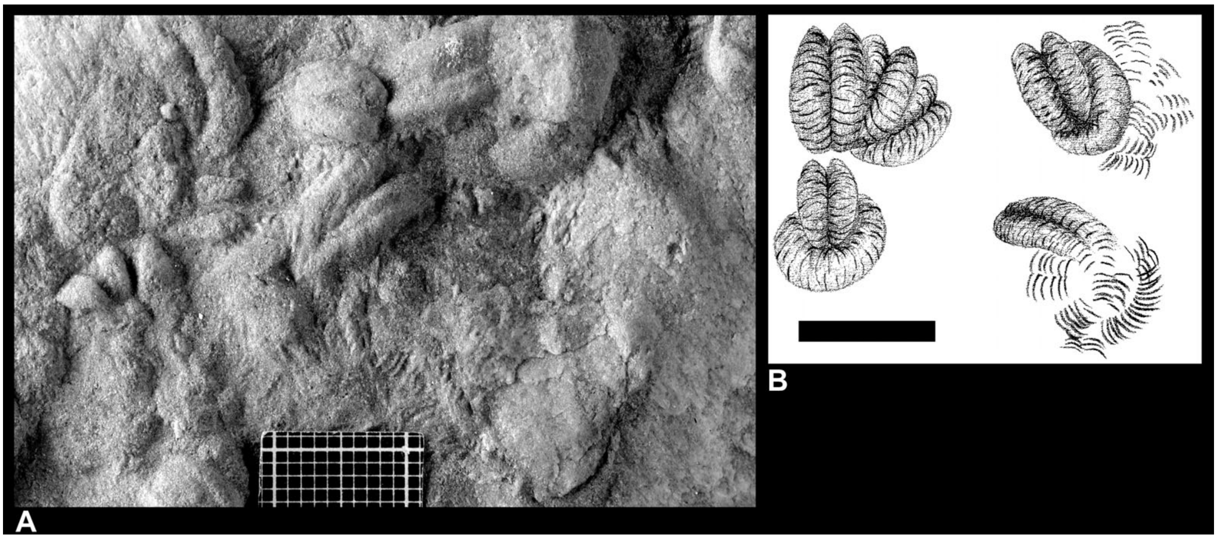


Figure 102: A-E. *Rusophycus versans* Schlirf & Uchman, 2001. **A**. SMNS 65500, Kieselsandstein, Hassberge Fm, Middle Keuper, Benning near Kleinbottwar, Baden-Württemberg, southern Germany. Positive hyporelief. **B**. Sketch of morphological variants of *Rusophycus versans*. Scale bar: 1cm.

Rusophycus versans Schlirf & Uchman, 2001

Fig. 101-102

? 1955 *Cruziana* cf. *irregularis* (Fenton) [sic = Fenton & Fenton, 1937]. – Seilacher: 105, fig. 5(8).
?p 1970 *Asteriacites stelliformis* (Miller & Dyer, 1878). – Osgood: 313, pl. 57, fig. 2 [*non* pl. 59, fig. 2, pl. 62, fig. 5 = *Heliophycus stelliformis*].
p 1970 *Rusophycus cryptolithi* n. sp. – Osgood: 307, pl. 59, fig. 4 [*non* pl. 58, figs. 1-2 = *Rusophycus cryptolithi*].
?p 1987 *Rusophycus*. – Wright & Benton: 418, pl. 52 fig. 5 [*non* pl. 52 fig. 4 = *Rusophycus carbonarius*].

Emended diagnosis: Clusters of short, poorly or well sculptured, bilobate, coffee-bean-shaped, hypichnial mounds, displaying additional, more-or-less fan-like or irregularly arranged side lobes.

Material: Holotype, PIW1998VIII-18; paratypes, PIW1998VIII-7A, 8, 9, 11B, 12A, Coburger sandstone, Hassberge Fm, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany. SMNS 65500, Kieselsandstein, Middle Keuper, Benning near Kleinbottwar, Baden-Württemberg, southern Germany.

Description: Clusters of variably oriented, small, very short, bilobate, hypichnial mounds, with or without anterior splay. Width 10-11mm, length 8-9mm. Lobes smooth or rarely covered with oblique striation. Median groove very narrow and shallow, commonly indistinct. Burrow density high, overlaps common.

Discussion: All other known ichnospecies of *Rusophycus* only consist of one bilobate element. These morphological difference suggests a different behavioural pattern of the tracemaker. The additional radiating lobes resulted from rotating movements of the progenitor. The rotation enabled the tracemaker to exploit the sediment more efficiently. Deposit-feeding notostracan crustaceans are considered as possible producers for the herein described material. The specimens of SEILACHER (1955) and OSGOOD (1970) that are put in synonymy with *R. versans* probably have been produced by trilobites, and, by contrast to the Keuper material they, occur in marine sediments.

SEILACHER (1955: fig. 5.8) figured a specimen as *Cruziana* cf. *irregularis* and recognised that - according to the kind of striation shown on the specimen - the producer must have changed the direction of movement. In addition, SEILACHER stated that the specimen is much deeper than what he called an 'ordinary' *Rusophycus*. These observations make it likely that this specimen belongs to *Rusophycus versans*.

OSGOOD (1970) introduced *Rusophycus cryptolithi* and regarded ornamentation as distinctly enough to differentiate ichnospecies of *Rusophycus*. In his diagnosis, OSGOOD (1970) defined *R. cryptolithi* as a small, ovoid, button-shaped *Rusophycus* with a coarse striated outer zone and a more finely striated inner zone. In addition, OSGOOD (1970) pointed out that *R. cryptolithi* differs from all other ichnospecies of *Rusophycus* by having a width to length ratio of nearly 1 to 1. Among his type series there is a single specimen (OSGOOD, 1970: pl. 59, fig. 4) that clearly features the behavioural pattern of *R. versans*.

SCHLIRF & UCHMAN (2001) based their new ichnospecies *Rusophycus versans* on poorly ornamented clusters of bilobate coffee-bean-shaped hypichnial elements. The diagnosis of *R. versans* is emended above, and well ornamented structures also are included in *R. versans*. However, the material figured by OSGOOD (1970: pl. 59, fig. 4) is only sparsely ornamented as well and OSGOOD (1970) stated that these structures are 'incipient' forms. The fact that *R. versans* consists of more than one bilobate element reflects a behaviour of high significance at the ichnospecific level of *Rusophycus* and is considered more important than ornamentation.

An additional structure, *Heliophycus stelliformis* (=*Asteriacites stelliformis* in OSGOOD 1970: pl. 57, fig. 2) shows interesting similarities with *R. versans*. As stated by OSGOOD (1970), there are similarities between *Heliophycus* and *Rusophycus* concerning the V-shaped striation. Interestingly OSGOOD (1970) did not discuss the problem of these morphological similarities and the possible consequences for the taxonomy of *Rusophycus* and *Heliophycus*. However, he found that the striae must have been formed differently. He stated that in *Rusophycus* the striae are a result of moving sediment towards the median furrow, thus taking into account that the possible producer was a

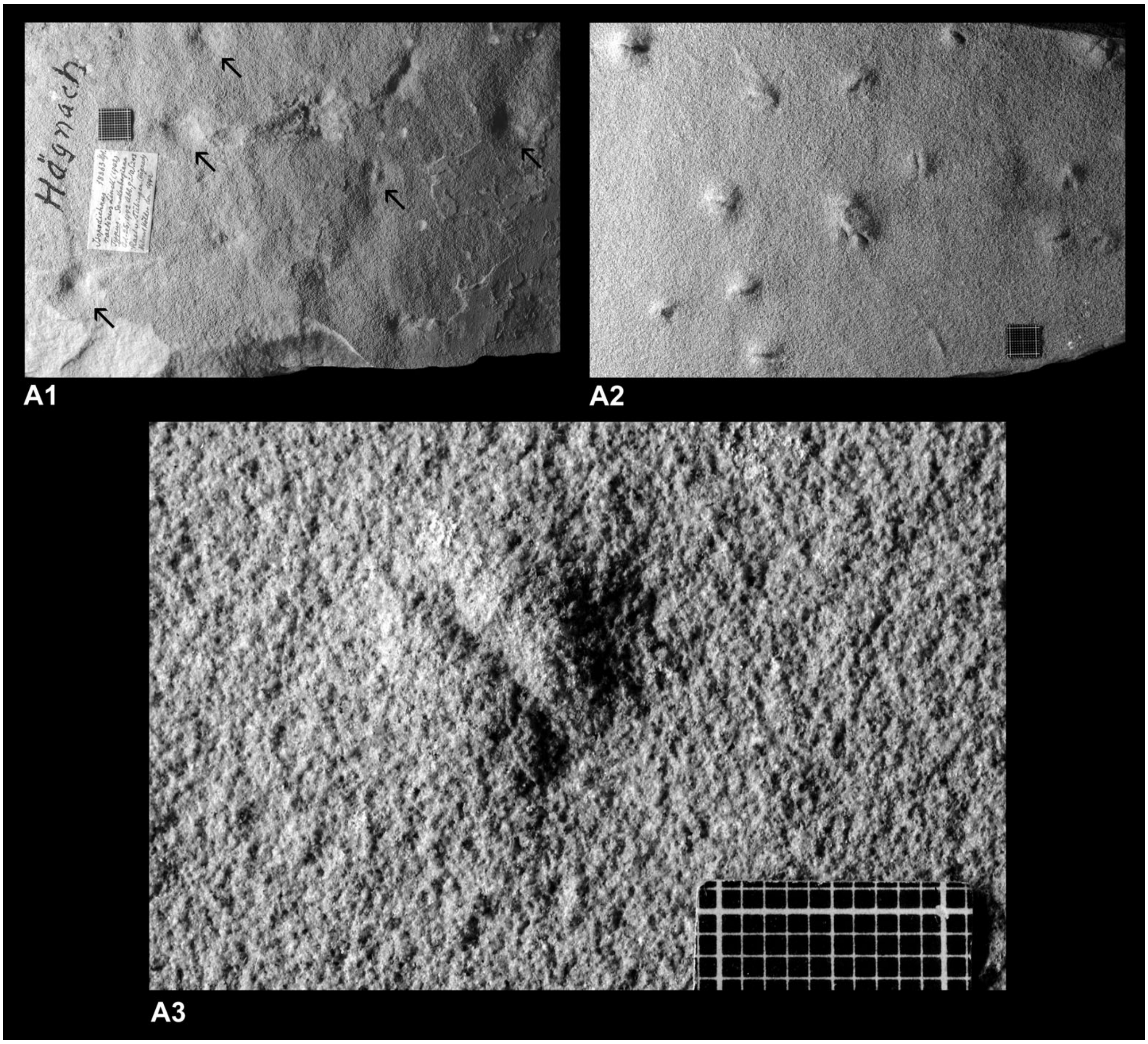


Figure 103: A1-3. *Rusophycus* isp., SMNS 18863, Rhätsandstein, Exter Fm, Upper Keuper, Hägnach quarry near Tübingen, Baden-Württemberg, southern Germany. **A1**. Indistinct bisymmetrical depressions, top view, negative epireliefs. **A2**. Sole of same slab with distinct, coffeebean-shaped positive hyporeliefs. **A3**. Detail of A2, showing smooth surface of *Rusophycus* isp. Millimetre grids for scale.

trilobite. In *Heliophycus*, by contrast the sediment must have been moved in the opposit directions, namely from the interior part to the outside. Otherwise the sediment would have become clogged in the central region of the 'arms' of the producer, presumed that the producer was a stelleroid. WRIGHT & BENTON (1987: pl. 52 fig. 5) figured a specimen of *Rusophycus* that resembles *R. versans*. Seemingly a 'deep' structure with poor striation. It also suggests varying movements of the producer characteristic of *R. versans*.

Rusophycus isp.

Fig. 103

v 1942 *Isopodichnus raeticus* n. sp. – LINCK: 242, fig. 9.

Material: SMNS 18863, Rhätsandstein, Exter Fm, Upper Keuper, Hägnach quarry near Tübingen, Baden-Württemberg, southern Germany.

Description: Hypichnial preservation: variably oriented, small, short, bilobate, smooth, coffee-bean shaped hypichnial mounds. Width 8-14mm, length 16-19mm. Median groove wide and deep. Epichnial preservation: indistinct, bisymmetrical, depressions.

Discussion: LINCK (1942) introduced *Isopodichnus raeticus*. Re-study of the type material suggests no diagnostic features are present that would justify a separation from other known ichnospecies of *Rusophycus*. The specimens occur in a massive, medium-grained sandstone, and thus the chances to preserve scratch ornaments are low. The slab bearing the specimens is approximately 4cm thick. This means that the structures apparently reach deeply into the sediment. However, it cannot be decided if the structures are deep burrows, or if the hypichnial expressions are undertracks of the epichnial expressions.

Ichnogenus *Kouphichnium* NOPCSA, 1923

Type ichnospecies: *Ichnites lithographicus* OPPEL, 1862: 121; by monotypy.

* 1862 *Ichnites lithographicus* OPPEL 1862: 121
v 1943 *Limuludichnulus* n. g. – LINCK: 10.
v 1949b *Limuludichnus* n. g. – LINCK: 56.
1993 *Kouphichnium* NOPCSA, 1928. – HASIOTIS & DUBIEL: 176.
1993 limuloid trackway. – HUNT et al.: 205.
1998 *Kouphichnium* NOPCSA, 1928. – BUATOIS et al.: 160.
2003 *Kouphichnium* NOPCSA, 1928. – ROMANO & WHYTE: 259.

Diagnosis: Heteropodous trackway of great variability; complete trackway consisting of two kinds of track series: (1) two chevron-like series each of four oval, round, or bifid V-shaped impressions or scratches, forwardly directed; and (2) one pair of digitate or flabellar, toe-shaped or otherwise variable imprints; trackway with or without median drag ornament. All elements negative in epirelief and positive in hyporelief (modified after ROMANO & WHYTE 2003).

Remark: The diagnosis provided by ROMANO & WHYTE (2003) contains interpretative information and is thus slightly modified by omitting their interpretations. Diagnoses should generally be free of interpretations.

Discussion: The first four chevron tracks are supposed to be produced by the anterior four pairs of walking-legs; the second set of imprints is interpreted as produced by the birdfoot-like ‘pushers’ of the fifth pair of walking-legs, with their four or five leaf-like movable blades (CASTER 1938, ROMANO & WHYTE 2003). The median drag-ornament is produced by the telson (CASTER 1938, 1944). Lateral drag ornaments are either produced by the edges of the cephalothorax or the telson (BUATOIS et al. 1998; CASTER 1938, 1940).

LINCK (1943, 1949b) introduced two ichnogenera for supposed limulinid trackways. In 1943 he introduced *Limuludichnulus nagoldensis* from the Lower Triassic (Buntsandstein), in 1949 he erected *Limuludichnus variabilis* from Upper Triassic deposits (Keuper). Both trace fossils are very similar in general morphology. Although describing and discussing the new forms in detail, LINCK (1949b) did not mention why he introduced a new ichnogenus for the Keuper forms and what distinguishes the Keuper structures from the Buntsandstein structures. Both ichnogenera were considered synonyms of *Kouphichnium* by HÄNTZSCHEL (1975). This view is supported here. SCHLIRF et al. (2001) did not recognize the slightly different spelling of the two ichnogenera and confused them. However, since both ichnogenera are synonymous with *Kouphichnium*, this mistake is of minor importance and apologized here.

Following ROMANO & WHYTE (2003) and GOLDRING & SEILACHER (1971), the trackways are interpreted as limulid trackways. According to GOLDRING & SEILACHER (1971), the main habitats of limulinids have always been shallow marine environments. However, reports such as those of the modern *Carcinoscorpius rotundicauda*, which can be found 150km upstream from the open sea in the Hoohgly River, India, show that even long distances in a freshwater environment can be covered by usually marine invertebrates (SHUSTER 1957). If the Schilfsandstein (Middle Keuper), the host rock of *Kouphichnium variabilis* and *K. gracilis*, has been deposited under marine, nonmarine conditions, or both is controversially discussed (see GEYER 2002 for a summary). However, short periods of marine incursions cannot be excluded (see discussion of *Biformites insolitus* above).

Kouphichnium gracilis (LINCK, 1949b)

Fig. 104, 106A

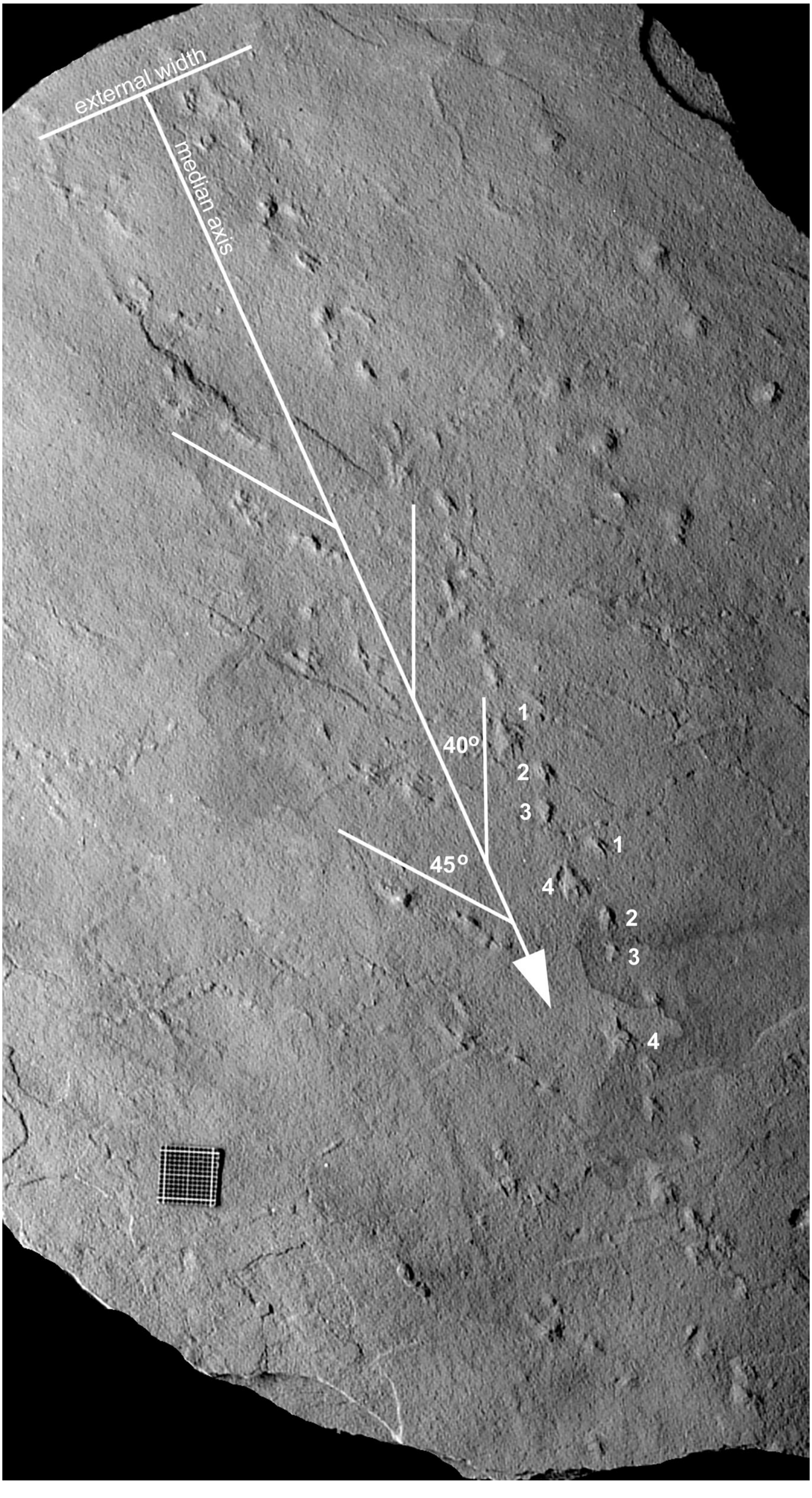
	1943	*L. gracilis* n.g. n. sp. – LINCK: 19 [= *nomen nudum*].
**v*	1949b	*Limuludichnulus gracilis* n. sp. LINCK: 57, fig. 4, pl. 6 fig. 5-6, pl. 7 fig. 2.
v	2001	*Kouphichnium* isp. – SCHLIRF et al.: 95, tab. 1.

Diagnosis: *Kouphichnium* trackway composed of regularly arranged three V-shaped tracks and one multifid, ideally quatrifid track; with or without median or lateral drag ornament.

Material: Holotype SMNS 22007, uppermost Schilfsandstein, Stuttgart Fm, Middle Keuper, Sternenfels, Baden-Württemberg, southern Germany.

Description: Two asymmetric, chevron-shaped, lateral series of distinct tracks of variable form; with faint lateral drag ornament; each series consist of four transverse oriented tracks. Shapes of tracks are irregularly subrounded to elliptical, subquadrangular, bifid, V-shaped and trifid. The series of tracks of the trackway forms a 40° angle with the median axis; the opposite side (with the lateral drag ornament) forms an angle of 45° with the median axis. Each series consists of four tracks (1-4, Fig. 106A); track 1 is obliquely oriented, bifid; tracks 2 and 3 are nearly parallel, bifid to ellipsoidal; track 4 is nearly parallel, trifid (orientation with respect to median axis). The series length is approximately 4cm, the external width is approximately 5cm.

Discussion: Three of the four transversely oriented tracks are interpreted as imprints of the anterior four pairs of walking-legs, most likely pairs 2 to 4. The trifid tracks are interpreted as imprints of the fifth pair of walking-legs (‘pushers’). The lateral drag-ornament may be produced either by the edges of the cephalothorax or the telson. The fact that the telson imprint is not in a median position but lateral is frequently observed in limulinid trackways (e.g. BUATOIS et al. 1998; ROMANO & WHYTE 2003). However, in this case the sublateral imprint remains in the same position with respect to the tracks, and the entire trackway is straight. Lateral telson drag ornaments are generally observed in bended tracks (see *Kouphichnium variabilis*).


external width
median axis
40°
45°
1
2
3
4
1
2
3
4

Previous page:

Figure 104: *Kouphichnium gracilis* (LINCK, 1949b), positive hyporelief, bottom view, holotype, SMNS 22007, uppermost Schilfsandstein, Stuttgart Fm, Middle Keuper, Sternenfels, Baden-Württemberg, southern Germany. 1-4 indicates tracks. Note faint cephalothorax imprint on left side of trackway. Arrow indicates direction of movement (top to bottom). Millimetre grid for scale.

The different angles of the track series with the median axis and the fact that the lateral imprint is preserved on one side of the trackway only suggests an inclined position of the progenitor with respect to its lateral axis.

The delicate and detailed preservation of the imprints of the fifth pair of walking-legs suggests moderately cohesive sediment conditions, which allow such a mode of preservation. By contrast, the tracks of *Kouphichnium variabilis* are preserved in less detail and are interpreted as being produced in less cohesive sediment.

Kouphichnium gracilis was described in detail by LINCK (1949b). The call for a general detailed revision of all ichnospecies of *Kouphichnium* as expressed by ROMANO & WHYTE (2003) and BUATOIS et al. (1998) is supported here. The three ichnospecies introduced by LINCK (1943, 1949b) appear to be distinctive. There are various morphological details which differentiate *Kouphichnium nagoldensis*, *K. variabilis*, and *K. gracilis*. Accordingly their hitherto used ichnospecific separation is maintained. In order to make a final statement on the value of the morphological differences among the ichnospecies of *Kouphichnium* further detailed studies are necessary. It appears that *K. gracilis*, *K. nagoldensis*, and *K. variabilis* are preservational variants. Sediment cohesiveness and grain size strongly influence the preservation of arthropod trackways (e.g., BRADDY 1998). This are 'primary preservational influences' (Fig. 105); 'primary', because it is neither a taphonomic overprint nor influenced by diagenesis. Such influences could be called 'secondary preservational influences'. Primary preservational influences may have an effect on the progenitor in such a way that – as an example – an animal walking over very soft substrate behaves differently from walking over stiff substrate. Crabs walking over a beach with sediments of varying water saturation would not show a difference in behaviour. How far such abiogenic primary factors should influence the taxonomy of arthropod trackways needs further general detailed investigations on arthropod trackways. BERTLING et al. (in rev.) favour a complete exclusion of abiogenic factors for ichnotaxonomy. This is supported here, but a priori a practicable and consistent classification scheme must be the result. Currently there is no general agreement on how to deal with primary preservational variants of arthropod trackways.

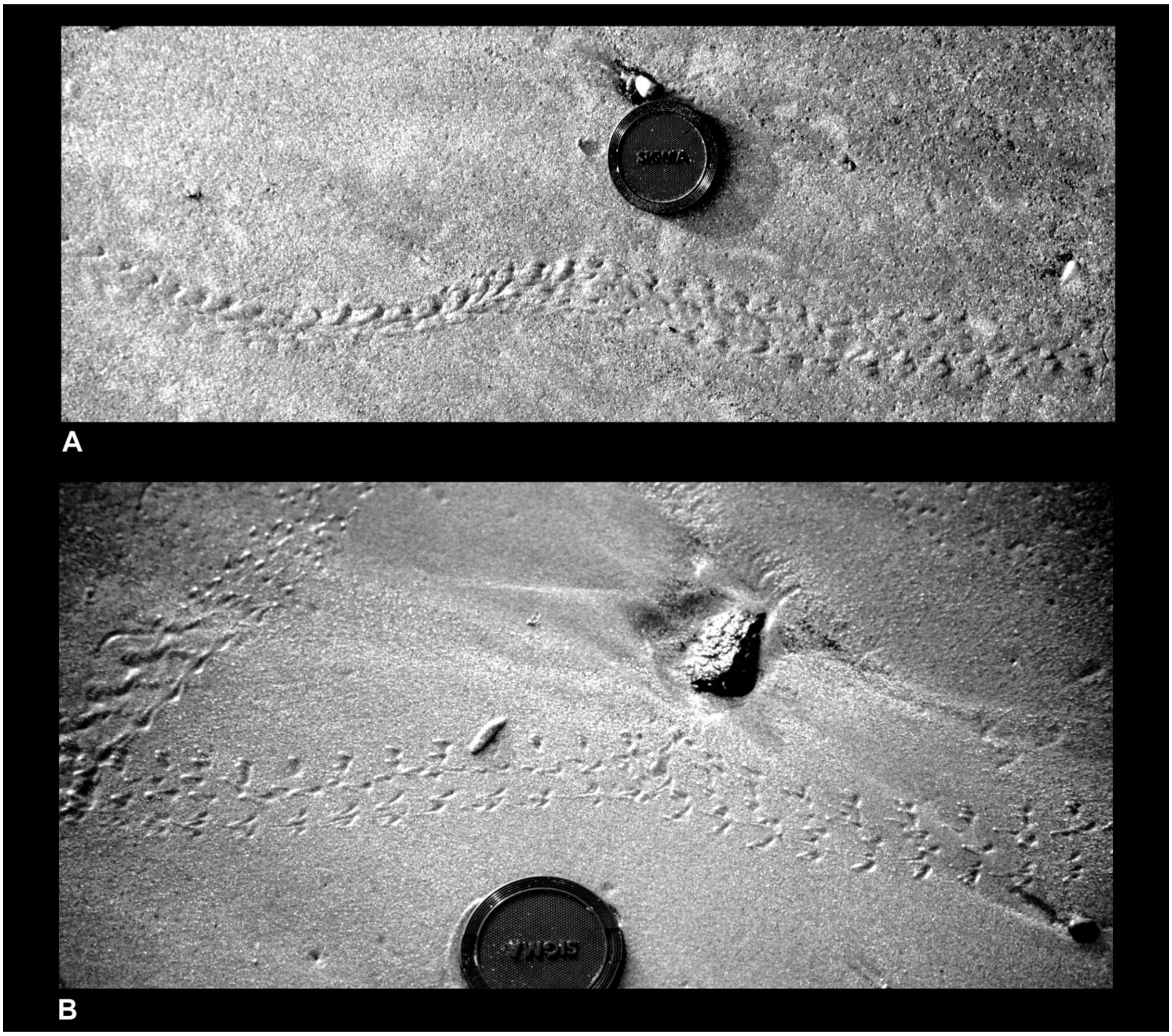


Figure 105: A-B. Trackways of crabs on a beach during low tide. Note variable forms of tracks which are a result of water saturation of the sediment. No behavioural diffences of the tracemaker were observed; all trackways were produced by one individual. Lens cap 72mm across.

Kouphichnium variabilis (LINCK, 1949b)

Fig. 106B, 107

**v*	1949	*Limuludichnus variabilis* n. sp. LINCK: 57, pl. 5 fig. 1, pl. 7 fig. 1.
v	2001	*Kouphichnium* isp. – SCHLIRF et al.: 95, tab. 1.
?	2003	*Kouphichnium* aff. *variabilis* (LINCK, 1949). – ROMANO & WHITE: 259, fig. 2-8.

Diagnosis: *Kouphichnium* trackways with two lateral series of more-or-less distinct tracks of variable form; each series consists of up to five transverse, irregular, or winding tracks; with or without median or lateral drag ornament. Tracks are bifid, V-shaped, hook-shaped, trifid, quatrifid, elliptical, elongate, subtriangular, or irregular with no definite outline.

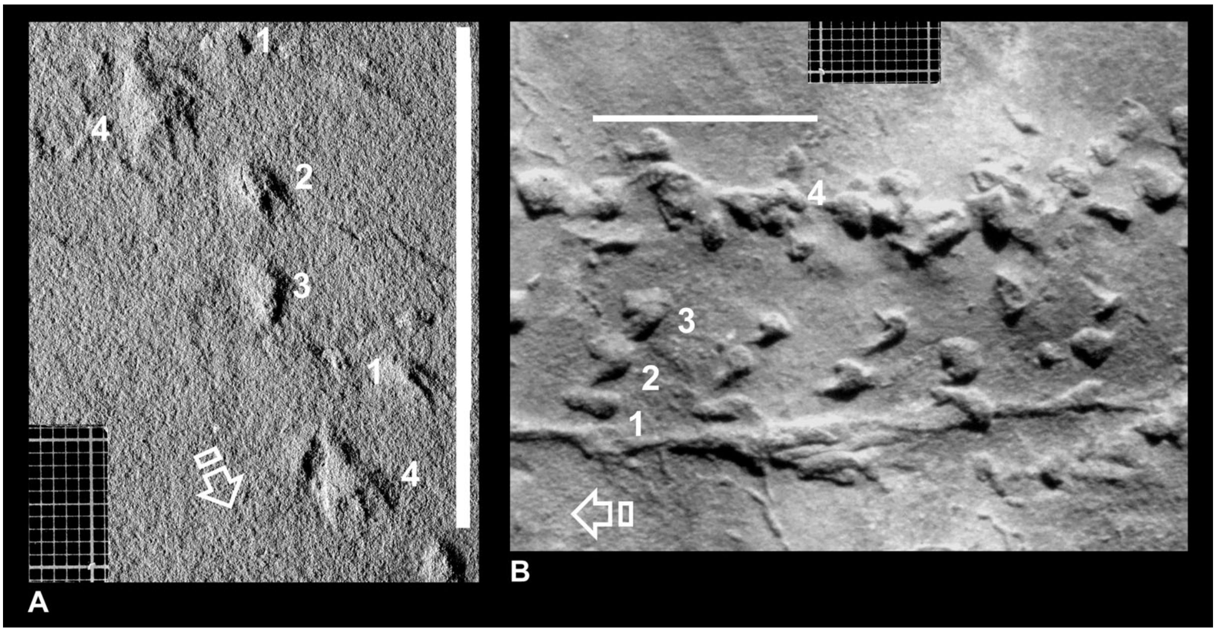


Figure 106: **A**. *Kouphichnium gracilis* (LINCK, 1949b). Detail of Fig. 104. 1-4 indicates tracks. Tracks 1 to 3 are bifid, and track 4 is trifid. **B**. *Kouphichnium variabilis* (LINCK, 1949b). Detail of Fig. 107. 1-4 indicates tracks. Track 1 is elongate, 2 and 3 are bifid, track 4 consists of one to three separate irregular structures with no definite outline to spike-shaped imprints. **A, B**. Positive hyporeliefs, bottom view; arrows indicate direction of movement (top to bottom); white bars indicate series length. Millimetre grids for scale.

Material: Holotype of LINCK (1949b: pl. 5 fig. 1) SMNS 22008, upper Schilfsandstein, Freudenstein; paratypes of LINCK (1949b: pl. 5 fig.2, pl. 7 fig. 1) SMNS 22009, uppermost Schilfsandstein, Sternenfels; both Stuttgart Fm, Middle Keuper, Baden-Württemberg, southern Germany.

Description: Asymmetrical, curving trackway, made up of variable series of four tracks. External width 5cm, length 65cm. Series consists of four, more-or-less transverse or irregular oriented tracks; drag ornament varies in position from left lateral to medial to right lateral with respect to the direction of movement. Individual tracks 1 to 3 are bifid, V-shaped, hook-shaped, elliptical, elongate, subtriangular; track 4 is made up of two subrounded and one irregular imprint with no definite outline.

Discussion: Three of the four transversely oriented tracks are interpreted as imprints of the anterior four pairs of walking-legs, most likely pairs 2 to 4. The irregularly shaped tracks 4 are interpreted as imprints of the fifth pair of walking-legs ("pushers"). The drag ornament is interpreted as produced by the telson (tdo). The variation of the telson imprint in its position from left lateral to medial to right lateral with respect to the direction of movement is interpreted as a result of balancing the body of the progenitor (ROMANO & WHYTE 2003). The trackway describes a curve, the progenitor apparently had to balance its body. The body of the tracemaker apparently was held in an inclined position with respect to its lateral axis and thus was responsible for the asymmetry of the trackway. As a result the imprints of the tracks are preferably preserved on one side of the trackway.

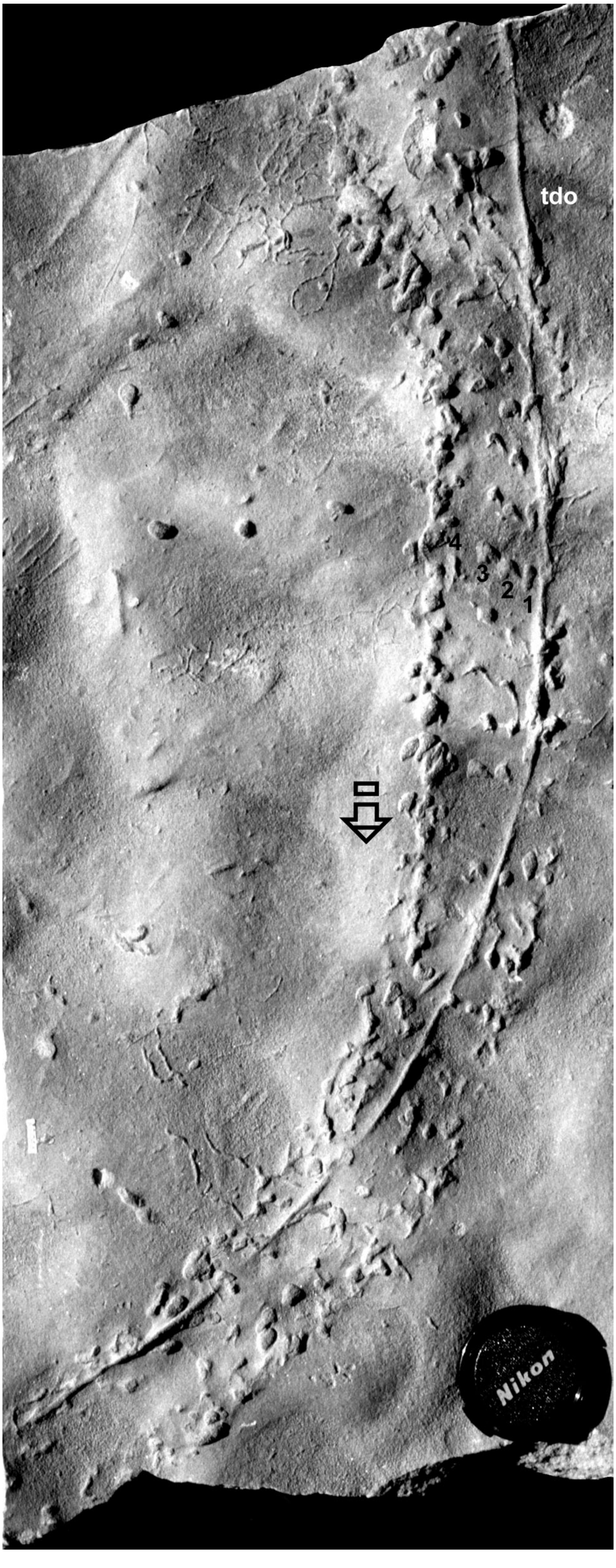


Figure 107: *Kouphichnium variabilis* (LINCK, 1949b), holotype, positive hyporeliefs, bottom view, SMNS 22008, upper Schilfsandstein, Stuttgart Fm, Middle Keuper, Freudenstein, Baden-Württemberg, southern Germany. 1-4 indicates tracks; arrow indicates direction of movement (top to bottom); tdo = telson drag ornament. Lens cap 52mm in diameter.

A preferred angle of the track series with the median axis has not been determined because the trackway has a curved nature and thus no straight median axis. However, the series describe an acute angle with a supposed median axis.

By contrast to *Kouphichnium gracilis*, the individual tracks are less detailed in *K. variabilis*. This may be due to sediment cohesiveness; soft sediments do not allow a detailed preservation. Another explanation is that the tracks are from a greater depth than those of *K. gracilis*, known as undertracks *sensu* GOLDRING & SEILACHER (1971). Associated trace fossils on the same slab have a detailed preservation so that an interpretation as undertracks is more likely than poor preservation due to low sediment cohesiveness.

Ichnogenus *Tasmanadia* CHAPMAN, 1929

Type ichnospecies: *Tasmanadia twelvetreesi* CHAPMAN, 1929: 5; by monotypy.

* 1929 *Tasmanadia* CHAPMAN: 5.
v 1937 *Incisifex*. – DAHMER: 525.
v 1949b *Ichnyspica*. – LINCK: 32.
non 1981 *Ichnyspica*: LINCK 1949 [sic]. – CHIPLONKAR et al.: 147.
non 2002 *Ichnyspica* LINCK, 1949. – FERNANDES et al.: 77.

Diagnosis: Double series of very sharp transverse imprints, commonly single but some joined internally or rarely externally to form bifid impressions (HÄNTZSCHEL 1975: W114).

Tasmanadia twelvetreesi CHAPMAN, 1929

Fig. 108

* 1929 *Tasmanadia twelvetreesi* CHAPMAN: 5.
v 1937 *Incisifex rhenanus* n.g. n.sp. – DAHMER: 525, pl. 32 fig. 2, pl. 35. fig. 1.
v 1938 *Incisifex rhenanus.* – DAHMER: 66, fig. 1-2.
v 1949b *Ichnyspica pectinata* n. sp. – LINCK: 37.
v 1949b *Ichnyspica pectinata* n. g. n. sp. – LINCK: pl. 2, fig. 1-2.
1957 *Tasmanadia twelvetreesi.* – GLAESSNER: 104, pl.11 fig. 4.
v 1962 *I. pectinata.* – HÄNTZSCHEL: *W*201, fig. 123.4.
v 1962 *I. rhenanus.* – HÄNTZSCHEL: *W*201, fig. 125.6
v 1965 *I. pectinata* LINCK 1949. – HÄNTZSCHEL: 48
v 1965 *I. rhenanus* DAHMER 1937. – HÄNTZSCHEL: 49.
v 1975 *I. pectinata.* – HÄNTZSCHEL: *W*74, fig. 44.3.
v 1975 *I. rhenanus.* – HÄNTZSCHEL: *W*74, fig. 46.2.
non 1981 *Ichnyspica guptai* ichno sp. nov. [sic]. – CHIPLONKAR et al.: 147, fig. 1B; [= *Protovirgularia dichotoma*].
1994 *Tasmanadia twelvetreesi* CHAPMAN, 1929. – RINDSBERG: 59, pl. 18 fig. A-C.
v 2001 ?*Diplichnites* isp. – SCHLIRF et al.: 95, tab. 1.
v 2001 ?inorganic structure. – SCHLIRF et al.: 95, tab. 1.
v 2002 *Incisifex rhenanus* DAHMER, 1937. – SCHLIRF et al.: 58, pl. 5 fig.2.

Diagnosis: As for ichnogenus (because of monotypy).

Material: SMNS 22015 (holotype of *Ichnyspica pectinata* = *Tasmanadia twelvetreesi*), Upper Schilfsandstein, Stuttgart Fm, Middle Keuper, Stetten a. H.; SMNS 20958 (paratype of *Ichnyspica pectinata* = *Tasmanadia twelvetreesi*), Upper Schilfsandstein, Stuttgart Fm, Middle Keuper, Sternenfels; both Baden-Württemberg, southern Germany. NMW-Collection Rose, unnumbered (holotype of *Incisifex rhenanus* = *Tasmanadia twelvetreesi*), Taunus quartzite, Lower Devonian, am 'Rossel', west of Rüdesheim, Hesse, Germany.

Description: Double series of perpendicular, opposed, more-or-less equidistant, hypichnial elongate ridges; each ridge laterally tapering; distance between individual ridges 1-3mm; length of individual ridges 7-10mm; width of entire trace 20-2mm; length of entire trace max. 23cm (holotype, SMNS 22015). Specimen on slab SMNS 20958 similar to holotype but with only one series preserved. The specimen from the Taunus quartzite is a short double series of simple, short, closely spaced, equidistant, parallel, hypichnial ridges (specimens from NMW).

Discussion: The double series of perpendicular, opponing, equidistant hypichnial ridges are best assigned to *Tasmanadia twelvetreesi* CHAPMAN, 1929. There are no significant differences between *T. twelvetreesi* and *Ichnyspica pectinata* LINCK, 1949b which is thus considered a subjective junior synonym of the first. The sole morphological difference that could be observed is the lateral tapering of the individual ridges (not yet reported from *Tasmanadia* specimens). However, the preservation of such features is more influenced by sediment cohesiveness and grain size than by the behaviour of the progenitor. For this reason the tapering of the individual ridges is not considered an ichnotaxobase.

The type material of *Incisifex rhenanus* DAHMER, 1937 (Fig. 108C) consists of a simple double series of hypichnial ridges, and is thus also considered a subjective junior synonym of *Tasmanadia twelvetreesi* CHAPMAN, 1929.

SCHLIRF et al. (2003) discussed a possible assignment of *Incisifex rhenanus* to *Diplichnites* DAWSON, 1873. RINDSBERG (1994) showed that the type material of *Diplichnites* is a very large and wide trackway and most of the subsequent assignments are better kept in *Tasmanadia*. FILLION & PICKERILL (1990) stated that the ichnotaxonomy of *Diplichnites*, especially the various ichnospecies of *Diplichnites*, are in need of revision. BUATOIS et al. (1998) while reviewing the invertebrate trace fossils previously reported by BANDEL (1967a,b) from the Upper Pennsylvanian did not follow RINDSBERG (1994) and assigned their double series of perpendicular hypichnial ridges to *Diplichnites* – a decision not supported here.

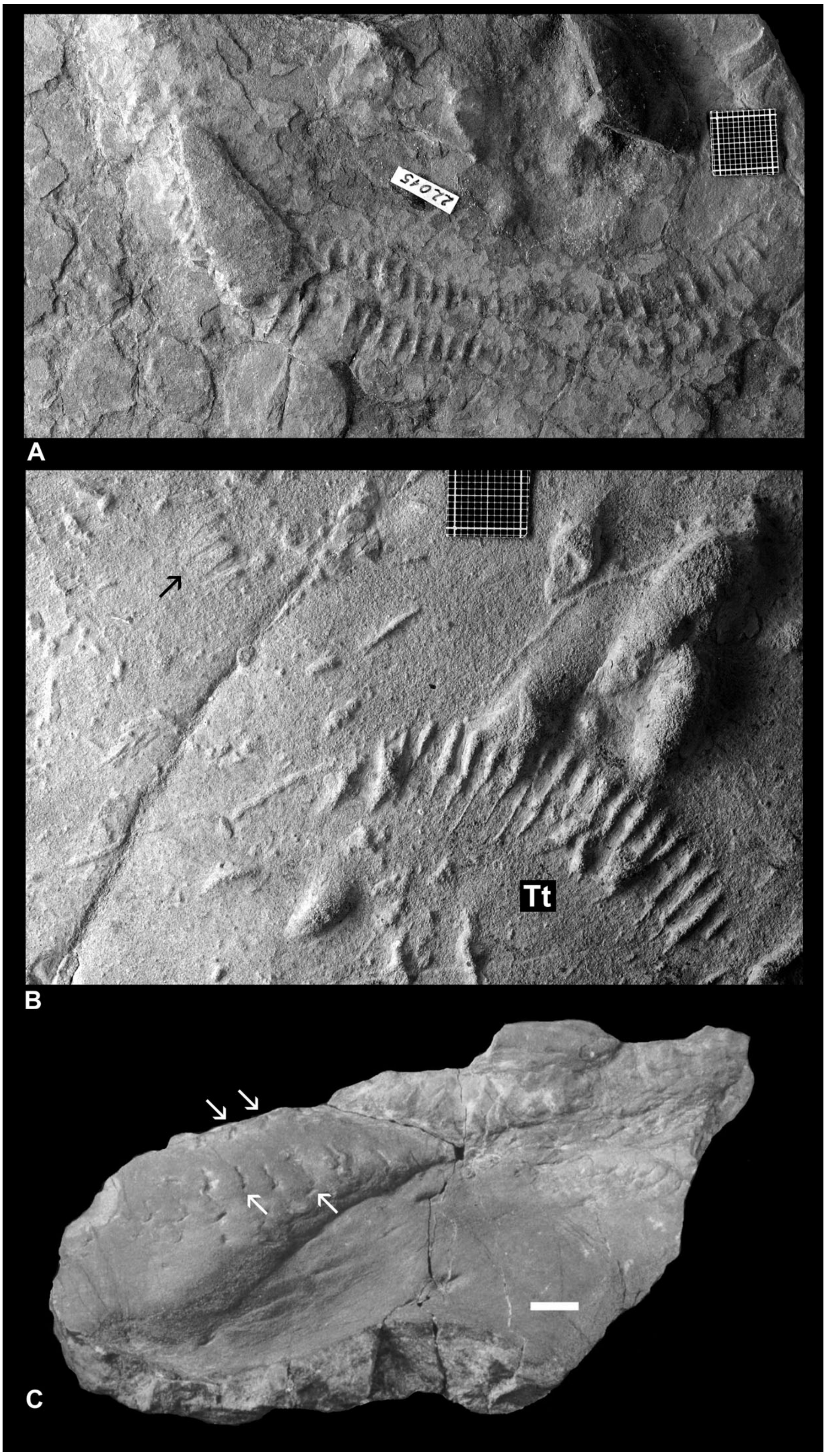


Figure 108: *Tasmanadia twelvetreesi* CHAPMAN, 1929. **A**. Complete double row of perpendicularly arranged elongate tracks; SMNS 22015, Upper Schilfsandstein, Stuttgart Fm, Middle Keuper, Stetten a. H. **B**. Incomplete specimen, with only one side of the row preserved (Tt); arrow indicates faint tracks, most likely produced by the same progenitor as *T. twelvetreesi*; SMNS 20958, Upper Schilfsandstein, Stuttgart Fm, Middle Keuper,

Sternenfels. Both positive hyporeliefs; bottom view; Baden-Württemberg, southern Germany. Millimetre grids for scale. **C**. Arrows indicate double row of perpendicular tracks. Taunus quartzite, Lower Devonian, am ‘Rossel’, west of Rüdesheim, Hesse, Germany. Scale bar: 1cm.

Tasmanadia is generally interpreted as an arthropod trackway (GLAESSNER 1957). Depending on the age and particular morphological details trilobites are plausible candidates (e.g., = *Diplichnites* of OSGOOD 1970; = *Diplichnites* of FILLION & PICKERILL 1990; RINDSBERG 1994). This might be true for the Devonian material from the Taunus quartzite. The Triassic material is also best explained as trackways of arthropod origin. LINCK (1949b) considered annelids as likely progenitors because of the regularity of the imprints and the tapering of each individual imprint. However, none of these morphological features contradicts an arthropod origin, and an annelid as progenitor seems unlikely. The locomotion of most annelids is by peristaltic movement of the body and the nature of the imprints is better explained as made by arthropod appendages (walkin-legs) rather than parapodia of polychaetes.

Coprolites

Ichnogenus *Helicerina* BRÖNNIMANN & MASSE, 1968

Type ichnospecies: *Helicerina spinosa* BRÖNNIMANN & MASSE, 1968: 154, fig. 3A; pl. 1 fig. 2, 4, 7; pl. 2 fig. 2; by original designation.

Diagnosis: Cylindrical coprolite characterized by triangular or diamond-shaped canals within the symmetry plane of cross sections. Laterally, rounded canals can develop from spine-like extensions of the central canals on each side of the symmetry plane (after SCHWEIGERT et al. 1997).

cf. *Helicerina* isp.

Fig. 109

Material: Numerous specimens on three slabs, SMNS11136a-c, Lettenkeuper, Erfurt Fm, Lower Keuper, near Seebronn, Baden-Württemberg, southern Germany.

Description: Clusters of cylindrical microcoprolites, 0.2-0.3mm in diameter and 0.6-1.2mm in length. Parallel to the long axis indistinct canals exist.

Discussion: The microcoprolites are assigned to *Helicerina* with reservations only because no cross-section has been observed. The occurrence in clusters, the general shape, the internal canals and the size range are similar to those of *Helicerina*.which is assigned to crustacean coprolites (Schweigert et al. 1997). SEEGIS in SCHWEIGERT et al. (1997) described *Helicerina keuperina* SEEGIS, 1997 from the Lehrberg beds of southern Germany. To date, these are the oldest finds of *Helicerina*. If the herein presented material can be assigned to this ichnogenus without doubts, they were the oldest coprolites of this ichnogenus reported from the Germanic Triassic. Another crustacean coprolite occurring in the Late Triassic is *Bactryllium* HEER, 1853. However, its size is usually larger, several millimetres to more than a centimetre, and it shows delicate transverse striations on the exterior. Although size generally is not a suitable ichnotaxobase, it can be used as a hint in the case of coprolites because their final morphology is strongly related to the producers. This is due to the anatomy of the anus of the producer, which forms the shape and internal canals of the coprolites. Accordingly, there is a relation between the classification of coprolites and the size of their producers.

Helicerina is interpreted as microcoprolites of decapod crustaceans which lived in a limnic to brackish environment (SCHWEIGERT et al. 1997). The sediments bearing the microcoprolites, grey to yellowish silty claystones of the so-called 'Lettenkeuper', are generally interpreted as marine to brackish (GEYER & GWINNER 1986).

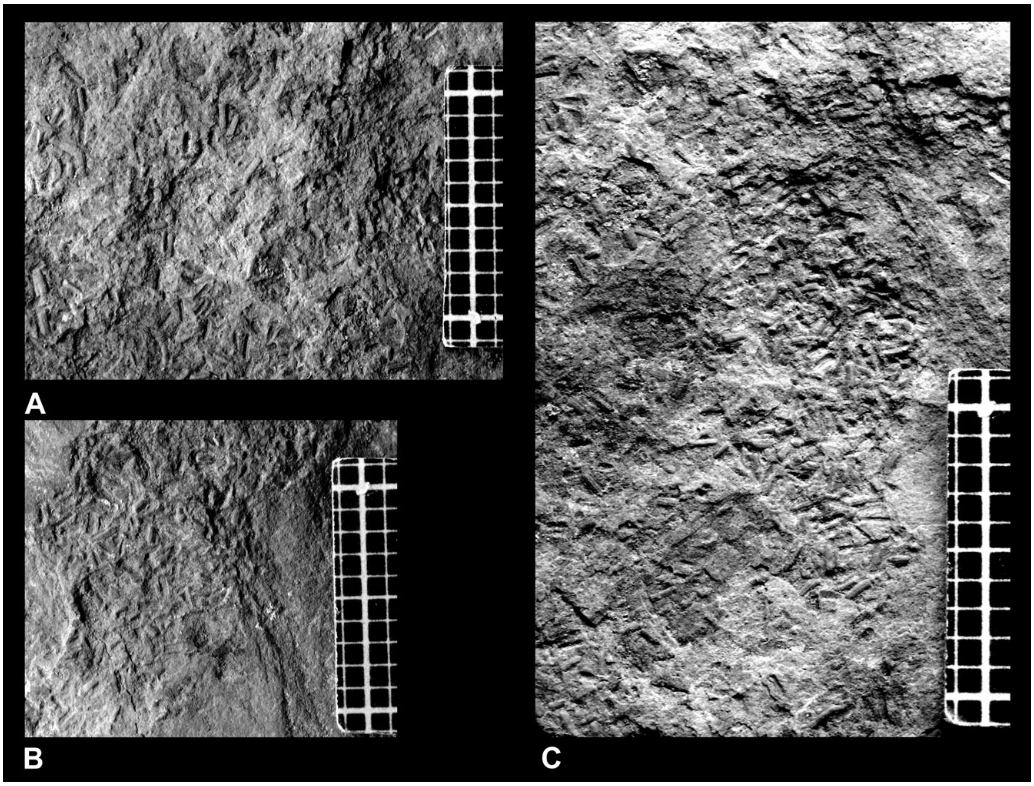


Figure 109: **A-C**. Clusters of cf. *Helicerina* isp. Fullreliefs and casts, top view; Erfurt Fm, Lower Keuper, near Seebronn, Baden-Württemberg, southern Germany. **A**. SMNS 11136a. **B**. SMNS 11136b. **C**. SMNS 11136c. Millimetre grid for scale.

Unidentified biogenic structures

Probable *Triops* resting trace

Fig. 110

Material: One specimen, PIW2002-I-12; Werksandstein, Würzburg Fm, Lower Keuper, between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

Description: Very small, positive hyporeliefs building a more-or-less bisymmetrical structure. The structure consists of two 2mm long, longitudinal posterior ornaments (LPO), which slightly diverge towards the posterior, one 1.5mm long, V-shaped posterior ornament (VPO), one elliptical, 4mm long, up to 1.5mm wide, segmented median ornament (SMO). Maximum width of entire structure: 4mm; length: 10mm. The structure is surrounded by hemispherical (0.3mm in diameter) positive hyporeliefs which are regarded not as belonging to the trace fossil.

Discussion: MÁNGANO et al. (1997) introduced *Tonganoxichnus*, a monuran insect resting and/or feeding trace. Their material clearly reflects the impression of a small, elongate multisegmented insect. The herein

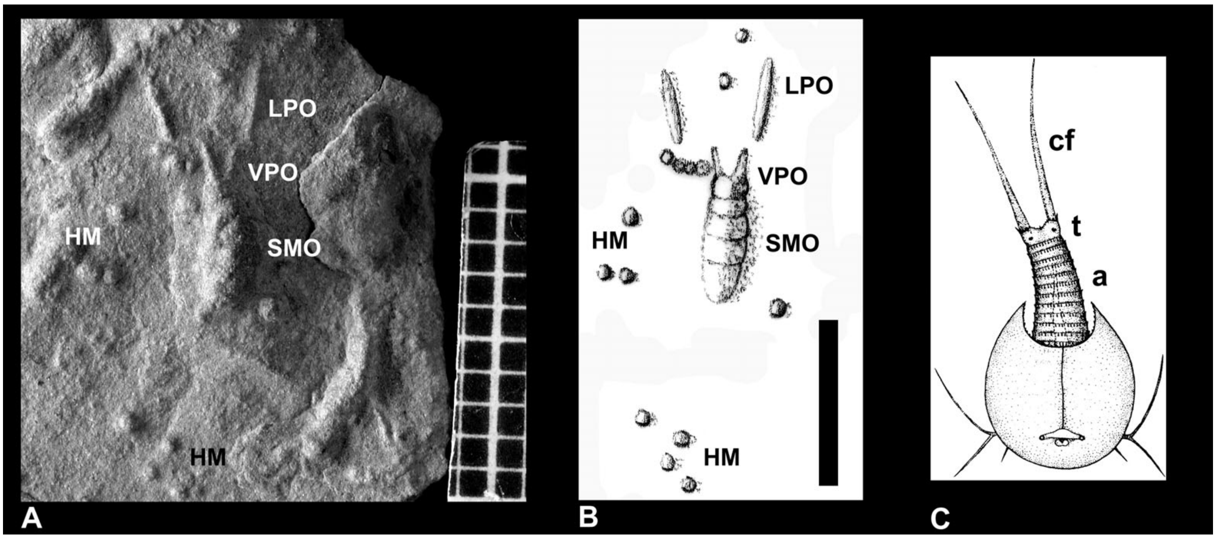


Figure 110: A-B. Probable *Triops* resting trace. **A**. Positive hyporelief, bottom view; PIW2002-I-12. Millimetre grid for scale. **B**. Sketch of trace fossil. Scale bar: 0.5cm. LPO = lateral posterior ornament, VPO = V-shaped posterior ornament, SMO = segmented median ornament, HM = hemispherical marks of unknown origin. **C**. Sketch of *Triops cancriformis;* cf = caudal furca, t = telson, a = abdomen (pleon). Not to scale. Modified after TRUSHEIM 1937.

presented material is of same size range and, in parts, reflects the morphology of *Tonganoxichnus*. However, upon close examination, the Triassic material is better explained as resting trace of a *Triops*. The longitudinal posterior ornaments (LPO) are interpreted as imprints of the caudal furca and the V-shaped posterior ornaments (VPO) are interpreted as imprints of the telson plus the anteriormost part of the caudal furca. The elongate, segmented median ornament (SMO) is interpreted as abdomen (pleon) imprint. The hemispherical marks are of unknown origin (HM). Why only the abdomen, the telson, and the caudal furca are preserved as imprints is difficult to answer. However, incomplete preservation of the body of the producer is common in resting traces.

Triops, a notostracan phylopod is well known from the Coburger Sandstein, Hassberge Fm, Middle Keuper (TRUSHEIM 1937). Currently one subspecies, *Triops cancriformis minor* is described from the Germanic Triassic. These crustaceans lived in ephemeral lakes or ponds (GEYER 2002).

The sediments bearing the resting trace, fine-grained sandstones to siltstones with claystone intercalations are interpreted as fluvial deposits of the so-called Werksandstein (Würzburg Fm). The deposits represent fluvial overbank deposits.

Small irregular networks

Fig. 111A-B

Material: Several specimens on slab, PIW1998-VIII-73, -74, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Irregularly bifurcating, semi-tubular burrows preserved as negative epirelief, with a distinct positive marginal rim on both sides of the semi-tube. Diameter of semi-tube including rim: 1.5-2mm; entire burrow length 3.5-5cm.

Discussion: These small burrows may be interpreted as produced by small insects or insect larvae.

Row of small knobs

Fig. 111C-D

Material: PIW1998VIII-16, one field photograph, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Slightly arcuate, single row of hemispherical knobs, about 25mm long; number of knobs eleven, almost touching each other; diameter of knobs 1.5-2.0mm.

Discussion: The overall morphology resembles the pearl chain trace fossil *Hormosiroidea* SCHAFFER, 1928. However, the burrow size is very small and connecting strings between the individual knobs, a characteristic feature of *Hormosiroidea*, were not observed.

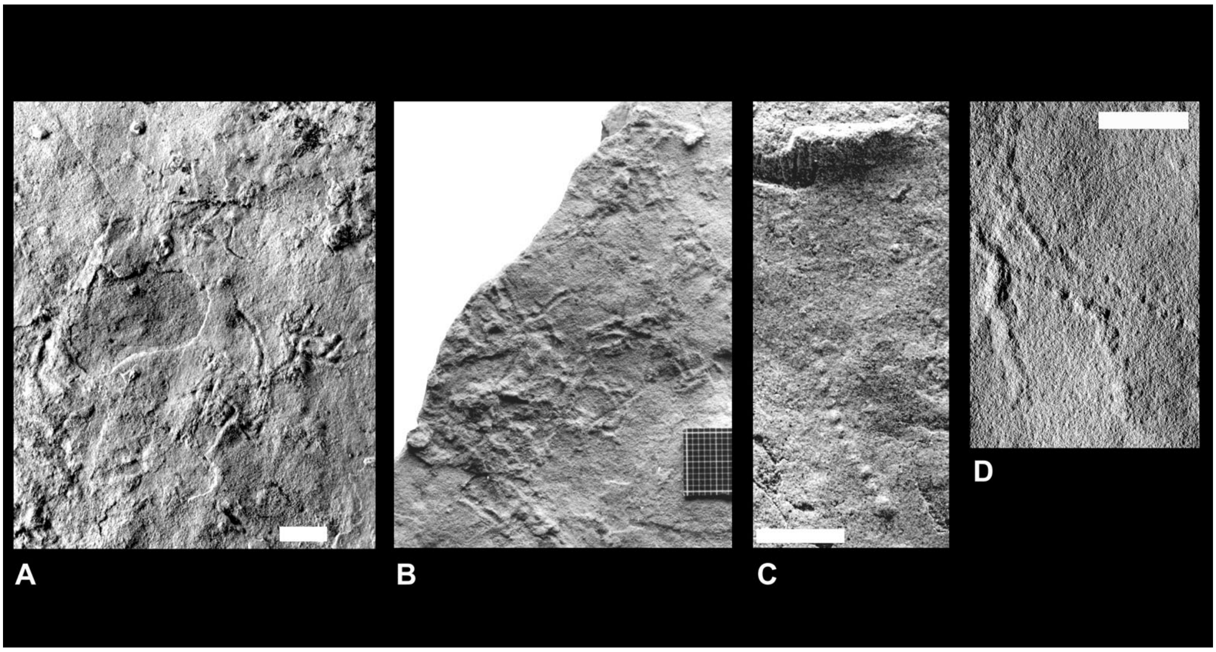


Figure 111: A-B. Small irregular network. **A**. Negative epirelief, top view; PIW1998-VIII-73. **B**. Negative epirelief, top view; PIW1998-VIII-73. Millimetre grid for scale. **C-D**. Row of small knobs. **C**. Positive epirelief, top view; PIW1998-VIII-16. **D**. Positive and negative epireliefs, top view; field photograph. **A-D**. Coburger Sandstein Hassberge Fm, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany. Scale bars: 1cm.

Large parallel hypichnial ridges

Fig. 112

Material: One field observation, several specimens on slab PIW1998-VIII-56, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Hypichnial, subparallel ridges, triangular to subtrapezoidal in cross-section; 10-20mm wide, up to 10mm high, and about 100mm long. Ridges bend acutely into the bedding-plane at one side, and end abruptly at the other side.

Discussion: The ridges are interpreted as casts of drag marks produced by legs of swimming tetrapods, possibly reptiles. Structures of similar morphology, interpreted as traces of swimming dinosaurs *sensu lato* have been reported, for example, from the Triassic of Wyoming (BOYD & LOOPE 1984), the Middle Triassic of New Mexico (HUNT & LUCAS 1993: fig. 23C-D), and from Jurassic rocks of England (ROMANO & WHYTE 1996: fig. 4).

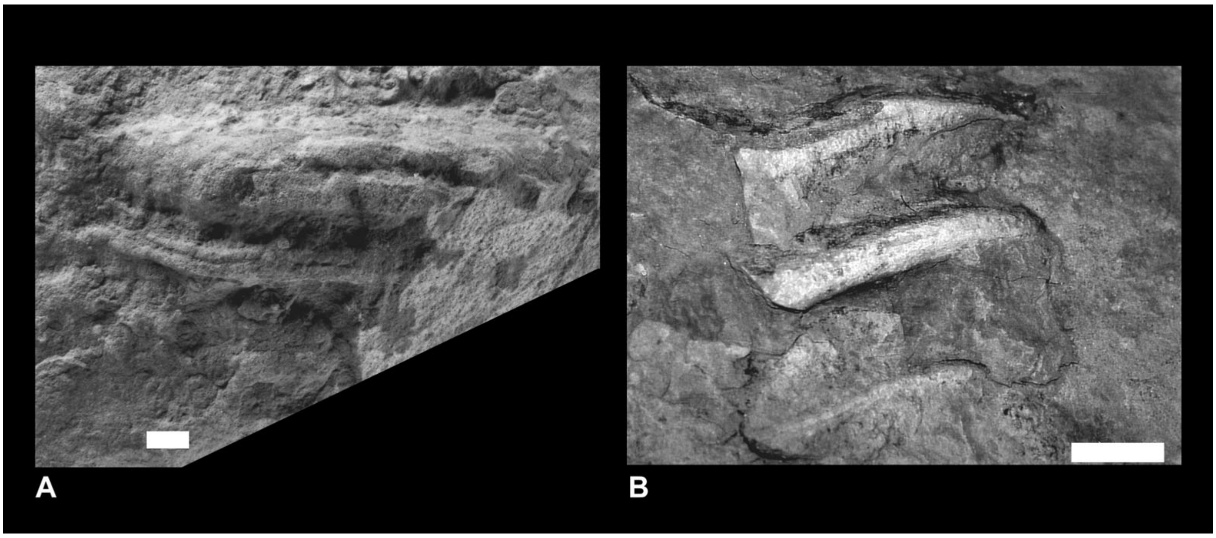


Figure 112: A-B. Large parallel hypichnial ridges. **A**. Positive hyporelief, basal view; PIW1998-VIII-56. **B**. Positive hyporelief, basal view; field photograph. All Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany. Scale bars: 1cm.

Small hypichnial ridges

Fig. 113

Material: Several specimens on slab PIW2002-I-18, Werksandstein, Würzburg Fm, Lower Keuper, outcrops between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

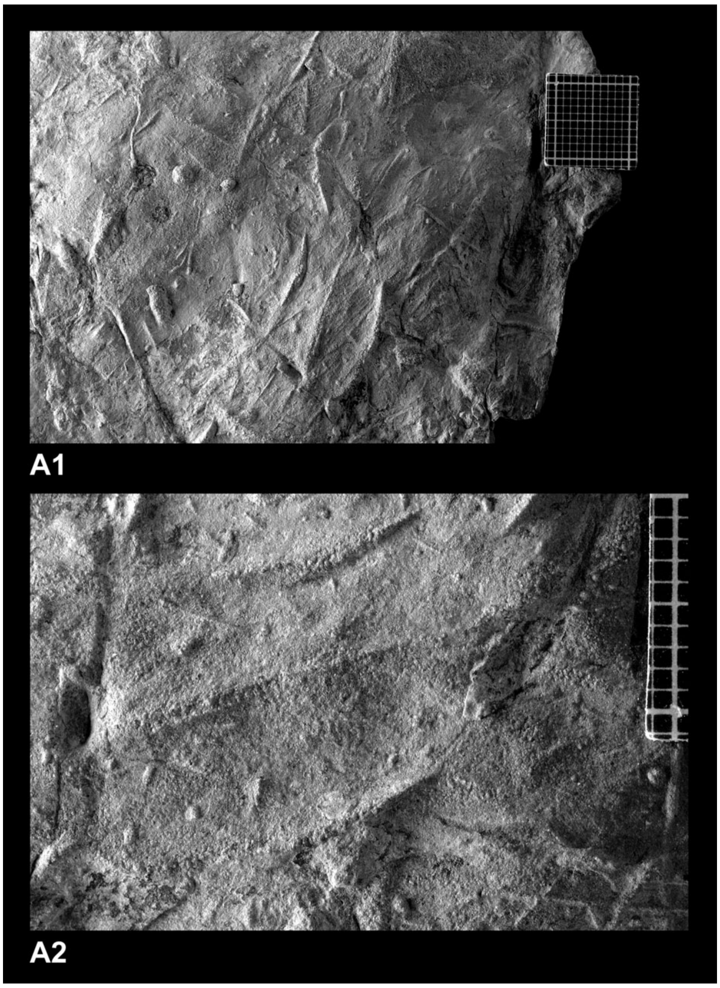


Figure 113: Small hypichnial ridges. PIW2002-I-18; Werksandstein, Würzburg Fm, between Seubrigshausen and Thundorf i. Ufr. The ridges are interpreted as casts of marks produced by the fin of a swimming fish. **A2** is an enlargement of **A1** and shows an arrangement of three parallel ridges. Millimetre grids for scale.

Description: Straight to slightly curved, hypichnial ridges; triangular in cross-section; 0.5-1mm wide, up to 1mm high and 6-25mm long.

Discussion: The ridges are interpreted as casts of marks produced by either the pelvic or pectoral fins of a swimming fish. These and the trace of the tail fin usually are observed in *Undichna*, the most common trace fossil of swimming fish, revised by TREWIN (2000). Recently SIMON et al. (2003) reported swimming traces of a coelacanth fish from the Late Triassic of the Germanic Basin. Their structures are much more complex and do show a distinct sinusoidal pattern. Although no pattern is present, the scratches on the sole of sandstones may be interpreted as being produced by fish fins. Similar structures, associated with *Undichna*, have been reported by TREWIN (2000). He referred to these structures as brush-like imprints.

Bilobed burrow indet.

Fig. 114

Material: One specimen on slab PIW2002-I-13; Werksandstein, Würzburg Fm, Lower Keuper, outcrops between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

Description: Short, fragment of a bilobed, fullrelief structure, with an angular, laying eight-shaped cross-section; width 5mm, height 1-2mm.

Discussion: Similar structures have commonly been assigned to *Aulichnites*. However, the revision of *Psammichnites* by MÁNGANO et al. (2003) suggests that *Aulichnites* is a younger subjective synonym of *Psammichnites*. The authors showed that *Aulichnites* is a preservational variant of *Psammichnites*, and not, as frequently assumed, a bilobed trace fossil. As a consequence, *Aulichnites* is not applicable for bilobed structures. Currently no name is available for such structures, and the herein presented material is considered insufficient to introduce a new ichnogenus. HAGADORN & SCHLIRF (in prep.) will provide a revision and the introduction of a new name for bilobed trace fossils.

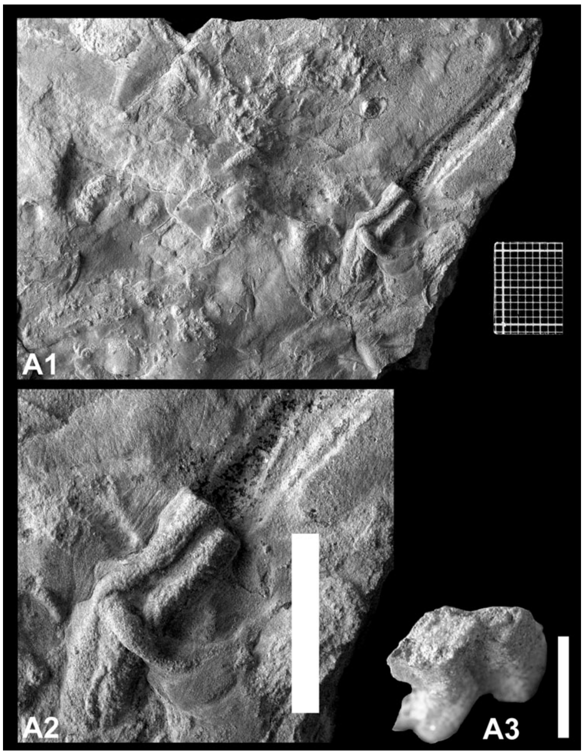


Figure 114: Bilobed burrow indet. PIW2002-I-13; Werksandstein, Würzburg Fm, outcrops between Seubrigshausen and Thundorf i. Ufr. Millimetre grid for scale. **A2**. Detail of **A1**. Both top view. Scale bar: 1cm. **A3**. Cross-section of bilobed burrow. Note laying eight-shaped cross-section; picture taken with a slight angle. Scale bar: 3mm.

Flat-conical hypichnial structures

Fig. 115

Material: Several specimens on three slabs PIW2002-I-11 and 20; Werksandstein, Würzburg Fm, Lower Keuper, outcrops between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany.

Description: Flat-conical positive, hypichnial structures (width 0.5-1mm, length 0.5-2mm) made up of thin, irregular tubular structures.

Discussion: The small tubular structures are interpreted as faecal castings. The entire structure is likely to be a deposit-feeding structures. Probably a small vermiform animal has exploited a small area of sediment rich in nutrients. Similar structures are present on several slabs (Fig. 115).

Enigmatic structures

Ichnogenus *Sagittichnus* SEILACHER, 1953b

Type ichnospecies: *Sagittichnus lincki* SEILACHER, 1953b: 115, pl. 13 fig. 1, by monotypy.

Diagnosis: Small arrowhead-shaped hypichnial structures with a median keel (after HÄNTZSCHEL 1972: *W*102).

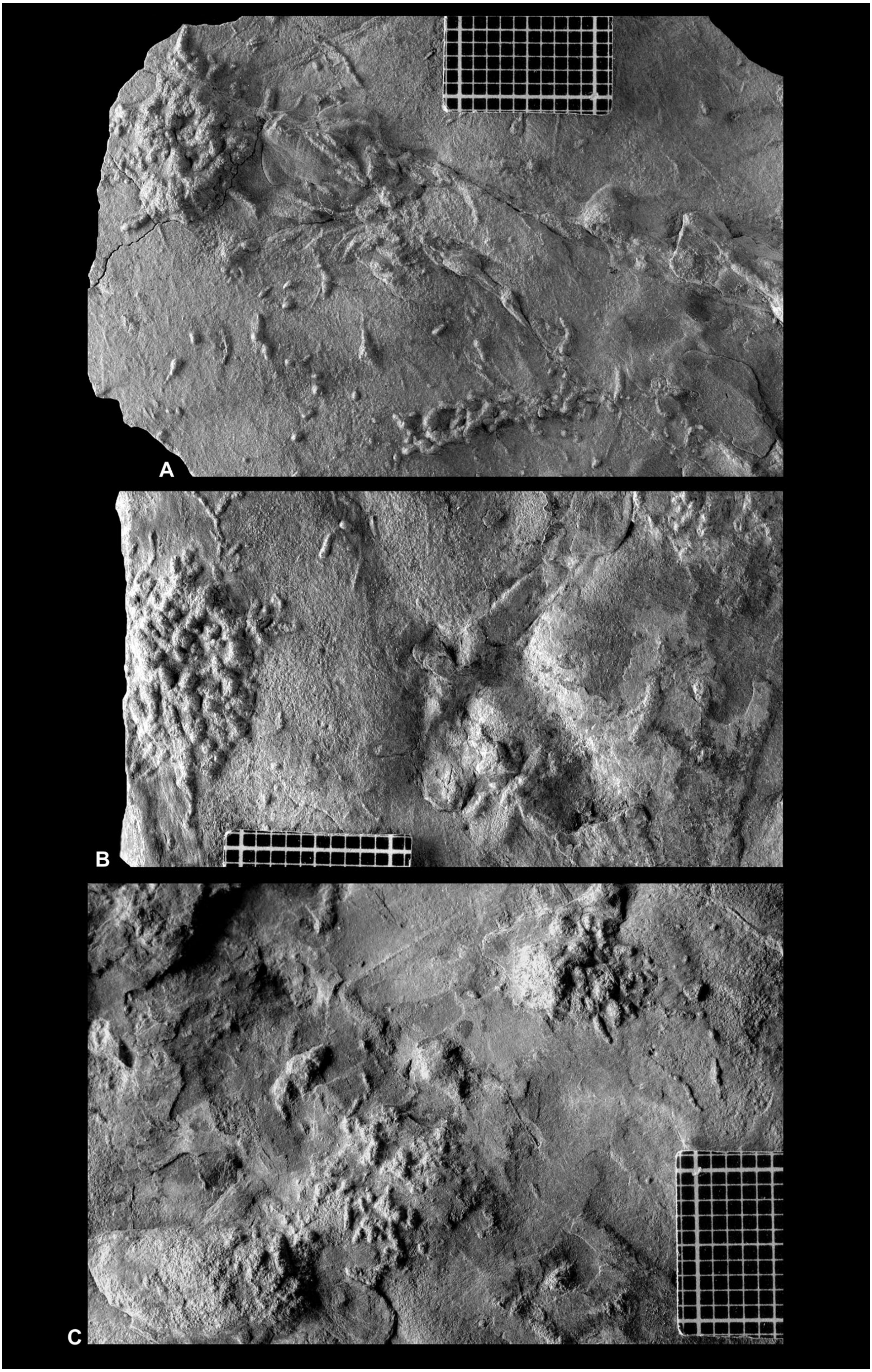
Sagittichnus lincki SEILACHER, 1953b

Fig. 9C-D

Diagnosis: As for ichnogenus (because of monotypy).

Material: Paratypes SMNS 22013 from the Schilfsandstein, Stuttgart Fm, Middle Keuper, Sternenfels, Baden-Württemberg, southwestern Germany.

Discussion: SEILACHER (1953b) introduced *Sagittichnus lincki* from the Keuper (Schilfsandstein) at Sternenfels, southern Germany, where the structures are more-or-less oriented with the individual acute angles pointing in one direction. Earlier, LINCK (1949: 72) described them from the same formation as “pfeilspitzenförmige Ausgüsse” (‘arrowhead-shaped casts’), and interpreted them as swimming traces, a suggestion not followed here. SEILACHER (1953b) interpreted *S. lincki* as resting traces of epipsammonts of unknown origin. He stated that the large number of structures on the sole of


A
B
C

Previous page:

Figure 115: A-C. Flat-conical, hypichnial structures consisting of small tubular structures, interpreted as faecal castings. All Werksandstein, Würzburg Fm, Lower Keuper, outcrops between Seubrigshausen and Thundorf i. Ufr., Lower Franconia, Bavaria, southern Germany. Bottom view. Millimetre grids for scale.

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thin sandstone slabs were all of same size and form, and thus are not purely accidental. A close look at the slab with the paratypes (Fig. 117C-D) shows, however, that the structures are not equal sized and show different forms. The slab chosen as holotype (SEILACHER 1953b: pl. 13 fig. 1) has very few specimens of *S. lincki*, all oriented in the same direction but also of various size and form. It cannot be excluded that *S. lincki* is a trace fossil. Maybe the structures are washed out resting traces. Accepting this, the original structures were most likely similar to *Rusophycus*, and received their final arrowhead-shape due to currents. This explanation is favoured by the orientation of the structures in one direction. According to the point of view of the author, the structures cannot be unambiguously related to behaviour, and thus are of doubtful origin and therefore placed under "enigmatic structures". Additional triangular structures, similar to *S. lincki* (Fig. 117E-F), were found in the Werksandstein near Effeldorf (see "Small triangular structures" below).

Clusters of small pits

Fig. 116

Material: PIW1998VIII-73, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Epichnial clusters of small, oval or subpolygonal pits, 1.5-2.5mm in diameter. Pits separated by narrow ridges, about 0.5mm wide. Some clusters small and discrete. Clusters 20-25mm across contain 25-35 pits.

Discussion: The formation of the studied material is not clear. Similar pits were described as imprints of tests of *Euestheria minuta* from Upper Triassic deposits of East Greenland (BROMLEY & ASGAARD 1979). However, this origin cannot be proved for the forms described here, since no morphological details, such as concentric ribs, were observed. Similar, but distinctly larger structures were described as pits made by tail-wagging of tadpoles ("Schwänzel-Gruben von Kaulquappen") by LINCK (1954). Despite the fact that LINCK's material is larger, the general morphology is very similar to the Franconian material. Furthermore, there are morphological similarities to egg-masses figured in GRAUVOGEL-STAMM & KELBER (1996). However, their material is always adhering to leaf sheeths, whereas the material presented herein is isolated. Since the Franconian material lacks further details a precise classification is impossible.

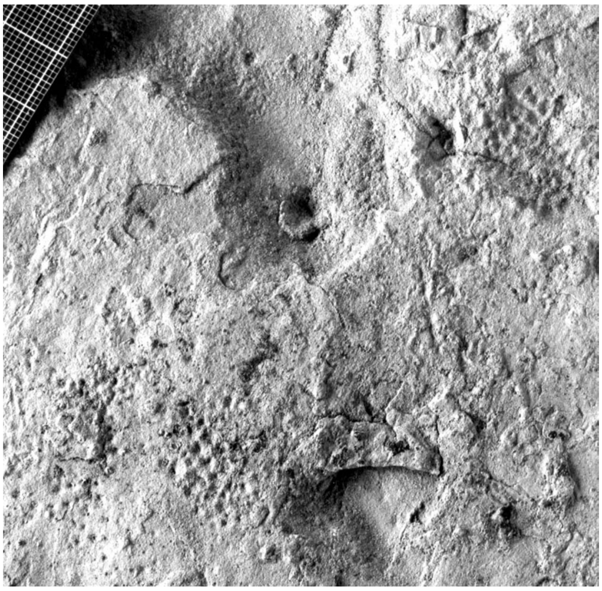

Figure 116: Clusters of small pits. Negative epirelief, top view; PIW1998-VIII-73; Coburger sandstone, Hassberge Fm, Vetter quarry at Schönbachsmühle. Millimetre grid for scale.

Concentric rings

Fig. 117A-B

Material: Four specimens on slab PIW1998VIII-2, Coburger Sandstein, Hassberge Fm, Middle Keuper, Eltmann quarry, Lower Franconia, Bavaria, southern Germany.

Description: Endichnial, hemispherical structure composed of an inner cylindrical to subcylindrical area in a centric or eccentric position, surrounded by 4-5 concentric rings; distance between rings varying from 1 to 2.5mm; entire structure 12-25mm across, depth about 10mm, central area 0.8-12mm, with an irregular, uneven, flat mound.

Discussion: Structures of this type were described from the Triassic of northern Spain as *Cyclozoon philippi* by WURM (1911), which was later included in *Laevicyclus* QUENSTEDT (HÄNTZSCHEL 1965). SCHMIDT (1934) and PIA (1935) regarded *Cyclozoon philippi* and related forms as inorganic structures produced by gas expulsion. This view was confirmed by BOYD (1975). However, at least some *Laevicyclus* such as *L. mongraensis* VERMA, are true trace fossils (UCHMAN 1995). Nevertheless, the studied material is most likely of inorganic origin and may represent concretions. Cone-in-cone structures are similar to this material and as a consequence earthquake waves might be responsible for their formation. The concentric rings were found at the same stratigraphical level as the below described “enigmatic sedimentary structures”, which are also interpreted as being formed by earthquake waves.

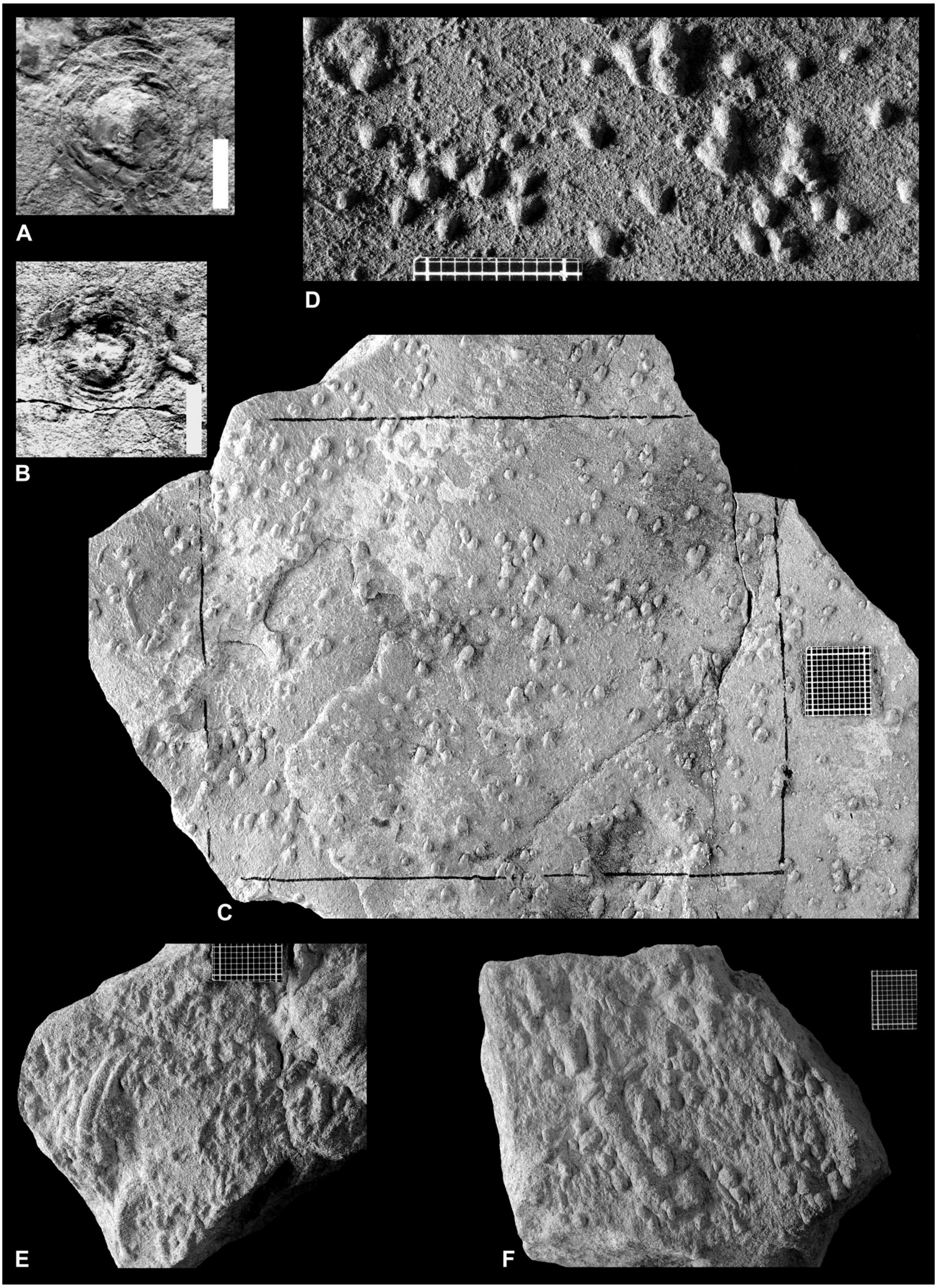

Figure 117: A-B. Concentric rings; PIW1998-VIII-2; positive epireliefs, Eltmann quarry. Scale bar: 1cm. **C-D**. *Sagittichnus lincki* SEILACHER 1953b, paratypes, SMNS 22013. **C**. Sole of a slab with numerous specimens. Clearly visible is the equal orientation but the structures are of varying size and form. **D**. Detail of **C** that shows the differences in shape and size. **E-F**. Structures similar to *Sagittichnus lincki*; Werksandstein, Würzburg Fm, near Effeldorf, Lower Franconia, Bavaria, southern Germany. **E**. PIW2002-I-21. **F**. PIW2002-I-22. Millimetre grids for scale.

Small triangular structures

Fig. 94, 117E-F

Material: PIW1998VIII-12B, C, F, 73, Coburger Sandstein, Hassberge Fm, Middle Keuper, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany. PIW2002-I-21 & 22, Werksandstein, Würzburg Fm, Lower Keuper, near Effeldorf, Lower Franconia, Bavaria, southern Germany.

Description: Variably oriented, hypichnial, minute, almond- or arrowhead-shaped mounds, rarely bilobate; 4-8mm, exceptionally 14mm long, 2-4mm wide. Arrowhead-like forms occasionally display a short tail. Angle of arrowhead varies, but mostly acute.

Discussion: The described structures resemble *Sagittichnus lincki* (see above). In the studied material, the structures post-date *Cruziana pascens*. It seems improbable that prod marks could be formed without destruction of *C. pascens*. On the other hand, the structures may be diagenetic features, such as halite crystal casts.

Wrinkle marks

Fig. 118

Material: Two slabs PIW2002-I-23 & 24 from the Whitehill Fm, Permian, southern Namibia.

Description: Polygonal network of positive ridges on top of a bedding surface. Diameter of ridges: 3-4mm, mesh-size: 7-12mm.

Discussion: Some authors (e.g., ARCHER & MAPLES 1984; PICKERILL 1992) report *Paleodictyon* MENEGHINI, 1850 from nonmarine deposits. However, such finds are better explained as *Multina* (see there) if they are irregular, or may even be of abiogenic origin. The well-preserved wrinkle marks are presented to show how regular such structures can be, and how difficult it may be to distinguish such sedimentary structures from true trace fossils.

Paleodictyon is generally preserved as positive hyporelief and is characteristic of flysch deposits (UCHMAN 1995, 2003).

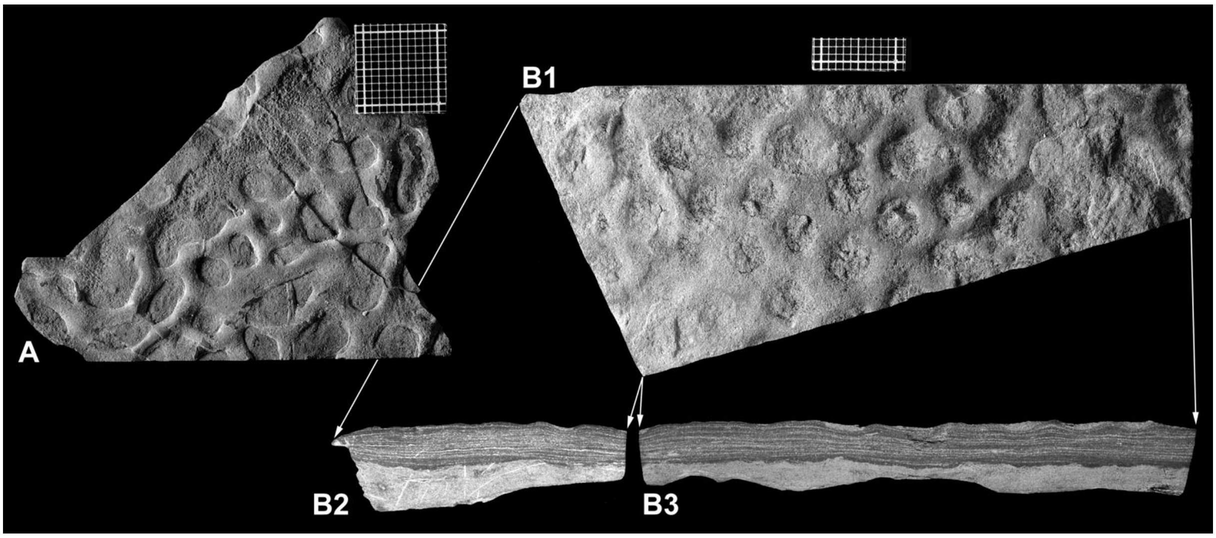

Figure 118: A-B. Well preserved wrinkle marks from the Whitehill Fm, Permian, southern Namibia; positive ridges on bedding surfaces. The polished cross sections (**B2** & **B3**) clearly show that the structures are minute ripples and no burrows. **A**. PIW2002-I-23. **B**. PIW2002-I-24. Millimetre grids for scale.

Enigmatic sedimentary structures

Fig. 119

Material: Numerous field observations, Coburger Sandstein, Hassberge Fm, Vetter quarry at Schönbachsmühle, Lower Franconia, Bavaria, southern Germany.

Description: Large, several decimetres across, 7-11cm high, lenticular structures made up of sigmoidal layers of claystone (dark) and fine-grained sandstone (light). The structures occur only in one bed in the upper part of the section at Schönbachsmühle. Unfortunately, the structures are so fragile that it was impossible to separate a specimen for collection purposes.

Discussion: The structures are very difficult to explain. No hints for a biogenic origin were found. The structures may have formed earthquake waves. The area was tectonically active during the Late Triassic (GEYER 2002), and thus sedimentary structures reflecting earthquake activities are not unlikely to be found. NEUWEILER et al. (1999) described sinusoidally deformed veins ("Sigmoidalklüftung") from the Muschelkalk and suggest various modes of formation but did not exclude earthquake activity.

Figure 119: Enigmatic sedimentary structure. Lenticular structures made up of sigmoidal layers of claystone (dark) and fine grained sandstone (light); field photograph, Coburger Sandstein, Hassberge Fm, Vetter quarry at Schönbachsmühle. Scale bar: 10cm.

Spongeliomorpha group including *Gyrolithes*

Introduction

Although only rarely found in Keuper deposits (e.g. FLEISCHER 2003) this particular group of trace fossils has attracted my special attention. As in this thesis apart from a revision of Keuper trace fossils also general methodologies of how to name and group trace fossils are presented, this widely known group of trace fossils may be taken as an example for ichnological methodology as applied by me.

The three ichnogenera *Spongeliomorpha* SAPORTA, *Ophiomorpha* LUNDGREN and *Thalassinoides* EHRENBERG (in the following abbreviated as SOT) have long been the issue of highly controversial debates among ichnologists (e.g., FÜRSICH 1973; BROMLEY & FREY 1974; BROMLEY 1990, 1996; UCHMAN 1995). It was only lately that SCHLIRF (2000) reanimated the dormant debate on how to handle these three ichnogenera. Following FÜRSICH (1973), SCHLIRF (2000) favoured a synonymisation of the three ichnogenera. Soon after publication a discussion on the ichnology listserver 'SKOLITHOS' (URL: http://www.listserv.rediris.es/archives/skolithos.html) arose. From the very first beginning of the debate it was clear that it was going to be difficult to convince a majority for either of the positions. Neither the arguments of the pro-synonymisation party nor the ones of the contra-synonymisation party could convince a majority of the listserver members. After re-thinking the whole problem again, it became clear that, as it often is the case, the truth may lay somewhere between the two positions. The following new attempt is not meant as a compromise in order to please everybody, but is understood as the logical consequence of a long lasting debate.

Generations of ichnotaxonomists were discussing whether a particular trace fossil belongs to the one or the other ichnogenus. In the case of SOT, morphological similarities among these three ichnogenera are obvious. Certainly there are also differences; however, the question is how important these differences are for their systematics. Unfortunately, the debate was much about names, and the actual subject, morphology, was thrust into the background. By no means all the various morphologies we know from recent crustacean burrows are *Spongeliomorpha* because of a herein proposed synonymisation of one particular morphologic variant.

A frequently used argument in favour of a separation of SOT at the ichnogeneric level is exactly the wall lining. Mostly ichnologists working with ichnofabric favour a separation. In ichnofabric analyses on core material the identification of trace fossils often is very difficult due to the limited exposure. Sometimes it seems that a statement on environment, sediment conditions, tier level and the resulting value as possible hydrocarbon reservoir is so important that the systematics of the occurring trace fossils are of only minor interest. However, this is no biologic argument and we are bound to biology, at least as long as we even use a biologic code to name trace fossils.

Historical overview

In this brief historical overview, the major landmarks in the classification of SOT structures are given, and are not understood as a complete synonymy. For additional references see HÄNTZSCHEL (1952), KENNEDY (1967), FÜRSICH (1973) and SCHLIRF (2000).

The first mentioning and figuring of SOT structures in literature was made by SCHULZE (1760; Fig. 120) in his 'Betrachtung über die fossilen Seesterne und ihrer Theile' (Observations on the fossil starfish and their parts). As the title of his work already implies, SCHULZE thought the structures he found belonged to echinoderms. However, SCHULZE recognized differences between body fossils and these so-called "Walzensteine" ('roller stones'). SCHULZE (1760) considered them not as body fossils but suggested they were better interpreted as cavities produced by vagile starfish, a very early interpretation of these structures as trace fossils. In 1833, STERNBERG introduced *Halymenites* in his work on the fossil flora of the ancient world. Unfortunately his drawings and his descriptions are very vague. MIKULÀŠ & UCHMAN (1996) have re-described material from the STERNBERG collection that was thought to be lost and found again in the Natural History Museum in Prague. They could not find any specimens that could be assigned to SOT structures. Interestingly the name *Halymenites* was commonly used for SOT structures occurring in Cretaceous deposits of the Western Interior Seaway in the USA (e.g., PATTERSON 1942). This is a good example of misunderstood 'well established' names resulting in pseudo-stability. If one argues like that, American authors should further use *Halymenites*. Some authors seem to follow this because a web page (http://www.cretaceousfossils.com) still uses *Halymenites* for U.S. Cretaceous SOT structures.

In 1842 the SOT story became very interesting since two authors published a new name for SOT structures: GÖPPERT (1842) introduced *Cylindrites spongioides* and GEINITZ (1842) introduced *Spongites saxonicus*. The material figured by GEINITZ is undoubtedly a tubular, Y-shaped branching burrow system with a knobby exterior (GEINITZ 1842: pl. fig.; Fig. 121C2). HÄNTZSCHEL (1952) was aware of the problem but while revising *Ophiomorpha* he simply stated that this (his paper) was not the place to discuss the nomenclature of these structures, a strange decision in a review paper with serious consequences. KENNEDY (1967) figured well-preserved SOT material from Cretaceous deposits in southern England and Wales. He also designated a neotype for '*Thalassinoides paradoxica*' (WOODWARD, 1830) and a lectotype for *Thalassinoides saxonicus* (GEINITZ, 1842). The diagnoses presented by KENNEDY (1967) could hardly be used to differentiate the described forms of

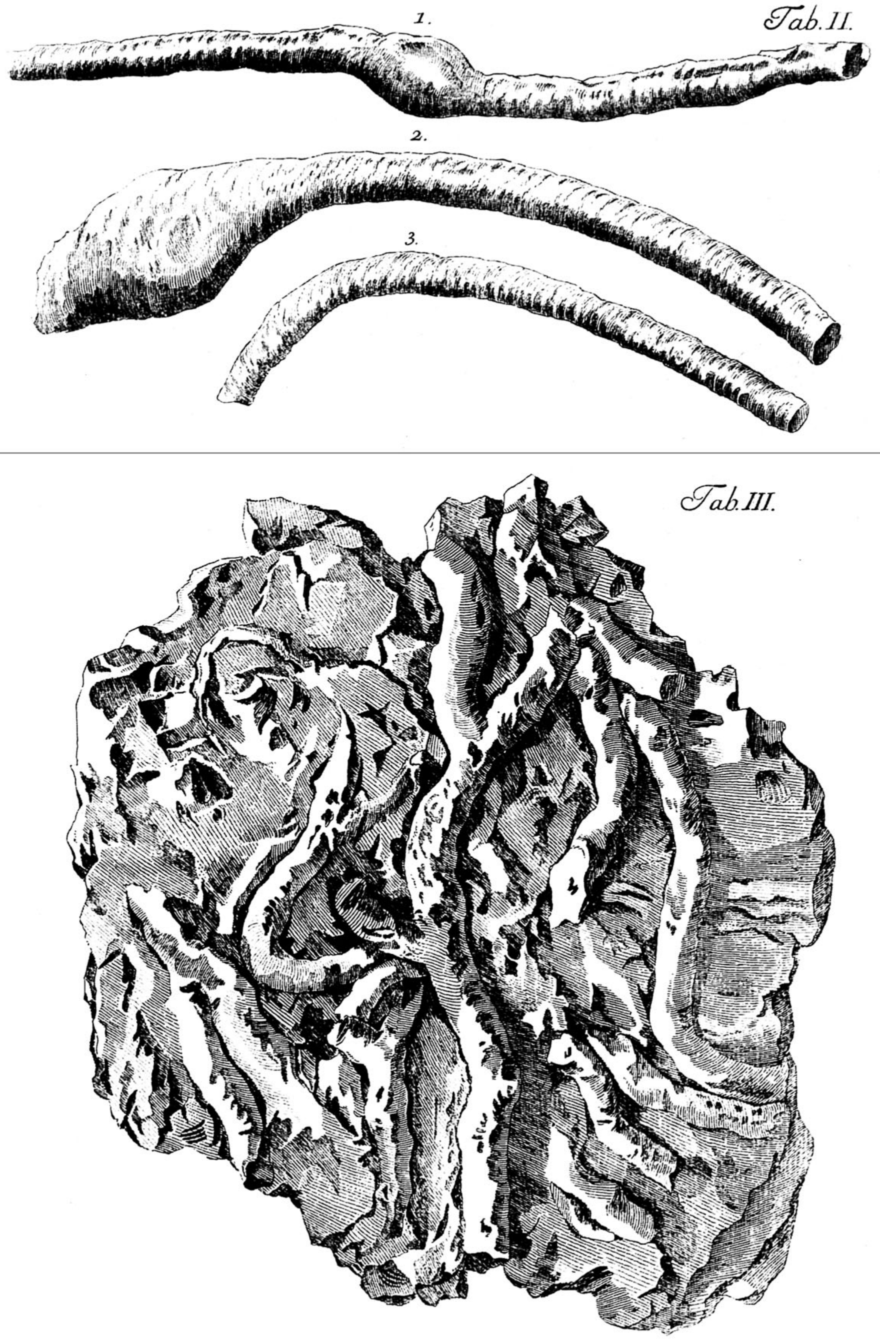

Figure 120: Reproduction of plates 2 and 3 of SCHULZE (1760), which can be considered the oldest publications of SOT structures. SCHULZE interpreted the so-called “Walzensteine” (‘roller stones’) as cavities made by vagile starfish. Most likely they are of Cretacous age, the locality where they were collected is near Dresden, Saxony, eastern Germany. Length of the longest specimen approximately 30cm.

SOT. This was the reason for FÜRSICH (1973) to rearrange the entire group. His concept is predominantly concise and convincing but bears some nomenclatural inconsistencies. *Spongeliomorpha iberica* was considered an unrecognizable ichnospecies. This fact as such is understandable from a 1973 viewpoint when *Spongeliomorpha* indeed was poorly understood and no type material known. Unfortunately, *S. iberica* is the type ichnospecies of *Spongeliomorpha* and thus an unrecognizable *S. iberica* makes *Spongeliomorpha* unrecognizable, a fact already pointed out by BROMLEY & FREY (1974) and MARCINOWSKI & WIERZBOWSKI (1975). After detailed revisions of type material (CALZADA 1981), *Spongeliomorpha* is well defined and certainly not a *nomen dubium*. BROMLEY (1990, 1996) mentioned that *Spongeliomorpha* was not an appropriate name and that *Granularia* POMEL, 1849 was the oldest available name. However, although recognizing an older available name he did not place *Ophiomorpha* in synonymy with *Granularia*. If *Granularia* were the oldest available name it should have been put in synonymy with one of the SOT genera, in this case *Ophiomorpha*, irrespective of a probable later synonymysation of all three ichnogenera. However, after FU (1991) revised *Phymatoderma granulatum*, based on *Algacites granulatus* SCHLOTHEIM, 1822, by BRONGNIART (1849), and UCHMAN (1995) showed that *Granularia* POMEL, 1849 is also based on *Algacites granulatus* SCHLOTHEIM, 1822 the name *Granularia* POMEL, 1849 is invalid. However, *Spongeliomorpha* SAPORTA is valid and available after the revisions of MARCINOWSKI & WIERZBOWSKI (1975) and CALZADA (1981). For further details on the type ichnospecies and its synonymy, see below.

The fact that the name *Spongeliomorpha* is not really fortunate has no effect on the nomenclature of the structures. In the sense of the Code a name is just a series of letters. In palaeontological history many names have turned out to be unfortunate because at the time when they were introduced their authors assumed they have found a new fossil, a plant, for instance. Later this new phycus turned out to be a trace fossil made by an animal and is now known as the 'ancient plant' (*Palaeophycus*), not a very fortunate name.

In order to place all morphologically similar structures of the SOT group in one ichnotaxon it appears that we only have two possibilities: 1) to put them in one ichnofamily 2) to put them in one ichnogenus (e.g., FÜRSICH 1973, BROMLEY & FREY 1974, SCHLIRF 2000). Anyway, the synonymy problem of SOT structures and their often poorly defined types would still remain open. This rather seems an argument of workers who have no real arguments against a synonymisation. Any attempt of synonymisation could be blocked with the argument to put the genera in question into one ichnofamily. If this was the solution to all the problems one should create the phylum Ichnia in which all trace fossils are placed and stop working.

For this reason a synonymisation at the ichnogeneric level is favoured here, but in contrast to previous attempts, a lowering of *Ophiomorpha* to ichnosubgenus rank is proposed; *Thalassinoides* is considered a synonym of *Spongeliomorpha*. *Ophiomorpha* based on *Ophiomorpha nodosa* could well be considered a *nomen dubium*, because the holotype originated from an erratic block, its orientation is unknown, its age is unknown, the locality is unknown, and the holotype is unbranched

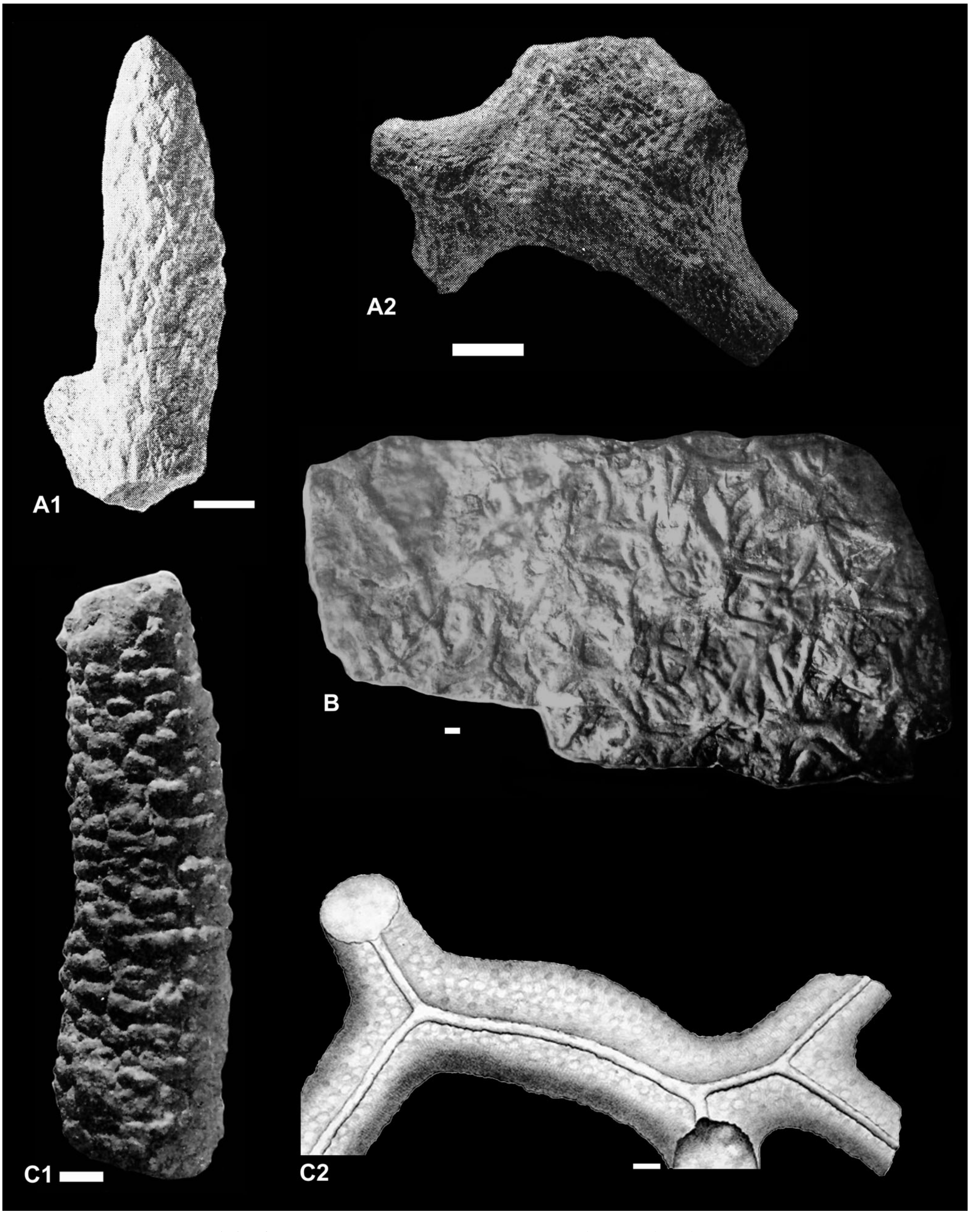

Figure 121: Type material of some SOT structures. **A1**. *Spongeliomorpha iberica* Saporta, 1887; neotype (taken from Calzada, 1980: pl. 2 fig. 2). **A2**. *Spongia sudolica* Zaręcni, 1878; lectotype (taken from Marcinowski & Wierzbowski, 1975: pl. 2 fig. 1a). **B**. *Cylindrites suevicus* Rieth, 1933; lectotype (taken from Rieth: pl. 1 fig. a.). **C1**. *Ophiomorpha nodosa* Lundgren, 1891; lectotype (taken from Häntzschel, 1953: pl. 14 fig 3). **C2**. *Spongites saxonicus* Geinitz, 1842, lectotype (original of Geinitz, 1842: pl 12 fig.1); note knobby exterior. Scale bars: 1cm.

(HÄNTZSCHEL 1952; ANDERSSON 1981). In the sense of the type material *Ophiomorpha* only is the name for short, unbranched burrows of unknown orientation. Ever since its introduction *Ophiomorpha* was used in many different ways. We need clearly defined type material for such complex structures to stop the long lasting debate. Fortunately, GEINITZ'S (1842) description and figures are good quality (Fig. 121C2), so that there can be no doubt that *Spongites saxonicus* GEINITZ, 1842 is synonymous with what currently is understood as *Ophiomorpha nodosa* LUNDGREN, 1891. *Ophiomorpha* was introduced as a new genus based on a species that later turned out to be synonymous with another species. The genus name remains valid and available, the species, however, has to be suppressed in favour of the older synonym. For this reason, *Ophiomorpha nodosa* LUNDGREN, 1891 is considered a synonym of *O. saxonica* (GEINITZ, 1842). Stability in nomenclature is stability on the long run, not only for ten to 15 years. The species *O. nodosa* was more frequently used than *O. saxonica*, but *O. saxonica* certainly is no *nomen oblitum* (see additional remarks on *nomina oblita* below). Presuming that the new concept is subsequently used, finds its way in the new *Treatise*, and new generations of ichnologists are taught the new concept, the new concept will soon be the old and a well established concept. Stability can only be achieved with good type material. For this reason well-defined and typified ichnogenera and ichnosubgenera are introduced here. As a result, all predominantly horizontally oriented Y- to T-shaped branching structures are assigned to the ichnogenus *Spongeliomorpha*, with the introduction of ichnosubgenera as the most practicable solution and logical consequence. Thus, in the following, the introduction of several new ichnogenera for complex three-dimensional burrow systems and predominantly vertical structures, and ichnosubgenera of *Spongeliomorpha* (predominantly horizontal burrow systems) is proposed.

FREY et al. (1978; Fig. 122) and BROMLEY (1996) show a large variety of recent crustacean burrows and stated that these burrows are celebrated for ichnologists, because constructional parallels between them and the ichnogenera *Ophiomorpha* and *Thalassinoides* can be drawn. If one studies these crustacean burrows one cannot deny the fact that there is a large variety of such structures. BROMLEY (1996) arranged the burrows according to their gross morphology and trophic behaviour resulting in the following scheme: boxworks, spiral and dendritic burrows, Y-burrows (vertical). An attempt to assign all these structures (if they were fossil) to one single ichnogenus certainly is too simplistic and not justified. Ichnology with all its weaknesses should always try to give a picture of the past that reflects ancient environments and their inhabitants as exactly as possible. This is why FÜRSICH'S (1974) concept of significant and accessory features is so important for ichnology. In order to be as close to biology as possible the first and certainly most difficult problem to be solved is to find out what is biologically relevant and what not. As already pointed out by FÜRSICH (1973) and again by SCHLIRF (2000) there are no major morphological differences between *Spongeliomorpha*, *Ophiomorpha* and *Thalassinoides* that would justify a separation at the ichnogeneric level. On the

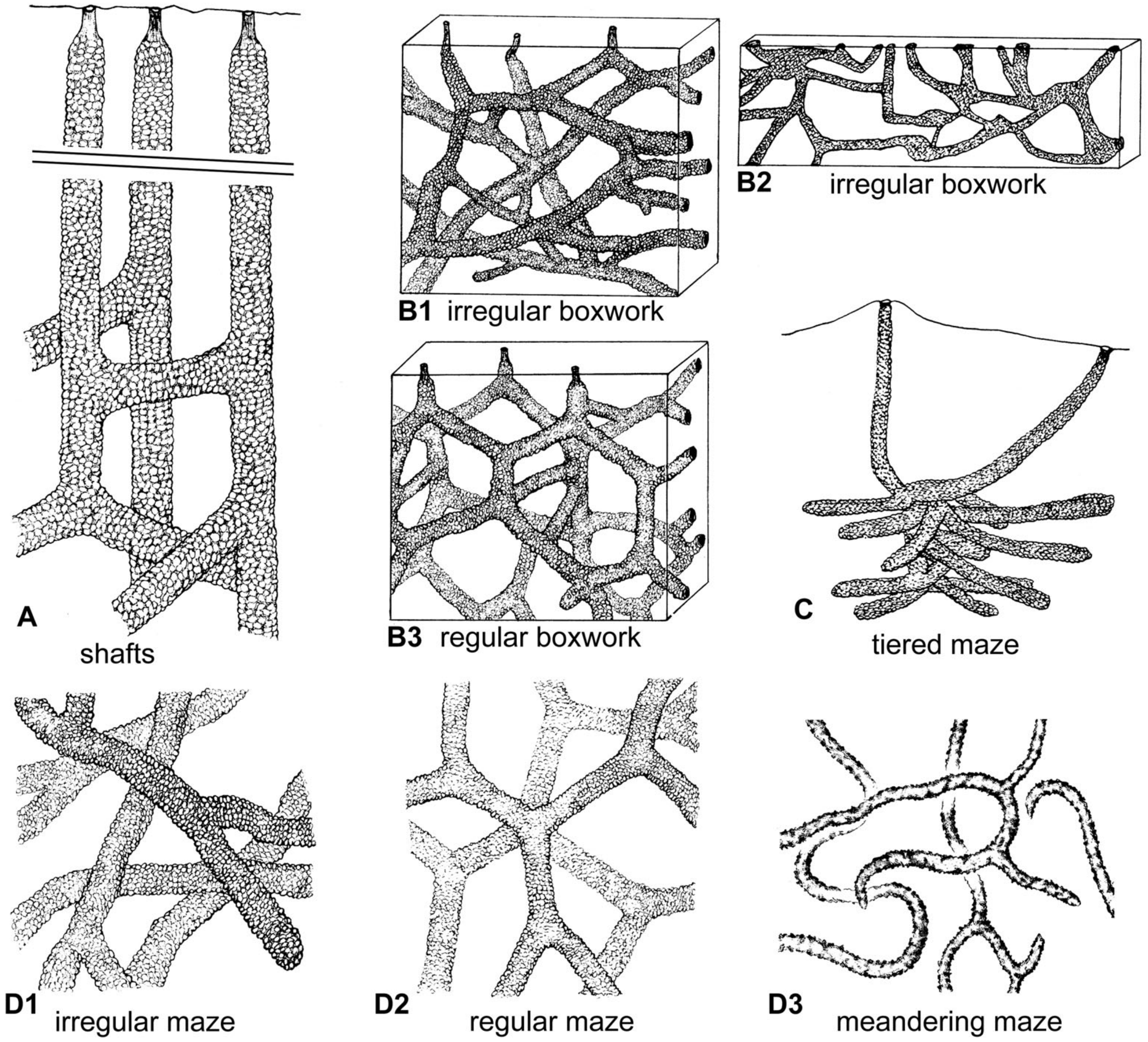

Figure 122: Structures produced by Recent decapod crustaceans as observed and reconstructed by FREY et al. (1978). **A**. Structures dominated by vertical shafts. **B1-3**. Regular and irregular boxwork structures. **C**. Tiered mazes. **D1-2**. Regular and irregular, bedding plane parallel mazes. **D3**. Meandering mazes. Modified after FREY et al. (1978: fig. 2). All are not to scale.

other hand, a separation of all ichnospecies belonging to *Spongeliomorpha*, *Ophiomorpha*, and *Thalassinoides* only at the ichnospecific level would create two qualities of ichnospecies. In the case of a synonymisation, *Spongeliomorpha saxonica* (knobby exterior, consisting of spherical pellets), *S.* nomen novum 1 (knobby exterior, consisting of pellets flattened perpendicularly toward the main axis of the burrow), and *S. sudolica* (unlined with scratched exterior) would all be of the same systematic status, although there are more distinct features that separate *S. sudolica* from *S. saxonica* than there are between *S. saxonica* and *S.* nomen novum 1. As a consequence, the use of ichnosubgenera is suggested. *Ophiomorpha* is lowered in its systematic rank and introduced as an ichnosubgenus of the ichnogenus *Spongeliomorpha*. In contrast to ichnosubspecies the use of ichnosubgenera leaves more flexibility for further systematic treatment of this trace fossil group, and

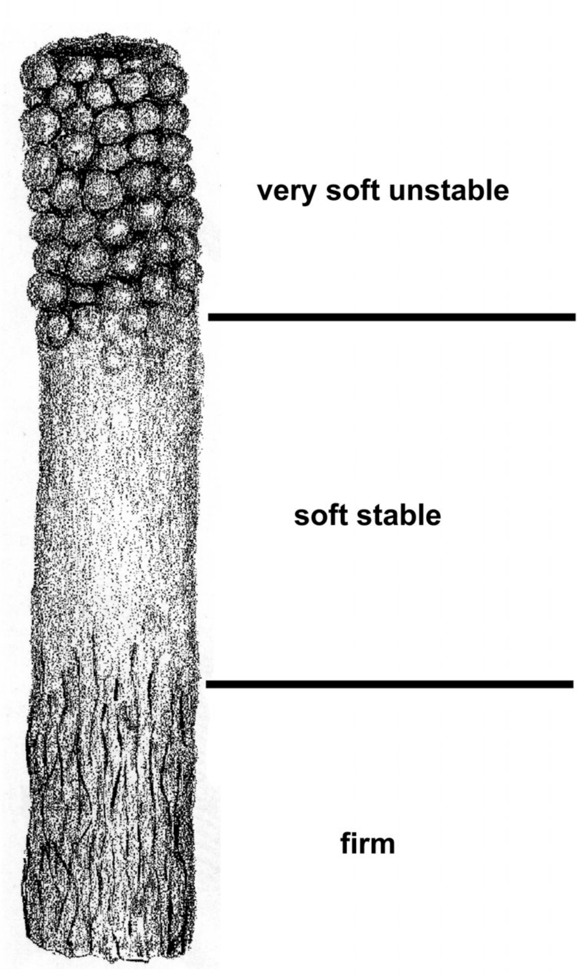

Figure 123: Exterior morphology of *Spongeliomorpha* structures. Upper part with pelletal wall-lining in very soft and unstable substrate; middle part smooth in a soft but stable substrate, and lower part with scratch ornaments as a result of excavation in a firm substrate.

is thus favoured here. *Thalassinoides* is considered synonymous with *Spongeliomorpha* because of lacking a wall-lining, and further use is not recommended.

In order to define the value of ichnotaxobases, the behavioural affinity to the resulting structure is important (FÜRSICH 1974). Generally, ichnogenera are based on their entire burrow morphology, presence or absence of branching, if present frequency of branching or branching pattern, orientation, passive/active filling, presence or absence of a wall-lining, and bioglyphs. An identification of an ichnogenus is only possible if enough material can be studied, similar to *Hillichnus* (BROMLEY et. al 2003). Individual parts of this ichnogenus may be identified as several ichnogenera, the entire system is something different since it represents a complex behavioural pattern. For this reason solely the presence or absence of one particular form of wall-lining cannot be the unique criterion for the distinction between the various forms of *Spongeliomorpha* and other related structures.

Admittedly, it may become difficult in the one or the other case to assign fragments of burrows to one particular ichnogenus, but ichnologists should use open nomenclature more often. This would increase stability because many arguments concerning the stability of certain ichnotaxa are based on misidentified material. It is of no importance what an author wrote and what an author did observe, if the collected and/or figured specimens and especially the type material does not show such observations, they are obsolete. Once again: only the type material counts!

In the following ichnospecies are only discussed when considered relevant for the understanding of the ichnogeneric classification or where homonyms are created due to the synonymisation.

Ichnogenus *Spongeliomorpha* SAPORTA, 1887

Type ichnospecies: *Spongeliomorpha iberica* SAPORTA, 1887: 299, pl.6 figs. 2-3 [= *Spongia sudolica* ZARĘCNI, 1878].

Synonym: *Thalassinoides* EHRENBERG, 1944

Diagnosis: Cylindrical to elliptical, predominantly horizontal burrow systems, showing Y-shaped and/or rarely T-shaped branching; with subordinate sub-vertical and vertical elements. Burrow wall lined or unlined; when lined, distinctly lined with agglutinated sediment; exterior smooth, knobby, or with sub-parallel longitudinal or crossing ridges. Meniscate backfill structures and/or spreite structures may be subordinately present.

Discussion: *Spongeliomorpha iberica* SAPORTA, 1887 is type species of *Spongeliomorpha* SAPORTA, 1887. However *S. iberica* is invalid as an ichnospecies name since MARCINOWSKI & WIERZBOWSKI (1975) revised *Spongia sudolica* ZARĘCNY, 1878 which is a subjective senior synonym of *Spongeliomorpha iberica*. According to Article 23 (ICZN 1999), ZARĘCZNY's *Spongia sudolica* has priority and, as a consequence, *Spongeliomorpha iberica* SAPORTA, 1887 is considered a junior synonym of *Spongeliomorpha sudolica* (ZARĘCZNY, 1878); this however, does not effect the validity of the ichnogenus *Spongeliomorpha*.

The diagnosis states that meniscate backfill structures or spreite structures may be subordinately present. There are several examples known where apparently abandoned burrow parts were stuffed with sediment by the inhabitants. If such features are observed they should be documented, but they do not justify an assignment of this particular burrow part to a separate ichnogenus, nor should synonymisations be justified with such observations. Again, *Hillichnus* (BROMLEY et al. 2003) is a good example.

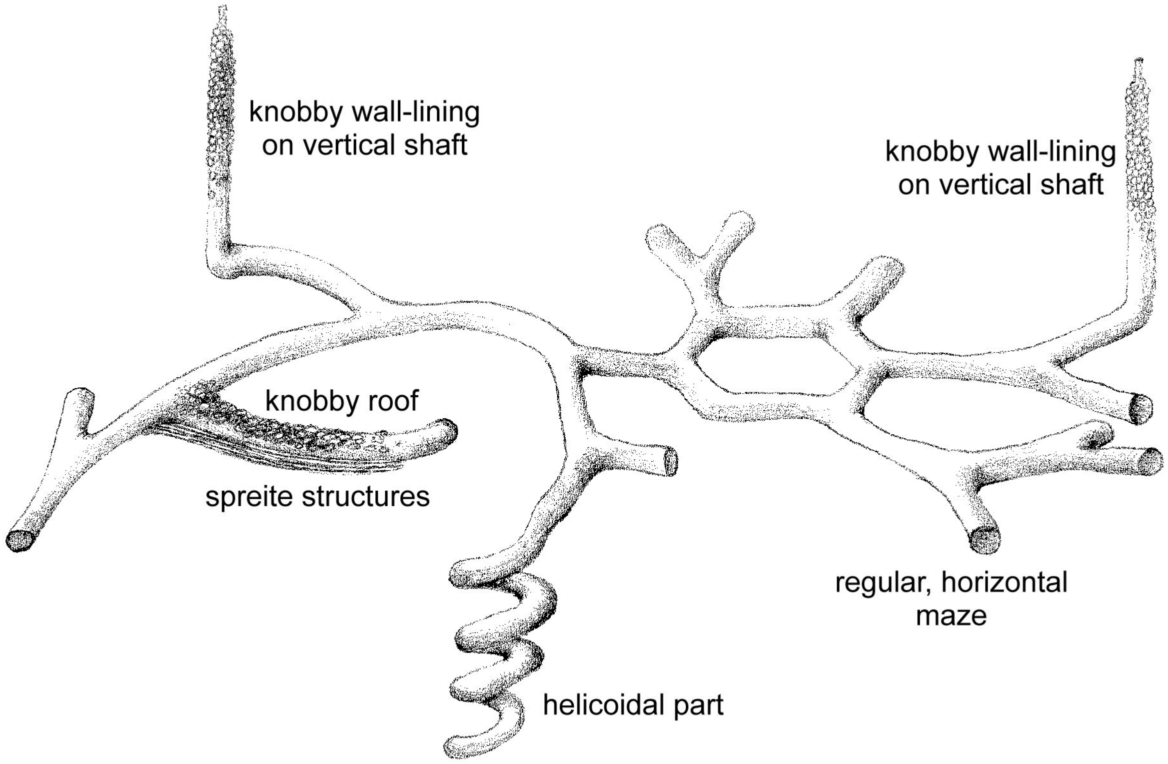

Figure 124: Reconstruction of Spongeliomorpha (Spongeliomorpha) suevica with structures, which, if found separately, are commonly assigned to different ichnogenera. However, it seems better to name them only if they occur separately but to describe their nature if found connected to a larger system. Due to space limitation the dominant maze structure is underrepresented in the reconstruction. Not to scale.

MILLER (2000, 2001) reported multiple branching trace fossils from the Paleocene of Italy and interpreted them as compounds of *Thalassinoides* and *Phycodes* and used this as an argument against a synonymisation of SOT structures, because *Phycodes* RICHTER, 1850 would then have to be considered as synonymous as well, and would be the oldest available name. If the observed structures were *Phycodes* and the branching burrow systems were *Thalassinoides* the following points would have to be considered: it would have been an exceptional find and as such would not justify a synonymisation, for the same reason as *Skolithos* should not be synonymised with *Paleodictyon* because small vertical tubular elements connected to the polygonal networks can occasionally be observed. Even if such vertical elements were very frequently found connected to the polygonal networks this would not justify a synonymisation but would show how complex *Paleodictyon* is. The structures reported by MILLER (2000, 2001) show a highly complex three dimensional multibranching burrow system that has very little in common with SOT structures and *Phycodes*. The branching pattern is almost throughout T-shaped, enlargements at points of bifurcation are rarely identifiable, the entire structure is a complex three dimensional system and the terminations identified as *Phycodes* show a two dimensional fan-like arrangement rather than a three dimensional bundle as it would be typical of *Phycodes*. There is one slightly dubious trace fossil, *Lennea*, hitherto almost only reported from Devonian deposits in Germany (e.g., KRÄUSEL & WEYLAND 1932, 1934; PAULUS 1957; FISCHER & PAULUS 1969, MILLER & KNOX 1985) that shows some similarities with the material presented by MILLER (2000, 2001). Although listed under the available trace fossil names and figured by HÄNTZSCHEL (1962, 1975) the validity of *Lennea* is questionable and needs further detailed investigations[1].

Trace fossils often are highly complex structures and have to be identified as such. As the example of *Paleodictyon* has already shown, it would be possible to reduce almost all trace fossils to a combination of *Planolites* and *Skolithos*. Since these are the most simple structures known and could be found in nearly all other trace fossils in various combinations, most trace fossils would end as being synonymous with either *Skolithos* or *Planolites*. As stated above, it is not the intergradation of wall structures in *Spongeliomorpha* that makes *Thalassinoides* synonymous with *Spongeliomorpha* it is the entire burrow morphology that counts.

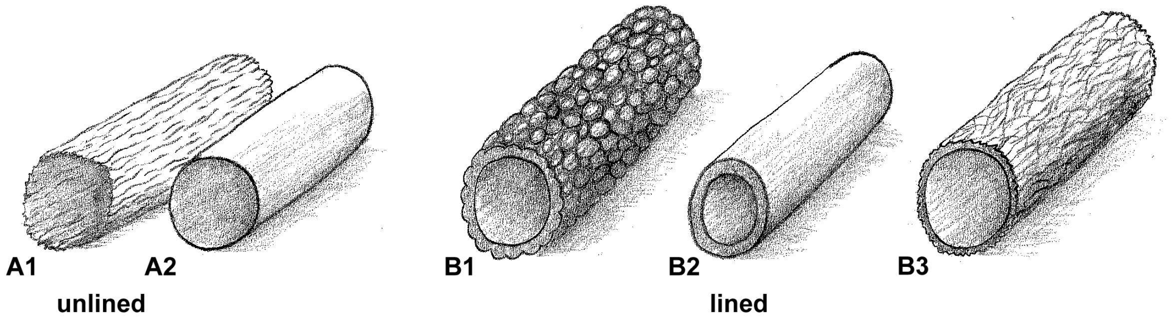

Figure 125: Various external burrow morphologies and different types of wall-lining. A1-2. Unlined. A1. Burrow with scratch ornaments on the exterior. A2. Burrow with smooth exterior. B1-3. Lined. B1. With pelletal wall-lining and resulting knobby exterior. B2. With heavy wall-lining but smooth exterior. B3. With heavy wall-lining and scratch ornaments on the exterior. Not to scale.

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[1] In their original description KRÄUSEL & WEYLAND (1932) neither figured a specimen nor did they refer to a specimen in a collection, they only provided a description, which is sufficient according to Article 13 (ICZN 1999). Two years later (KRÄUSEL & WEYLAND 1934) they stated that the new name introduced in 1932 was only provisional, however, they then provided detailed descriptions and figures and gave reference where the material is deposited. The figured material shows very complex structures and a variety of morphologies, thus an undoubted assignment from the figures alone cannot be made. In order to guarantee long-term stability a lectotype should be designated. Thus, currently *Lennea* can be considered a *nomen dubium*. For a detailed revision a restudy of the original material is necessary, but this was beyond the scope of this study. As an anecdote it might be added that *Lennea* as a genus name was already preoccupied in 1932 for a plant. *Lennea* was introduced by KLOTZSCH (1842) for a magnoliacean plant from Mexico, thus the name introduced by KRÄUSEL & WEYLAND (1932), at that time thought to be a new plant genus, was a younger homonym. However, after realizing that *Lennea* KRÄUSEL & WEYLAND, 1932 was a trace fossil this problem does not exist any more, since trace fossil names, treated by the ICZN, and plant names do not compete for homonymy.

Ichnosubgenus *Spongeliomorpha* (*Spongeliomorpha*) SAPORTA, 1887

Type ichnospecies: *Spongeliomorpha iberica* SAPORTA, 1887: 299, pl. 6. fig. 2-3 [= *Spongia sudolica* ZARĘCNI, 1878].

Diagnosis: Predominantly horizontal, Y- to T-shaped branched burrow systems, forming irregular to regular mazes, with vertical to oblique shafts; dominantly no wall-lining, exterior smooth or rough (longitudinal to transverse ridges and grooves).

Currently recognized ichnospecies:
Spongeliomorpha (*Spongeliomorpha*) *sudolica* (ZARĘCNI, 1878)
S. (*S.*) *harefieldensis* (WHITE, 1923)
S. (*S.*) *sublumbricoides* (AZPEITIA MOROS, 1933)
S. (*S.*) *suevica* (RIETH, 1933); SCHWEIGERT (1998) designated a lectotype and mentioned that the publication date of RIETH was 1933, not 1932 as usually cited.
S. (*S.*) *oraviense* (KSIĄŻKIEWICZ, 1977)
S. (*S.*) *carlsbergi* BROMLEY & ASGAARD, 1979 emend. EKDALE et al. 1984
S. (*S.*) *chevronensis* MUÑIZ & MAYORAL, 2001

Tentatively assigned ichnospecies:
S. (*S.*) *milfordensis* METZ, 1993
S. (S.) paradoxica (WOODWARD, 1830) emend. KENNEDY, 1967

Discussion: The aim of this study is to present a new ichnogenus concept for vertical and horizontal Y- to T-shaped branching systems. Many ichnospecies belonging to this group are in need of a detailed revision. This, however, was far beyond the scope of this study. However, some remarks on certain ichnospecies belonging to *Spongeliomorpha* (*Spongeliomorpha*) are given. Table 1 & 2 give short descriptions of the various ichnospecies currently thought to belonging to the *Spongeliomorpha* group.

Thalassinoides ornatus KENNEDY, 1967 is synonymous with *Spongeliomorpha* (*S.*) *sudolica* (ZARĘCNI, 1878). KENNEDY mentioned reticulate ridges as diagnostic for his *T. ornatus*, however, *S.* (*S.*) *sudolica* also shows reticulate ridges and can thus be considered a younger synonym. If *S. (S.) paradoxica* (WOODWARD, 1830) emend. KENNEDY, 1967 remains a separate ichnospecies can only be decided after a detailed revision of the type material of all other forms showing scratch ornaments on the exterior.

Figure 126: Mazes of *Spongeliomorpha* (*Spongeliomorpha*) *suevica* (RIETH, 1933). Field photograph, full reliefs, top view; Grès de la Crèche, Tithonian, Upper Jurassic, Cap Gris Nèz, Boulonnais, northern France. Hammer head for scale.

The ichnospecies of *Spongeliomorpha* (*Spongeliomorpha*) introduced by MUÑIZ & MAYORAL (2001) do show differences in the striation pattern. Whether these differences are recurrent morphologies only future investigations will show, especially since the observed angles of branching and angles of scratch pattern overlap with other ichnospecies, making a distinction between them sometimes impossible (see MUÑIZ & MAYORAL 2001: tab. 1,2 & 3). Moreover, the holotypes of each of the newly introduced ichnospecies by MUÑIZ & MAYORAL (2001) are unfortunate, non of them shows branching. As in the case of *Maiakarichnus*, it would have been better if the authors had chosen a syntype series instead of designating a holotype. In addition, a discussion on *Spongeliomorpha* (*Ophiomorpha*) *annulata* (KENNEDY, 1967) is missing. The authors seem to have studied the scratch pattern on the exterior but they have completely neglected the fact that *S.* (*O.*) *annulata* (KENNEDY) has a heavy clay lining; a fact that is absolutely not in line with their own ichnogenus concept and not with the herein presented one. The holotype of '*Terebella*' *harefieldensis* WHITE, 1923 in KENNEDY (1967: pl. 7 fig. 2) exactly matches the diagnosis of *Spongeliomorpha sinuostriata* MUÑIZ & MAYORAL (2001), which, thus, is a younger synonym of *Spongeliomorpha* (*S.*) *harefieldensis* (WHITE, 1923). *Spongeliomorpha* (*S.*) *sudolica*, although being the oldest available name, is also dismissed by MUÑIZ & MAYORAL (2001).

UCHMAN (1998) stated that *Spongeliomorpha* (*Spongeliomorpha*) *milfordensis* METZ, 1993 is morphologically very similar to *S.* (*S.*) *sublumbricoides* (AZPEITIA MOROS, 1933). UCHMAN (1998) retained from a synonymisation of both ichnospecies because *S.* (*S.*) *milfordensis* occurs in fresh water environments whereas *S.* (*S.*) *sublumbricoides* occurs in marine sediments. Palaeoenvironment is no ichnotaxobase, however, for a final decision the type material of both ichnospecies has to be consulted again. For this reason *S.* (*S.*) *milfordensis* is assigned to *Spongeliomorpha* (*Spongeliomorpha*) with reservations only.

Ichnosubgenus *Spongeliomorpha* (*Ophiomorpha*) (LUNDGREN, 1891)

Type ichnospecies: *Ophiomorpha nodosa* LUNDGREN, 1891 [= *Spongites saxonicus* GEINITZ, 1842].

Diagnosis: *Spongeliomorpha* with a distinct wall lining; wall-lining may be knobby, smooth or with longitudinal to transverse grooves and ridges on the exterior.

Currently recognized ichnospecies:

Spongeliomorpha (*Ophiomorpha*) *saxonica* (GEINITZ, 1842)
S. (*O.*) *rectus* (FISCHER-OOSTER, 1858)
S. (*O.*) *borneensis* (KEIJ, 1965)
S. (*O.*) *annulata* (KENNEDY, 1967)
S. (*O.*) *rudis* (KSIĄŻKIEWICZ, 1977) emend. UCHMAN (2001)
S. (*O.*) *irregulare* (FREY, HOWARD & PRYOR, 1978) emend. BROMLEY & EKDALE (1998); the spelling of *Ophiomorpha irregulaire* FREY et al. should be corrected and spelled *S.* (*O.*) *irregulare*; *irregulaire* certainly was a lapsus (already mentioned by BROMLEY & EKDALE 1998) and must be corrected. According to Article 32.5 ICZN spelling errors of names are to be corrected.
S. (*O.*) nomen novum 1 to replace *S.* (*O.*) *annulata* (KSIĄŻKIEWICZ, 1977).

Discussion: The wall-lining distinguishes this ichnosubgenus from the other ichnosubgenus. A wall-lining is considered an ichnotaxobase at a high level of significance, but in complex three dimensional structures a distinction of ichnogenera purely on the basis of presence or absence of wall-linings seems an oversimplification. As a result, some structures thought to belong to *Spongeliomorpha* (*Spongeliomorpha*) are placed under *S.* (*Ophiomorpha*) because the actual form of the wall-lining is not considered to be very significant. The significant behavioural pattern is the building of a wall-lining (Fig. 123 & 125). Whether or not this wall-lining has a smooth, a knobby or a scratched exterior

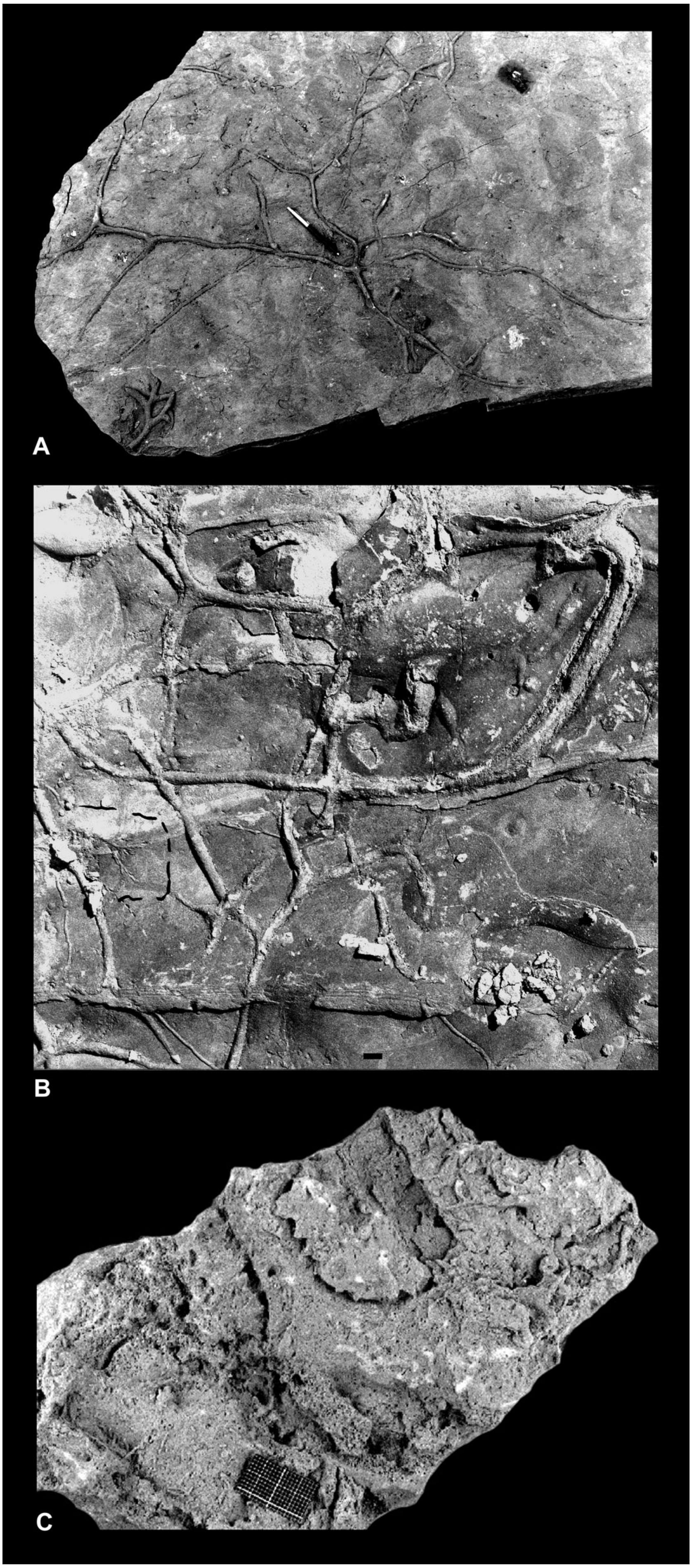

Figure 127: **A**. *Spongeliomorpha* (*Ophiomorpha*) *saxonica* (GEINITZ, 1842). Field photograph, fullrelief, top view. Ballpen for scale. **B**. *Spongeliomorpha* (*O.*) *saxonica* (GEINITZ, 1842) with smooth exterior over large distances. Field photograph, fullrelief, top view. Scale bar 1cm. **C**. *Spongeliomorpha* (*O.*) *irregulare* variatio *densa*, sensu SCHLIRF (2000). Fullreliefs, top view. Millimetre grid for scale. **A-C**. Grès de la Crèche, Tithonian, Upper Jurassic, Le Portel. Boulonnais, northern France.

pattern is considered less relevant, and should therefore be used as ichnotaxobase at the ichnospecific level. As a consequence, the mere existence of a scratch ornament pattern on the exterior of a burrow alone is insufficient as a diagnostic criterion. This concept is totally in line with the taxonomy of *Palaeophycus* except for the fact that *Planolites* and *Palaeophycus* are primarily distinguished at the ichnogeneric level by having a wall-lining or not. In this case it seems well justified because *Planolites* and *Palaeophycus* are more-or-less simple structures, and thus the value of a wall-lining may be higher than in complex three-dimensional burrow systems.

As shown in Fig. 121C2, *Spongites saxonicus* GEINITZ, 1842 [= *Spongeliomorpha* (*O.*) *saxonica* (GEINITZ, 1842)] clearly shows a knobby exterior and therefore is best assigned to the ichnosubgenus *Spongeliomorpha* (*Ophiomorpha*) and not as stated by KENNEDY (1967) and lately by KIM et al. (2002) to *Thalassinoides* [= *Spongeliomorpha* (*S.*)].

Ichnogenus new Ichnogenus 3

Type ichnospecies: New Ichnogenus 3 new ichnospecies 3.1.

Diagnosis: Predominantly vertical, lined or unlined, tubular shafts with occasional oblique to horizontal Y- to T-shaped branching tunnel systems associated with it. When lined, dominantly knobby, subordinately smooth or with longitudinal to transverse grooves and ridges on the exterior; if unlined, smooth or with longitudinal to transverse grooves and ridges on the exterior.

Derivatio nominis:

New Ichnogenus 3 new ichnospecies 3.1

Fig. 128

Type material: Specimens from Madsegrav, Bornholm, Denmark; specimens in the coastal cliff section in Freemantle harbour, below Round House (oldest public building of Western Australia, Australia); specimens at Alice Wainright Park, Miami Limestone, Pliocene, Miami, Florida, USA.

Remarks: Yet I have not made a final decision on the type locality, thus the introduction of the new ichnogenus and ichnospecies is provisional only. In January 2005 I will visit the locality in Bornholm which hosts a varierty of well-preserved specimens suitable as types for new Ichnogenus 3 new ichnospecies 3.1 (pers. comm. R. BROMLEY, Copenhagen).

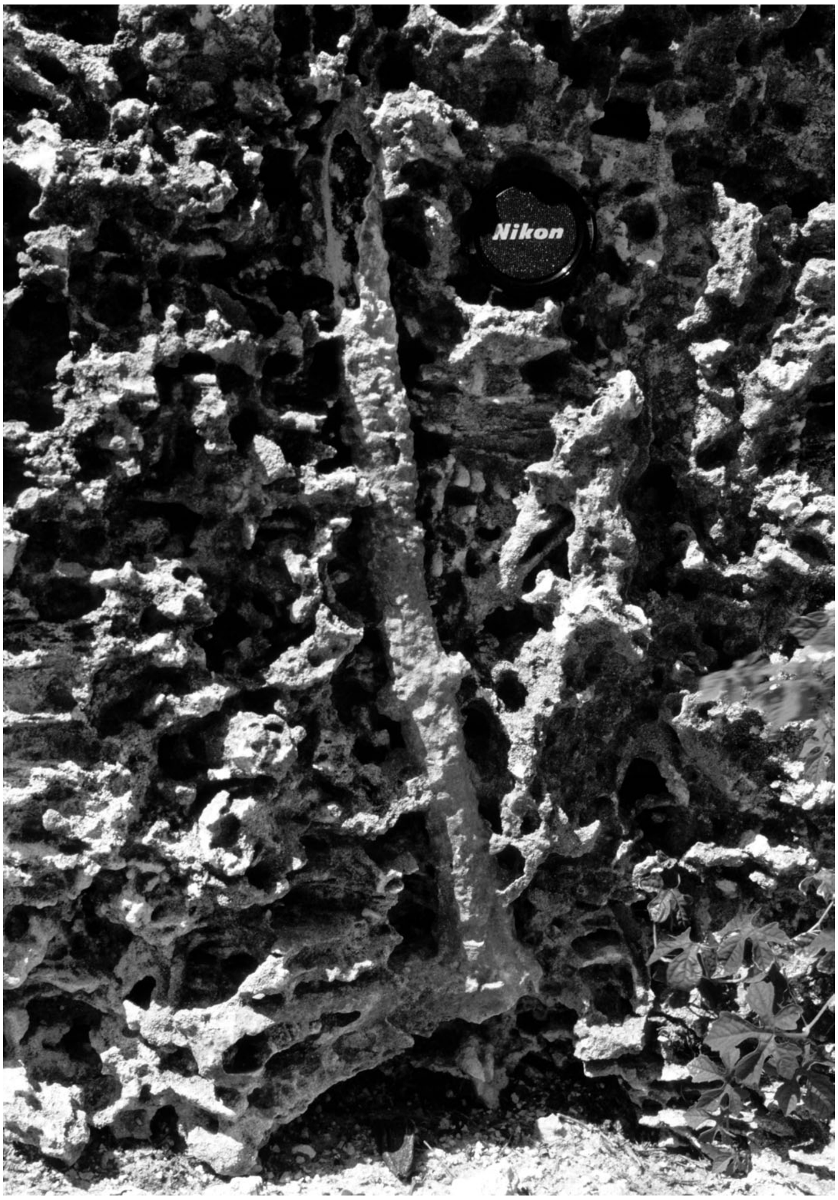

Figure 128: Vertical shaft of new Ichnogenus 3 new ichnospecies 3.1. Field photograph, fullrelief, side view, Alice Wainright Park, Miami Limestone, Pliocene,Miami, Florida, USA. Lens cap 52mm across.

Diagnosis: Dominantly vertical, lined, tubular shafts with occasional oblique to horizontal, Y- to T-shaped branching tunnel systems associated with it. Generally lined with knobby exterior; subordinately smooth or with longitudinal to transverse grooves and ridges on the exterior.

Derivatio nominis: From *nodi* = Latin for knots and *struere* = Latin for to pile up, with respect to the pellets used for the wall-lining.

Discussion: In order to pay respect to the fact that the specimens of the new ichnogenus and ichnospecies are very large and uncollectable, a syntype series is assigned. The author is aware that usually specimens have to be collected and reposited in official collections. However, for large trace fossils this is impossible. Although by the time specimens will be destroyed by erosion the chosen outcrops are large enough and rich enough in specimens to guarantee sufficient material for a very long time.

Especially in Cenozoic rocks these trace fossils are very common. A coastal cliff section in Freemantle harbour below the oldest public building of WA, Australia bears hundreds of up to five meter long, vertical specimens associated with short horizontal tubular structures. The entire specimens are completely pellet lined.

Ichnogenus new Ichnogenus 4

Type ichnospecies: *Thalassinoides bacae* EKDALE & BROMLEY, 2003: 224, fig. 2A-F.

Derivatio nominis:

Diagnosis: Dominantly horizontal, smooth walled, unlined, anastomizing, Y- to T-shaped branching, tubular structures with numerous, closely spaced, strictly vertical shafts aligned along the horizontal tunnels.

Currently recognised ichnospecies: new Ichnogenus 4 *bacae* (EKDALE & BROMLEY, 2003), new combination.

Discussion: The new ichnogenus New Ichnogenus 4 differs from smooth *Spongeliomorpha* (*Spongeliomorpha*) in showing an anastomizing nature and by having numerous, closely spaced, short vertical shafts. The morphology of this burrow system is unique and significantly distinct to justify a separation at the ichnogeneric level.

The morphology clearly is a reflection of behaviour. New Ichnogenus 4 is interpreted as an agrichnial trace fossil representing some type of chemosymbiotic feeding behaviour (EKDALE & BROMLEY, 2003).

Ichnogenus new Ichnogenus 5a

Type ichnospecies: new Ichnogenus 5a (new Subichnogenus 5a) new ichnospecies 5a.1

Diagnosis: Branching tunnel systems, forming irregular to regular complex three-dimensional boxworks. Burrow wall lined or unlined, distinctly lined with agglutinated sediment; exterior smooth,

Figure 129: Complex, unlined, three-dimensional boxwork of new Ichnogenus 5a (new Subichnogenus 5a) new ichnospecies 5a.1. Grès de la Crèche, Tithonian, Upper Jurassic, Point de la Crèche, Boulonnais, northern France. Lens cap 52mm.

knobby, or with sub-parallel longitudinal or crossing ridges and grooves. Meniscate backfill structures and/or spreite structures may be subordinately present.

Derivatio nominis:

Remarks: In consistency with the new classification concept complex three dimensional boxwork structures are divided into two ichnosubgenera. The two ichnosubgenera are based on the presence or absence of a wall-lining. The different ichnospecies are separated in the same way as the ichnospecies of *Spongeliomorpha*, based on details of the wall-lining.

Ichnosubgenus new Ichnogenus 5a (new Subichnogenus 5a)

Type ichnospecies: new Ichnogenus 5a (new Subichnogenus 5a) new ichnospecies 5a.1

Diagnosis: Branching tunnel systems, forming irregular to regular complex three-dimensional boxworks. Burrow unlined, exterior smooth, or with sub-parallel longitudinal or crossing ridges and grooves. Meniscate backfill structures and/or spreite structures may be subordinately present.

new Ichnogenus 5a (new Subichnogenus 5a) new ichnospecies 5a.1

Fig. 129

Iconotypes: Specimens occurring in the Upper Jurassic Grès de la Crèche at Point de la Crèche, Boulonnais, northern France (Fig. 129).

Diagnosis: Unlined new Ichnogenus 5a forming irregular to regular complex three-dimensional boxwork systems. Exterior smooth or with sub-parallel longitudinal or crossing ridges and grooves.

Derivatio nominis:

Discussion: new Ichnogenus 5a (new Subichnogenus 5a) new ichnospecies 5a.1 designates a new ichnogenus, ichnosubgenus and ichnospecies for long known forms of three-dimensional boxworks hitherto assigned to *Thalassinoides*. As already discussed above such highly complex three dimensional burrow systems deserve an own name. BROMLEY (1996) has shown that modern crustacean burrows can also be assigned to maze and boxwork structures. The newly introduced ichnogenus thus pays respect to these neoichnological observations.

Ichnosubgenus new Ichnogenus 5a (new Subichnogenus 5b)

Type ichnospecies: new Ichnogenus 5a (new Subichnogenus 5b) new ichnospecies 5b.1

Diagnosis: Branching tunnel systems, forming irregular to regular complex three-dimensional boxworks. Burrow wall lined with agglutinated sediment; exterior smooth or knobby. Meniscate backfill structures and/or spreite structures may be subordinately present.

Derivatio nominis:

new Ichnogenus 5a (new Subichnogenus 5b) new ichnospecies 5b.1

Fig. 131

Iconotypes: Specimens in the Paleogene-Neogene Upper Gaiman Formation, Bryn Gwyn Palaeontological Park, Chubut, Patagonia, Argentina.

Remarks: Due to technical problems currently no photographic reproductions of the specimens can be given.

Diagnosis: Branching tunnel systems, forming irregular to regular complex three-dimensional boxworks. Burrow wall lined with agglutinated sediment; exterior smooth or knobby (pellets); form of pellets spherical or ovoid; distinct pellet lining may be present at tops of cylindrical tunnels only or mantles entire tunnels. Meniscate backfill structures and/or spreite structures may be subordinately present.

Derivatio nominis:

Ichnogenus new Ichnogenus 6

Type ichnospecies: *Spongeliomorpha sicula* D’ALESSANDRO & BROMLEY, 1995.

Derivatio nominis:

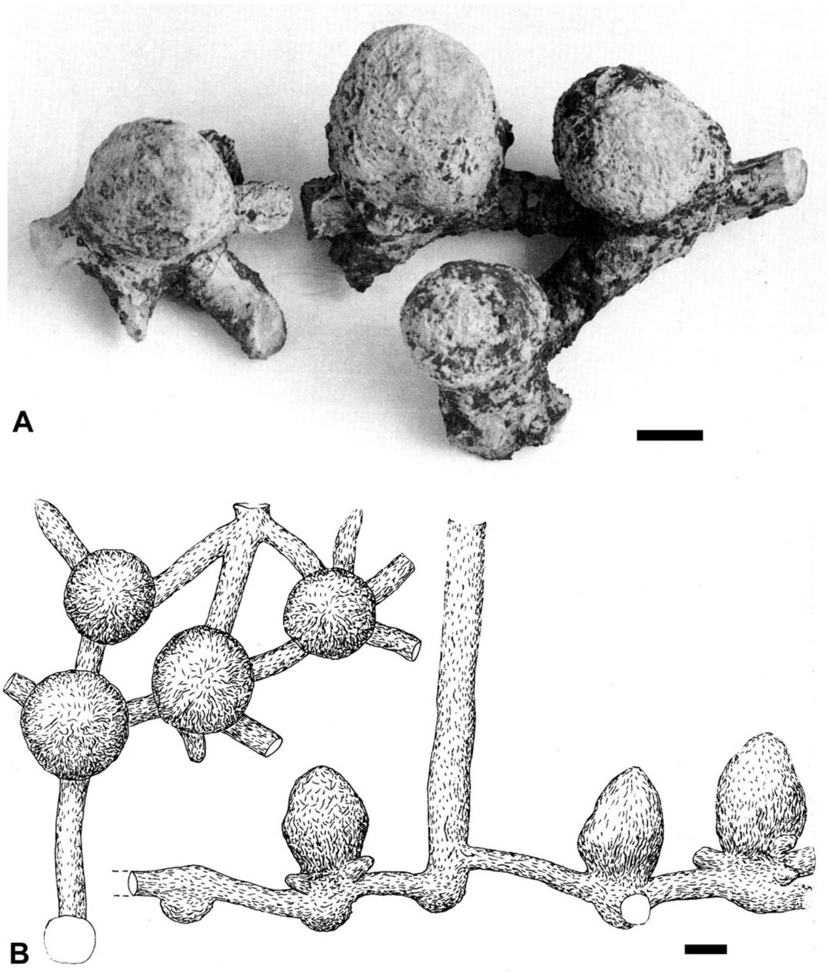

Figure 130: New Ichnogenus 6 *sicula* (D’ALESSANDRO & BROMLEY, 1995). **A**. Holotype, Early Pleistocene, Vallone Lodiero, Scordia, Sicily, southern Italy. Taken from D’ALESSANDRO & BROMLEY, 1995: fig 6. **B**. Reconstruction of *B. sicula*. Taken from D’ALESSANDRO & BROMLEY, 1995: fig 4. Scale bars: 1cm.

Currently recognised ichnospecies: New Ichnogenus 6 *sicula* (D’ALESSANDRO & BROMLEY, 1995) new combination.

Diagnosis: Dominantly horizontally oriented networks of tubular burrows with multiple branching (3-5) from one point, with slight enlargements at points of bifurcation. Terminations of tubular burrows bluntly pointed. Vertically elongated, ovoid chambers located above multiple branching points of burrow network; commonly small hemispherical swellings at the bottom of the tubes oppose ovoid chambers. Base of the ovoid chambers locally adorned by several small, obliquely upward directed, conical structures. More than one horizontal maze developed as discrete tiers, connected to larger vertical shafts. Surfaces bear acutely angled, crisscross ornament of sublongitudinal ridges and grooves.

Discussion: This particular trace fossil, originally assigned to *Spongeliomorpha* (D'ALESSANDRO & BROMLEY 1995) can be distinguished from *Spongeliomorpha* by having a morphology dominated by vertical shafts and ovoid chambers. In addition, the branching pattern of *Bromleya* n. ig. is different from *Spongeliomorpha*. *Spongeliomorpha* predominantly has triple junctions in one plane whereas new Ichnogenus 6 is clearly dominated by closely spaced branching points from which up to five branches emerge. The enlargements at the points of bifurcation in *Spongeliomorpha* are generally more strongly developed than in new Ichnogenus 6. D'ALESSANDRO & BROMLEY (1995) already mentioned that these burrows clearly differ from all other known *Spongeliomorpha* but considered the scratch ornaments on the burrow walls as only ichnogeneric taxobase in this case. According to the new concept presented herein this seems oversimplified and as a consequence these structures are assigned to a new ichnogenus.

Ichnogenus *Maiakarichnus* VERDE & MARTÍNEZ, 2004

Type ichnospecies: *Maiakarichnus currani* VERDE & MARTÍNEZ, 2004: 42, fig. 3-5; by original designation.

Emended diagnosis: Dominantly horizontal, irregular networks of tubular structures with multiple branching; with slight to strong enlargements at points of bifurcation. Terminations of tubular structures rounded to slightly bulbous. Subspherical chambers, with clay lining, preserved in full relief located at termination of tubular structures; with numerous thin shafts radiating mainly in an upward direction from the upper part and from the sides.

Discussion: The diagnosis provided by VERDE & MARTÍNEZ (2004) included forms with and without clay lining. The holotype, as stated and figured by VERDE & MARTÍNEZ (2004) shows a clay lining. In order to provide a concise taxonomy, forms without a wall lining should be placed in a subgenus different from *Maiakarichnus*. Although stated, not one of the figured specimens shows a wall-lining and *Maiakarichnus* is considered a lined burrow unless the existence of such material is not proved.

Interestingly, the authors state that *Maiakarichnus* is frequently found in association with *Spongeliomorpha* (*Ophiomorpha*), however, no good photographic evidence was provided. The specimen figured in VERDE & MARTÍNEZ (2004: fig. 5C) does not show a nodular exterior but rather is a highly irregular structure that can hardly be assigned to a known ichnogenus. The forms the authors refer to as *Thalassinoides* are very irregular and named separately. Single elements of complex structures should not be named separately. The irregular network associated with the chambers unambiguously is part of the trace fossil and should thus be mentioned in the diagnosis.

Unfortunately the holotype is incomplete. Due to the large size of the trace fossils it certainly was impossible to excavate a complete specimen. In highly complex, large structures one has to refer to the entire type series. The type locality, although possibly eroded in a few decades, becomes very important since it is the only known locality to provide the entire structures for study. BROMLEY et al. (2003) had similar problems with *Hillichnus*. The structure is too large and too complex to be excavated, as a consequence BROMLEY et al. (2003) have designated an iconotype. The Code demands complete type material. Such complex structures need exceptional treatment and the specimens of the type locality should be regarded as highly important. If an author introduces a new species it is not necessary to designate a holotype. If no holotype is designated (in a publication before 1999) the entire material referred to by the author in the original publication is a syntype series (Article 72.3). Every specimen is equally important. In future it is recommended that no holotypes but syntypes are designated for large and complex structures, because this guarantees that all aspects of a complex structure are represented. In publications after 1999, the author has to state which of the specimens belong to the syntype series (Article 73.2). Of course subsequent authors are also well advised not to designate a lectotype subsequently.

Ichnogenus *Sinusichnus* GIBERT, 1996

Type ichnospecies: *Sinusichnus sinuosus* GIBERT, 1996: 251, pl. 1 fig. 1-5 by original designation.

Emended diagnosis: Horizontal, regularly sinusoidal, Y- to T-shaped, rarely X-shaped branching, unlined, tubular structures, with subordinate short vertical shafts originating at points of branching; cross-section of tubular elements elliptical. Branches always originate at the convex side of tubes.

Currently recognized ichnospecies: *Sinusichnus sinuosus* GIBERT, 1996.

Remarks: The original diagnosis by GIBERT (1996) did not contain any information on burrow cross-section and wall-lining and is therefore emended.

GIBERT et al. (1999) interpreted *Sinusichnus sinuosus* as an open burrow system produced by crustaceans following a mixed deposit-feeding and farming (or trapping) mode of life.

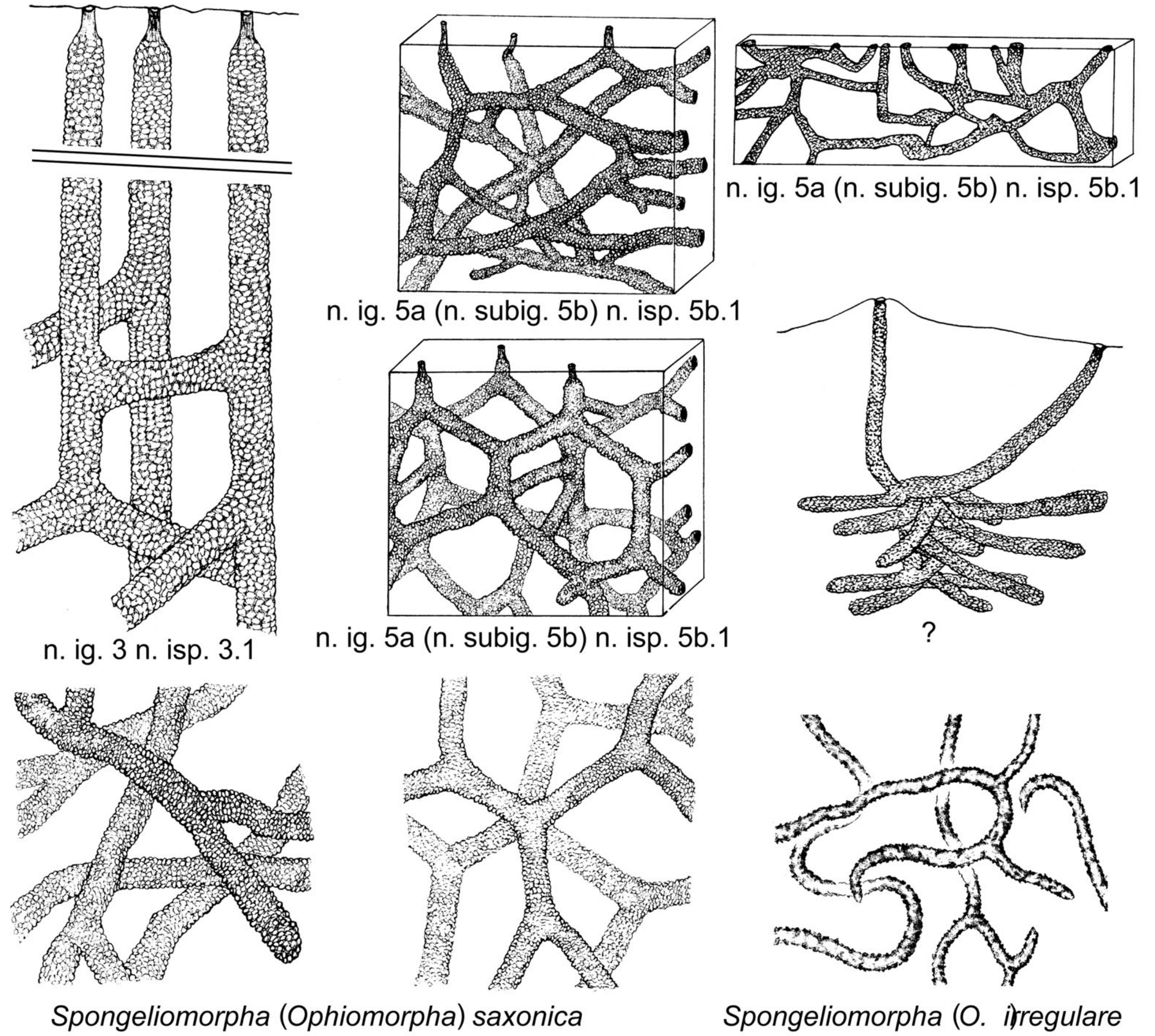

Figure 131: Morphological structures of Recent decapod crustacean burrows after FREY et al. (1978). If these structures were found fossilized, the names below would apply after the newly introduced classification scheme. Modified after FREY et al. (1978: fig. 2). Not to scale.

Ichnogenus *Gyrolithes* SAPORTA, 1884

Type ichnospecies: *Gyrolithes davreuxi* SAPORTA, 1884; by subsequent designation by HÄNTZSCHEL (1962: *W*200).

? 1922 *Dinocochlea ingens* n.gen. et sp.– WOODWARD: 243, pl. 1 fig 1-4 [= difficult to judge since the material consists of concretions, but most likely *Gyrolithes* (*Xenohelix*) isp.].
? 1935 Flint with spiral form. – THOMAS: 9, fig. 1 [= most likely *Gyrolithes* (*Xenohelix*) isp.].
non 1935 Ironstone concretion. – THOMAS: 17, pl. 1 figs. 1-2 [= concretions].
? 1935 Phosphatic nodule. – THOMAS: 17, pl. 1 fig. 3 [= most likely *Gyrolithes* (*Xenohelix*) isp.].
? 1935 Another small sinistral specimen. – THOMAS: 17, pl. 1 fig. 4 [= strongly weathered concretion, cf. *Gyrolithes* (*Xenohelix*) isp.].
? 1935 Another small specimen. – THOMAS: 17, pl. 1 fig. 4 [= strongly weathered concretion, cf. *Gyrolithes* (*Xenohelix*) isp.].
non 1935 Coprolite of a fossil shark. – THOMAS: 17, pl. 1 fig. 6.
non 1935 Clay ironstone. – THOMAS: 17, pl. 2 figs. 1+2 [= concretions].
1935 Clay ironstone concretion. – THOMAS: 17, pl. 2 fig. 3 [= *Gyrolithes* (*Xenohelix*) *clarki*].
1962 Ansicht des Zwischenmittels. – KILPPER: 58, pl. 7 fig.1 [= *Gyrolithes* (*Xenohelix*) *nodosa*].
1962 *Xenohelix* cf. *marylandica.* – KILPPER: 58, pl. 7 figs. 2-3, 5 [= *Gyrolithes* (*Xenohelix*) *nodosa*].
1962 *Xenohelix.* – KILPPER: 58, pl. 7 fig. 4 [= *Gyrolithes* (*Xenohelix*) *nodosa*].
pt 1997 *Gyrolithes* DE SAPORTA, 1884. – JENSEN: 51 [all genera listed in synonymy except for *Spiroscolex* = *nomen dubium*; *Daemonelix* = separate ichnogenus].

Emended diagnosis: Systems built up of tubular structures with circular to elliptical cross-section, more-or-less describing one or more dextral, sinistral, or mixed circular helix structures (coils) essentially upright in the sediment; coils may be connected to each other by horizontal to oblique or vertical unbranched or branched tubular structures; with or without wall-lining; exterior morphology smooth, knobby, with criss-cross ridges and grooves or longitudinal ridges and grooves; radius of individual whorls may increase, decrease or remain constant; diameter of tubular structures may vary.

Remarks: *Gyrolithes* is revised in the course of the revision of the members of the *Spongeliomorpha* group, because *Gyrolithes* structures are assumed to co-occur with *Spongeliomorpha*. However, as stated above, a trace fossil should receive its own name if it is a frequently recurring morphologic unit. In the case of *Gyrolithes*, separate occurrence of complex burrow systems with coiled structures justifies a separate naming. JENSEN (1997) discussed the taxonomy of vertical spiral burrows. Additional ichnogenus synonyms of *Gyrolithes* can be found there. His general concept is followed here, except for the synonymisation of *Daemonelix* with *Gyrolithes* (see below). There are various morphological details that can be measured in *Gyrolithes* (Fig. 132). Among all these morphological features, there seem to be only a few of ichnotaxonomic relevance. MAYORAL & MUÑIZ (1993, 1995, 1998) have shown that most morphometric parameters are irrelevant for the taxonomy of the various ichnospecies of *Gyrolithes*. Their analyses show that almost all morphometric parameters overlap and are, thus, of no use for distinguishing ichnospecies. These investigations support that the currently best way of distinguishing the various ichnospecies of *Gyrolithes* is the gross morphology plus the wall ornamentation and/or wall-lining.

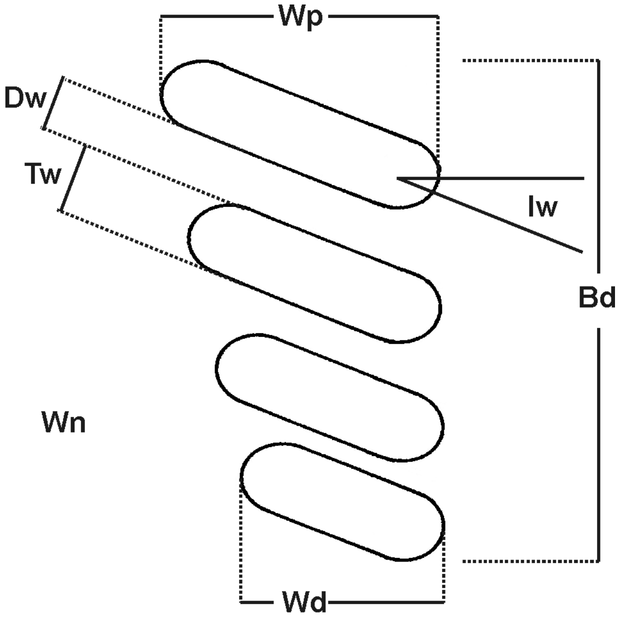

Figure 132: Morphometric parameters which can be measured in *Gyrolithes* structures. **Wp** = proximal width; **Wd** = distal width; **Dw** = distance between whorls; **Tw** = thickness of whorls; **Iw** = inclination of whorls with respect to bedding plane; **Wn** = number of whorls; **Bd** = burrow depth. After measuring the parameters following ratios can be calculated: **Wp** : **Wd**; **Dw** : **Tw**; proximal **Dw** : distal **Dw**; proximal **Tw** : distal **Tw**; **Wp** : proximal **Tw**. However, the currently recognized ichnospecies of *Gyrolithes* can be distinguished on morphological criteria which do not necessarily be described by formula.

Ichnosubgenus *Gyrolithes* (*Gyrolithes*) SAPORTA, 1884

Type ichnospecies: *Gyrolithes davreuxi* SAPORTA, 1884; by subsequent designation by HÄNTZSCHEL (1962: *W*200).

Diagnosis: *Gyrolithes* without wall-lining, external morphology of burrow smooth or with longitudinal to transverse grooves and ridges.

Discussion: In their description of the type material, BROMLEY & FREY (1974) state that one of the most consistent and characteristic features of *Gyrolithes* (*Gyrolithes*) *davreuxi* is the glauconitic wall-lining. So far glauconite is only known from marine environments supposed to form during early diagenesis (ODIN & MATTER, 1981). The wall-lining in the type material of *Gyrolithes* is considered a secondary mineralisation, and thus the wall-lining is considered passive and no relevant ichnotaxobase. In the description such phenomena should be mentioned of course because such observations help in reconstructing the building and diagenetic history of such specimens. In many trace fossils, especially near or at omission surfaces a secondary mineralisation of the burrow boundary and/or wall-lining is known.

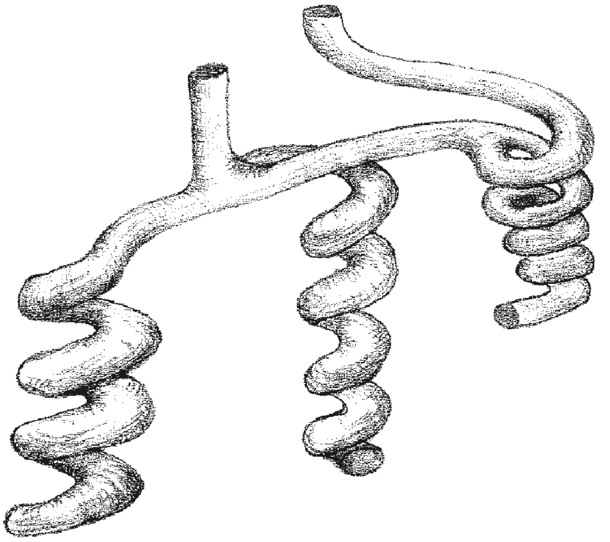

Figure 2: Reconstruction of complex, unlined burrow system of *Gyrolithes* (*G.*) isp. The connecting tubular horizontal burrow parts and the shaft are part of the structure, and thus not named separately. Not to scale

Currently recognized ichnospecies:

Gyrolithes (*Gyrolithes*) *davreuxi* SAPORTA, 1884 [with irregular coils, and occasional branching with enlargements at points of bifurcation]

G. (*G.*) *clarki* (MANSFIELD, 1930) [with more than two regular coils, smooth wall]

G. (*G.*) *mexicanus* (MANSFIELD, 1930) [with regular coils, longitudinal scratch ornaments]

G. (*G.*) *bularti* MACOSTAY, 1967 [with a furrow on the interior of the whorls]

G. (*G.*) *polonicus* FEDONKIN, 1981 [up to two regular coils, tapering terminations]

G. (*G.*) *okinawaensis* MYINT & NODA, 2000 [regular coils with wide galleries]

Tentatively assigned ichnospecies:

G. (*G.*) *vidali* MAYORAL 1986a

G. (*G.*) *variabilis* MAYORAL 1986b

G. (*G.*) *isabeli* MAYORAL 1986b

Discussion: ?*Xenohelix clarki* MANSFIELD, 1930 and ?*Xenohelix mexicana* MANSFIELD, 1930 were only placed with reservations to this ichnogenus by MANSFIELD. They clearly show a spiral nature and tubes with no wall-lining, thus they should be assigned to *Gyrolithes* (*Gyrolithes*). *Xenohelix saxonica* HÄNTZSCHEL, 1935 is synonymous with *G.* (*G.*) *clarki* because no significant differences can be identified. HÄNTZSCHEL (1935) referred to his earlier publication (1934: fig. 1) and designated this specimen as holotype, which shows no wall-lining. A diagnosis was not provided by HÄNTZSCHEL (1935) but the figures and the descriptions are of good quality. One specimen shows a wall-lining and was considered a special form by HÄNTZSCHEL (1934: fig. 4). This specimen should be assigned to *Gyrolithes* (*Xenohelix*) *nodosus*.

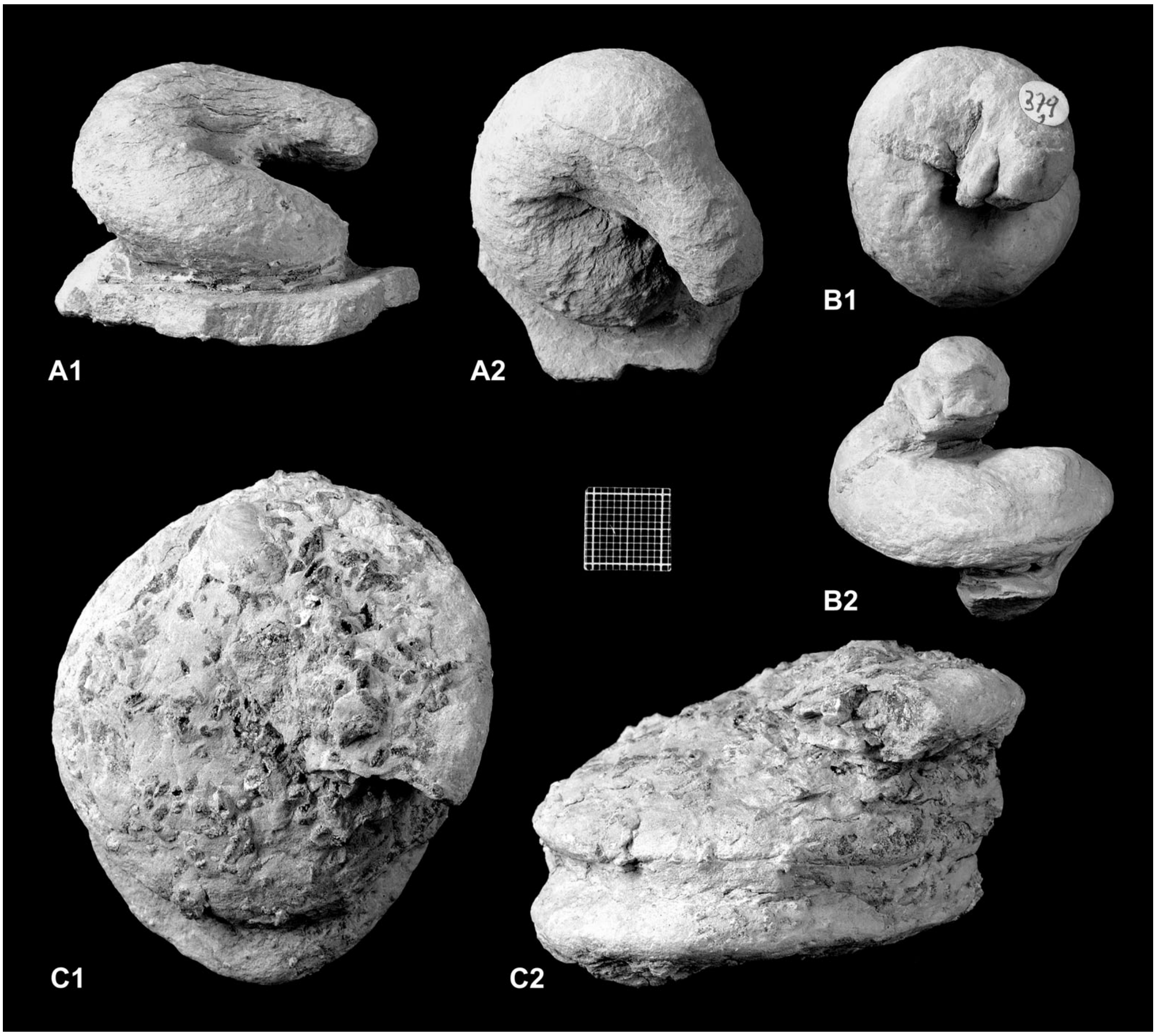

Figure 3: A-B. One complete whorl and tapering terminations of *Gyrolithes* (*Gyrolithes*) *polonicus* FEDONKIN, 1981. **A1**. SMNS 194, Zeiern, Baden-Württemberg, Upper Muschelkalk fullrelief, side view, upside down. **A2**. Same as A1, bottom view. **B1**. SMNS L248a, Dietersweiler, Baden-Württemberg, Upper Muschelkalk, fullrelief, top view. **B2**. Same as B1, side view, upside down. **C1.** *Gyrolithes* (*G.*) *clarki* (MANSFIELD, 1930), SMNS L248c, Haase quarry, Dietersweiler, Upper Muschelkalk 2, fullrelief, top view. **C2**. Same as C1, side view. Millimetre grid for scale.

Gyrolithes (*G.*) *polonicus* FEDONKIN, 1981 is regularly coiled, has a smooth exterior and no wall-lining. However, *G.* (*G.*) *polonicus* seems to have 1 to 2 whorls and tapering terminations, whereas *G.* (*G.*) *clarki* has more than two whorls and blunt terminations. *Gyrolithes* (*G.*) *vidali* MAYORAL 1986a, *G.* (*G.*) *variabilis* MAYORAL 1986b, and *G.* (*G.*) *isabeli* MAYORAL 1986b are likely to be synonymous with *Gyrolithes* (*Gyrolithes*) *clarki* since no significant differences can be identified. However, for a final judgement a restudy of the type material is necessary. For this reason these ichnospecies are only assigned with reservations to *Gyrolithes* (*Gyrolithes*).

Ichnosubgenus *Gyrolithes* (*Xenohelix*) (MANSFIELD, 1927)

Type ichnospecies: *Xenohelix marylandica* MANSFIELD, 1927; by original designation because of monotypy.

Diagnosis: *Gyrolithes* with wall-lining, wall-lining may be smooth or knobby exteriorly.

Currently recognized ichnospecies:

Gyrolithes (*Xenohelix*) *marylandica* (MANSFIELD, 1927) [with smooth wall-lining].
G. (*X.*) *nodosus* MAYORAL & MUÑIZ, 1998 [with knobby wall-lining].

Ichnogenus *Daemonelix* BARBOUR, 1892

Type ichnospecies: *Daemonelix circumaxilis* BARBOUR, 1892: 99, figs. 1-3; by subsequent designation by HÄNTZSCHEL (1975: *W*58).

Emended diagnosis: Tubular structure building one dextral or sinistral helix with constant diameter; lowermost end of helix connected to surface by an oblique, slightly conical structure (tapering upward).

Remarks: The original spelling used by BARBOUR (1892) was *Dæmonelix*. Since the ICZN does not allow letters such as "æ" in scientific names, the former spelling has to be transcribed. This was already done and the name was corrected to *Daimonelix*. However, the letter æ is used in several languages (e.g., French, Danish and Norwegian) and is better transcribed with ae resulting in *Daemonelix*. JENSEN (1997) put *Daemonelix* in synonymy with *Gyrolithes* with reservations, according to his opinion they only differ in size and palaeoenvironmental distribution, which, of course, should not be considered ichnotaxobases. If one compares only fragments of the helix structure, JENSEN's (1997) considerations may be correct. However, this is frequently the case with incomplete material. Considering the entire burrow morphology, there are significant differences between these two ichnogenera (Fig. 135). The long oblique tunnel connecting the lowermost end of the helix with the surface is known only from *Daemonelix* and can be used to separate *Daemonelix* from other coiled ichnogenera.

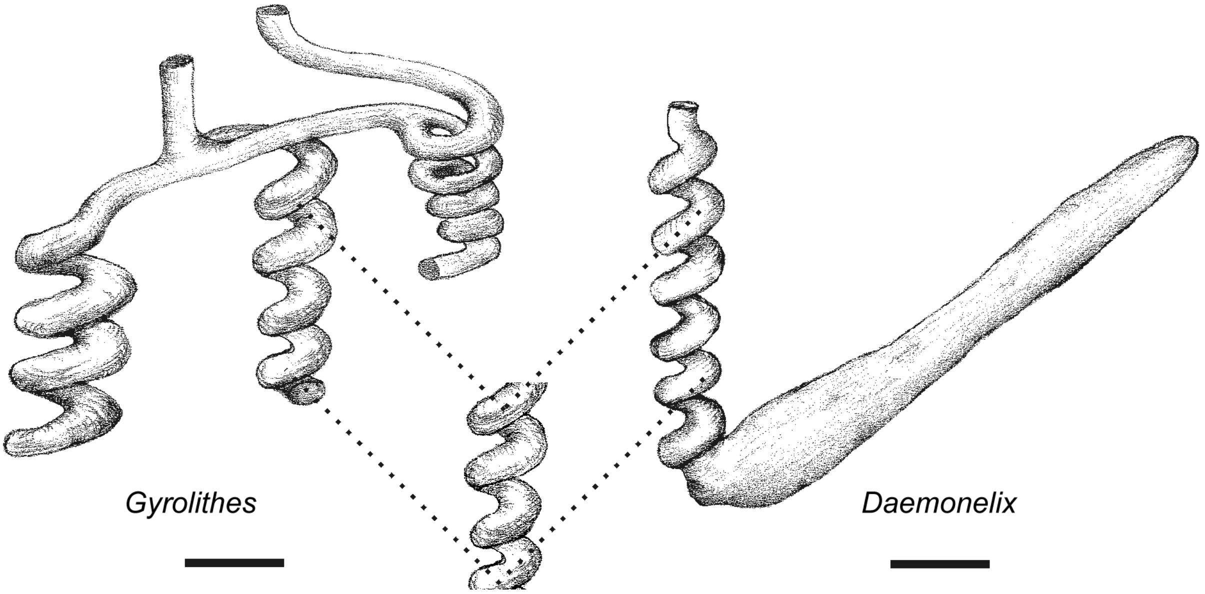

Figure 135: Morphologically similar helicoidal structures of *Gyrolithes* (scale bar: 5cm) and *Daemonelix* (scale bar: 50cm). Entire burrow morphology clearly distinguishes *Gyrolithes* structures from *Daemonelix* burrows.

Ichnogenus *Lapispira* LANGE, 1932

Type ichnospecies: *Lapispira bispiralis* LANGE, 1932: 537, pl. 17 fig. 3a-c, by original designation.

Remarks: The ichnogenus *Lapispira* is supposed to consist of two interconnected helix structures. LANGE (1932: figs. 1-2) presented two wire models of this ichnogenus, which later entered the Treatise. The original material, especially the holotype, which was kept in a private collection, is not as instructive as one would wish for such complex structures. The holotype shows spirals of various diameters, however, not in one plane. The holotype is a more-or-less conical concretion with pyritized tubular structures building a helix. Paratype material shows two spirals in one plane in some specimens but the supposed turn around at the bottom from the larger outer spiral to the smaller, interconnected inner spiral could not be observed. The original material should be restudied, if still available. HÄNTZSCHEL & REINECK (1968) and WINCIERZ (1973), which long were the only references apart from the original description, made their assignments with restrictions because no double helix, and neither the top nor the bottom of a single specimen could be observed. Unfortunately no figures were provided. Recently, LANES et al. (2004) have reported well preserved *Lapispira* from Lower Jurassic deposits of the Neuquén Basin, Mendoza, Argentina, which give new data on the morphology of this rare trace fossil.

Concerning the publication date of WINCIERZ (1973), it should be emphasized that the publication date is 1973 and not 1974as usually cited. The first two issues of *Neues Jahrbuch für Geologie und*

Paläontologie, Abhandlungen **144** were published in October 1973. This affects the newly introduced ichnogenus and ichnospecies by WINCIERZ, which should have the date 1973.

Table 1: Overview of currently recognized ichnospecies of the ichnosubgenus *Spongeliomorpha* (*Spongeliomorpha*) SAPORTA, 1887 and their main morphological differences.

currently recognized ichnospecies of *Spongeliomorpha* (*Spongeliomorpha*) SAPORTA, 1887	**diagnostic morphological features**
S. (*S.*) *paradoxica* (WOODWARD, 1830)	longitudinal scratch ornaments
S. (*S.*) *sudolica* (ZARĘCNI, 1878)	reticulate scratch ornaments
S. (*S.*) *harefieldensis* (WHITE, 1923)	sinuous scratch ornaments
S. (*S.*) *sublumbricoides* (AZPEITIA MOROS, 1933)	short, irregular, oblique to perpendicular scratch ornaments
S. (*S.*) *suevica* (RIETH, 1933)	smooth
S. (*S.*) *oraviense* (KSIĄŻKIEWICZ, 1977)	short, fine, oblique, parallel oriented and grouped scratch ornaments
S. (*S.*) *carlsbergi* BROMLEY & ASGAARD, 1979	heavy perpendicularly arranged scratch ornaments
S. (*S.*) *milfordensis* METZ, 1993	heavy, regular ornamentation forming an acute angle with respect to the median axis
Spongeliomorpha (*S.*) *chevronensis* MUÑIZ & MAYORAL, 2001	chevron-shaped scratch ornaments

Table 2: Overview of currently recognized ichnospecies of the ichnosubgenus *Spongeliomorpha* (*Ophiomorpha*) LUNDGREN, 1891 and their main morphological differences.

currently recognized ichnospecies of *Spongeliomorpha* (*Ophiomorpha*) (LUNDGREN, 1891)	**diagnostic morphological features**
S. (*O.*) *saxonica* (GEINITZ, 1842)	wall-lining with irregularly arranged, single spherical to ovoid pellets
S. (*O.*) *rectus* (FISCHER-OOSTER, 1858)	rarely branching and winding; wall-lining with small, single, spherical to ovoid pellets
S. (*O.*) *borneensis* (KEIJ, 1965)	wall-lining with irregularly arranged, double pellets
S. (*O.*) *annulata* (KENNEDY, 1967)	distinct clay wall-lining with irregular scratch ornaments on the exterior
S. (*O.*) *rudis* (KSIĄŻKIEWICZ, 1977)	irregular mazes; wall-lining with irregular ovoid pellets, smooth and scratched exterior
S. (*O.*) *irregulare* (FREY, HOWARD & PRYOR, 1978)	irregularly arranged conical pellets
S. (*O.*) nomen novum 1	perpendicularly arranged ovoid pellets

Table 3: Overview of currently recognized ichnospecies of the ichnosubgenus *Gyrolithes* (*Gyrolithes*) SAPORTA, 1884 and their main morphological differences.

currently recognized ichnospecies of *Gyrolithes* (*Gyrolithes*) SAPORTA, 1884	**diagnostic morphological features**
G. (*G.*) *davreuxi* SAPORTA, 1884	unlined, irregular coils, and occasional branching with enlargements at points of bifurcation
G. (*G.*) *clarki* (MANSFIELD, 1930)	unlined, regular coils, smooth exterior
G. (*G.*) *mexicanus* (MANSFIELD, 1930)	unlined, regular coils, longitudinal scratch ornaments
G. (*G.*) *bularti* MACOSTAY, 1967	unlined, with a furrow on the interior of the whorls
G. (*G.*) *okinawaensis* MYINT & NODA, 2000	unlined, wide galleries

Table 4: Overview of currently recognized ichnospecies of the ichnosubgenus *Gyrolithes* (*Xenohelix*) (MANSFIELD, 1927) and their main morphological differences.

currently recognized ichnospecies of *Gyrolithes* (*Xenohelix*) (MANSFIELD, 1927)	**diagnostic morphological features**
Gyrolithes (*Xenohelix*) *marylandica* (MANSFIELD, 1927)	wall-lining, smooth exterior
Gyrolithes (*Xenohelix*) *nodosus* MAYORAL & MUÑIZ, 1998	wall-lining, knobby exterior

DISTRIBUTION AND PALAEOECOLOGY OF KEUPER TRACE FOSSILS

PALAEOENVIRONMENTS AND ICHNOCOENOSES

Covering a large area of southern Germany (Fig. 9) Keuper beds containing invertebrate trace fossils suitable for palaeoecological studies are rare. Although invertebrate trace fossils are frequently found in Keuper beds they are dominantly monospecific with a rather limited distribution. The distributional pattern of nonmarine trace fossils in the Germanic Triassic – as it is common for nonmarine environments – is the major problem for detailed palaeoecological analyses (BUATOIS & MÁNGANO 2004). One of the studied outcrops, Vetter quarry at Schönbachsmühle, is an active quarry. One summer season hundreds of specimens of various ichnotaxa were collected. Six month later a second visit and for additional search of invertebrate trace fossils was not successful. Only a few poorly preserved *Skolithos* isp. A were found.

This study is mainly focusing on general ichnotaxonony and the systematics of the invertebrate trace fossils from the Keuper and related forms. However a few comments on two ichnofaunas are presented. As stated above most finds are limited to one slab with a few specimens, which is insufficient for palaeoecological reconstructions. The ichnofauna from the Hassberge Formation in the Haßberge area and the one from the Würzburg Formation between Seubrigshausen and Thundorf in Ufr. are worth being mentioned.

HASSBERGE AREA

The studied sediments of the Coburger Sandstein (Hassberge Fm) are traditionally interpreted as fluvial and playa lake deposits (e.g., AIGNER & BACHMANN 1998). The trace fossils described here support this view but offer a more precise interpretation. The trace fossil assemblage contains vertical domichnial forms (e.g., *Skolithos, Polykladichnus*) and horizontal pascichnial forms (e.g., *Cruziana problematica*), including very characteristic meniscate trace fossils (*Scoyenia gracilis*, *Taenidium barretti*), which are typical of the *Scoyenia* ichnofacies (SEILACHER 1967). The definition of this ichnofacies was specified by BUATOIS & MÁNGANO (1995). This ichnofacies is typical of non-marine, inundated environments, such as floodplains and lake margins (BUATOIS & MÁNGANO 1998).
Two frequently occurring palaeo-ichnocoenoses can be identified in the studied Triassic rock sections.

The *Cruziana* – cf. *Polykladichnus* ichnocoenosis

This ichnocoenosis contains *Cruziana problematica*, cf. *Polykladichnus* isp., and *Skolithos* isp. B and occurs in marginal parts of trough cross-bedded sandstones. *C. problematica* was produced under subaqueous conditions in shallow fluvial channels in a lake-margin plain setting or in a floodplain environment. *Skolithos* isp. B and cf. *Polykladichnus* isp. point to non-aquatic conditions after filling and/or drying out of the channels. This view is also supported by desiccation cracks associated with these trace fossils.

The *Rusophycus versans* ichnocoenosis

This ichnocoenosis is dominated by *Rusophycus versans*, *Taenidium barretti*, *Scoyenia gracilis* and *Skolithos* isp. A. It is typical of an ephemeral lake setting characterized by coarse-grained, platy, poorly sorted, locally rippled sandstones, occasionally with desiccation cracks, rare trough cross-bedded sandstones, intercalated with greenish mudstones/siltstones with a high content of detrital mica.

The massive fluvial sandstones, like those at the base of the succession in the Vetter quarry at Schönbachsmühle, are almost barren of trace fossils. Traces occur only at the base of a single sandstone bed in that quarry. They are double ridges interpreted as traces of swimming tetrapods.

The two ichnocoenoses occur in several outcrops within the study area in the same facies context. The high burrow density as well as the great variety of different trace fossils cotradicts an interpretation as purely fluvial or as playa setting. At least for a certain period of time, stable palaeoenvironmental conditions must have been established, otherwise the diversity of the ichnofossils would not have been so high. According to the palaeogeographical setting, close to an active half-graben fault, the existence of persistent lake systems appears plausible. The value of these described ichnocoenoses as indicators of particular palaeonvironments is high. However, the value for more generalized use awaits further studies in areas with similar depositional histories.

SEUBRIGSHAUSEN AND THUNDORF AREA

The trace fossils occur in grey to green, fine-grained, trough cross-bedded sandstones to siltstones with mudstone intercalations of the Werksandstein (Würzburg Fm) in outcrops between Seubrigshausen and Thundorf i. Ufr. The deposits are interpreted as overbank deposits. Due to the fine grain-size a trace fossil fauna of minute burrows, trackways, and trails has been preserved. Among the structures which can be assigned to ichnotaxa are: *Halopoa imbricata*, *Halopoa* isp., *Palaeophycus* isp., *Planolites beverleyensis*, *Planolites* isp., *Lockeia siliquaria*, *Rusophycus* cf. *carbonarius*, *Cruziana* cf. *problematica*. Apart from these structures some remarkable additional forms can be identified, however, they cannot be assigned to an ichnogenus. These are: flat-conical hypichnial structures and a bilobed trace indet. In addition, a probable resting trace of a *Triops* could be identified (Fig. 110).

Although being of small size the ichnocoenosis is moderately to highly diverse. Some of the trace fossils can be related to arthropods (*Cruziana*, *Rusophycus*, and a probable *Triops* resting trace). The minute *Lockeia siliquaria* specimens also are most likely produced by small arthropods, maybe conchostracans (see discussion above). The other trace fossils (*Halopoa*, *Planolites*, and *Palaeophycus,* bilobed burrow indet., flat-conical hypichnial structures) may be explained as being produced by vermiform deposit feeders. Associated with the invertebrate trace fossils are structures which can be related to fish (Fig. 113). It appears that the ichnocoenosis from the Werksandstein represents one of the rare occasions in fluvial settings where the colonization window was open long enough to allow the development of a fauna, and subsequent sedimentation did not destroy their traces left in the sediment.

STRATIGRAPHICAL AND GEOGRAPHICAL DISTRIBUTION OF THE STUDIED TRACE FOSSILS FROM THE KEUPER

The table below lists the studied trace fossils from the Keuper formations. The Stuttgart Formation, the Hassberge Formation, and the Würzburg Formation in general host most of the trace fossils. The Upper Erfurt Formation seems barren of trace fossils where as the Trossingen and the Steigerwald Formations at least host one report. Although the Stuttgart formation in Baden-Württemberg bears a moderate number, its Bavarian counterpart appears barren of invertebrate trace fossils.

Apart from the Schilfsandstein, the Coburger Sandstein and the Werksandstein fluvial deposits show the highest trace fossil diversity in the Keuper. However, most of the trace fossils occur in the overbank facies not in the channel facies.

Table. 5: Stratigraphical and geographical distribution of the studied Keuper trace fossils. The sizes of the fields for the formations in the stratigraphical column is not to age scale.

Baden-Württemberg		**Formations**	**Bavaria**	
	Teichichnus duplex	Exter Formatiom		
	Diplocraterion parallelum			
	Gyrochorte comosa			
	Heliophycus seilacheri			
	Solemyatuba ypsilon			
	Rusophycus isp.	Trossingen Fm		
	Skolithos isp. A	Löwenstein Fm		
	Nereites cf. *jacksoni*			
	Taenidium crinoidiforme			
	Planolites montanus			
		Hassberge Fm	*Arenicolites* isp.	
			Planolites beverleyensis	
			Planolites montanus	*Lockeia cunctator*
			Planolites cf. *montanus*	*Lockeia siliquaria*
			Arenicolies isp.	*Skolithos* isp. A & B
			Polykladichnus aragonensis	Cruziana pascens
			cf. *Planolites* isp.	Cruziana problematica
			Helminthoidichnites tenuis	*Rusophycus carbonarius*
	Arthrophycus alleghaniensis		cf. *Multina* isp.	*Rusophycus versans*
	Protovirgularia cf. *rugosa*		*Scoyenia gracilis*	rows of small knobs
	Rusophycus versans		*Taenidium barretti*	small irregular networks
Helicerina keuperina		Steigerwald Fm		
	Linckichnus pseudoxylotrypanon	Stuttgart Fm		
	Lockeia vagans			
Rusophycus eutendorensis	*Biformites insolitus*			
Kouphichnium gracilis	*Skolithos* isp. A & B			
Kouphichnium variabilis	*Arthrophycus alleghaniensis*			
Tasmanadia twelvetreesi	*Arthrophycus* isp.			
		Grabfeld Fm	*Protovirgularia dichotoma*	
			cf. *Chomatichnus* isp.	
		Upper Erfurt Fm		
		Würzburg Fm	*Cruziana* cf. *problematica*	*Halopoa imbricata*
			Rusophycus cf. *carbonarius*	*Halopoa* isp.
			Arthrophycus isp.	*Palaeophycus* isp.
			Gyrochorte comosa	
	Lockeia siliquaria		cf. *Planolites* isp.	*bilobed burrow indet*
	Arthrophycus alleghaniensis		(*Alcyonidiopsis* isp.)	flat-conical hypichnial structures
	Arthrophycus isp.		*Planolites beverleyensis*	probable *Triops* resting trace
	cf. *Helicerina* isp.	Lower Erfurt Fm		

ACKNOWLEDGEMENTS

I am deeply indebted to my lovely wife SILKE for her continuous support of my work and her faith in me. I wish to express my thanks to JAN-NIKLAS for his smiles.

I am grateful to my supervisor Professor Dr. FRANZ T. FÜRSICH, Würzburg for giving me the possibility to carry out this PhD study, his support and his patients with me handing in my thesis.

Special thanks are due to apl. Professor Dr. GERD GEYER (Würzburg) for endless discussions and his steady advice. He is also acknowledged for language improvements and constructive criticism on various manuscripts.

Many thanks to PD Dr. MARKUS WILMSEN and Dr. MICHAEL HAUTMANN (both Würzburg) for their constructive criticism and language improvements of the text.

My dear colleagues Dr. MARKUS BERTLING (Münster), Dr. SIMON J. BRADDY (Bristol), Prof. Dr. RICHARD G. BROMLEY (Copenhagen), Dr. JORGE F. GENISE (Trelev), Dr. DUNCAN MCILROY (Newfoundland), Dr. ANDY K. RINDSBERG (Tuscalosa), and especially my collaborator Prof. Dr. ALFRED UCHMAN (Krakov) are gratefully acknowledged for fruitful discussions, inspirations and advice.

Dr. CONRAD C. LABANDEIRA (Washington) is acknowledged for his help with *Linckichnus pseudoxylotrypanon.* Dr. SÖREN JENSEN (Extremadura) is acknowledged for his constructive criticism on the *Sabellarifex* and especially *Monocraterion* issue.

All fair trade coffee farmers in Africa and South Amerika are gratefully acknowledged for providing the *sine qua non* of scientific existence.

AUGUST ILG (Düsseldorf) is gratefully acknowledged for his help in creating a pdf file out of a vast number of word-documents.

Composers BEETHOVEN, MOZART, and TSCHAIKOWSKI as well as AC/DC, Deep Purple and Rammstein permanently supported this study with good music.

Everybody not explicitly named here (whom I might have forgotten) but who has contributed to the success of this study is also wholeheartedly thanked.

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APPENDIX I

Nomenclatural rules

Although many of the terms presented here are explained in the glossary of the *Code* (ICZN 1999 and previous versions) their frequent misuse prompts a separate short communication of how to use them. This counts especially for frequently misused terms such as *nomen novum*, *nomen oblitum* etc., or the difference between an available name and an invalid name. In the following, several lists of terms and their meanings are given, differentiated between official defined (means explained in the glossary of the *Code*) and recommended for use, officially defined and not recommended for use, and old fashioned and/or not officially defined terms not recommended for use. Although any zoologist or palaeozoologist, respectively, should consult the ICZN when introducing new names it seems that this is not the case. Apparently not every university library holds a copy of the *Code*. The number of possible references of bad examples that could be cited at this place is nearly endless. However, the author resigns to name examples here. By using the lists given below readers may go through publications and find negative examples on their own. In order to make ‘systematic life’ a bit easier especially for young palaeozoologist I have compiled several frequently used terms but also apparently old-fashioned terms, which were used by our predecessors. By no means the author intends to question the authority of the International Commission on Zoological Nomenclature, hence officially used terms are clearly separated and explained in the exact wording of the English version of the text of the fourth edition of the International Code of Zoological Nomenclature, with exact reference to the bibliographic source. In addition, inofficial terms are explained in order to help understanding their meaning, and hopefully resulting in a more uniform use of official terms and non-use of unofficial terms. The presented list may also content some terms frequently and officially used in botany or palaeobotany, respectively, which are not recommended for use in a zoological context. The recommendations are only relevant for zoological publications and not for botanical publications since this subject is covered by the ICBN. The lists provided only contain the most frequently used terms and are by no means considered complete. Authors writing articles on zoological topics are asked to read the *Code* carefully and to follow the recommendations given in the *Code* as well. Although not being official rules or articles, the recommendations given in the *Code* do make sense and should be followed. Since this contribution only deals with the most frequently used terms in a zoological context and not the plethora of additional terms I recommend LINCOLN et al. (1998) for further reading.

List and explanation of official terms as explained in the glossary of the *Code* (1999: and recommended for use in nomenclatural acts.

combination: The association of a generic name and a specific name to form the name of a species; or of a generic name with a specific name and a subspecific name to form the name of a subspecies.

new combination: The first combination of generic name and a previously established species-group name.

available name: A scientific name applied to an animal taxon that is not excluded under ICZN Article 1.3 and that conforms to the provisions of ICZN Articles 10 to 20.

conserved name: A name otherwise unavailable or invalid that the Commission, by use of its plenary power, has enabled to be used as a valid name by removal of the known obstacles to such.

excluded name: A name that under ICZN Article 1.3 cannot be an available name, or one that has been disclaimed (see ICZN Articles 8.2, 8.3).

inappropriate name: A name that denotes a character, a quality, or an origin not possessed by the taxon bearing that name.

invalid name: An available name which either (1) is objectively invalid (i.e. it is a junior homonym or a junior objective synonym of a **potentially valid name**, or must be rejected under the provisions of the *Code*, or has been suppressed by the Commission), or (2) is subjectively invalid (because it is considered subjectively to be a junior synonym or to be inapplicable to a taxonomic taxon).

new replacement name (*nomen novum*): A name established expressly to replace an already established name. A nominal taxon denoted by a new replacement name (*nomen novum*) has the same name-bearing type as the nominal taxon denoted by the replacement name [ICZN Arts. 67.8, 72.7].

potentially valid name: An available name which is not objectively invalid.

replacement name: See **new replacement name (*nomen novum*)** and **substitute name**.

rejected name: (1) A name which, under the provsions of the *Code*, cannot be used as a valid name which is set aside in favour of another name. (2) A name which, as a matter of taxonomic judgment, is either treated as a junior subjective synonym of a name used as valid or is believed not be applicable to the taxon under consideration.

substitute name: Any available name, whether new or not, used to replace an older available name.

suppressed name: see **suppression**.

unavailable name: A scientific name that does not conform to ICZN Articles 10 to 20, or that is an excluded name under ICZN Article 1.3.

valid name: The correct name for a taxonomic taxon, i.e. the oldest potentially valid name of a name-bearing type which falls within an author's concept of the taxon.

vernacular name: A name of an animal or animals in a language used for general purposes as opposed to name proposed only for zoological nomenclature.

***nomen dubium* (pl. *nomina dubia*):** Latin term meaning "a name of unknown or doubtful application".

***nomen novum* (pl. *nomina nova*):** Latin term equivalent to "new replacement name".

nomen nudum **(pl. *nomina nuda*):** Latin term referring to a name that, if published before 1931, fails to conform to ICZN Article 12; or, if published after 1930, fails to conform to ICZN Article 13. A *nomen nudum* is not an available name, and therefore the same name may be made available later for the same or a different concept; in such a case would the authorship and date [ICZN Arts 21, 50] from that act of establishment, not from any earlier publication as a *nomen nudum*.

nomen oblitum **(pl. *nomina oblita*):** Latin term (meaning "forgotten name") applied after 1 January 2000 to a name, unused since 1899, which as a result of an action taken under ICZN Article 23.9.2 does not take precedence over a younger synonym or homonym in prevailing usage; the younger name which takes precedence over a *nomen oblitum* may be called a *nomen protectum* (see there). The term *nomen oblitum* was also applied to a disused senior synonym rejected between 6 November 1961 and 1 January 1973 under ICZN Article 23b of the *Code* editions then in force (see ICZN Article 23.12.2). *Nomina oblita* remain available names; see ICZN Articles 23.9 and 23.12 for conditions controlling their use as valid names.

nomen protectum **(pl. *nomina protecta*):** Latin term (meaning "protected name") applied to a name which has been given precedence over its unused senior synonym or senior homonym relegated to the status of nomen oblitum (see there, and IZCN Article 23.9.2).

I strictly recommend the use of officially recommended and defined terms only. If, for instance, an author wants to express that the particular name she or he is dealing with is used in different senses, it is recommended to state this in an explanatory sentence rather than using a term such as '*nomen ambiguum'* although this term may be used by palaeobotanists. In the long run this will help creating a clear and uniform understanding of official nomenclatural terms in a zoological context.

List and explanation of inofficial Latin terms not recommended for use in nomenclatural acts; terms in bold are official equivalents, for their explanation see above.

nomen ambiguum: ambiguous name
nomen confusium (= ***nomen dubium***)
nomen conservandum (= ***nomen protectum***)
nomen corrigendum: corrected name, in case of an original misspelling.
nomen substitutum (= **replacement name**)
nomen triviale (= **vernacular name**)
nomen nullum (= ***nomen nudum***)

Explanations of additional frequently used terms explained in the glossary of the Code if not otherwise stated:

***corrigendum* (pl. *corrigenda*):** A note published by an author, editor, or publisher of a work, expressly to cite one or more errors or omissions in that work together with their corrections.

emendation: (1) Any intentional change in the original spelling of an available name [ICZN Article 33.2]. (2) An available name formed by intentionally changing the original spelling of an available name.

justified emendation: The correction of an incorrect original spelling [ICZN Article 33.2.2].

unjustified emendation: Any emendation other than a justified emendation [ICZN Article 33.2.3].

Erratum (pl. Errata): Error in printing or writing (not an official term).

errata slip: List of errors, misprints, etc. in a printed book (not an official term).

***lapsus calami* (sing. and pl.):** Latin term meaning "slip (or slips) of the pen", i.e. an error (or errors) made by an author in writing a text, such as a misspelling of a name; contrasted with copyist's or printer's errors [ICZN Article 32.5.1].

suppression (suppress): A ruling by the Commission, using its plenary power, (1) that a work is to be deemed, for nomenclatural purposes, as unpublished, or that names and acts in it are not available; or (2) that an available name is never to be used as valid because (a) it is available only for the purpose of homonymy ("partial suppression") or (b) it is not available for the purposes of priority and homonymy ("total suppression"; but a totally suppressed species-group name may still denote the type species of a nominal genus or subgenus [ICZN Article 81.2.1]); or (3) that an available name is only to be used as valid under stated conditions (e.g. when not considered a synonym of a particular later name) ("conditional suppression").

synonym: Each of two or more names of the same rank used to denote the same taxonomic taxon.

junior synonym: Of two synonyms: the later established, or in the case of simultaneous establishment that not given precedence under ICZN Article 24. See also ICZN Article 23.9.

objective synonym: Each of two or more synonyms that denote nominal taxa with the same name-bearing type, or (in the cases of family-group and genus-group) that denote nominal taxa with name-bearing types whose own names are themselves objectively synonyms.

senior synonym: Of two synonyms: the earlier established, or in the case of simultaneous establishment given precedence under ICZN Article 24. See ICZN Article 23.9.

subjective synonym: Each of two or more names whose synonymy is only a matter of individual opinion , i.e. it is not objective. See also ICZN Article 61.3.1.

type: A term used alone, or forming part of a compound term, to denote a particular kind of specimen or taxon.

allotype: A term, not regulated by the *Code*, for a designated specimen of opposite sex to the holotype [ICZN Recommendation 72A].

cotype: A term not recognized by the *Code*, formerly used for either syntype or paratype, but that should not now be used in zoological nomenclature [ICZN Recommendation 73E].

genotype: Taxonomy: A term not recognized by the *Code*, formerly used type species, but that should not now be used in zoological nomenclature [ICZN Recommendation 67A].

Evolutionary biology: Genetic constitution of an organism, as opposed to its physical appearance (**phenotype**).

hapanotype: One or more preparations consisting of directly related individuals representing distinct stages in the life-cycle, which together form the name-bearing type in an extant species of protistan [ICZN Article 72.5.4]. A hapanotype, while a series of individuals, is a holotype that must not be restricted by lectotype selection; however, if a hapanotype is found to contain individuals of more than one species, components may be excluded until it contains individuals of only one species [ICZNN Article 73.3.2].

holotype: The single specimen (except in the case of a **hapanotype**, see there) designated or otherwise fixed as the name-bearing type of a nominal species or subspecies when the nominal taxon is established.

lectotype: A syntype designated as the single name-bearing type specimen subsequent to the establishment of a nominal species or subspecies [ICZN Article 74].

name-bearing type: The type genus, type species, holotype, lectotype, series of syntypes (which together constitute the name-bearing type) or neotype that provides the objective standard of reference whereby the application of the name of a nominal taxon can be determined.

neotype: The single specimen designated as the name-bearing type of a nominal species or subspecies when there is a need to define the nominal taxon objectively and no **name-bearing type** is believed to be extant. If stability and universality are threatened, because an existing name-bearing type is either taxonomically inadequate or not in accord with the prevailing usage of a name, the Commission may use its plenary power to set aside that type and designate a **neotype**.

paralectotype: Each specimen of a former syntype series remaining after the designation of a **lectotype** [ICZN Article 72.1.3, Recommendation 74F].

paratype: Each specimen of a type series other than the **holotype** [ICZN Recommendation 73D].

syntype: Each specimen of a type series (see there) from which neither a **holotype** nor a **lectotype** has been designated [ICZN Articles 72.1.2, 73.2, 74]. The syntypes collectively constitute the name-bearing type.

topotype (topotypic): A term, not regulated by the *Code*, for a specimen originating from the type locality of the species or subspecies to which it is thought to belong, whether or not the specimen is part of the type series.

type series: The series of specimens, defined in ICZN Articles 72.4 and 73.2, on which the original author bases a new nominal species-group taxon. In the absence of a **holotype** designation, any such specimen is eligible for subsequent designation as the name-bearing type (**lectotype**); pending **lectotype** designation, all the specimens of the type series are **syntypes** and collectively they constitute the name-bearing type. Excluded from the type series are any specimens the original author expressly excludes or refers to as distinct variants, or doubtfully includes in the taxon.

type specimen: A term used in previous editions of the *Code* for a **holotype**, **lectotype** or **neotype**, or for any **syntype**; also used generally for any specimen of the type series (see there).

Old terms not recommended for further use:

archetype, archetypical: The hypothetical ancestral type or the earliest common ancestor.

morphotype: A specimen selected to represent a given intrapopulational variant.

phenotype: The sum of all observable structures and functional properties of an organism; the product of the interaction between the **genotype** (in the evolutionary biological sense!) and the environment.

Additional terms that should be explained:

monotypy: The situation arising (1) when an author establishes a nominal genus or subgenus for what he or she considers to be a single taxonomic species and denotes that species by an available name (the nominal species so named is the type-species by monotypy) [68.3]; or (2) when an author bases a nominal species-group taxon on a single specimen but does not explicitly designate it as **holotype** (**holotype** by monotypy; see ICZN Article 73.1.2].

polytypic

Principle of the First Reviser: The principle that the relative precedence of two or more names or nomenclatural acts published on the same date, or of different original spellings of the same name, is determined by the First Reviser [ICZN Article 24.2].

Principle of Priority: The principle that the valid name of a taxon is the oldest available name applied to it (taking into consideration the other provisions of ICZN Article 23), provided that the name is not invalidated by any provision of the *Code* or any ruling of the Commission [ICZN Article 23].

type horizon: (*stratum typicum*)**:** The geological stratum from which the name-bearing type of a nominal species or subspecies was collected.

type locality: (*locus typicus*)**:** The geographical (and, where relevant, the stratigraphical) place of capture, collection, or observation of the name-bearing type of a nominal species or subspecies [ICZN Article 76.1, Recommendation 76A].

ex grege (ex gr.): In its original meaning: “Rising above the flock” means exeptional.

In nomenclature: To connect two names of two authors when the second author validly published a name proposed by, but not validly published by, the first author.

page priority: Does not exist as such; only if there are no other provisions of the *Code* it is recommended [ICZN Recommendation69A10] that in a publication the first validly introduced and aviailable name in that publication should be taken into account (also see **Principle of Priority**).

Although the disciplines of nomenclature, taxonomy, and systematics are not very popular among todays' scientists these disciplines are the backbone not only of vertebrate palaeontology. Only with well-understood and well-defined terms and taxa reliable statements can be made on evolutionary patterns, palaeoecological value of certain animals or trace fossils etc. With this small contribution I hope to take away a bit of the fear people seem to have while reading and/or writing papers dealing with systematics, nomenclature, or taxonomy.

APPENDIX II

List of trace fossils described from the Germanic Keuper. * traditional names of lithostratigraphic units.

original determination	**author, formation, locality**	**recommended taxonomic use**
Tubifex antiquus PLIENINGER (pl. 1 fig. 5)	PLIENINGER 1845, Keuper near Stuttgart	*Skolithos* cf. *magnus*
Isopodichnus moenanus KUHN (text-fig. 1)	KUHN (1937), Hassberge Formation (*Semionotensandstein), Schmachtenberg/Main	*Cruziana problematica*, *Rusophycus carbonarius* (after KEIGHLEY & PICKERILL 1996)
Steigerwaldichnium heimi KUHN (text-fig. 2a, b)	KUHN (1937), Grabfeld Formation (**Acrodus* Bank), Zell (Unterfranken), Zeil (Steigerwald)	*Arthrophycus* isp.
Annelidichnium triassicum KUHN (text-fig. 3)	KUHN (1937), Grabfeld Formation (**Acrodus* Bank), Oberschwappach	*Scoyenia gracilis*
sternförmige Lebensspur (star-shaped trace) (fig. 4)	KUHN (1937), Grabfeld Formation (**Acrodus* Bank), Zell (Steigerwald)	inorganic structure (most probably desiccation cracks)
Palaeophycus-Typ (text-fig. 5).	KUHN (1937), Grabfeld Formation (**Acrodus* Bank), Dingolshausen	*Planolites montanus*
Wurmgänge (= worm burrows) (pl. 2 fig. 2-3)	HAARLÄNDER 1938, Hassberge Formation (*Blasensandstein), Raindorf quarry	*Planolites montanus*
Corophioides ? RIETH (text-fig. 232e)	SCHMIDT 1938, Exter Formation (*Rhätsandstein), Tübingen	*Diplocraterion parallelum*
Isopodichnus sp. (text-fig. 1-2)	LINCK 1942, Stuttgart Formation (*Schilfsandstein), Mühlbach, Weser Formation (*Ob.Gipskeuper), Eutendorf	*Rusophycus* isp. (after KEIGHLEY & PICKERILL 1996)
Isopodichnus eutendorfensis LINCK (text-fig. 3, 5, 7)	LINCK 1942, Hassberge Formation (*Kieselsandstein), Eutendorf	*Rusophycus eutendorfensis*
Isopodichnus eutendorfensis LINCK (text-fig. 8)	LINCK 1942, not indicated	*Rusophycus carbonarius*
Isopodichnus raeticus LINCK (text-fig. 9)	LINCK 1942, Exter Formation, Tübingen	washed-out *Rusophycus* isp.
Cylindricum gregarium LINCK (pl. 1 fig. 1-3)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Skolithos* isp. B
skulpturierte Rinnen-Ausgüsse (= sculptured channel-fills) (pl. 3 fig. 2)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Arthrophycus* isp.
Isopodichnus sp. (pl. 2 fig. 3)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Rusophycus* isp.
Ichnyspica pectinata LINCK (pl. 2 fig. 1)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Tasmanadia twelvetreesi*
Ichnyspica pectinata LINCK (pl. 2 fig. 2)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Tasmanadia twelvetreesi*
Zopfwülste (plaited pads) (pl. 3 fig. 3)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Arthrophycus alleghaniensis*
gekörnelte Tunnel-Geflechte (knobbed 'tunnel-garlands') (pl. 3 fig. 1)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	indet.
Biformites insolitus LINCK (text-fig. 1, pl. 4 fig. 1-2)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Biformites insolitus*
bogenförmige, zuweilen dreistrahlige Lebensspuren (= arched trace, occasionally three times radiating) (pl. 4 fig. 3)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	desiccation cracks
Limuludichnus variabilis LINCK (text-fig. 2, pl. 5 fig. 1-2, pl. fig. 1)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Kouphichnium variabilis*
Limuludichnulus gracilis LINCK (text-fig. 4, pl. 6 fig. 5-6, pl. 6)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Kouphichnium* isp.
Limuludichnus variabilis LINCK (pl. 7 fig. 1)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Kouphichnium gracilis*.
einzeilige Reihenhöcker-Spur (= single row of humps) (pl. 8 fig. 1-3)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Lockeia vagans*
Pelecypodichnus amygdaloides SEILACHER (pl. 12 fig. 1)	SEILACHER 1953, ?württembergischer Keuper, locality unknown, age questionable	*Lockeia siliquaria*
Cruziana? *rhaetica* LINCK	SEILACHER 1953, Exter Formation (*Rhät-Sandstein), Hängnach quarry	*Rusophycus* isp.
Saggitichnus lincki SEILACHER (pl. 13 fig. 1-2)	SEILACHER 1953, Stuttgart Formation (*Schilfsandstein), Sternenfels	*Saggitichnus lincki* SEILACHER [maybe washed out *Rusophycus* isp.]
Planolites sp. (pl. 1 fig. 1)	LINCK 1961, Löwenstein Formation (*Stubensandstein), Stromberg	?*Planolites* isp.
Taenidium crinoidiforme LINCK (pl. 1 fig. 2)	LINCK 1961, Löwenstein Formation (*Stubensandstein), Cleebronn	*Taenidium crinoidiforme*
Taenidium sp., kleine büschelige Form (= small	LINCK 1961, Löwenstein Formation	*Planolites montanus*

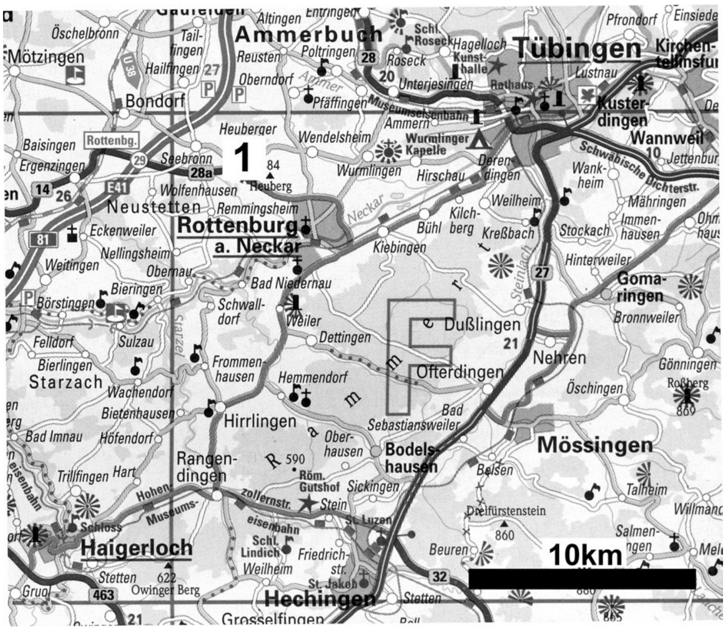
fascicular form) (pl. 2 fig. 1)	(*Stubensandstein), Ochsenbach	
Taenidium duplum LINCK (pl. 3 fig. 1)	LINCK 1961, Löwenstein Formation (*Stubensandstein), Feuerbach	*Nereites* cf. *jacksoni*
Cylindricum grande LINCK = *Tubifex antiquus* PLIENINGER (text-fig. 1, pl. 4 fig. 1-2, pl. 5 fig. 1-2)	LINCK 1961, Löwenstein Formation (*Stubensandstein), Stromberg	*Skolithos* cf. *magnus*
Palaeophycus sp., kleine Form (= small form) (pl. 1 fig. 3)	LINCK 1961, Löwenstein Formation (*Stubensandstein), Stromberg	?*Planolites montanus*
Palaeophycus sp. große Form (= large form) (text-fig. 2, pl. 2 fig. 2)	LINCK 1961, Löwenstein Formation (*Stubensandstein), Stromberg	?*Palaeophycus* isp.
Isopodichnus (p. 31, pl. 14. fig. 4), 'Kaffebohnen' (= coffee-bean)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Rusophycus* cf. *eutendorfensis*
Isopodichnus 'Langform' (= long form) (pl. 15 fig 1)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Planolites montanus*
Cylindricum antiquum (pl. 9 fig. 1, pl. 10 fig. 2)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Skolithos* isp. A
Stopftunnel (= stuffed tunnels) (pl. 10 fig. 1)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Scoyenia gracilis*
Cylindricum	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Skolithos* isp. A
Stopftunnel (= stuffed tunnels) (pl. 11 fig. 4)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Taenidium barretti*
Cylindricum antiquum (pl. 11 fig. 5)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Skolithos* isp.
Stopftunnel (= stuffed tunnels) (pl. 14 fig. 2-3)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	?*Scoyenia gracilis*
sandige Gangfüllungen (= sandy fillings of burrows)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Rusophycus carbonarius* *Cruziana problematica*
Wurmspur (= worm trace) (text-fig. 1)	WELZEL 1968, Hassberge Formation (*Blasensandstein), east of Leinach	*Taenidium* cf. *serpentinum*
ichnog. et ichnosp. incert. (text-fig. 9)	GEYER 1987, Grabfeld Formation (**Modiola* Bank), Franconia	*Chomatichnus* isp.
Solemyatuba ypsilon SEILACHER (text-fig. 5)	SEILACHER 1990, Exter Formation (*Rhaetic Sandstone), Bebenhausen	*Solemyatuba ypsilon*
Helicerina keuperina SEEGIS (text-fig. 4a-f, 5)	SEEGIS in SCHWEIGERT et. al. 1997, Steigerwald Fm (Lehrberg Schichten), Lengröden SE Eschwege	*Helicerina keuperina* SEEGIS

APPENDIX III

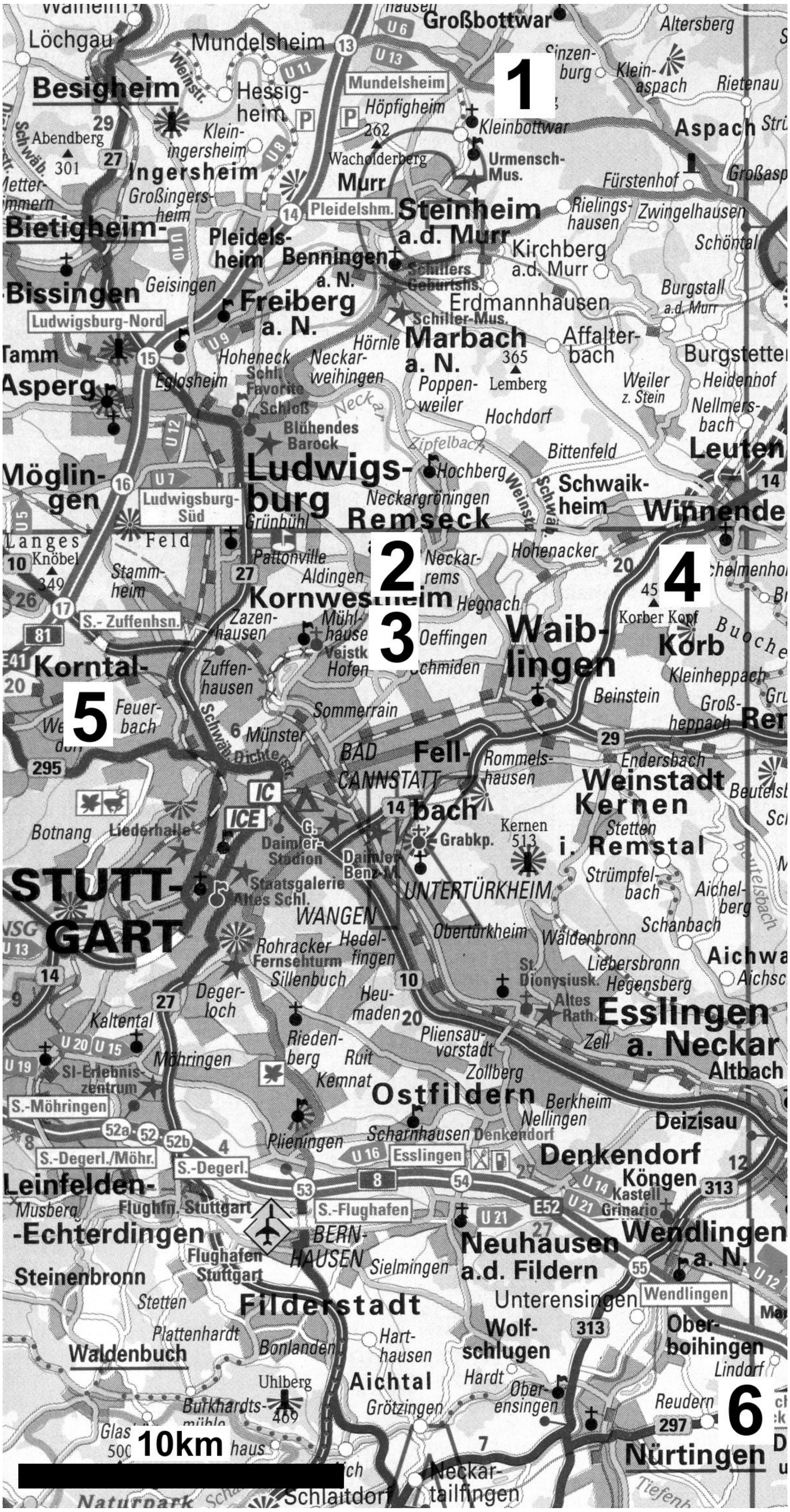
DETAILED LOCALITY MAPS

Map 1: Outline map of the study area.

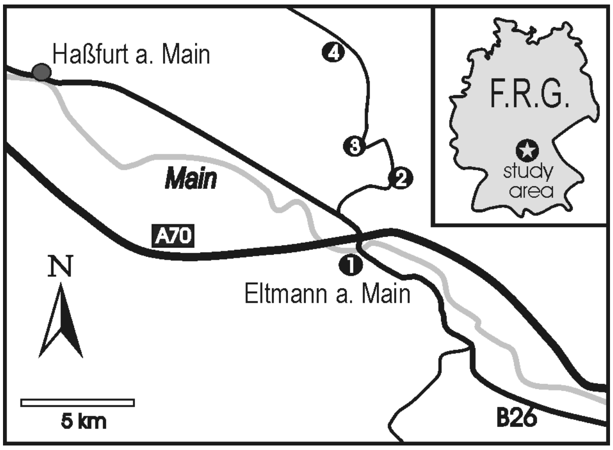
Map 2: Localities in the Nature Reserve Stromberg and Heuchelberg, Baden-Württemberg. 1) Stocksberg and Stocksheim; 2) Stetten; 3) Sternenfels; 4) Mühlbach; 5) Maulbronn; 6) Diefenbach; 7) Eibensbach; 8) Cleebronn; 9) Ochsenbach.



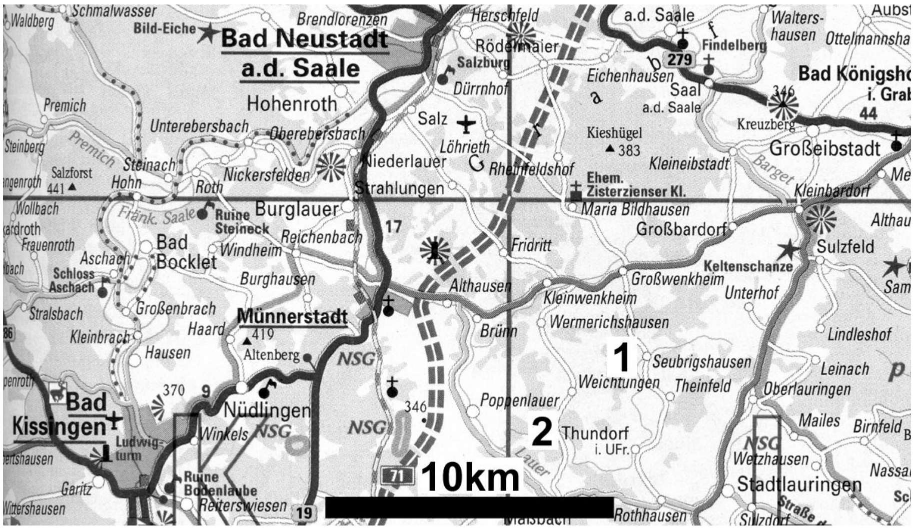
Map 3: Tübingen and 1) Seebronn.



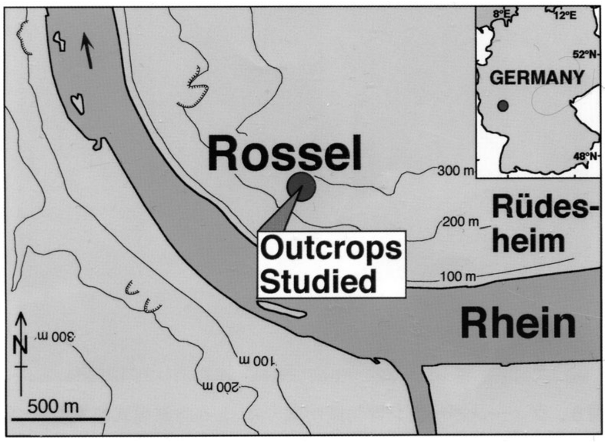
Map 4: 1) Kleinbottwar; 2) Neckarrems; 3) Oeffingen; 4) Korb and Korber Kopf; 5) Feuerbach; 6) Nürtingen.



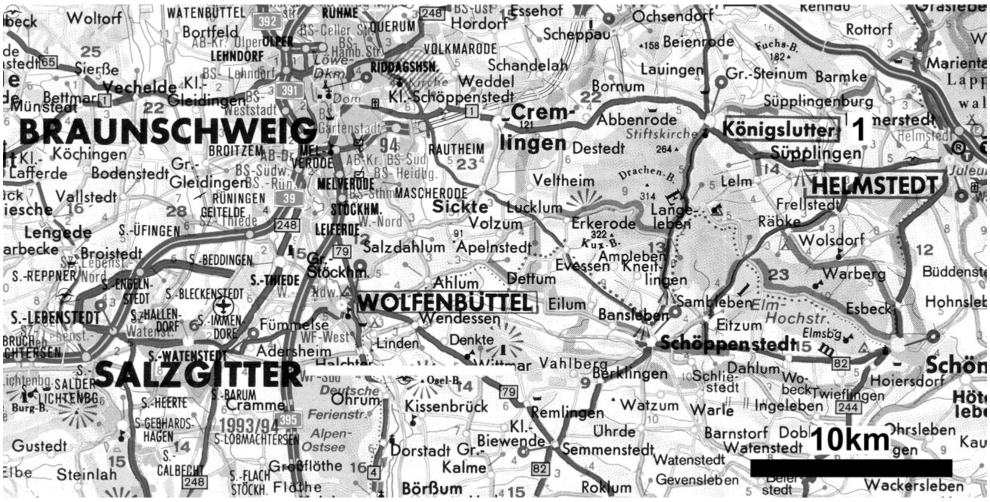
Map 5: Haßberge area. 1) Eltmann am Main; 2) Schleifsteinwerke quarry; 3) Vetter quarry at Schönbachsmühle; 4) Natursteinwerke quarry near Dörflis.



Map 6: 1) Seubrigshausen; 2) Thundorf in Unterfranken.



Map 7: 'Rossel' near Rüdesheim.



Map 8: Königslutter, Lower Saxony.