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Upper Triassic (Keuper) non-marine trace fossils from the Haßberge area (Franconia, south-eastern Germany)

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with 21 figures and 1 table

Abstract: Various trace fossils from the Hassberge Formation and the Löwenstein Formation (Middle Keuper, Upper Triassic) of the Haßberge region are described. Twenty-three different forms have been identified, 17 of which are named, including *Cruziana pascens* n. isp., *Lockeia cunctator* n. isp., and *Rusophycus versans* n. isp. *Lockeia siliquaria* JAMES, 1879, *L. amygdaloides* (SEILACHER, 1953), *L. triangulichnus* KIM, 1994, and *L. elongata* (YANG, 1984) are revised and synonymized under the oldest available name, *L. siliquaria* JAMES, 1879. *Rusophycus eutendorfensis* (LINCK, 1942) and *R. carbonarius* DAWSON, 1864 are revised. The diagnosis of *Polykladichnus* FÜRSICH, 1981 is emended, and a diagnosis for *Helminthoidichnites* FITCH, 1850 is given for the first time. Among the described ichnotaxa, *Skolithos* ispp., *Rusophycus carbonarius*, and *Taenidium barretti* are the most common forms. The trace fossil association is typical of the *Scoyenia* ichnofacies, which indicates non-marine, periodically or completely inundated environments, such as floodplains and lake margins. Two palaeoichnocoenoses are identified. One ichnocoenosis, dominated by *Cruziana problematica*, cf. *Polykladichnus* isp., and *Skolithos* isp. B characterizes margins of trough cross-bedded sandstones. Another ichnocoenosis, dominated by *Rusophycus versans* n. isp., *Taenidium barretti*, *Scoyenia gracilis* and *Skolithos* isp. A is related to ephemeral lake deposits. Taxonomic recommendations for the use of hitherto described and figured invertebrate Keuper trace fossils from Germany are given.

Keywords: Upper Triassic, Keuper, non-marine, trace fossils, south-eastern Germany.

Zusammenfassung: Aus dem mittleren Keuper (Hassberge Formation, Löwenstein Formation) der Haßberge in Unterfranken wird eine sehr reichhaltige Spurenfauna beschrieben. Es können insgesamt 23 verschiedene Formen unterschieden werden, wovon 17 formell beschrieben werden. Unter ihnen werden *Cruziana pascens* n. isp., *Lockeia cunctator* n. isp und *Rusophycus versans* n. isp. erstmals beschrieben. *Lockeia siliquaria* JAMES, 1879, *L. amygdaloides* (SEILACHER, 1953), *L. triangulichnus* KIM, 1994 und *L. elongata* (YANG, 1984) werden revidiert und unter dem ältesten verfügbaren Synonym *L. siliquaria* JAMES, 1879 zusammengefaßt. *Rusophycus eutendorfensis* (LINCK, 1942) und *R. carbonarius* DAWSON, 1864 werden ebenfalls revidiert. Die Diagnose von *Polykladichnus* FÜRSICH, 1981 wird emendiert, und zu *Helminthoidichnites* FITCH, 1850 wird erstmals eine Diagnose erstellt. Unter den bearbeiteten Formen sind *Skolithos* ispp., *Rusophycus carbonarius* und *Taenidium barretti* die häufigsten Spurenfossilien. Die Spurengemeinschaft kann der *Scoyenia*-Ichnofazies zugeordnet werden, die charakteristisch für nichtmarine Ablagerungen randlicher Bereiche ephemerer Seen sowie für Überflutungsebenen ausgedehnter Flusssysteme ist. Innerhalb der gesamten Spurenassoziation können zwei Paläoichnozönosen unterschieden werden: (1) Eine von *Cruziana prolematica*, cf. *Polykladichnus* isp. sowie *Skolithos* isp. B dominierte Ichnozönose, die auf randliche Bereiche rinnenförmiger Sandsteinkörper beschränkt ist, und (2) eine hauptsächlich von *Rusophycus versans* n. isp., *Taenidium barretti*, *Scoyenia gracilis* sowie *Skolithos* isp. A aufgebaute Ichnozönose. Diese Ichnocoenose ist typisch für die Ablagerungen ephemerer Seen. Abschließend werden Vorschläge zur Nomenklatur von Spurenfossilien gegeben, die bereits früher aus dem Keuper Deutschlands beschrieben wurden.

Schlüsselwörter: Ober Trias, Keuper, nicht marin, Spurenfossilien, Südost-Deutschland.

Introduction

The Keuper beds (Upper Triassic) of southern Germany are predominantly composed of rocks representing various non-marine environments but dominated by red bed

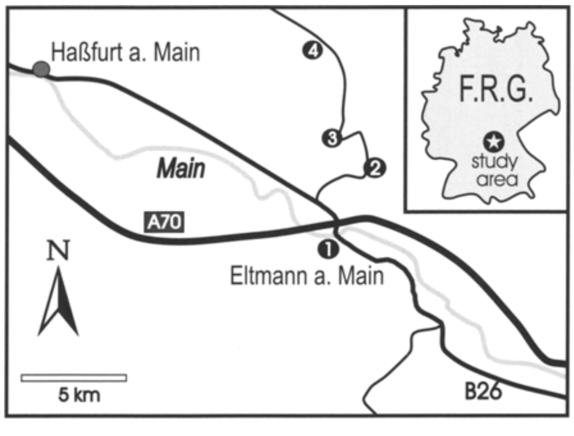

Fig. 1. Location map of the study area (Haßberge, Franconia). (1) quarry south of Eltmann, (2) Fränkische Schleifsteinwerke GmbH, (3) Vetter GmbH near Schönbach, and (4) Bamberger Natursteinwerk near Dörflis.

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Eltmann quarry
lake
fluvial
lake margin
lake
fluvial
lake margin
c s fs ms cs
Schleifsteinwerke quarry
fluvial
lake and lake margin
fluvial
c s fs ms cs
Schönbach quarry
lake margin
lake
fluvial
lake margin
c s fs ms cs
Dörflis quarry
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-scale
carbonate concretions
intraclasts
rootlets
structureless, massive
horizontal bedding
dm-scale horizontal bedding
siltstone
arcosic sandstone
sandstone
soil (Recent)
intercalation of subarcose and siltstone, cm-scale
channelled subarcoses (cm-scale) in siltstone matrix

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

A great variety of trace fossils has been found in the Keuper deposits around Eltmann, Franconia, SE Germany (Fig. 1). The main purpose of this article is a systematic description and discussion of these trace fossils, followed by a brief discussion of their value for palaeoenvironmental reconstructions of non-marine environments.

Geological setting

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. 2). The studied sections are about 40 m thick and belong to the Hassberge Formation (previously known as Coburger Sandstein and Blasensandstein) and the Löwenstein Formation (previously known as Burgsandstein) (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) gives a latest Carnian to early Norian age for the mentioned formations, whereas the upper and lower boundaries of the Hassberge Formation are diachronous (Fig. 3).

Trace fossils

Trace fossils have been collected in the following quarries: (1) south of Eltmann, (2) Fränkische Schleifsteinwerke GmbH, (3) Vetter GmbH near Schönbach, and (4) Bamberger Natursteinwerk near Dörflis (all Hassberge and Löwenstein formations; Fig. 3). The described specimens are housed in the collection of the Institut für Paläontologie der Universität in Würzburg (acronym PIW1998VIII).

Fig. 2. Generalized graphic logs of the Keuper deposits in the studied outcrops.

Systematic ichnology (M. SCHLIRF & A. UCHMAN)

Stationary domichnia/fodinichnia

Ichnogenus *Polykladichnus* FÜRSICH, 1981

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

1991 *Arborichnus* new ichnogen. – EKDALE & LEWIS: 264, fig. 3-4.

Emended diagnosis: Lined or unlined, vertical tubes with Y- or U-shaped bifurcations with slight enlargements at points of bifurcation; usually connecting to the bedding surface.

Remarks: *Polykladichnus* is typified by *P. irregularis* FÜRSICH, 1981 from marginal marine Jurassic deposits in Portugal. It is described as a small vertical burrow with a lined tube, 2-5 mm in diameter, and with Y-shaped bifurcations. The material herein described is unlined. Like *Spongeliomorpha*, however, a lining is not considered a diagnostic feature on the ichnogeneric level (see SCHLIRF 2000 for further discussion). In addition, similar trace fossils were observed in Miocene non-marine sediments from northern Spain (UCHMAN & ÁLVARO 2000), but these have U-shaped bifurcations. The upwardly directed, Y- or U-shaped bifurcations are regarded as the most diagnostic feature of this ichnogenus. For this reason, the original diagnosis of FÜRSICH (1981) is emended.

Arborichnus sparsus EKDALE & LEWIS (1991: 265, fig. 3-4) from Quaternary fan delta deposits of New Zealand is synonymous with *Polykladichnus irregularis*.

cf. *Polykladichnus* isp.
Fig. 4A

Material: PIW1998VIII-36.

Description: Vertical to subvertical, slightly arcuate, cylindrical shafts with a lateral, upward bending branch, showing slight enlargements at points of bifurcation. Shaft diameter 2-3 mm, length 55-95 mm. Lower part filled with sandstone similar to host rock, upper part filled with silty clay from overlying bed.

Remarks: *Polykladichnus* in non-marine environments may be interpreted as a burrow of insects. Similar forms are, for example, produced by staphylinid beetles of the genus *Bledius* (LARSEN 1936; RATCLIFFE & FAGERSTROM 1980). *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,

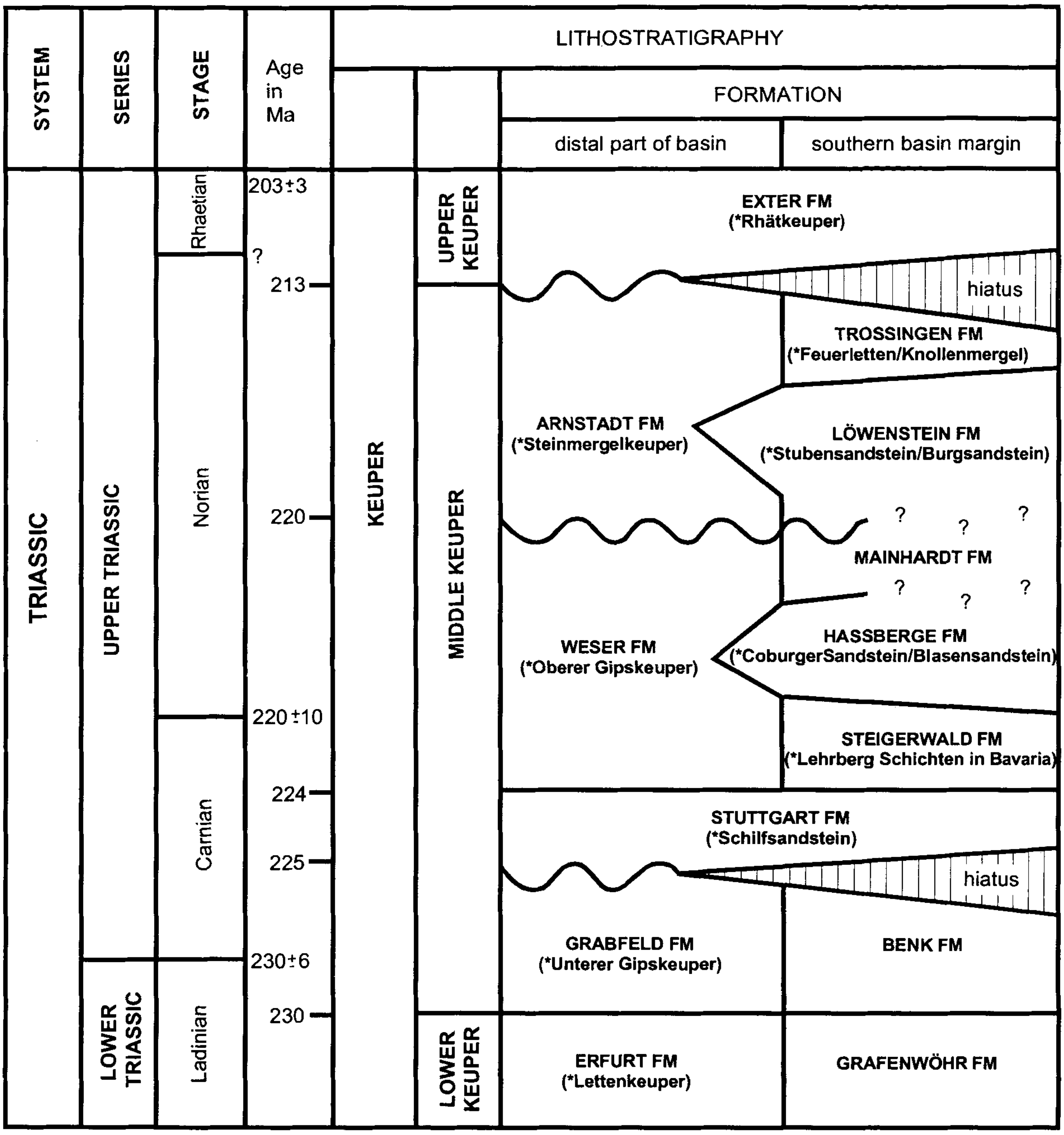

Fig. 3. Chrono- and lithostratigraphy of the studied rock sections (modified after BEUTLER 1998, age dates for stages from International Stratigraphic Chart; absolute ages on the right site of age-column from BEUTLER 1998); * traditional lithostratigraphic names.

among their specimens of *Arenicolites* isp. are obvious U-shaped burrows. These trace fossils were interpreted by the authors 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.

Ichnogenus *Skolithos* HALDEMAN, 1840

Type ichnospecies: *Fucoides*? *linearis* HALDEMAN, 1840: 3.

Diagnosis: see SCHLIRF 2000: 151.

Skolithos isp. A
Fig. 4B, D-E

Material: PIW1998VIII-31-35, 39-40, 45-46, 51, 54-55, 82, 86, numerous field observations.

Description: Cylindrical, vertical, slightly curved, rarely straight, unlined burrows, with or without smooth or indistinctly striated external burrow surface and hemispherical terminations. Burrow length 65-90 mm, burrow diameter 9-10 mm; 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 (Fig. 4D-E). Burrows are relatively isolated and appear predominantly as circular projections on the tops of bedding planes.

Remarks: 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* LINCK, 1949 (see Tab. 1); an ichnogenus which was partly included in *Skolithos* by ALPERT (1974).

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).

Skolithos isp. B
Fig. 4C, F-H

Material: PIW1998VIII-26, 31, 38, 40-43, 47-53, 57-64, 82-85.

Description: Vertical, cylindrical, slightly curved, rarely straight, thinly lined or unlined burrows; length 19-50 mm, width 3-4 mm. 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.

Remarks: *Skolithos* isp. B occurs together with cf. *Polykladichnus* isp. 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 our cf. *Polykladichnus* isp., *Skolithos* isp. B is interpreted as an insect burrow.

Cubichnia/fodinichnia

Ichnogenus *Lockeia* JAMES, 1879

Type ichnospecies: *Lockeia siliquaria* JAMES, 1879: 17.

Emended 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.

Remarks: 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, are modified.

Isolated *Lockeia* is commonly interpreted as a bivalve resting trace most probably produced by an animal with a wedge-foot (SEILACHER & SEILACHER 1994). The newly introduced ichnospecies *Lockeia cunctator* is interpreted as 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 n. isp.
Fig. 5, 6A

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

Derivatio nominis: *cunctator* (Latin) = waverer.
Holotype: PIW1998VIII-17.
Locus typicus: Quarry of the Vetter GmbH near Schönbach.
Stratum typicum: Hassberge Formation.

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.

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 9-10 mm long and up to 4.5 mm 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* n. isp. 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 and demands the introduction of a new ichnospecies. 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*. However, this is no objection against the introduction of a new ichnospecies, because single parts of the burrow parts can easily be mistaken. For example, smooth segments of *Spongeliomorpha* (sensu SCHLIRF 2000) can easily be confused with *Planolites*.

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

Remarks: Similar asymmetric traces were produced experimentally as undertracks of the bivalve *Macoma* kept

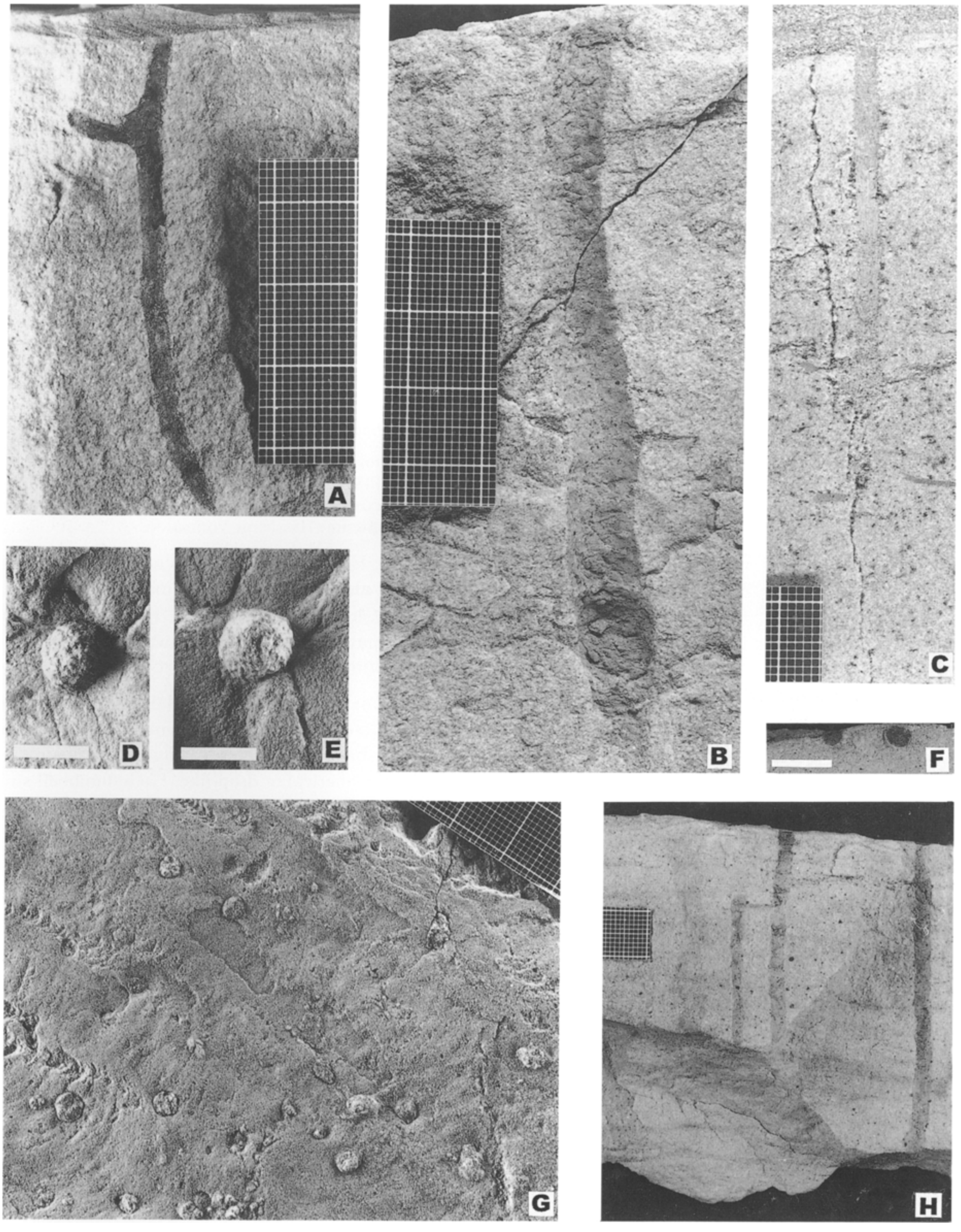

Fig. 4. – **A:** cf. *Polykladichnus* isp. Full relief, lateral view; Schleifsteinwerke quarry; × 1.3; PIW1998VIII-36. **B:** *Skolithos* isp. A. Full relief, lateral view; Vetter quarry; × 1.3; PIW1998VIII-32. **C:** *Skolithos* isp. B. Full relief, lateral view; Schleifsteinwerke quarry; × 1.3; PIW1998VIII-41. **D-E:** Sculptured terminations of *Skolithos* isp. A. Positive hyporelief, basal view; Natursteinwerk quarry; × 1.3; PIW1998VIII-86. **F-H:** *Skolithos* isp. B. **F.** Epirelief, top view; natural size; **H.** full relief, lateral view; × 0.75; Schleifsteinwerke quarry; PIW1998VIII-42; **G.** positive epirelief, top view; Natursteinwerk quarry; natural size; PIW1998VIII-26. Scale bars: 1 cm.

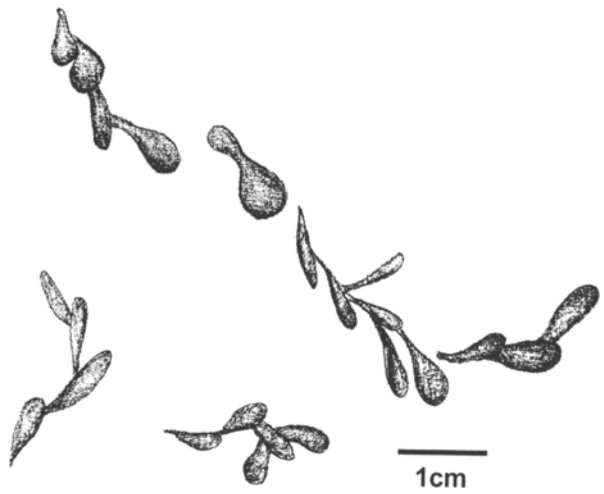

Fig. 5. Interpretative sketch of *Lockeia cunctator* n. isp.

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, we regard the studied form as both pascichnial and cubichnial.

Treptichnus bifurcus MILLER, 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. Nevertheless, the type material of *T. bifurcus* MILLER 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.

Lockeia siliquaria JAMES, 1879
Fig. 6B-C

* 1879 *Lockeia siliquaria* JAMES: 17.
1953b *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.

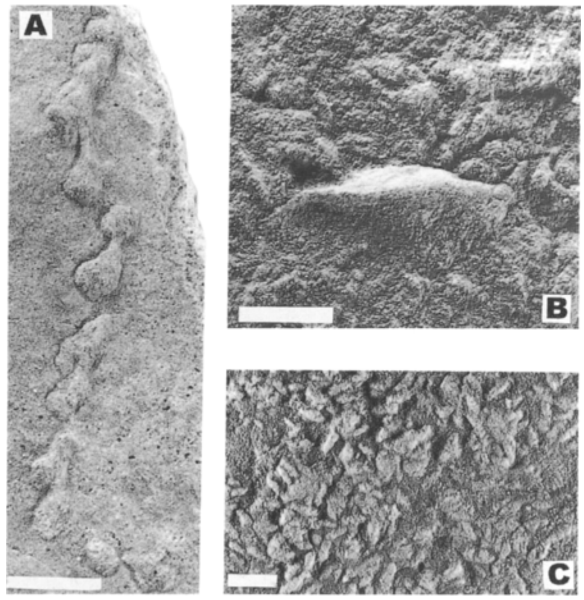

Fig. 6. – A: *Lockeia cunctator* n. isp. Positive hyporelief, basal view; Vetter quarry; × 1.3; **holotype**, PIW1998VIII-17. **B-C:** *Lockeia siliquaria* JAMES, 1879. **B.** Positive hyporelief, basal view; Eltmann quarry; × 1.3; PIW1998VIII-23. **C.** Dense occurrence, positive hyporelief, basal view; Vetter quarry; × 0.7; PIW1998VIII-76. Scale bars: 1 cm.

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).

Material: PIW1998VIII-23, 76-78.

Emended diagnosis: Thin, elongated to stout, generally high-relief, almond-shaped, smooth hypichnial ridges, with strongly arcuate to almost obtuse terminations; occasionally showing vertical spreite.

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. Two size classes can be distinguished: (a) 26 mm long, and 7 mm across in the widest portion, and (b) 5 mm long and 2 mm 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, we regard *L. amygdaloides* (SEILACHER, 1953), *L. avalonensis* FILLION & PICKERILL, 1990, and *L. triangulichnus* KIM, 1994 as junior synonyms of *Lockeia siliquaria* JAMES, 1879. *Lockeia elongata* (YANG, 1984) is considered a *nomen nudum* since no holotype was mentioned and figured. SEILACHER & SEILACHER (1994) designated 'Muschelspur' in LINCK (1949) as holotype of *L. serialis*. However, there are neither specimens, illustrations, nor descriptions related to 'Muschelspur' in LINCK 1949 and, thus, *L. serialis* is considered a *nomen nudum*.

Ichnogenus *Rusophycus* HALL, 1852

Type ichnospecies: *Fucoides biloba* VANUXEM, 1842: 79.

Emended 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; sculptured with oblique to transverse or longitudinal striae in various arrangements, or almost smooth.

Remarks: Apart from obvious *Rusophycus*, there are transitional forms to *Cruziana*, which show a length to width ratio of about 2:1. This ratio has been recommended by KEIGHLEY & PICKERILL (1996) as the diagnostic criterion for distinguishing between *Cruziana* and *Rusophycus*. However, the 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 than bilobate *Rusophycus* (see *Rusophycus versans*) made an emendation of the diagnosis necessary.

In the Palaeozoic, *Rusophycus* is said to be produced predominantly by trilobites (see OSGOOD 1970 and RINDSBERG 1994 for discussion). Mesozoic to Cenozoic forms can be related to arthropod activities in general.

Rusophycus eutendorfensis (LINCK, 1942)
no Fig.

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

Lectotype: Vertically oriented specimen at the centre of the slab illustrated by LINCK (1942: 238, fig. 5), below the coin.

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.

Discussion: LINCK (1942) in his original description of *Rusophycus eutendorfensis* (= *Isopodichnus eutendorfensis* in his paper) pointed out that the most important feature and morphological difference to other *Rusophycus* known so far, is the fact that his material 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 (LINCK 1942: 240, fig. 8) under the same name, 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 is not according to the rules of I.C.Z.N. (Paragraph 74). Other authors also 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, we designate a new lectotype (see above). A confusion of *R. eutendorfensis* and *R. didymus* (SALTER) as discussed by FILLION & PICKERILL (1990: 55) is irrelevant, since the longitudinal striation in *R. eutendorfensis* is a characteristic feature unknown in *R. didymus*.

Rusophycus carbonarius DAWSON, 1864
Fig. 7A-E

* 1864 *Rusophycus carbonarius* – DAWSON: 364, fig. 3.
1942 *Isopodichnus eutendorfensis*. – LINCK: 240, fig. 8.
pt 1979 *Cruziana problematica* (SCHNDEWOLF, 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: 17 D, 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.

Emended diagnosis: Small, coffee-bean-shaped form with transverse to oblique, generally fine striation. Lobes parallel or slightly gaping.

Material: PIW1998VIII-1A-B, 7A-B, 9, 11A-B, 25, 81, 82, 85.

Description: Variably oriented, hypichnial, bilobate mounds, 5-15 mm across, and 6-15 mm long, with a distributional maximum of 10-12 mm. Lobes separated by median furrow, commonly wider and deeper towards anterior end, where lobes are splayed. Lobes predomi-

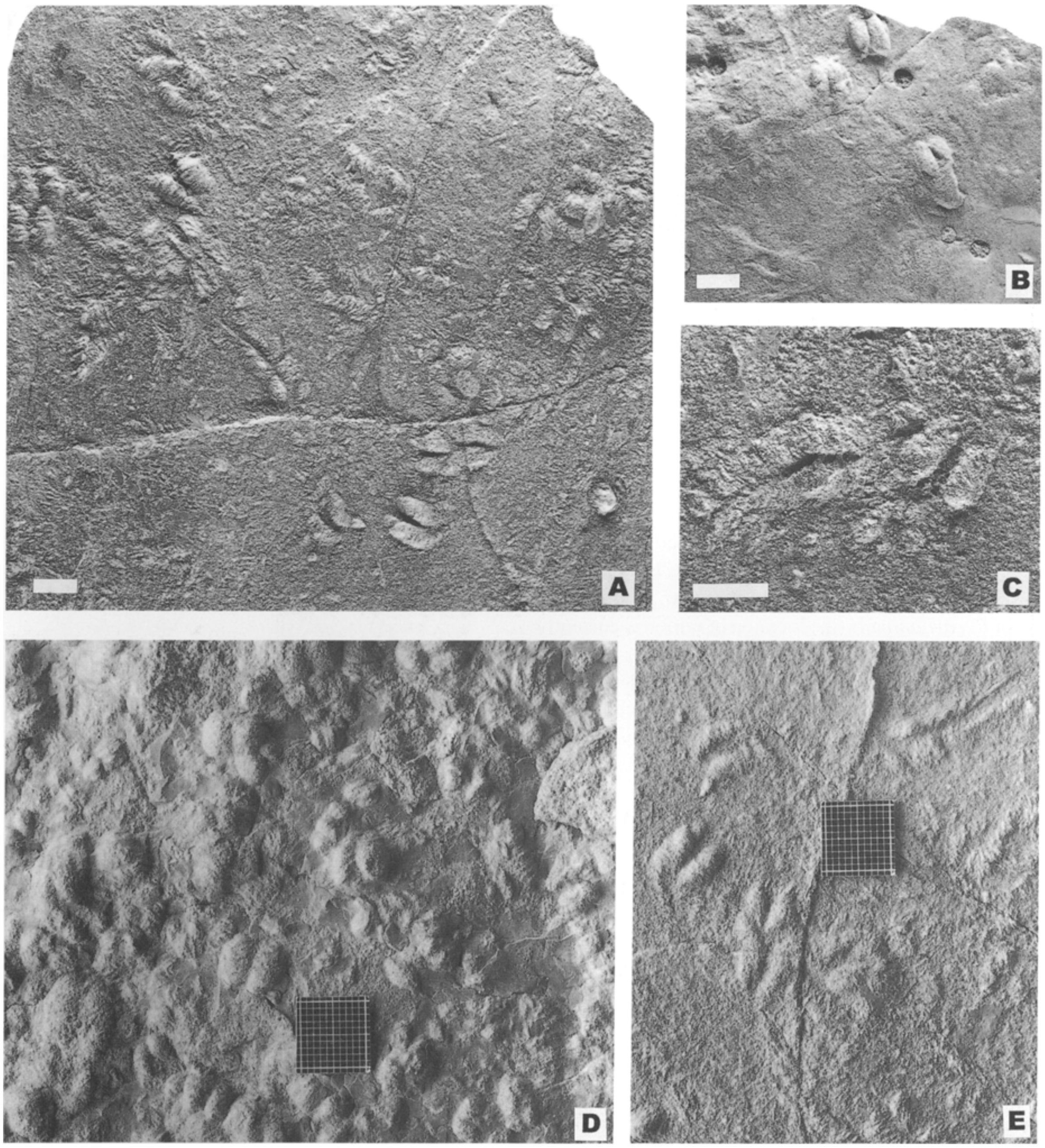

Fig. 7. – **A-E:** *Rusophycus carbonarius* DAWSON, 1864. Positive hyporelief, basal view; **A:** × 0.7; PIW1998VIII-1. **B:** × 0.7; PIW1998VIII-81. **C:** × 1.2; PIW1998VIII-1. **D:** Natural size; PIW1998VIII-7. **E:** Natural size; PIW1998VIII-1. All Vetter quarry. Scale bars: 1 cm.

nantly smooth, rarely covered with fine oblique striae. Overlaps common in case of dense occurrences (e.g., PIW1998VIII-7). Intergradation with *Cruziana problematica* common.

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

Remarks: KEIGHLEY & PICKERILL (1996) revised *Rusophycus carbonarius* (DAWSON) and separated it from *R. eutendorfensis* sensu FILLION & PICKERILL (1990) (see discussion of *R. eutendorfensis*) on the basis of the lateral range of the striation. They regarded the striation in *R. carbonarius* as not extending beyond the margin of the lobes in contrast to their *R. eutendorfensis*, in which the striation extends beyond the margin. 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. 8). Moreover, the lectotype of *R. eutendorfensis* selected by FILLION & PICKERILL (1990) and discussed by KEIGHLEY

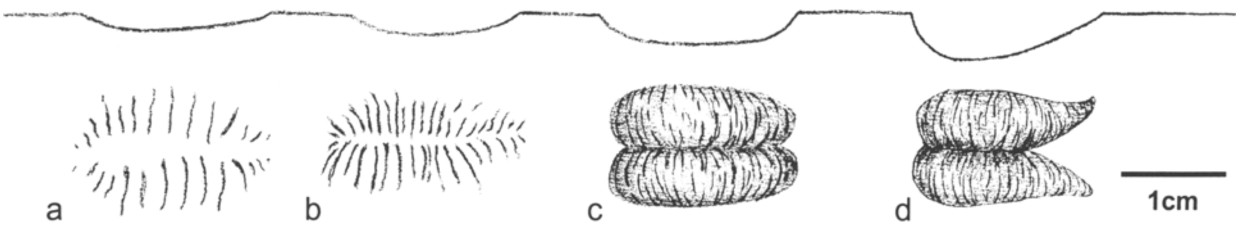

Fig. 8. Preservational variants of *Rusophycus carbonarius* as a result of burrow depth. Upper line depicts vertical section at sediment surface, lower part indicates resulting hypichnial preservation. (a) Very flat burrowing activity resulting in a wide gap between the two lobes and poorly defined coffeebean-shape with scratches of different length resulting in a poorly defined burrow outline. (b) Slightly deeper burrow resulting in a narrower gap, a better defined coffeebean-shape and burrow outline. (c) Deep burrow with both ends similar in shape, resulting in a well defined coffeebean-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.

& PICKERILL (1996) does not belong to *R. eutendorfensis* (see discussion above). These facts allowed us to emend the diagnosis of *R. carbonarius* DAWSON. However, for the final solution of the discussed problem, 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 characterization.

Rusophycus carbonarius was discussed by BROMLEY & ASGAARD (1979) (= *R. eutendorfensis* in their paper) who regarded their Triassic material as cubichnia of notostracans. This interpretation can also be applied to our material. BROMLEY & ASGAARD (1979) mentioned that Palaeozoic forms related to trilobites show a comparable behavioural pattern. The forms described herein do not display a distinct change of direction in the striation, which was described by BROMLEY & ASGAARD (1979).

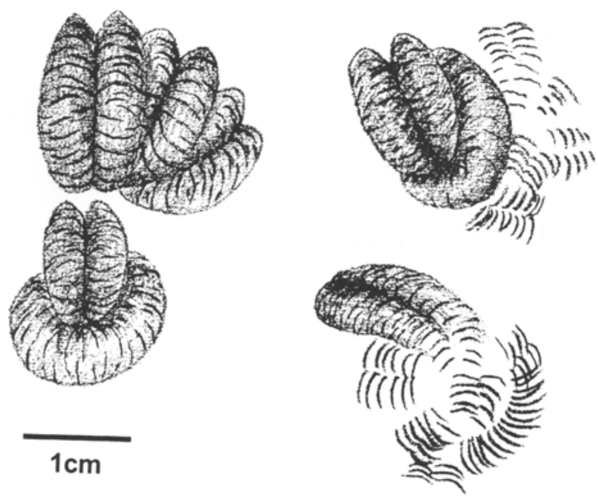

Fig. 9. Morphological variants of *Rusophycus versans* n. isp.

Rusophycus versans SCHLIRF & UCHMAN n. isp.
Fig. 9, 10A-E

? 1955 *Cruziana* cf. *irregularis* (FENTON). [sic = FENTON & FENTON] – SEILACHER: 105, fig. 5 (8).

Derivatio nominis: *versare* (Latin) = to twist, to rotate.
Holotype: PIW1998VIII-18.
Paratypes: PIW1998VIII-7A, 8, 9, 11B, 12A.
Locus typicus: Quarry of Vetter GmbH near Schönbach.
Stratum typicum: Hassberge Formation.

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

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

Remarks: All other known *Rusophycus* ichnospecies only consist of one bilobate element. These morphological differences suggest a different behavioural pattern of the tracemaker. The additional radiating lobes resulted from rotating movements of the tracemaker. The rotation enabled the tracemaker to exploit the sediment more efficiently. Deposit-feeding notostracan crustaceans are considered as possible producers.

Pascichnia/repichnia

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).

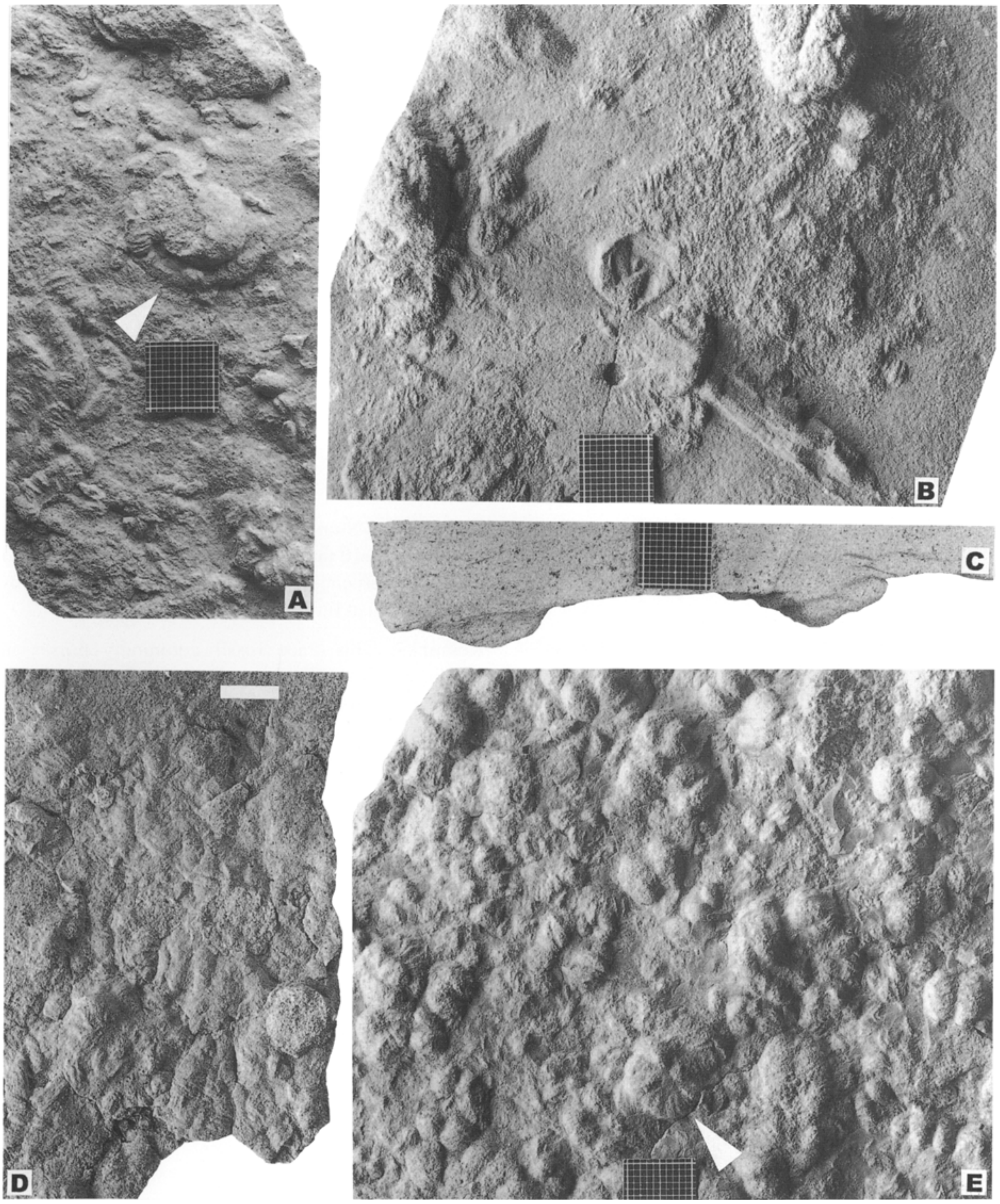

Fig. 10. – **A-E:** *Rusophycus versans* n. isp. **A.** Arrow indicates trace segment caused by rotating movement of the tracemaker; positive hyporelief, basal view; natural size; syntype, PIW1998VIII-9. **B.** Positive hyporelief, basal view; natural size; **holotype**, PIW1998VIII-18. **C:** Full relief, lateral view; natural size; **holotype**, PIW1998VIII-18. **D.** Positive hyporelief, basal view; natural size; syntype, PIW1998VIII-10. **E.** Arrow indicates trace segment caused by rotating movement of the tracemaker; positive hyporelief, basal view; natural size; syntype, PIW1998VIII-8. All Vetter quarry. Scale bar: 1 cm.

Remarks: *Cruziana* was synonymized 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 ichnolgical procedures (see also Fillion & Pickerill 1990 for discussion). The fact, that in contrast to Palaeozoic forms, no Mesozoic and Cenozoic *Cruziana* can be produced by trilobites is no objection for a synonymization, since the possible producers of trace fossils are generally regarded as irrelevant for ichnotaxonomy.

Cruziana pascens SCHLIRF & UCHMAN n. isp.
Fig. 11, 12A-D

Derivatio nominis: *pascere* (Latin) = to graze.
Holotype: PIW1998VIII-12C.
Paratypes: PIW1998VIII-11D-H, 29.
Locus typicus: Quarry of Vetter GmbH near Schönbach.
Stratum typicum: Hassberge Formation.

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.

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 10-14 mm. Number of striae: 15 per centimetre. Rows tend to be parallel and occur in high density.

Remarks: *Cruziana pascens* n. isp. differs from all other known *Cruziana* ichnospecis 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 on the ichnogeneric level (HÄNTZSCHEL 1965, 1975).

There is a transition of *Cruziana pascens* n. isp. to *Cruziana problematica* and to *Rusophycus eutendorfensis*, and the three taxa can be referred to the same tracemaker, such as notostracan crustaceans. The behaviour reflected by *Cruziana pascens* n. isp. 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 scratches 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 problematica (SCHINDEWOLF, 1921)
Fig. 13

Emended 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 (modified after FILLION & PICKERILL 1990).

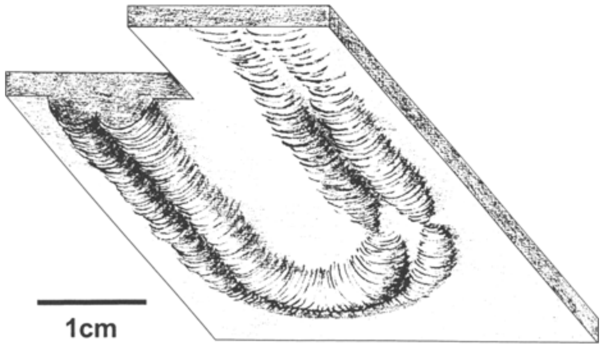

Fig. 11. Hypichnial preservation of a curved segment and undulose pattern of *Cruziana pascens* n. isp.

Material: PIW1998VIII-11A- B, 15.

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

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

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

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.

Remarks: In contrast to *Gordia* EMMONS, 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). *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).

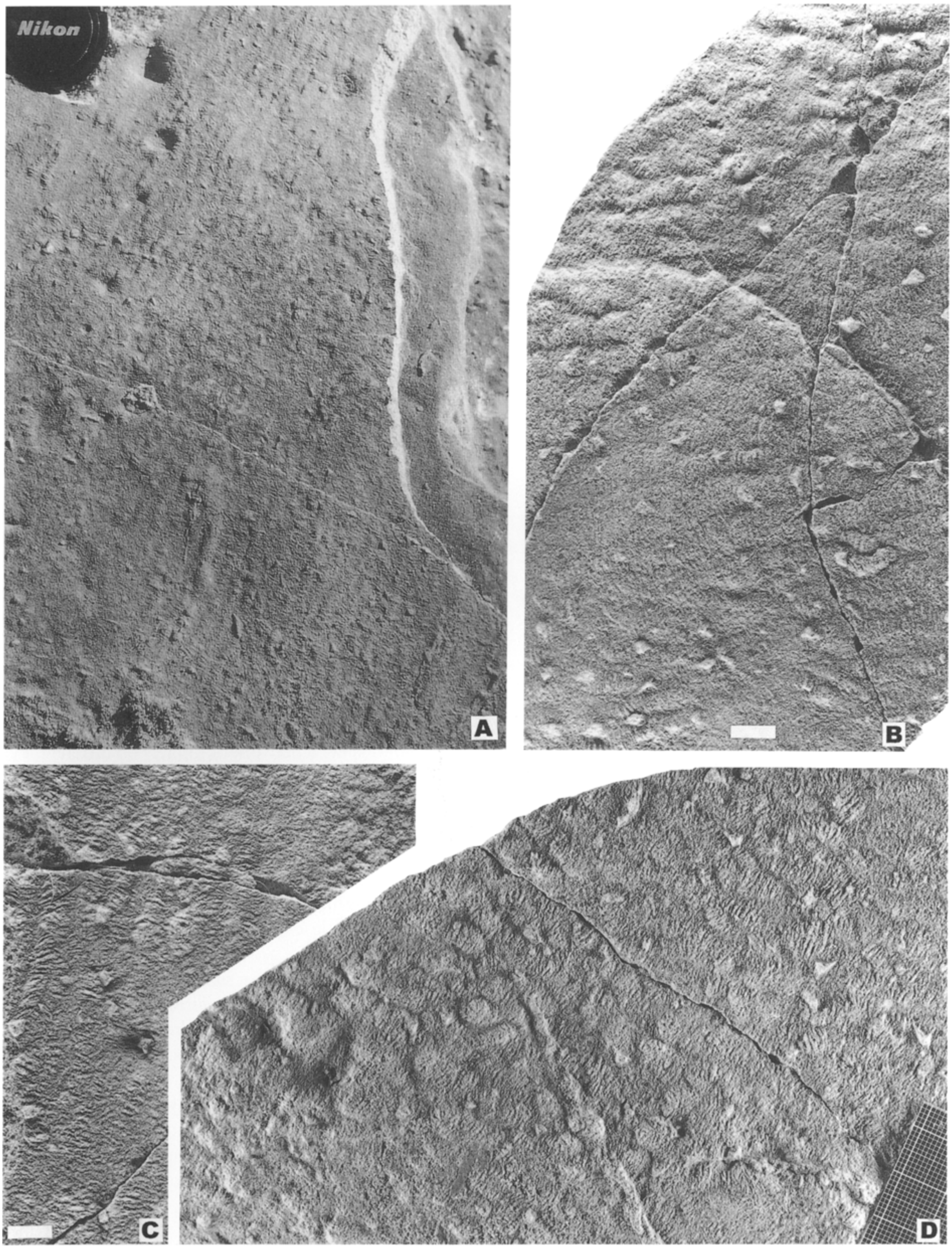

Fig. 12. – A-D: *Cruziana pascens* n. isp. **A.** Positive hyporelief, basal view; × 0.4; field photograph. **B.** Detail of **holotype**, PIW1998VIII-12B. In addition, small triangular structures can be identified; positive hyporelief, basal view; × 0.8. **C.** Detail of **holotype**, PIW1998VIII-12F. Positive hyporelief, basal view; × 0.8. **D.** Detail of **holotype**, PIW1998VIII-12C. In addition, small triangular structures can be identified; positive hyporelief, basal view; × 0.8. All from Vetter quarry, lens cap 52mm across. Scale bar: 1 cm.

Fig. 13. *Cruziana problematica* (SCHINDEWOLF, 1921). Positive hyporelief, basal view; natural size; PIW1998VIII-11A. Vetter quarry.

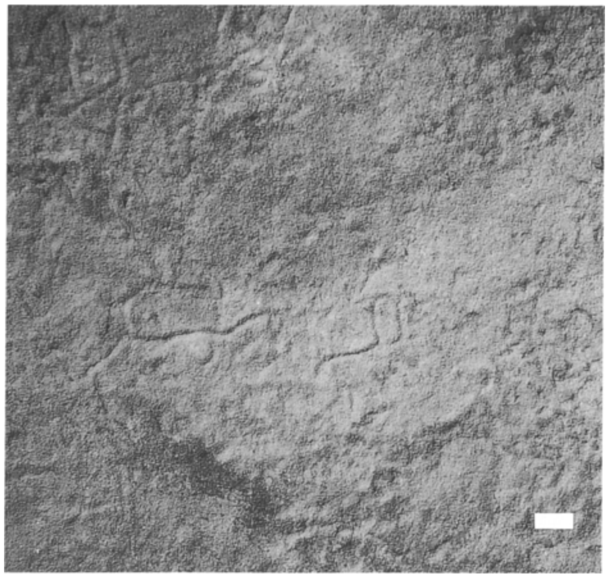

Fig. 14. *Helminthoidichnites tenuis* FITCH, 1850. Negative epirelief, top view; × 0.5; Vetter quarry, field photograph. Scale bar: 1 cm.

Helminthoidichnites tenuis FITCH, 1850
Fig. 14

Diagnosis: As for ichnogenus.

Material: PIW1998VIII-75.

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

Ichnogenus *Multina* ORŁOWSKI, 1968

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

? 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 0.5-2 mm), and locally undulating in the vertical plane. Vertical or oblique burrow parts can be present.

Remarks: *Megagrapton* KSIAZKIEWICZ, 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 & ZYLIŃSKA 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 synonymized under the oldest available name *Multina* ORŁOWSKI, 1968. Clarification of how many species belong to *Multina* requires a detailed revision of this ichnotaxon.

cf. Multina isp.
Fig. 15

Material: PIW1998VIII-80.

Description: Hypichnial, horizontal, irregular, more or less polygonal network composed of winding, cylindrical tubes with a diameter of 1.5 mm; meshes 5-10 mm 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.

Remarks: *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.

Ichnogenus *Planolites* NICHOLSON, 1873

Type ichnospecies: *Planolites vulgaris* NICHOLSON & HINDE, 1875: 138-139.

Diagnosis: see FILLION & PICKERILL (1990).

Planolites beverleyensis (BILLINGS, 1862)
Fig. 16C

Material: PIW1998VIII-4; occasional field observations.

Description: Hypichnial, horizontal, slightly curved, thinly lined, smooth, cylindrical burrows, about 11 mm in diameter and up to 16 cm long.

Planolites cf. *montanus* RICHTER, 1937
Fig. 16A-B

Material: PIW1998VIII-4, 5, 14, 21, 87-89.

Description: Variably oriented, undulose, short, unlined, cylindrical burrows, preserved as full relief; 4-7 mm across, mostly between 10 and 20 mm long. Burrow margins uneven, with local change in width.

Remarks: 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.
no Fig.

Material: PIW1998VIII-19, 41 76, 81.

Description: Short, straight, cylindrical, smooth ridges, either 2 mm wide (PIW1998VIII-19) or 15 mm wide (PIW1998VIII-41); or slightly winding, horizontal, cylindrical burrows, either 4.5 mm wide (PIW1998VIII-81) or 6 mm wide (PIW1998VIII-76).

Remarks: 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).

Ichnogenus *Scoyenia* WHITE, 1929

Type ichnospecies: *Scoyenia gracilis* WHITE, 1929: 115.

Diagnosis: see HÄNTZSCHEL (1975).

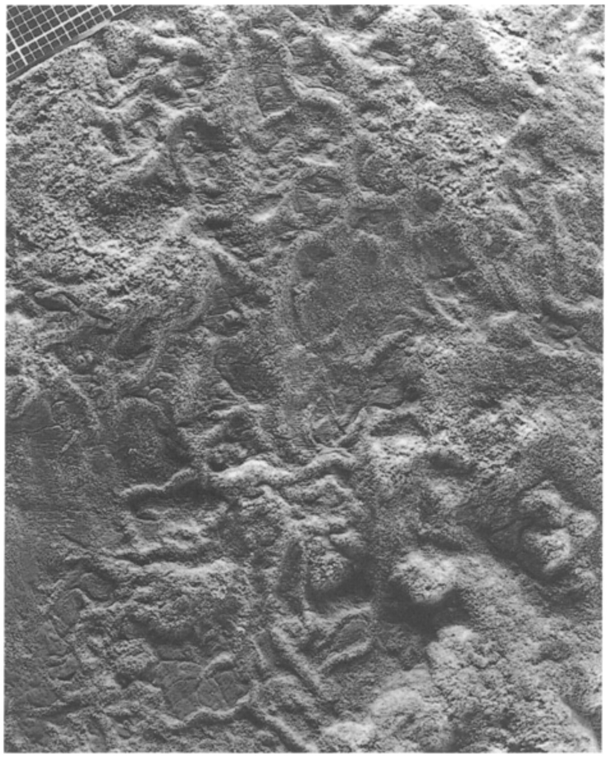

Fig. 15. cf. *Multina* isp. Positive epirelief/full relief, top view; × 1.3; PIW1998VIII-80; Natursteinwerk quarry.

Scoyenia gracilis WHITE, 1929
Fig. 17A-B

Material: PIW1998VIII-13A-B, 19, 20.

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

Remarks: The external striation as well as the meniscate backfill are characteristic of *Scoyenia*. Monospecific *Scoyenia*, typified by *S. gracilis*, is regarded as burrow of deposit-feeding organisms in different non-marine environments, presumably in moist or wet substrates near water bodies, in periodically inundated areas, or in permanent, shallow subaqueous environments. Arthropods are favoured as possible producers, but insects or decapods can be excluded (FREY et al. 1984). *Scoyenia* occurs since the Permian (SCHWAB 1966).

Ichnogenus *Taenidium* HEER, 1877

Type ichnospecies: *Taenidium serpentinum* HEER, 1877: 117, pl. 45 fig. 9, 10B.

Diagnosis: see KEIGHLEY & PICKERILL (1994).

Remarks: Taxonomic problems of *Taenidium* and related meniscate backfilled burrows and their formation

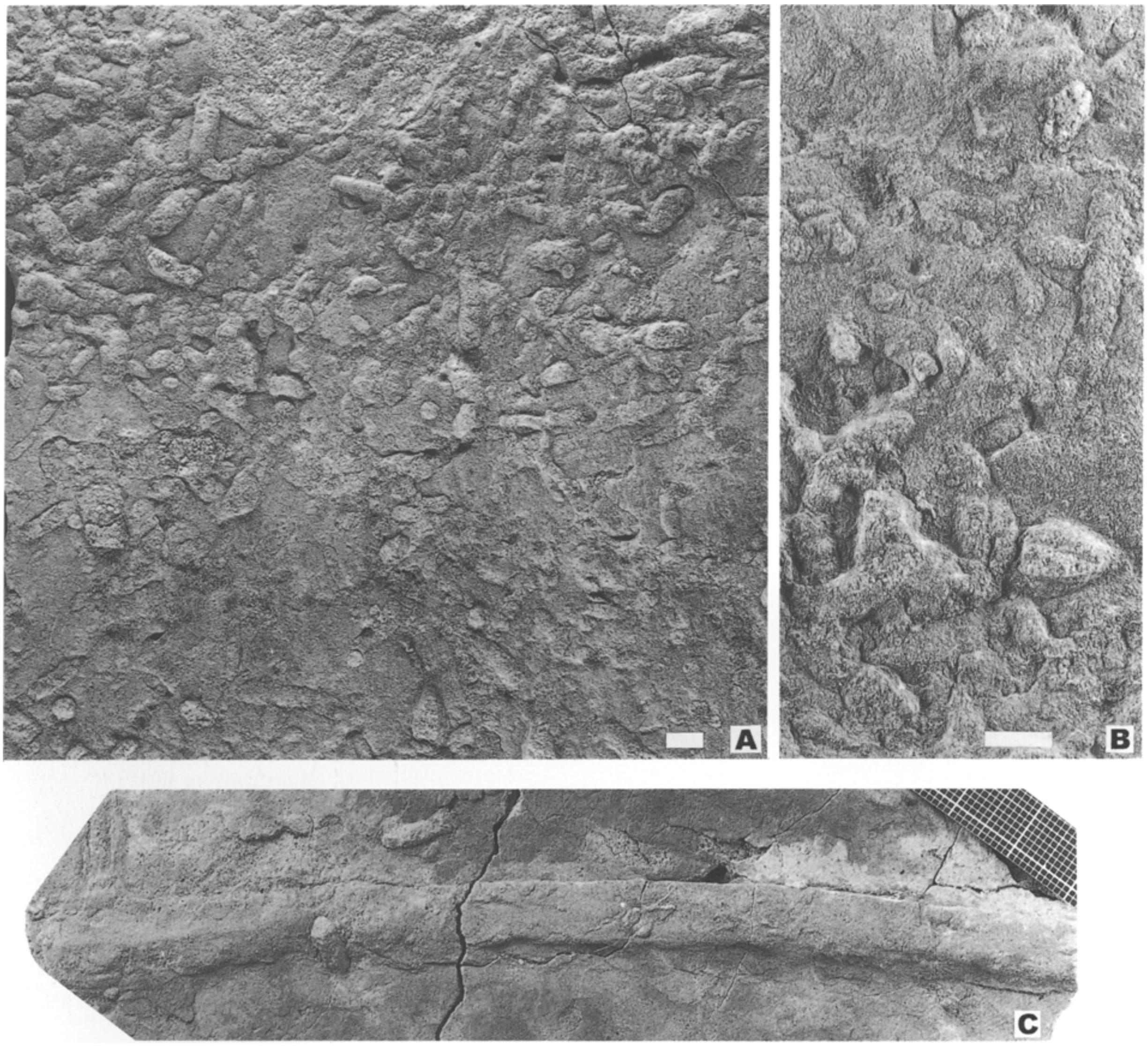

Fig. 16. – **A-B:** *Planolites* cf. *montanus* RICHTER, 1937. **A:** Positive epirelief/full relief, top view; ×0.5; PIW1998VIII-14; Natursteinwerk quarry. **B:** Detail of (a) natural size; Vetter quarry. **C:** *Planolites beverleyensis* (BILLINGS 1862) [large trace] *Planolites* cf. *montanus* RICHTER, 1937 [small trace]. Full relief, top view; natural size; PIW1998VIII-4; Schleifsteinwerke quarry. Scale bar: 1 cm.

were discussed in detail by D'ALESSANDRO & BROMLEY (1987), KEIGHLEY & PICKERILL (1994), and UCHMAN (1995). *Taenidium* occurs from the Lower Cambrian (CRIMES et al. 1992) to the ?Quaternary (WETZEL 1983; synonymized by D'ALESSANDRO & BROMLEY 1987).

Taenidium barretti (BRADSHAW, 1981)
Fig. 17C-F

Material: PIW1998VIII-3A-F, 6, 13.

Description: Endichnial, horizontal, oblique to vertical, slightly winding, cylindrical, unlined burrows with meniscate filling, 8-18 mm wide and up to 35 cm 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: 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.

Remarks: *T. barretti* occurs in different non-marine environments from the Lower Ordovician to the Pleistocene (KEIGHLEY & PICKERILL 1994).

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 this ichnospecies (as ?*Muensteria* isp.) from a Miocene section in

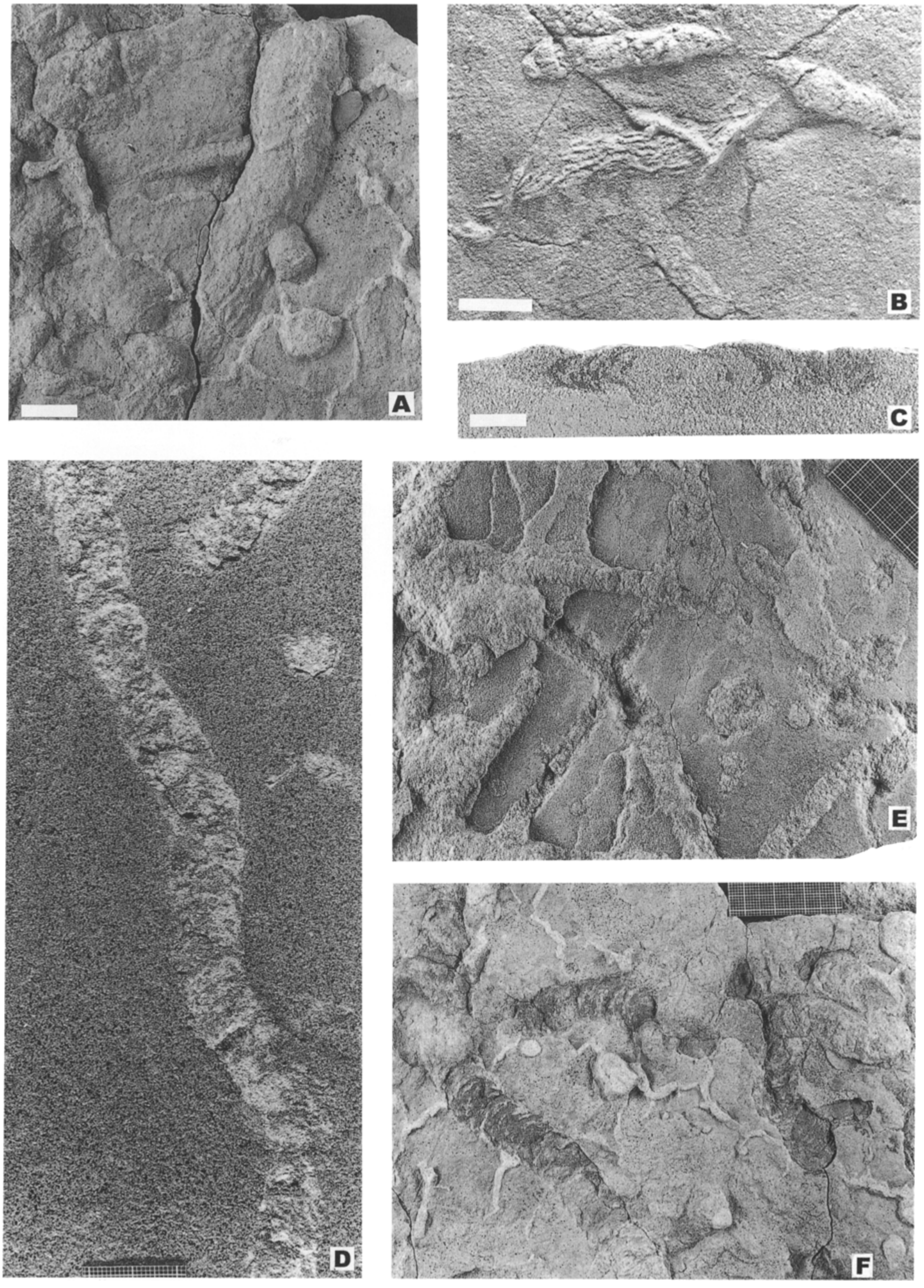

Fig. 17. – A: *Scoyenia gracilis* WHITE 1929 (sculptured burrow), *Skolithos* isp. A (circular projections). Positive epirelief, top view; natural size; PIW1998VIII-13A. **B.** *Scoyenia gracilis* WHITE 1929. Positive epirelief, top view; × 1.3; PIW1998VIII-19. **C-F:** *Taenidium barretti* (BRADSHAW, 1981). **C.** Two specimens crossing each other, full relief, lateral view; natural size; PIW1998VIII-13B. **D.** Full relief, top view; × 0.7; PIW1998VIII-3C. **E.** High burrow density, full relief, top view; × 0.6; PIW1998VIII-6. **F.** Full relief, top view; × 0.5; PIW1998VIII-13B. All Natursteinwerk quarry. Scale bars: 1 cm.

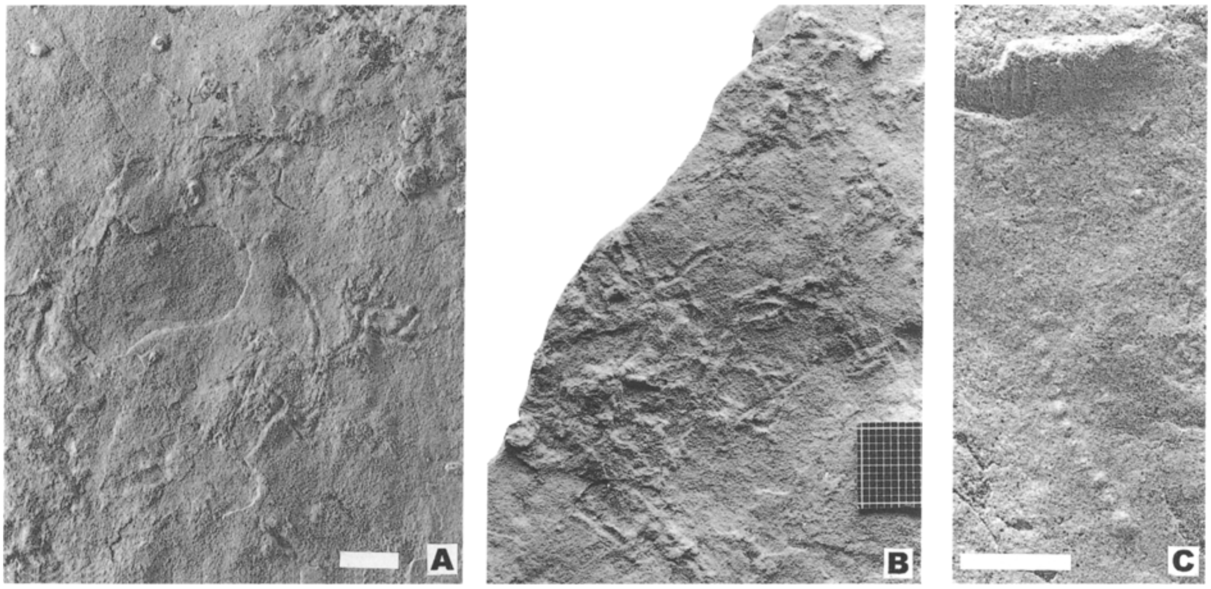

Fig. 18. – A-B: Small irregular network. **A.** Negative epirelief, top view; × 0.8, PIW1998VIII-73. **B.** Negative epirelief, top view; natural size, PIW1998VIII-73. **C.** Row of small knobs. Positive epirelief, top view; × 1.5, PIW1998VIII-16. All Vetter quarry. Scale bar: 1 cm.

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.

Unidentified biogenic structures

Small irregular networks
Fig. 18A-B

Material: Several specimens on slab PIW1998-VIII-73-74.

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

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

Parallel hypichnial ridges
Fig. 19A-B

Material: Several specimens on slab PIW1998-VIII-56, one field observation.

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

Remarks: 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 have been reported, for example, from the Triassic of Wyoming (BOYD & LOOPE 1984) and from Jurassic rocks of England (ROMANO & WHYTE 1996: fig. 4).

Row of small knobs
Fig. 18C

Material: PIW1998VIII-16.

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

Remarks: The overall morphology resembles *Hormosiroidea*. However, the burrow size is very small and connecting strings between the single knobs, a characteristic feature of *Hormosiroidea*, were not observed.

Enigmatic structures

Clusters of small pits
Fig. 20

Material: PIW1998VIII-73.

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

Remarks: 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,

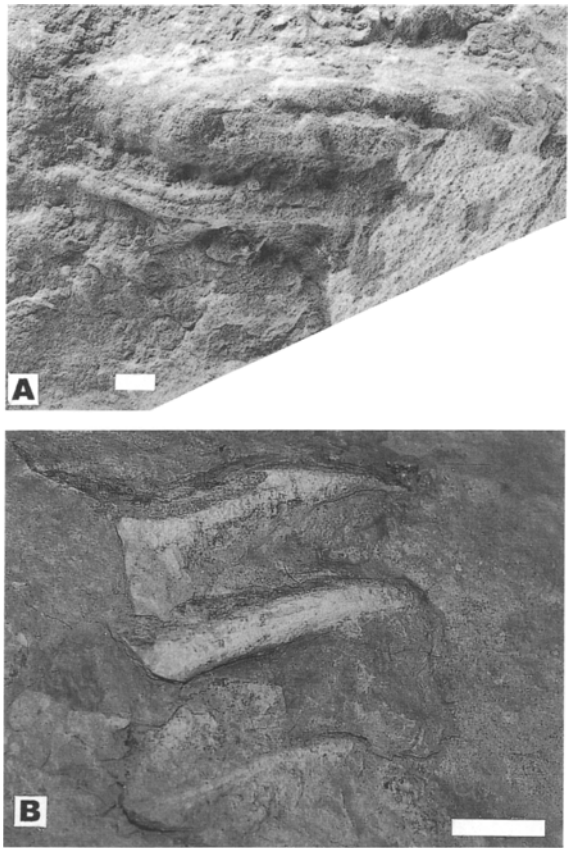

Fig. 19. – A-B: Parallel hypichnial ridges. **A.** Positive hyporelief, basal view; × 0.5; PIW1998VIII-56. **B.** Positive hyporelief, basal view; × 0.25; field photograph. All Vetter quarry. Scale bars: 1 cm.

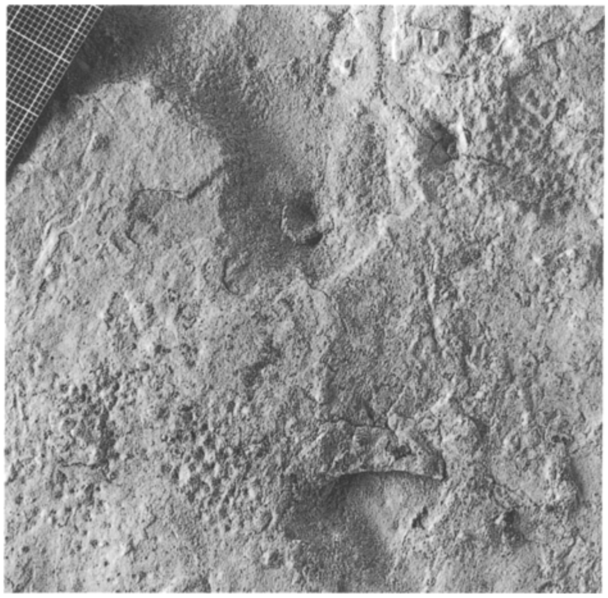

Fig. 20. Clusters of small pits. Negative epirelief, top view; × 0.8; PIW1998VIII-73; Vetter quarry.

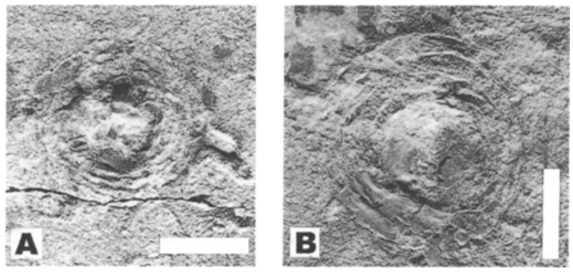

Fig. 21. – A-B: Concentric rings. Positive epirelief, top view; × 1.2; PIW1998VIII-2; Eltmann quarry. Scale bars: 1 cm.

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 ours is free. Since the Franconian material lacks further details a precise classification is impossible.

Concentric rings
Fig. 21

Material: Four specimens on slab PIW1998VIII-2.

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 2.5 mm; entire structure 12-25 mm across, depth about 10 mm, central area 0.8-12 mm, with an irregular, uneven, flat mound.

Remarks: 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.

Small triangular structures
Fig. 12B, D

Material: PIW1998VIII-12B, C, F, 74.

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

Remarks: The described stuctures resemble *Sagittichnus lincki* SEILACHER, 1953 from the Keuper (Schilfsandstein) at Sternenfels, southern Germany, where it is more-or-less oriented in a row with the individual acute angles pointing in one direction. Earlier, LINCK (1949: 72) described it from the same formation as "pfeilspitzenförmige Ausgüsse". In the studied material, the structures post-date *Cruziana pascens* n. isp. It seems improbable that prod marks could be formed without destruction of *C. pascens* n. isp. On the other hand, the structures may be diagenetic features, such as halite crystal casts.

Palaeoenvironments and ichnocoenoses

The studied sediments 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*, cf. *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 lately 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 mica content.

The massive fluvial sandstones, like those at the base of the succession in the Vetter GmbH quarry near Schönbach, 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.

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Appendix (next pages)

Literature data on other invertebrate Keuper trace fossils from Germany

In the following, invertebrate trace fossils from the Keuper of Germany described in the past are listed, and taxonomic recommendations for their further use are given.

Tab 1. List of invertebrate trace fossils described from German Keuper and taxonomic recommendations for their further use. * – 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* HOWELL
Isopodichnus moenanus KUHN (text-fig. 1)	KUHN 1937, Hassberge Formation (*Semionotensandstein), Schmachtenberg/Main	*Cruziana problematica* (SCHINDEWOLF), *Rusophycus carbonarius* (DAWSON) (after KEIGLEY & PICKERILL 1996)
Steigerwaldichnium heimi KUHN (text-fig. 2a, b)	KUHN 1937, Grabfeld Formation (**Acrodus* Bank), Zell (Unterfranken), Zeil (Steigerwald)	*Steigerwaldichnium heimi* KUHN
Annelidichnium triassicum KUHN (text-fig. 3)	KUHN 1937, Grabfeld Formation (**Acrodus* Bank), Oberschwappach	?*Planolites* isp.
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* RICHTER
Wurmgänge (= worm burrows) (pl. 2 fig. 2-3)	HAARLÄNDER 1938, Hassberge Formation (*Blasensandstein), Raindorf quarry	*Planolites montanus* RICHTER
Corophioides ? RIETH (text-fig. 232e)	SCHMIDT 1938, Exter Formation (*Rhätsandstein), Tübingen	*Diplocraterion parallelum* TORELL
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* (LINCK)
Isopodichnus eutendorfensis LINCK (text-fig. 8)	LINCK 1942, not indicated	*Rusophycus carbonarius* (DAWSON)
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 (this study)
skulpturierte Rinnen-Ausgüsse (= sculptured channel-fills) (pl. 3 fig. 2)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Steigerwaldichnium heimi* KUHN
Isopodichnus sp. (pl. 2 fig. 3)	LINCK 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Rusophycus* isp.

Tab. 1. (continued)

Ichnyspica pectinata Linck (pl. 2 fig. 1)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	?*Diplichnites* isp.
Ichnyspica pectinata Linck (pl. 2 fig. 2)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	?inorganic structure
Zopfwülste (plaited pads) (pl. 3 fig. 3)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Cruziana problematica* (Schindwolf)
gekörnelte Tunnel-Geflechte (knobbed 'tunnel-garlands') (pl. 3 fig. 1)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	?*Steigerwaldichnium* isp.
Biformites insolitus Linck (text-fig. 1, pl. 4 fig. 1-2)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Protovirgularia rugosa* (Miller & Dyer) (after Uchman 1998)
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. 7 fig. 1)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Kouphichnium* isp.
Limuludichnus gracilis Linck (text-fig. 4, pl. 6 fig. 5-6, pl. 7 fig. 2)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Kouphichnium* isp.
Limuludichnus gracilis Linck (pl. 7 fig. 2)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	?*Kouphichnium* isp.
einzeilige Reihenhöcker-Spur (= single row of humps) (pl. 8 fig. 1-3)	Linck 1949, Stuttgart Formation (*Schilfsandstein), NW Württemberg	*Lockeia* isp. (= most probably *Lockeia serialis* Seilacher & Seilacher = *nomen nudum*)
Pelecypodichnus amygdaloides Seilacher (pl. 12 fig. 1)	Seilacher 1953, ?württembergischer Keuper, locality unknown, age questionable	*Lockeia siliquaria* James
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
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* cf. *serpentinum* Heer
Taenidium sp., kleine büschelige Form (= small fascicular form) (pl. 2 fig. 1)	Linck 1961, Löwenstein Formation (*Stubensandstein), Ochsenbach	?*Planolites* isp.
Taenidium duplum Linck (pl. 3 fig. 1)	Linck 1961, Löwenstein Formation (*Stubensandstein), Feuerbach	non *Taenidium*, unidentified trackway similar to *Petalichnus* isp. sensu Rindsberg (1994)

Tab. 1. (continued)

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* HOWELL
Palaeophycus sp., kleine Form (= small form) (pl. 1 fig. 3)	LINCK 1961, Löwenstein Formation (*Stubensandstein), Stromberg	?*Planolites montanus* RICHTER
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* (LINCK)
Isopodichnus 'Langform' (= long form) (pl. 15 fig. 1)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Planolites montanus* RICHTER
Cylindricum antiquum (pl. 9 fig. 1, pl. 10 fig. 2)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Skolithos* isp. A (this study)
Stopftunnel (= stuffed tunnels) (pl. 10 fig. 1)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Scoyenia gracilis* (WHITE)
Cylindricum	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Skolithos* isp. A (this study)
Stopftunnel (= stuffed tunnels) (pl. 11 fig. 4)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Taenidium barretti* (BRADSHAW)
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* (WHITE)
sandige Gangfüllungen (= sandy fillings of burrows)	FREYBERG 1965, Hassberge Formation (*Coburger Bausandstein), Zeil-Ebelsbach	*Rusophycus carbonarius* (DAWSON) *Cruziana problematica* (SCHINDEWOLF)
Wurmspur (= worm trace) (text-fig. 1)	WELZEL 1968, Hassberge Formation (*Blasensandstein), east of Leinach	*Taenidium* cf. *serpentinum* HEER
ichnog. et ichnosp. incert. (text-fig. 9)	GEYER 1987, Grabfeld Formation (*Modiola* Bank), Franconia	*Chomatichnus* isp.
Solemyotuba ypsilon SEILACHER (text-fig. 5)	SEILACHER 1990, Exter Formation (*Rhaetic Sandstone), Bebenhausen	*Solemyotuba ypsilon* SEILACHER