

Dictyodora and associated trace fossils from the Palaeozoic of Thuringia

MICHAEL J. BENTON

LETHAIA



Benton, Michael J. 1982/07/01: *Dictyodora* and associated trace fossils from the Palaeozoic of Thuringia *Lethaia*, Vol. 15, pp. 115–132. Oslo. ISSN 0024-1164.

Dictyodora occurs in the *Hauptquarzit* (Late Ordovician; *D. zimmermanni*) and *Bordenschiefer* (Early Carboniferous; *D. liebeana*) of Thuringia, East Germany. It is absent in the Early Devonian *Nereitenquarzit*, and analysis of the trace fossil assemblages points to environmental partitioning within the 'deep-sea' *Nereites* Association. The Carboniferous *Dictyodora* was much larger than the Early Palaeozoic forms and had a long respiratory (?) wall organ. This may have been an adaptation to feeding deeper in anoxic sediments, and the animal developed large 'parapodia' to effect its progression through the sediment. □ *Trace fossils, Palaeozoic, Nereites Association, Thuringia, Dictyodora.*

Michael J. Benton, Nature Conservancy Council, Pearl House, Bartholomew Street, Newbury, Berkshire, RG14 5LS, England, U.K.; 13th May, 1981 (revised 1982/01/19).

The Thuringian *Schiefergebirge*, in the southern DDR and partly in the BRD, consists of a series of Proterozoic to Carboniferous metasediments, only some of which are fossiliferous. Large tracts yield only deep-sea trace fossil faunas of Late Ordovician, Early Devonian, and Early Carboniferous age. *Dictyodora* occurs in the Ordovician and Carboniferous deposits, but is absent from the Devonian.

During a recent trip to East Germany, I was able to visit several localities and collect trace fossils (because of the politically sensitive nature of some of the localities, I would like to make it clear that I visited the sites as a holiday-maker and did so without the advice or assistance of anyone living in the DDR). The aim of this work is to offer new information on the evolution and biology of *Dictyodora*, and to review relevant features of the associated ichnofaunas.

Geological setting

The Lower Palaeozoic rocks of the Thuringian *Schiefergebirge* (Fig. 1) are exposed in two SW–NE trending horsts, the *Schwarzburger Sattel* (including the *Gräfenthaler Horst*) in the west, and the *Lobensteiner Horst* (passing north into the *Bergaer Sattel*) in the east. These structural highs were formed during the Variscan orogeny, and they are separated by a large area of Early Carboniferous (Culm) sediments. The Palaeozoic rocks are bounded to the north by the large

Permo-Triassic Thuringian basin, and to the south by a similar large basin in southeastern Thuringia and northern Franconia. During the Palaeozoic, Thuringia lay on the southern margin of Baltica, or Laurussia, which allowed continuous marine sedimentation until mid-Carboniferous times when the central European plate attached (Ziegler *et al.* 1979).

The stratigraphy of Thuringia is reviewed in Hoppe & Seidel (1974), and the main features, and the trace fossil-bearing beds, are summarised in Fig. 2. The Early Ordovician *Phycoden-Serie* is a shallow water deposit with trace fossils (Hundt 1941b) typical of the *Cruziana* Facies (Seilacher 1978), and it will not be considered further here. Rare *Dictyodora*, *Nereites* and *Neonereites* have been reported from the Late Devonian near Saalfeld (Fig. 1; Richter & Unger 1856; Pfeiffer 1954), but the main trace fossil horizons of interest here are the Late Ordovician *Hauptquarzit*, the Early Devonian *Nereitenquarzit*, and the Early Carboniferous *Bordenschiefer*.

Trace fossils of the Late Ordovician *Hauptquarzit*

The *Hauptquarzit* is dated as ?Llandeilo–Caradoc on the basis of the faunas of adjacent beds (Knüpfner 1967:69; Wiefel 1974:185–186), and it is exposed only in the eastern horst. Between Zeulenroda and Hohenleuben (Fig. 3A), this unit is about 170 m thick, and reaches its thickest

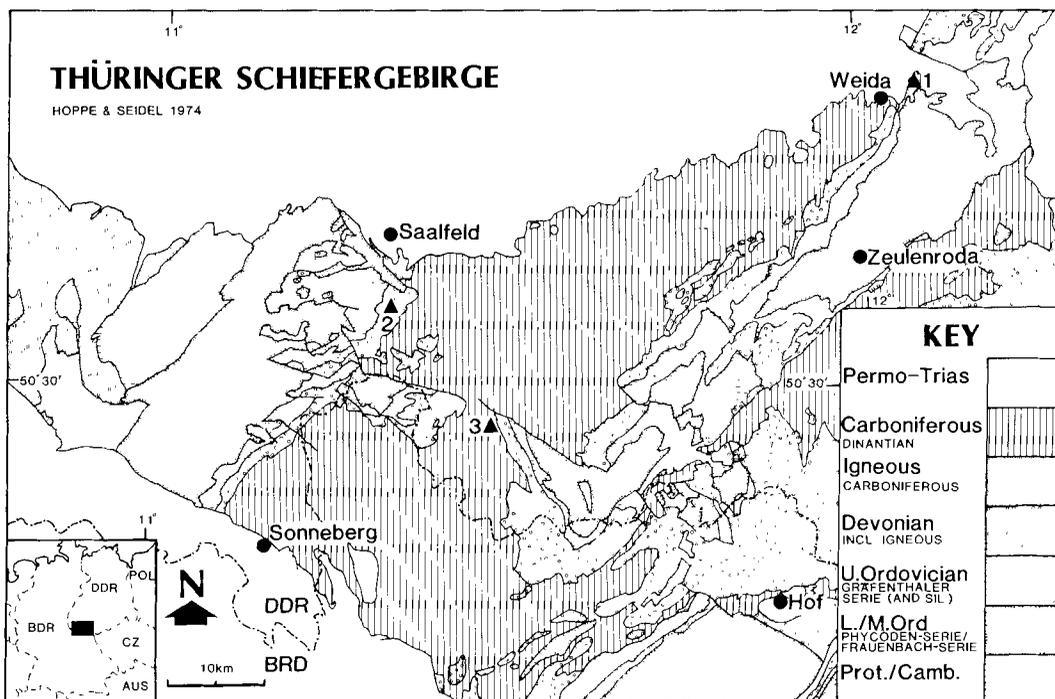


Fig. 1. Map of the Thuringian *Schiefergebirge* showing main Palaeozoic outcrop. Major towns are named, and the border between East and West Germany (DDR, BRD) is indicated. The western *Schwarzburger Sattel* runs SW from Saalfeld, and the eastern *Bergauer Sattel* runs SW from Weida. Main trace fossil localities are indicated with black triangles: 1. Wünschendorf (Upper Ordovician), 2. Schaderthal (Lower Devonian), 3. Wurzbach (Lower Carboniferous). Map modified from Deuber & Martini (1942), in Hoppe & Seidel (1974).

extent of 240 m at Wünschendorf. Two large quarries here on the Hüttchenberg, just south of the town, expose a considerable part of the *Hauptquarzit*, which is strongly folded, jointed, and mineralised in part of the northern quarry.

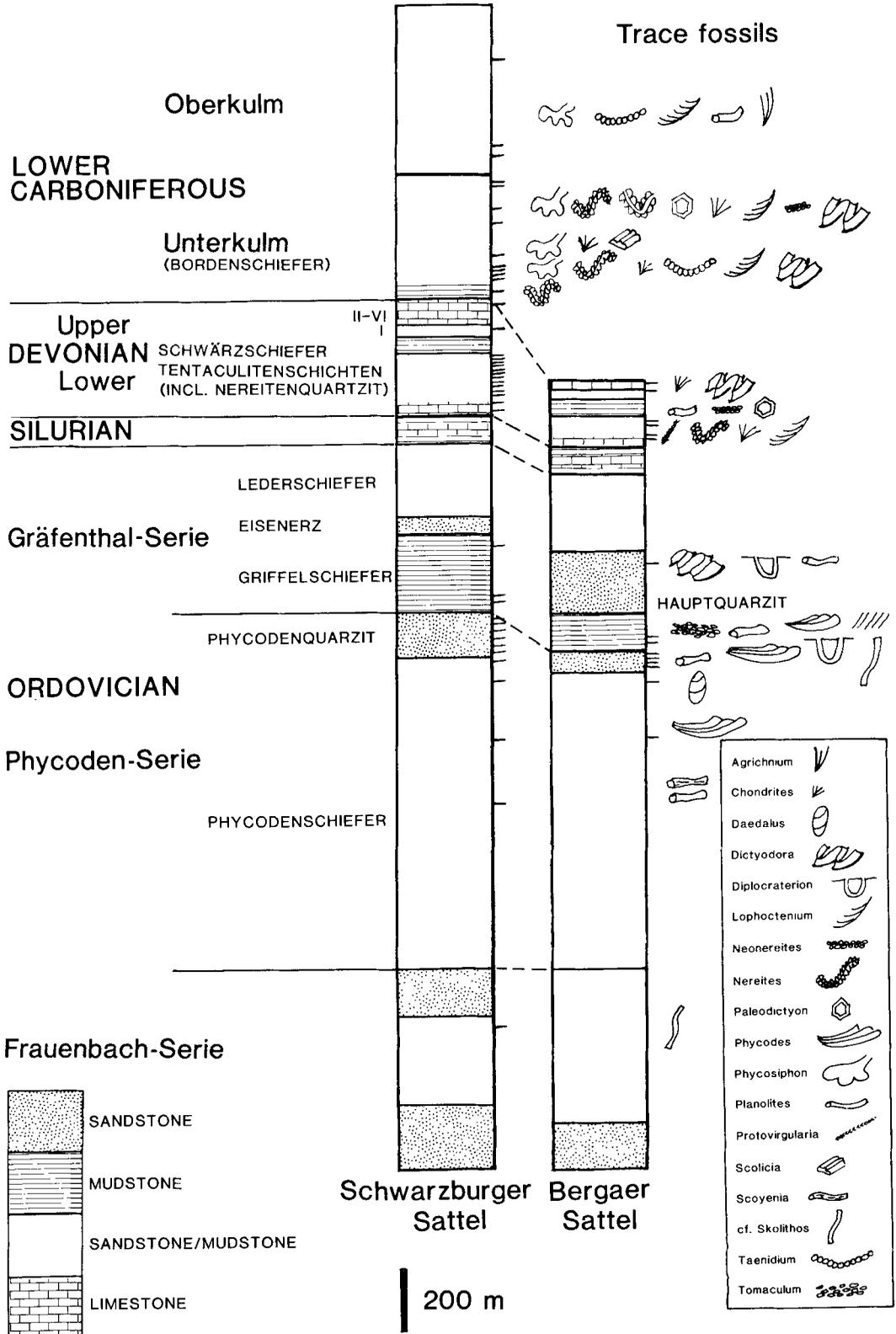
Body fossils are rare, and consist of an *Orthoceras* (Bachmann 1954) and some inarticulate brachiopods (Freyberg 1923:250). The *Hauptquarzit* was interpreted by Knüpfer (1967:72) as a shallow water deposit, and Wiefel (1974:189) wrote that it has 'numerous features of shallow water and in places of submarine slumping'. Unfortunately, there has been no detailed sedimentological study, and a definite conclusion as to the environment cannot be reached.

Trace fossils occur in maroon and grey-green mottled parallel- and cross-laminated siltstones and mudstones in the quarries at Wünschendorf (Hundt 1912, 1928). Other localities include hill-side sites and quarries on the road between Hohenölsen and Hoehnleuben, Reichenfels ruined castle, near Triebes (Hundt 1928, 1931a, 1941a),

and Lössau, near Schleiz (Zimmermann 1892:61; Fig. 3A herein).

The trace fossils have been named as *Dictyodora zimmermanni* Hundt 1913, *Paleodictyon eisleanum* Hundt 1913, *Arenicolites didyma* Salter 1857, *A. obliquiforans* Hundt 1928, *A. simplex* Hundt 1928, *A. pfeifferi* Hundt 1928, *A. pascholdi* Hundt 1931, *Phyllocytes geraensis* Hundt 1928, and *Arthropycus flabelliformis* Hundt 1940. Hundt's descriptions are poor, the last eight names are inappropriate, and most of the traces have never been figured adequately.

Fig. 2. Diagrammatic summary of Palaeozoic (Ordovician-Carboniferous) stratigraphy of the Thuringian *Schiefergebirge* in the *Schwarzburger Sattel* and the *Bergauer Sattel*. The main lithological types and average relative thicknesses of the units in each horst are shown. Trace fossil horizons are marked on the stratigraphic columns, and the pictographs on the right-hand side show main components of the ichnofaunas. Dating from graptolites (Ordovician-Silurian), ostracodes and tentaculitids (Devonian). Based on information in Volk (1964b), Pfeiffer (1968), Hoppe & Seidel (1974), and original data.



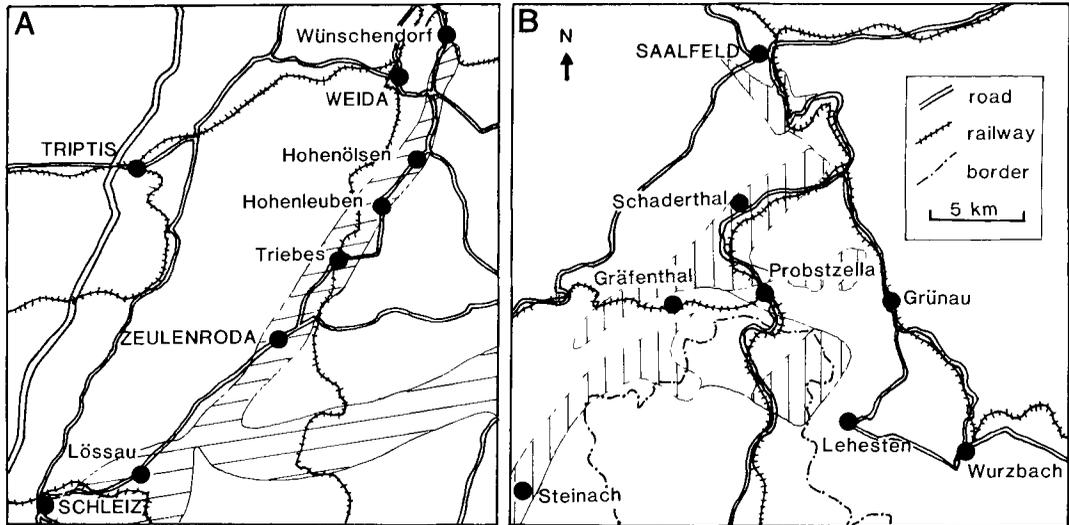


Fig. 3. Locality maps for trace fossil sites. □ A. Upper Ordovician *Hauptquarzit* of the *Bergaer Sattel*; approximate outcrop area shaded. □ B. Lower Devonian *Nereitenquarzit* of the *Schwarzbürger Sattel*; approximate outcrop area shaded. Lower Carboniferous *Unterkulm* of the *Teuschnitz-Ziegenrück Mulde*; outcrop east of the Devonian. Maps A and B include localities 1, and 2 and 3 of Fig. 1, respectively.

DICTYODORA ZIMMERMANNI Hundt 1913

Fig. 4A, B.

Synonymy. – □ 1892 *Palaeochorda*; Zimmermann, p. 61. □ 1912 *Silur-Dictyodora*; Hundt, p. 93. □ 1912 *Dictyodora liebeana* (Geinitz); Auerbach, pp. 127–128. □ * 1913 *Dictyodora zimmermanni* Hundt, pp. 180–181. □ 1928 *Dictyodora zimmermanni* Hundt; Hundt, pp. 27–31. □ 1928 *Phyllococites geraensis* Hundt, p. 32. □ 1929 *Dictyodora zimmermanni* Hundt; Korn, pp. 26, 38. □ 1931a *Dictyodora zimmermanni* Hundt; Hundt, pp. 184–186. □ 1940 *Arthropycus flabelliformis* Hundt, p. 211. □ 1941a *Dictyodora zimmermanni* Hundt; Hundt, pp. 150–151.

Material. – Auerbach Collection, Hundt Collection, Natural History Museum, Gera (?).

Description. – The material from Wünschendorf displays the characteristic features of *Dictyodora*: basal burrow and dorsal vertical wall. The basal burrow is preserved with a lenticular cross-section and varies from 4 mm to 5 mm wide and up to 3 mm high. The wall is placed centrally on top of the burrow and is up to 25 mm high (Fig. 4 B). It tapers upwards from a width of 2 mm at the base. Meandering is rather irregular (Fig. 4A), but when loops are developed, they are 40–60 mm long and spaced 10–20 mm apart. Frequently, the traces traverse large areas without displaying tight looping. At several points, the trace terminates in a large ovoid mark (Fig.

4A) which probably represents a point at which the animal has changed level in the sediment.

Dictyodora zimmermanni shows various preservational aspects, as in other examples of the same genus (e.g. Pfeiffer 1959; Benton & Trewin 1980). Most common are bedding plane views of horizontal sections through the wall (Fig. 4A). Bedding plane views of the basal burrow are rarer, probably because of the irregularly laminated nature of the sediment. The vertical wall represents a line of weakness through the sediment, and blocks may break in such a way as to reveal side views of the wall (Fig. 4B), as in other material of *Dictyodora* (e.g. Weiss 1884b; Benton & Trewin 1980). The striation pattern is not so well shown in the *Hauptquarzit* material because of the relatively coarse nature of the sediment, but there are clear oblique ‘ripples’ in the wall, probably reflecting jerky progression through the sediment. The basal burrow displays clear curved packing structures when sectioned longitudinally, and these appear to match the wall striations in spacing.

Discussion. – *Dictyodora zimmermanni* Hundt 1913 differs from *D. scotica* (M’Coy 1851) from the Lower Silurian of Scotland in its less regular looping pattern and greater wall height (average

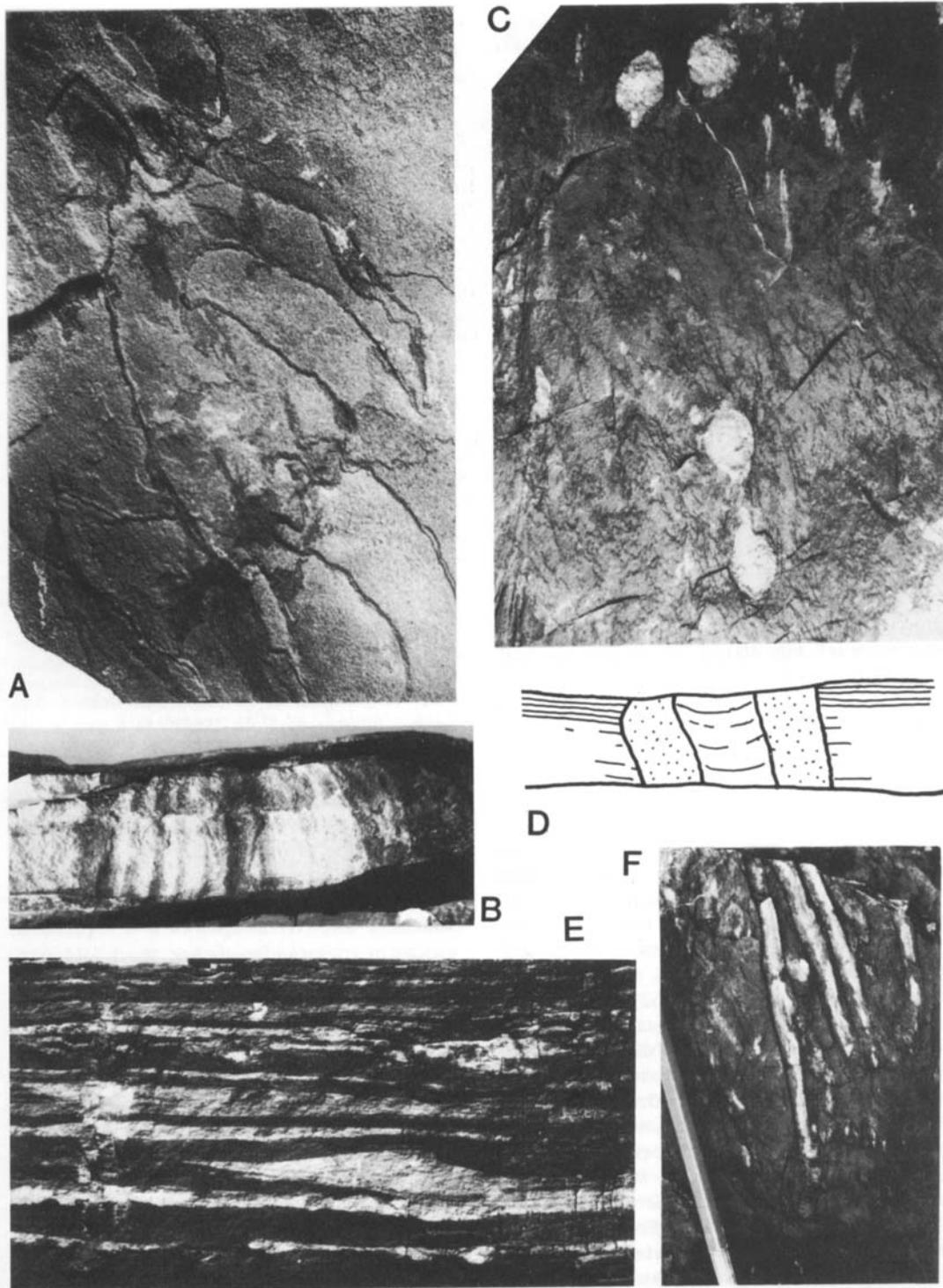


Fig. 4. Trace fossils from the *Hauptquarzit* (Upper Ordovician) of Wünschendorf, near Weida. □ A. *Dictyodora zimmermanni* Hundt 1913, bedding plane view of wall. $\times 0.9$. □ B. *Dictyodora zimmermanni*, side view of wall showing oblique 'waves'. $\times 1.0$. □ C. *Diplocraterion yoyo* Goldring 1962, bedding plane view of sections through two U-shaped burrows. $\times 1.0$. □ D. *Diplocraterion yoyo*, tracing of vertical section showing burrow fill and spreite. $\times 1.0$ □ E. Field photograph showing siltstone laminae, cross lamination, and cross-sections of *Planolites* burrows in light-coloured beds. $\times 0.4$. □ F. Bedding plane view of *Planolites* burrows. $\times 0.4$.

20–25 mm; *D. scotica*: 10–14 mm). It differs from *D. tenuis* (M'Coy 1851) in these features and in the absence of regular secondary sinuosity (Benton & Trewin 1980). It is concluded that *D. zimmermanni* Hundt 1913 is a valid name for Lower Palaeozoic *Dictyodora* with wall heights in excess of 15 mm and irregular meander pattern. These three forms all differ from Devonian and Carboniferous *D. liebeana* (Geinitz 1867b), which is a tighter complex with spiral units of considerable height.

Hundt's original description (1912:93) was rather imprecise ('Silurian *Dictyodora* ... The mode of preservation ... is the same as in the Culm. Differing from it is probably only the lower height of its cornet-shaped body ...'). He established the name *D. zimmermanni* in 1913 (pp. 180–181) without further description. Nevertheless, the description is probably adequate as an 'indication' (ICZN Code 1961, Article 16), and the name is regarded as valid. *Phyllodocites geraensis* Hundt 1928 is probably a basal burrow, and *Arthropycus flabelliformis* Hundt 1940 was based on specimens from Wünschendorf which are clearly views of the vertical wall of *D. zimmermanni* (cf. Fig. 4B).

Other trace fossils present in the HAUPTQUARZIT

Fig. 4C–F.

Diplocraterion yoyo Goldring 1962 (Fig. 4C, D). Small U-shaped burrows with protrusive spreite occur with *Dictyodora zimmermanni*. In bedding plane view, many slabs bear paired oval to sub-circular vertical burrows, 4–8 mm in diameter, whose colour differentiates them from the sediment. They are linked by a narrow zone of spreite ('septum': Goldring 1962), and these appear as deeply sagging meniscus structures in vertical section. The size and shape of the burrows, and the nature of the spreite fall well within the range of variation of *D. yoyo* from the Upper Devonian Baggy Beds of north Devon (Goldring 1962:239). The earlier identification as *Arenicolites didyma* Salter (Hundt 1912, 1928:21–24) is inappropriate because of the occurrence of spreite, and *A. pfeifferi* Hundt 1928 is identical. The other species of *Arenicolites* established by Hundt (1928, 1931a) are *Planolites* or *nomina nuda*.

Planolites vulgaris Nicholson & Hinde 1874 (Fig. 4E, F). Irregular, straight, smooth-walled

horizontal burrows, 2–8 mm in diameter, and elliptical to subcircular in cross-section. In vertical views (Fig. 4E), these burrows appear to be concentrated at certain horizons and they generally mix light-coloured sediment into the darker red horizons. There is no sign of backfill structures, they do not branch, and the burrow fill is different from the matrix, which suggests that these are *Planolites* rather than *Palaeophycus* (Osgood 1970:375, 376; Alpert 1975:512; Benton & Trewin 1978:6).

Some slabs bear *Caridolites*-like 'scratch' marks which have also been reported in association with *Dictyodora* in the Scottish Lower Silurian (Benton & Trewin 1980:510–511). *Cruziana-formen* and *Kriechspuren* described by Hundt (1928) may be *Planolites*, or inorganic structures.

Hundt (1912:93–94) described a 'worm-like problematicum' (*Paleodictyon eiseleanum* Hundt 1913) and 'worm crawling traces' from Wünschendorf, but no specimens have been found that match these meagre descriptions.

Trace fossils of the Early Devonian *Nereitenquarzit*

The *Nereitenquarzit* (= *Nereitenschichten*; *Steinach Schichten* of Volk 1964b) is a unit at the base of the *Tentaculitenschichten* (upper part of the *Tentaculitenschiefer*), dated as Emsian on the basis of tentaculitids and other fossils (Steinbach 1974:208, 247). It is exposed in a strip down the southeast side of the *Schwarzburger Sattel*, and thins from 120 m to 70 m in the east, passing conformably up into more typical *Tentaculitenschichten*. The *Nereitenquarzit* is a sequence of banded quartzite and mudstone, much folded and quartz-veined, and capped by a thin conglomerate in the west. Trace fossils occur in the laminated mudstones (burrows, *Chondrites*, *Nereites*) and in associated flaggy, unbedded, and coarse quartzites (burrows, *Chondrites*, *Lophoctenium*, *Protovirgularia*, *Protopaleodictyon*; Volk 1964b). Localities are the valley between Schaderthal and Probstzella, Gräfenthal, and Steinach (Hundt 1931b; Volk 1964b; Pfeiffer 1968; Fig. 3B herein). The *Tentaculitenschichten* were probably deposited in water of fluctuating depth. The trace fossils are mainly typical of the flysch *Nereites* Association, but autochthonous body fossils such as spiriferid brachiopods, crinoids, gastropods, and trilobites in associated beds point to shelf influences (Pfeiffer 1968:662).

On the basis of the trace fossils, these beds were long dated as Silurian by comparison with apparently similar trace fossil assemblages in Britain (Richter 1849, 1850, 1869; Murchison & Morris 1855; Marr 1889:415). Kayser (1894) corrected the stratigraphic assignment.

The trace fossils of the *Nereitenquarzit* have been described by several authors (Richter 1849, 1850, 1853, 1869; Hundt 1931b; Volk 1961, 1964a, b; Pfeiffer 1968), and the ichnofauna is summarised in Fig. 5. The important point to note is the absence of *Dictyodora*.

Pfeiffer gives a good series of plates of the Devonian and Carboniferous trace fossils, but the scales given on some of these at least should be multiplied by 1/2 or 2/3 where there is direct evidence of the actual size of the specimens (e.g. Pl. 1:1-2; Pl. 6:4-6; Pl. 7:1, 2, 4, 6-8; Pl. 8:1-7; Pl. 9:1-6).

Most of the identifications are based on those of Pfeiffer (1968), but the changes are noted here. Specimens identified here as *Neonereites biserialis* Seilacher 1960 (Hundt 1931b:30; Pfeiffer 1968, Pl. 1:5, Pl. 3:1, 3; Fig. 5G herein) correspond closely to examples from the Lower Silurian of the Southern Uplands of Scotland, and Co. Down, Northern Ireland (Doughty 1980). Thuringian material of *Nereites macleayi* (Murchison 1839; Fig. 5H herein) was called *N. tenuissimus* (Geinitz 1853) by Pfeiffer (1968:670-671, Pl. 3:1, 2), but these appear to be indistinguishable.

Protopaleodictyon spinata (Geinitz 1867; Fig. 5K herein) includes *Spinorhapha rubra* Pfeiffer (1968:682-683, Pl. 6:5, 6), which differs only in that the side branches of the former project at an angle from the main stem, whereas they merely continue in the same direction as one of the straight segments of the main stem in the latter. In view of the irregularity of this kind of trace fossil (Seilacher 1977b:306), it seems inappropriate to draw such fine distinctions.

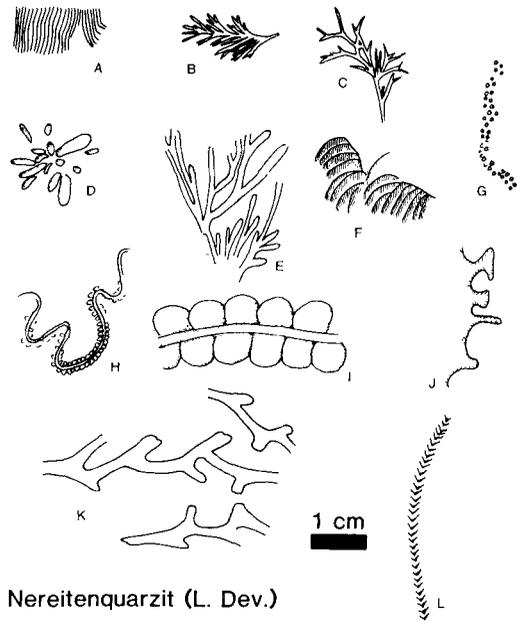
Thuringian specimens called *Protovirgularia nereitarum* (Richter 1853; Fig. 5L herein) are indistinguishable from *P. dichotoma* M'Coy 1850 from the Lower Silurian of the Southern Uplands of Scotland, and the species are synonymised.

Other trace fossils not figured here include abundant unbranched, smooth-walled horizontal burrows, varying from 2 mm to 10 mm in diameter (Hundt 1931b; Volk 1964b).

Trace fossils of the Early Carboniferous Culm

The Culm (Lower Viséan) of the Teuschnitz-Ziegenrück Mulde, between the two horsts, contains trace fossils at many levels, but no body fossils (Fig. 2; Pfeiffer 1968:659). The sediments are rhythmically layered black sapropelic mudstone and greywacke, and deposition evidently occurred in a deep basin. The trace fossil occurrences of the *Unter-* and *Oberkulm* have been correlated with major sedimentary cycles, and divided into five zones by Pfeiffer (1968).

The *Unterer Bordschiefer* (Lower *Unterkulm*) consists of three zones. The first, the Lehesten, has yielded only rare trace fossils (*Nereites*, *Dictyodora* and *Phycosiphon*) from Staats-



Nereitenquarzit (L. Dev.)

Fig. 5. Typical trace fossils of the *Nereitenquarzit*. □ A. *Agronidium brühmi* Pfeiffer 1968. □ B. *Chondrites antiquus* Göppert 1852. □ C. *Chondrites filifalx* Volk 1964a. □ D. *Chondrites glomeratus* (Ludwig 1869). □ E. *Chondrites goepperti* Geinitz 1853. □ F. *Lophoctenium comosum* Richter 1851. □ G. *Neonereites biserialis* Seilacher 1960. □ H. *Nereites macleayi* (Murchison 1839). □ I. *Nereites cambrensis* Murchison 1839. □ J. *Phycosiphon* sp. □ K. *Protopaleodictyon spinata* (Geinitz 1867). □ L. *Protovirgularia dichotoma* M'Coy 1850. Figures drawn to same scale, and based on Volk (1961): L, Volk (1964a); C-E, Volk (1964b); K, Pfeiffer (1968): A, B, F-J.

bruch Quarry, near Lehesten (Fig. 3B). The second zone, the Hasenthal, has a richer fauna, dominated by *Phycosiphon*, *Dictyodora*, *Lophoctenium*, *Nereites* and *Chondrites* (Fig. 9). Specimens are commonest in an old quarry at Obernitz, near Saalfeld, and the quarry Franzensberg, 5 km south of Wurzbach. The third zone, the Kaulsdorf, represented only by a quarry near Kaulsdorf, 6 km southeast of Saalfeld (Fig. 2), has yielded a similar, but less numerous, ichnofauna dominated by *Phycosiphon*.

The *Oberer Bordschiefer* (Upper *Unterkulm*) consists of one important zone, the Röttersdorf, which includes the quarries at Grünau, Koselstein, Röttersdorf, and Vogelsberg, near Wurzbach (Fig. 3B). These quarries have yielded vast numbers of specimens, and have attracted most attention. The ichnofauna is dominated by *Dictyodora*, but contains rarer examples of ten more genera.

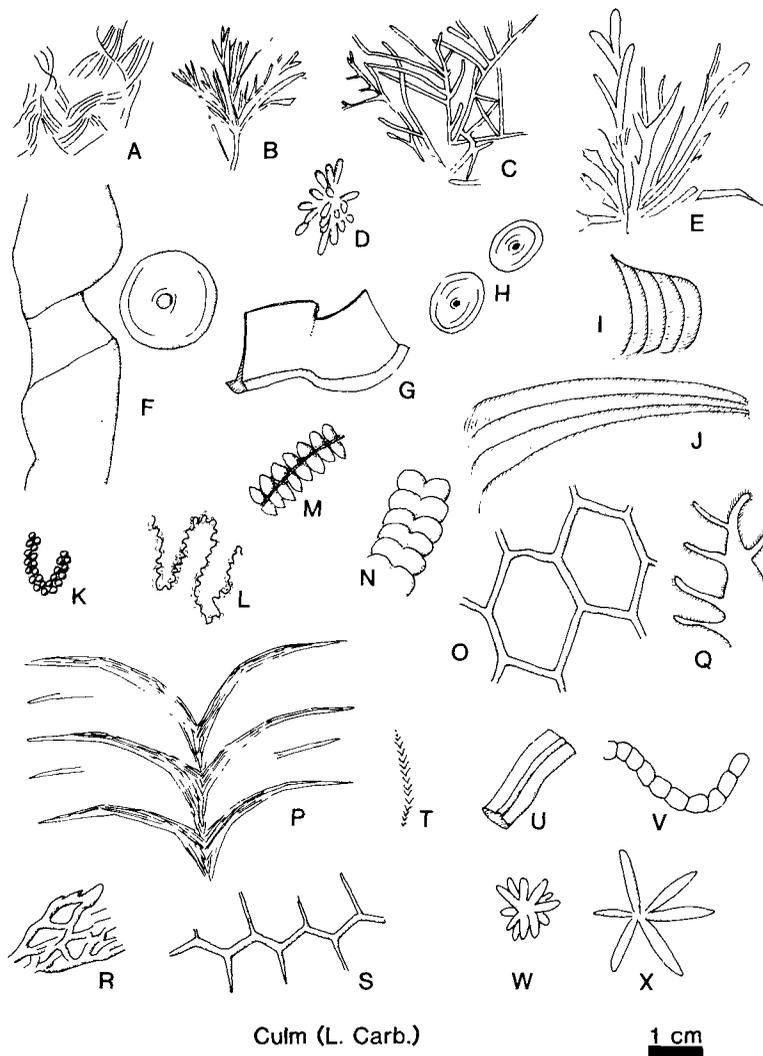


Fig. 6. Typical trace fossils of the Unter- and Oberkulm. Zones indicated as follows: F. *Fimbriatus Sandstein*, H. Hasenthal, K. Kaulsdorf, L. Lehesten, R. Röttersdorf, Z. Ziegenrück. □ A. *Agrichnium fimbriatum* (Ludwig 1869) (F). □ B. *Chondrites antiquus* Göppert 1852 (H, Z). □ C. *Chondrites filifalx* Volk 1964a (R). □ D. *Chondrites glomeratus* (Ludwig 1869) (R). □ E. *Chondrites goepperti* Geinitz 1853 (H, K, R). □ F. *Cylindrichnus* sp. (Z). □ G. *Dictyodora liebeana* (Geinitz 1867) (L-Z). □ H. *Laevicyclus* sp. (R). □ I. *Lophoctenium comosum* Richter 1851 (H, R, Z). □ J. *Lophoctenium hartungi* Geinitz 1864 (R). □ K. *Neoneireites biserialis* Scialacher 1960 (R). □ L. *Nereites macleayi* (Murchison 1839) (R). □ M. *Nereites cambrensis* Murchison 1839 (L-Z). □ N. *Nereites jacksoni* Emmons 1844 (K, R). □ O. *Paleodictyon* (*Glenodictyon*) sp. (R). □ P. *Palmichnium culmicum* Pfeiffer 1968 (H, K). □ Q. *Phycosiphon* sp. (R). □ R. *Megagraption hartungi* (Geinitz 1867) (R). □ S. *Protopaleodictyon spinata* (Geinitz 1867) (R). □ T. *Protovirgularia dichotoma* M'Coy 1850 (H, K). □ U. *Scolicia* sp. (H, K, Z). □ V. *Taenidium praecarbonicum* Gumbel 1879 (F). □ W. *Volkichnium volki* Pfeiffer 1965 (H, R). □ X. *Volkichnium minutum* Pfeiffer 1968 (H, R). Figures drawn to same scale, and based on Geinitz (1867): B, E, I, N; Pfeiffer (1968): A, C, D, F-H, J-M, O-X.

The Oberkulm Ziegenrück zone at Alter Presswitzer Weg and Könitz, 9 km east of Saalfeld, has yielded a sparse ichnofauna dominated by *Phycosiphon* with a few *Dictyodora*. The curious *Agrichnium fimbriatum* is found widely in a sandstone unit at the base of the Röttersdorf and Ziegenrück zones (*Unterer* and *Oberer Fimbriatus-Sandstein*).

The trace fossils of the *Bordenschiefer*, and particularly those from the Röttersdorf zone of Koselstein Quarry, near Wurzbach (Fig. 3B), have been described in some detail (Geinitz

1864, 1867a, b; Ludwig 1869; Weiss 1884b; Zimmermann 1889, 1891, 1892, 1893; Rauff 1892; Korn 1929; Pfeiffer 1959, 1968; Müller 1962, 1971; Volk 1964b). Pfeiffer (1968:660) lists 44 species of trace fossils from the Culm, but that figure may be reduced to 23 by ignoring rare, doubtful specimens, and by some synonymising. The Culm ichnofauna is summarised in Fig. 6. Some taxonomic notes follow, and *Dictyodora liebeana* is discussed in more detail below.

The specimens called *Cylindrichnus* sp. here (Fig. 6E) were described as *Ophthalmichnium heerwageri* Pfeiffer

(1968:691–693, Fig. 3 [No. 24], Pl. 7:6–8), and *Ophthalmidium* (misspelt!) was synonymised with *Planolites* by Häntzschel (1975:W97). However, these burrows are subvertical, tapering, and have a central core, which suggests an assignment to *Cylindrichnus*. *Laevicyclus* sp. (Fig. 6H) may represent the tops of such vertical burrows (Häntzschel 1975:W77).

Lophotenus hartungi Geinitz 1864 (Fig. 6J) may include *Minichnium wurzbachensis* Pfeiffer (1968:683–684, Pl. 6:7, 8). Häntzschel (1975:W82) accepted the genus as valid, but noted that it was 'poorly figured'.

Megagraption hartungi (Fig. 6R) is a reassignment of *Palaeophycus hartungi* Geinitz 1867. Pfeiffer (1968:674) erected the new genus *Pseudopaleodictyon* for this irregular meshwork, but the name is probably unnecessary. Häntzschel (1975:W97) tentatively synonymised *Pseudopaleodictyon* with *Protopaleodictyon*, but a more appropriate assignment is to *Megagraption* Książkiewicz 1968. This genus was established for Eocene specimens (Häntzschel 1975:W82), but includes irregular net-like forms (Seilacher 1977b:320–321) like the Palaeozoic material.

Specimens assigned earlier to *Phyllocytes* are placed in *Nereites cambrensis* (Fig. 6M) and *N. jacksoni* (Fig. 6N) because of an overlap in the boundaries of these genera, and because the type species, *P. thuringiaca* Geinitz 1864 is probably a basal burrow of *Dictyodora* (see below).

Paleodictyon specimens (Fig. 6O) probably belong to *P. (Glenodictyon)* because of their regular hexagonal shape and lack of vertical outlets (Seilacher 1977b:324).

Specimens called *Cosmorhaphie timida* Pfeiffer (1968:667, 669, Pl. 2:1, 2) are assigned to *Phycosiphon* sp. here (Fig. 6Q). Pfeiffer (1968:675–676, Fig. 4) described a wide range of forms of *Phycosiphon* and his new species of *Cosmorhaphie* appears to fall within that range.

Taenidium praecarbonicum Gümbel 1879 (Fig. 6V) occurs in sandstone beds, while *Nereites jacksoni* is found in associated mudstone units. The size and appearance suggest that this *Taenidium* could be part of a *Nereites* trace, preserved in coarser sediment than usual. This interpretation was also suggested by Pfeiffer (1968:689) for a specimen ascribed to *Neonereites uniserialis* by Volk (1964b:174, Fig. 13).

Other traces not figured here include subcircular impressions identified as *Guillemmites* Geinitz by Pfeiffer (1968:692, Pl. 8:6) which could be pseudofossils (Häntzschel 1975:W175), and some isolated burrow-like structures (Pfeiffer 1968:692–693).

DICTYODORA LIEBEANA (Geinitz 1867)

Figs. 7, 8.

Synonymy. – □ 1852 *Noeggerathia rueckeriana* Göppert, p. 220, Pl. 42:2. □ 1853 *Noeggerathia rueckeriana* Göppert; Geinitz, p. 82, Pl. 18:8. □ 1864 *Gordia marina* Emmons; Geinitz, p. 1, Pl. 1:1. □ 1864 *Crossopodia thuringiaca* Geinitz, p. 3, Pl. 1:1, 2; Pl. 2:3a, b. □ 1865 *Conularia reticulata* Richter, p. 369, Pl. 11:3. □ 1867a *Dictyophyton? liebeanum* Geinitz, pp. 15–16, Pl. 6:1. □ 1867b *Phyllocytes thuringiaca* (Geinitz); Geinitz, pp. 3–4, Pl. 3:1. □ 1867b *Crossopodia henrici* Geinitz, p. 5, Pl. 5:1, 2. □ 1867b *Nereites loomisi* Geinitz, p. 6, Pl. 4. □ 1867b *Palaeochorda marina* (Emmons); Geinitz, pp. 14–15, Pl. 6:1, 2. □ 1867b *Palaeochorda spiralis* Geinitz, pp. 15–16, Pl. 6:1. □ 1870 *Nemerites sudeticus* Roemer, p. 33, Pl. 6:7. □ 1879 *Taonurus praecarbonicus* Gümbel, p. 535. □ 1879 *Noeggerathia rueckeriana* Göppert; Gümbel, p. 535. □ 1884a *Dictyodora liebeana* (Geinitz); Weiss, p. 17. □ 1884b *Dictyodora liebeana* (Geinitz); Weiss, pp. 84–89, Pls. 11, 12:1–5. □ 1889 *Dictyodora liebeana* Weiss; Zimmermann, pp. 165–167. □ 1891 *Dictyodora*; Zimmermann, pp. 551–555. □ 1892 *Dictyodora liebeana*

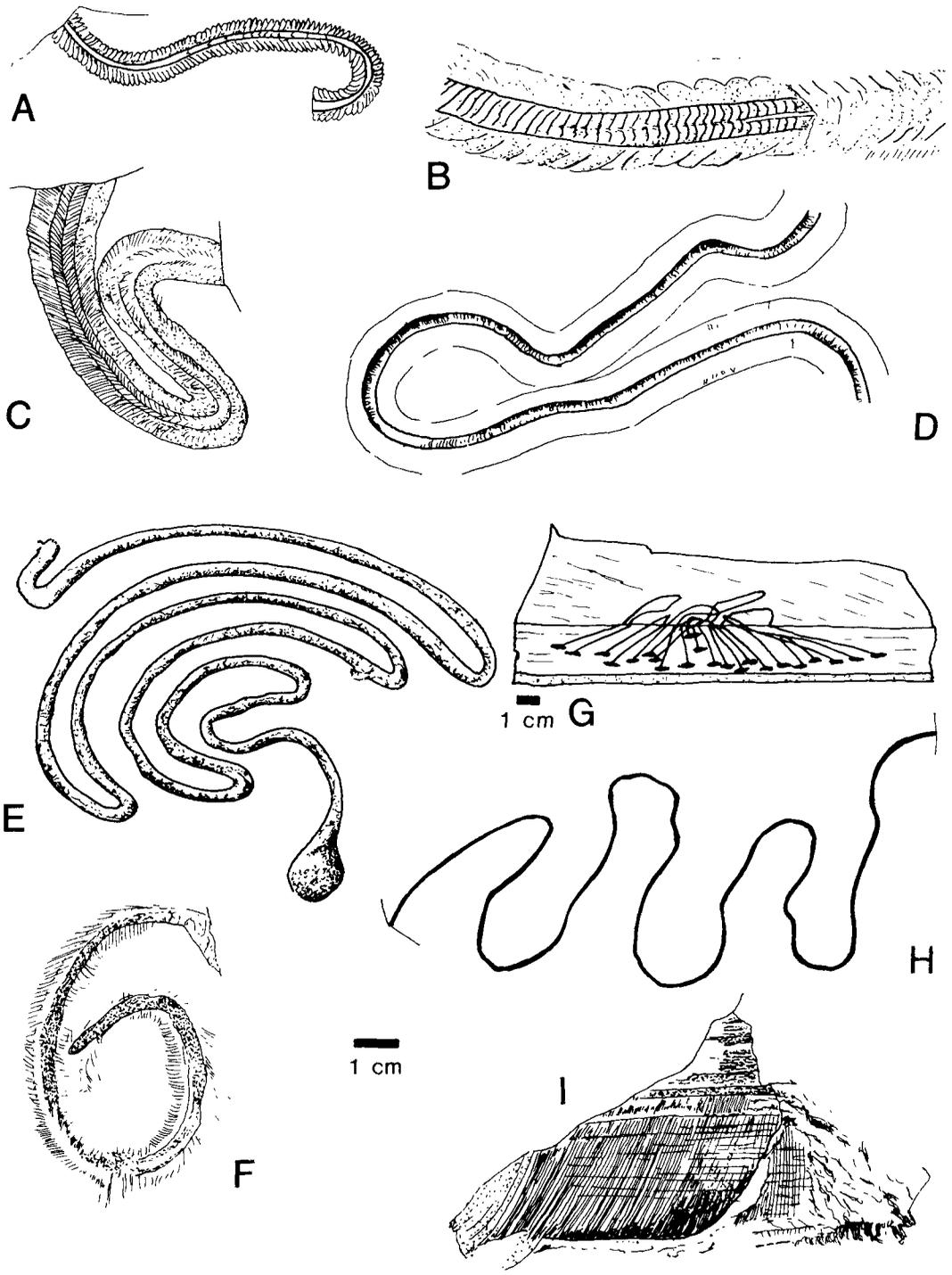
Weiss; Rauff, pp. 561–564. □ 1892 *Dictyodora liebeana* Weiss; Zimmermann, pp. 28–63, Fig. 1. □ 1893 *Dictyodora liebeana* Weiss; Zimmermann, pp. 155–158, Figs. 1–5. □ 1910 *Dictyodora liebeana* Weiss; Zimmermann, p. 49. □ 1910 *Palaeochorda spiralis* Geinitz; Zimmermann, p. 40. □ 1911 *Dictyodora liebeana* Weiss; Zimmermann, p. 50. □ 1929 *Dictyodora liebeana* Weiss; Korn, pp. 25–46, Fig. 1. □ 1935 *Dictyodora liebeana* (Weiss); Abel, pp. 429–441, Figs. 359–363. □ 1943 *Dictyodora*; Hundt, pp. 121–122, Fig. 1. □ 1954 *Dictyodora liebeana* (Weiss); Pfeiffer, p. 71, Pl. 5:2. □ 1959 *Dictyodora liebeana* (Weiss); Pfeiffer, pp. 425–434, Pls. 1, 2, 3. □ 1960 *Dictyodora liebeana* (Weiss); Pfeiffer, p. 40, Fig. 7e, f. □ 1962 *Dictyodora liebeana* (Geinitz); Müller, pp. 8–18, Figs. 1–4. □ 1964b *Dictyodora liebeana* (Geinitz). *Crossopodia henrici*, *Palaeochorda marina*; Volk, pp. 174–176, Figs. 14–16, Pl. 9:1. □ 1967 *Dictyodora* sp.; Ruchholz, pp. 509–512, Figs. 6, 7, 9, Pl. 2, Pl. 3:1. □ 1967 *Dictyodora liebeana* (Weiss); Ruchholz, pp. 514–516, Figs. 13–15, Pl. 4. □ 1967 *Dictyodora*; Seilacher, pp. 78–80. □ 1968 *Artikulation-Fährte*; Pfeiffer, p. 666, Pl. 1:3. □ 1968 *Spirodesmos spiralis* (Geinitz); Pfeiffer, pp. 673–674, Pl. 3:6; Pl. 7:1. □ 1968 *Phyllocytes thuringiacus* (Geinitz); Pfeiffer, pp. 686–687, Pl. 9:1–4. □ 1968 *Dictyodora liebeana* (Geinitz); Pfeiffer, pp. 689–690, Pl. 10:1–4. □ 1968 *Mäanderierender Fressbau mit Versatzlamellen*; Pfeiffer, p. 691, Pl. 7:5. □ 1971 *Dictyodora liebeana* (Geinitz); Müller, pp. 136–151, Figs. 1–11, Pls. 1–3. □ 1974 *Dictyodora liebeana* (Weiss); Gräbe, Photo 40 (p. 269), p. 282. □ 1974 *Dictyodora*; Seilacher, p. 240, Fig. 7.

Material. – The type specimen (Geinitz, 1867a, Pl. 3:3) was preserved in Gera or Dresden, but was probably lost during the war (Pfeiffer 1968:656). Many hundreds of specimens are preserved in various museums. Pfeiffer (1968:655–656) lists the current repositories of the collections of Geinitz, Gümbel, Weiss, Zimmermann, Korn, and Pfeiffer, in Berlin, Halle, Freiberg and Gera.

Description. – The most complex *Dictyodora* form, *D. liebeana*, always has the typical basal burrow and mid-dorsal vertical wall. The basal burrow is up to 20 mm wide, and may appear as a 2–5 mm broad tunnel, circular in section, or it may have broad side segments. Some specimens show regular backfill or packing structures in both the central and side portions (spacing 1–1.5 mm; Fig. 7C). In cross-section, the basal burrow is lens-shaped with a subcircular central portion and rather pointed lateral projections.

The vertical wall tapers upwards from a basal width of about 2 mm and may rarely reach a height of 16 cm (Weiss 1884b:87). In side view, the wall shows fine curved oblique and longitudinal streaks, 2–4 per mm (Fig. 7I), that probably reflect episodic movement through the sediment.

Characteristic of *D. liebeana* is the frequent development of complex spiral forms. The basal burrow clearly corkscrews down (or up) through the sediment, and the wall billows around to



produce a complex inverted cone structure (Fig. 10D).

As with other species of *Dictyodora*, *D. liebeana* occurs in a range of preservational aspects of the basal burrow and wall (Figs. 7, 8). Bedding planes near the level of the burrow may show the central tunnel, or that and the side sections, or the whole basal burrow as a single broad unit. Its looping pattern is usually regular. The vertical wall, when seen in bedding plane view, may form regular or irregular patterns. Vertical sections may show the striation patterns on the wall, or if cut through the middle of a spiral, may show its complex structure (*Tannenbaum-Typ*, Zimmermann 1893, Fig. 5; Pfeiffer 1968:690, Pl. 10:2; Fig. 7G).

Discussion. – The three-dimensional complexity of this trace fossil and its great variety of preservational aspects has led to the establishment of a large number of names for different views.

Noeggerathia rueckeriana Göppert (1852:220, Pl. 42) is possibly a side view of a high segment of wall showing the striations clearly. *Conularia reticulata* Richter (1865, Pl. 11:3) is probably a similar side view of the spreite.

Most of the genera and species of trace fossils established by Geinitz (1864, 1867a, b) are parts of the *Dictyodora* trace. He interpreted the specimens as the bodies of worms or algae, but his drawings appear to be faithful representations in general.

Nereites loomisi Emmons, as described and figured by Geinitz (1867b:6, Pl. 4), has been interpreted as the complete basal burrow of a small *D. liebeana* by Pfeiffer (1968:689), and the side segments drawn by Geinitz are probably not all as clear as the plate suggests ('drawn from a rather unclear photograph'). The specimens are 6–7 mm broad, the central band is about 1.5 mm broad, and there are about 8 backfill marks per cm (Fig. 7A).

I interpret another of Geinitz's specimens similarly, and the evidence seems even more conclusive. *Phyllocytes thuringiacus* Geinitz (1864:3, Pl.1:2; Pl. 2:3a, b; 1867b:3–4, Pl. 3:1) was de-

scribed as a worm 5–8 mm broad (the central strip) with a 5–8 mm zone of transverse marks on either side, 4–5 per cm length. Geinitz (1867b:3) also noted that 'along the middle of the body often appears a narrow keel-like elevation of nearly 1 mm thickness', and this is visible in his Pl. 3:1 (Fig. 7B). This feature is almost certainly the base of the vertical wall of a *Dictyodora*. The side marks are shown as irregular in occurrence, and even moreso in Pfeiffer's (1968, Pl. 9:1–4) photographs. These backfill structures are clear curving lines, in places only on the side segments, elsewhere traversing the central portion also. Some parts show only the central tunnel and no side marks; elsewhere the whole complex burrow fill seems to be absent, leaving a depressed hollow marked by faint transverse backfill structures that project slightly laterally. Pfeiffer (1968:686–687) accepted Geinitz's interpretation of the traces as *Phyllocytes* (i.e. large *Nereites*-like forms). Note that so-called *Phyllocytes thuringiaca* occurs almost exclusively at Koselstein and Grünau, in rather large numbers, and associated with *D. liebeana*.

Crossopodia henrici Geinitz (1867b:5, Pl. 5:1, 2) is a basal burrow form, rather similar to '*Nereites loomisi*'. The central canal is 2–3 mm broad, and the whole trace, 10–20 mm broad. There are 11–12 lateral backfill structures per cm length, and the central portion may be 'elevated keel-like' and may show complex chevron-like backfill marks (Geinitz 1867b, Pl. 5:1; Fig. 7C herein). The specimens of '*Crossopodia henrici*' figured by Volk (1964b, Figs. 14, 15; Fig. 7D herein) are identical in proportions to '*Phyllocytes thuringiaca*', but they lack clear backfill marks on the lateral margins. Geinitz (1867b:5) compared his specimens with *Crossopodia scotica* M'Coy 1851 from Scotland, and it has also recently been interpreted as the basal burrow of a *Dictyodora* (Benton & Trewin 1980).

Palaeochorda (Gordia) marina (Emmons 1844), as described and figured by Geinitz (1864:1; 1867b, pp. 14–15, Pl. 6:2, 3), has been interpreted by many authors (e.g. Zimmermann 1892; Volk 1964b:174–176; Pfeiffer 1968:689) as

Fig. 7. *Dictyodora liebeana* (Geinitz 1867). Koselstein Quarry, Wurzbach, Oberer Bordenschiefer, Unterkulm. Different preservational aspects and former taxonomic assignments. All figures drawn to the same scale, except G (scales shown on figure). □ A. '*Nereites loomisi*' view of basal burrow (after Geinitz 1867b, Pl. 4:2). □ B. '*Nereites thuringiacus*' view of basal burrow (after Geinitz 1867b, Pl. 3). □ C. '*Crossopodia henrici*' view of basal burrow (after Geinitz 1867b, Pl. 5:1). □ D. '*Crossopodia henrici*' view of basal burrow (after Volk 1964b, Fig. 14). □ E. '*Palaeochorda marina*' view of basal burrow (after Geinitz 1867b, Pl. 6:3). □ F. '*Palaeochorda spiralis*' view of basal burrow (after Geinitz 1867b, Pl. 6:1). □ G. Vertical section through part of a *Dictyodora liebeana* spiral (after Pfeiffer 1959, Fig. 3). □ H. Bedding plane view of regularly meandering wall (original). □ I. View of wall showing striation pattern (after Weiss 1884b, Pl. 12:5).

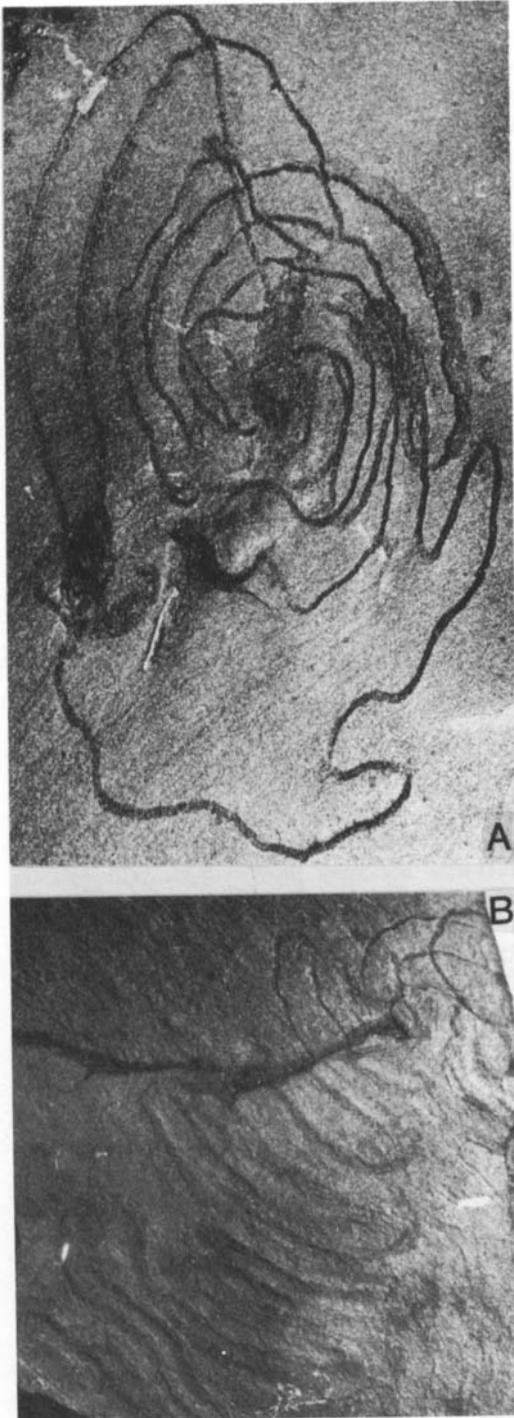


Fig. 8. *Dictyodora liebeana* (Geinitz 1867). Koselstein Quarry, near Wurzbach, Oberer Bordschiefer, Unterkulm. □ A. Bedding plane view of spiral pattern of wall. $\times 1.0$. □ B. Bedding plane view of regular meanders of wall passing into basal burrow at change of level. Small specimen. $\times 1.0$.

the central portion of the basal burrow (the 1–5 mm diameter circular tunnel) without the side marks. It is frequently preserved as a regular spiralling form, doubtless from the base of the conical structure (Fig. 7E).

A form that is very similar, but has not been interpreted as part of the *Dictyodora* structure hitherto, is *Palaeochorda spiralis* Geinitz (1867b:15–16, Pl. 6:1). The type specimen, and others referred to this species (as *Spirodesmos spiralis*) by Pfeiffer (1968:673–674, Pl. 3:6; Pl. 7:1) show partial spiral patterns formed by 1–3 mm broad smooth circular burrows. The spirals may be 40–70 mm in diameter. The specimen figured by Geinitz (1867b, Pl. 6:1) shows faint lateral marks (Fig. 7G). *P. spiralis* occurs with *D. liebeana* and it is most probably the central portion of the spiral structure.

Biology of *Dictyodora liebeana*

Much has been written on the biology of the supposed *Dictyodora* animal (e.g. Zimmermann 1892; Pfeiffer 1959; Müller 1962, 1971; Seilacher 1967; Raup & Seilacher 1969; Papentin 1973; Benton & Trewin 1980). It is interpreted as having travelled along the basal burrow, looping in a more or less regular fashion to utilise efficiently a patchy food source at one level in the sediment. It presumably moved in loose meanders when searching for food and looped tightly on a suitable area. Tightly looped areas with spirals also mark changes in level within the sediment as the animal moves up or down.

The pattern is highly regular in the tightly looped areas and the meander length and angle of turn increase and decrease rhythmically (Müller 1962, 1971). The meandering behaviour may be understood in terms of simple binary reactions to various stimuli, and these may be coded as a system of rules (Benton & Trewin 1980:510, modified from Seilacher 1967; Papentin 1973; Raup & Seilacher 1974; Papentin & Röder 1975):

- (1) Move horizontally keeping within a single stratum of sediment.
- (2) Always keep in touch with previously formed burrow while feeding (thigmotaxis).
- (3) Never come closer to a previously formed burrow than a particular distance 'd' (phobotaxis).
- (4) If contact is lost with a former burrow, make a 180° turn (homostrophy/strophotaxis).
- (5) When food content of sediment falls below a certain level, spiral up or down to a new level.

The reactions specified in rules 2, 3, and 4 depend on the detection of previously burrowed sediment over a short distance. Röder (1971) found that the living polychaete, *Paraonis fulgens*, which produces accurate planar spirals in sand, probably detects the 'movability of sand grains' with a sensory organ at the front end of its body (Papentin & Röder 1975). The *Dictyodora* animal may have employed a similar system.

Paraonis controls its depth by forming its spirals generally at the O_2/H_2S interface in the sediment. The *Dictyodora* animal may have controlled its depth by similar means, or more probably by the sensitivity of its wall organ (Benton & Trewin 1980:510).

The body of the animal was probably circular to subcircular in cross section with lateral limbs or parapodia of some sort by which it effected its progress through the sediment. The reinterpretation here of '*Phyllodocites thuringiaca*' offers possible new insights into the nature of the animal's movement. There is clear back-packing of sediment within the central tunnel, and regular lateral movement of parapodia producing unclear, almost *Nereites*-like, traces. This tripartite division of the basal burrow does not occur in the Lower Palaeozoic *Dictyodora*, but backfill structures are clear there also, and *D. scotica* shows possibly similar zonation in cross-sections of the basal burrow (Benton & Trewin 1980:504, Fig. 1B). The Carboniferous *Dictyodora* animal was probably larger, and certainly had a far longer wall organ than *D. scotica* or *D. zimmermanni*, and it may have required relatively larger 'parapodia' to be able to move.

The side marks run at an angle of about 45° from the direction of travel, and they may be slightly curved. They terminate in a sharp point, or fuse with adjacent marks. These features suggest a backwards sweeping movement of a simple conical, distally pointed 'limb' of some kind which, in combination with the peristaltic passage of sediment through the gut and backpacking, caused the animal to advance. This movement is envisaged as being relatively rapid, as the basal burrow may extend for a metre or more (Geinitz 1867b, Pls. 3, 4) with no apparent interruption to the motion.

The wall organ, possibly a respiratory device (Benton & Trewin 1980:508), was evidently very long in *D. liebeana* (up to 16 cm: Weiss 1884b:87), and yet its base was relatively narrow (1–2 mm). It apparently followed the progress of the animal's body in a passive fashion, curved

backwards, and dragging along the line of least resistance through the mud. This is shown by the wall striations (Fig. 71) and the fact that the wall always curves inwards and upwards at the bends, taking the shortest route possible. This model seems incredible when one considers the height and thinness of the wall organ.

The specimens of *D. liebeana* from Koselstein and elsewhere are apparently relatively little distorted during lithification of the mud, and the clear preservation of the trace also suggests that there was little compaction after it had been formed. This leads to the conclusion that measurements taken from the trace fossils are close to the original proportions, and that the mud in which the *Dictyodora* animal was performing was relatively water-free. The wall organ must have been an exceedingly tough, flexible structure, probably a mid-dorsal crest rather than a simple tube, and it may have had a sharp leading edge to cut through the stiff mud, and have been covered with cilia to ease its progress in small jerks as it followed the body hauling itself along below.

The Koselstein shales are black and the sediments were probably anoxic. However, the common assumption that all black shales were totally anoxic and azoic is clearly not true. Studies in present-day marine environments show that bottom waters with very low levels of dissolved oxygen support infaunas of tiny worm-like animals (Rhoads & Morse 1971). Ancient black shales may also contain burrows attributable to similar animals, generally with a diameter less than 2 mm (Byers 1979). The benthonic infauna of the Lower Carboniferous of Thuringia was abundant and diverse, and some of the animals were relatively large (e.g. *D. liebeana*), and they may have required special breathing devices. This tends to support our earlier interpretation of the wall organ as a respiratory device that poked up into the clear water above the sea bed and supplied the animal with oxygen while it fed on buried decomposing plant and animal material and anaerobic bacteria.

The spiral portion, characteristic of the *D. liebeana* trace, represents a point at which the animal passed up (or down) in a screw-like pattern to a particular level where normal meandering takes place. In order to do this, the animal evidently has to 'wind' its way, possibly as a means of thoroughly testing different levels for food until it reaches a suitable spot, or possibly because of mechanical constraints on the animal

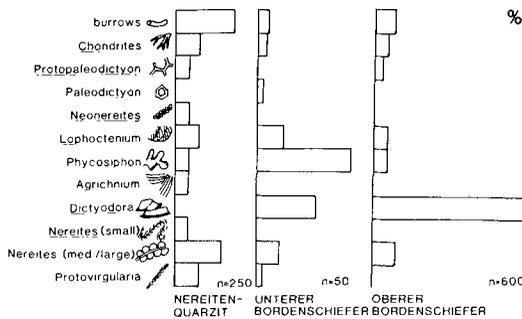


Fig. 9. Percentage presence of major trace fossils in three Thuringian ichnofaunas (others contain too few specimens for analysis): *Nereitenquarzit* (Lower Devonian), *Unterer Bordenschiefer* (Hasenthal zone: Lower *Unterkulm*), *Oberer Bordenschiefer* (Röttersdorf zone, Upper *Unterkulm*). Percentages estimated from my collections, and count of specimens mentioned by Hundt (1931b), Volk (1964b), and Pfeiffer (1968).

with its cumbersome wall organ. The basal burrow in the spiral areas generally lacks side marks, which may indicate a different, possibly slower, mode of locomotion without the use of the 'parapodia'. The basal burrow tends to slope down and inwards in the spiral areas (Fig. 7G), a kind of 'cornering' effect, presumably necessary to accommodate the steep inwards angle of the wall.

When travelling on the sea bed (? producing a typical *Nereites* trace), the *Dictyodora* animal may have folded its wall organ back, or allowed it to trail in the still water above.

Seilacher (1974:240) suggested that one *Dictyodora* trace represented the 'work of a lifetime', but this seems highly unlikely. The animal passed through the sediment only once – there is no indication of re-using the same burrow – and the regularity of backfill and striation marks suggests continuous movement. Individual traces may be followed for some distance without any evidence of growth. The living polychaete *Paraonis* produces roughly comparable spiral burrows deep in sediment within a few hours (Röder 1971).

Dictyodora and the 'deep-sea' *Nereites* Association

Dictyodora is normally regarded as typical of the deep-sea *Nereites* Facies (Seilacher 1978), and it occurs normally in flysch facies (e.g. Upper Ordovician Barrancos Shale of Portugal (Delgado 1910), Lower Silurian Gala Group of Scotland

(Benton & Trewin 1980), Lower Silurian Aberystwyth Grits of Wales (Crimes 1970:109–110), and Lower Carboniferous Bordenschiefer of Thuringia (Pfeiffer 1959, 1968; Müller 1962, 1971; Volk 1964b). The association of *Dictyodora* with *Diplocraterion* in the *Hauptquarzit* of Thuringia is unusual. *Diplocraterion* has hitherto been reported only from shelf situations (tidal zone to offshore; Goldring 1962; Häntzschel 1975:W62; Seilacher 1978:176). *Planolites* is a well-known facies-crossing trace fossil.

The *Nereitenquarzit* contains some trace fossils like *Nereites*, *Lophoctenium*, *Protovirgularia*, *Phycosiphon* and *Protopaleodictyon* (Fig. 9) that are typical of the *Nereites* Association (Seilacher 1978). However, the complete absence of *Dictyodora* from extensive collections in the *Nereitenquarzit*, the abundance of burrow forms, and the association of the trace fossil beds with sandstones containing shallow water body fossils suggests environmental control within the *Nereites* Association here.

The *Unterkulm Bordenschiefer* has a more typical flysch ichnofauna. However, its character changes over time, with *Phycosiphon* dominant at first, and *Dictyodora* becoming extremely abundant in the Röttersdorf zone (Koselstein, Grünau quarries; Fig. 9). This, again, suggests environmental control, since the same trace fossils are present, only in different proportions.

Seilacher (1974) divided his *Nereites* facies into a *Nereites* subfacies (distal parts of fans with thin laminae of mudstone and sandstone, characterised by *Oldhamia*, *Chondrites*, *Nereites*, *Dictyodora*, *Phycosiphon*, *Zoophycos*, etc.), and a *Paleodictyon* subfacies (thicker turbidites preserving secondary casts of *Paleodictyon* and similar open burrow systems). Analyses of trace fossils over the area of ancient deep-sea sand fans (Crimes 1970, 1977; Książkiewicz 1970) show different assemblages in proximal and distal portions. Burrows may occur in the former, and more typical flysch forms (meandering and patterned trails and burrows, faecal strings) in the latter. Since water depths probably did not vary greatly along the length of the fans, other environmental factors must be sought to explain the different assemblages: substrate (grain size, rate of deposition, degree of compaction, water content, substrate movement, aeration), bottom water (suspended material, currents, aeration, temperature), food availability (in suspension and buried), predation and competition, distance from shore.

Preservation potential is also of great importance (Crimes 1977), and it will also depend on many of the factors of substrate and bottom water just mentioned, but particularly on rate of deposition, thixotropy of mud, energy of turbidite flow, and size of producers. Książkiewicz (1970) found relationships between trace fossils preserved and thickness of sandstone layers, grain coarseness, character of the sole of sandstone units, and aeration of the bottom (as indicated by the colour of the sediments and abundance of microfossils).

Thus, the *Nereitenquarzit* probably represents a more proximal part of the flysch than the *Bordenschiefer*, and this is supported by evidence from trace fossils, sedimentology, and body fossils.

Seilacher (1974, 1977a) has shown that there is a general increase in diversity of trace fossils over time in flysch facies. The data presented here tend to support Seilacher's conclusions (Upper Ordovician, 3 species; Lower Devonian, 13 species; Lower Carboniferous, 23 species), although the latter figure is closer to those that he gives for Cretaceous–Tertiary flysch. Pfeiffer's (1968) figure of 44 species would be even more anomalous. Pickerill (1980) gives a total of 23 species for an Ordovician assemblage from New Brunswick, Canada, far higher than Seilacher's predicted diversity of 4–8. Pickerill suggests reasonably that diversity models at present suffer from inadequate study of certain geological periods, especially in the Palaeozoic and early Mesozoic. However, it is likely that a true picture of diversity evolution over time cannot be obtained simply by plotting totals for various flysch formations. It is clear that there is the possibility of a broad range of environmentally controlled ichnofaunas in any one sand fan, and the total figure may represent only one such assemblage, or several assemblages that may be as distinct as any series of shelf ichnofaunas. Preservation potential, dependent on sedimentary conditions, will also alter the figures. Thus, 'deep-sea' trace fossil diversity in any one geological period may show a broad range, dependent on environmental and preservational factors (e.g. Ordovician, 4–23; Carboniferous, 6–23), and this may mask real trends through time.

Evolution of *Dictyodora*

Seilacher (1967, 1974) has proposed an elegant model for the development of structural com-

plexity and efficiency of the *Dictyodora* animal through time. The Thuringian sequence, described here, contains one of the oldest and simplest representatives of the genus, *D. zimmermanni*, and the most advanced, *D. liebeana* (note that we regard the Precambrian *D. simplex* Seilacher 1955 as not a true *Dictyodora* since it lacks a distinguishable basal burrow and wall: Benton & Trewin 1980:502). The new information presented here confirms and supplements Seilacher's conclusions. Seilacher saw the evolution of *Dictyodora* as unusual in that size increased over time, whereas in other groups (e.g. *Paleodictyon*) size tends to decrease. It can be seen that size did decrease and efficiency of meandering improved between the Ordovician and the Silurian (Fig. 10). However, in general, the Carboniferous specimens are rather larger than *D. zimmermanni*.

The major developments over time, as shown by a comparison of *D. zimmermanni* and *D. liebeana* (Fig. 10), are:

- (1) Increase in height of wall.
- (2) Development of tight spiralling cone structure for level changes in the sediment.
- (3) Development of large 'parapodia' to effect progress through the sediment.
- (4) Increase in regularity of meandering.

The key feature seems to be the increase in the height of the wall. This may have led to problems in changing level in the sediment, and spiralling behaviour had to evolve in order to allow the longer wall organ to move vertically in the sediment (compare Fig. 10A and D). The long wall organ must have presented considerable resistance to movement through the mud, and relatively larger 'parapodia' were necessary. Finally, the improvement in regularity of meandering has been seen as evolution in efficiency of feeding on patchy food distributions (Seilacher 1967, 1974; Papentin 1973).

Why did the wall organ become so high in the Carboniferous animal? It could be an adaptation to feeding at an otherwise unexploited depth in the sediment, possibly occasioned by pressure from the increased diversity of new shallow infaunal feeders (e.g. *Chondrites*, *Lophoctenium*, *Phycosiphon*, *Protopaleodictyon*). It could also be associated with oxygen levels in the sediments and bottom waters. The Lower Palaeozoic forms from the *Hauptquarzit* of Thuringia, and the Gala Group of Scotland, occur mainly in red or purple mudstones, and the colour may indicate

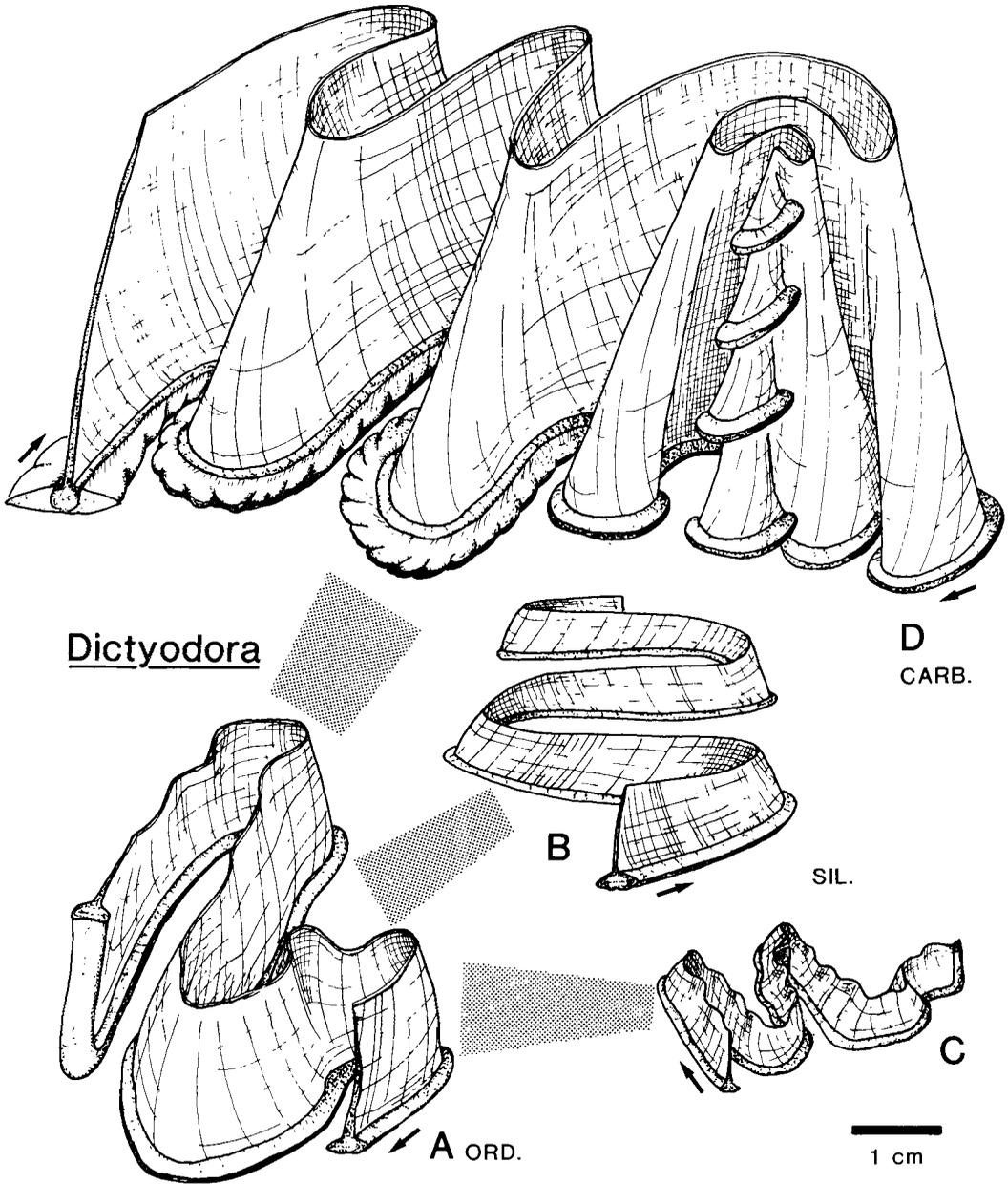


Fig. 10. Early evolution of *Dictyodora*. □ A. *D. zimmermanni*, Hauptquarzit (Upper Ordovician), Thuringia (based on specimens). □ B. *D. scotica*, Gala Group (Lower Silurian), Scotland (after Benton & Trewin 1980, Fig. 1A). □ C. *D. tenuis*, Gala Group (Lower Silurian), Scotland (based on Benton & Trewin 1980). □ D. *D. liebeana*, Bordenschiefer (Lower Carboniferous), Thuringia (based on specimens; Pfeiffer 1959, Fig. 3; Scilacher 1967). All drawn to same scale. More advanced spiral forms are figured by Seilacher (1967, 1974).

an oxidising depositional environment or an oxidising source area (Ziegler & McKerrow 1975). In any case, oxygen levels were probably higher

than in the Culm of Thuringia where a respiratory organ that projected well above the sea floor may have been essential for deep burrowers.

Conclusions

A comparison of Ordovician and Carboniferous *Dictyodora* shows that the most important evolutionary change was the increase in wall height. This led to an increase in size overall, and in complexity, and the changes probably all permitted the animal to feed deeper in anoxic sediment. *Dictyodora* became extinct at the end of the Early Carboniferous in East Germany and Austria, possibly with the closure of the Rheic Ocean. No living animal is known that produces such a trace, and it is unclear what animal fills the same adaptive zone in modern oceans. The *Dictyodora* animal may have belonged to a soft-bodied group as yet unknown.

Palaeozoic flysch mudstone trace fossil assemblages of East Germany and elsewhere show very different characters. Some are dominated by *Nereites*, and others by *Dictyodora*, often to the total exclusion of each other. Environmental control probably depended on subtle variations in oxygen content of the mud and bottom water, the physical characteristics of the sediment, frequency of turbidite influx, and nature of food. It is also likely that large depositional areas were dominated by the key controlling conditions since the character of the trace fossil assemblages is often constant in space and time within extensive formations. Many of these factors may be determinable from the sediments, and further studies of the trace fossils of Lower Palaeozoic ocean-floor and trench deposits should reveal what they are.

Acknowledgements. – I thank Dr. Nigel H. Trewin for reading various editions of the manuscript and for offering helpful comments.

References

- Abel, O. 1935: *Vorzeitliche Lebensspuren*. Fischer, Jena.
- Alpert, S. P. 1975: *Planolites* and *Skolithos* from the Upper Precambrian – Lower Cambrian, White Inyo Mountains, California. *J. Paleont.* 49, 508–521.
- Auerbach, A. 1912: *Dictyodora Liebeana* Weiss aus dem Untersilur von Wünschendorf. *Jb. Ges. Freunde Naturwiss. Gera* 53–54, 127–128.
- Bachmann, M. 1954: Das Ordovizium in der Gegend von Schleiz (Ostthüringen). *Neues Jahrb. Geol. Paläont. Mh.* 1954, 260–267.
- Benton, M. J. & Trewin, N. H. 1978: Discussion and comments on Nicholson's 1872 manuscript 'Contributions to the study of the Errant Annelides of the older Palaeozoic rocks'. *Publ. Dep. Geol. Miner. Univ. Aberdeen* 1, 1–16.
- Benton, M. J. & Trewin, N. H. 1980: *Dictyodora* from the Silurian of Peebleshire, Scotland. *Palaeontology* 23, 501–513.
- Byers, C. W. 1979: Biogenic structures of black shale palaeoenvironments. *Postilla* 174, 1–43.
- Crimes, T. P. 1970: The significance of trace fossils in sedimentology, stratigraphy and palaeoecology with examples from Lower Palaeozoic strata. In Crimes, T. P. & Harper, J. C. (eds.): *Trace Fossils. Geol. J. Spec. Issue* 3, 101–126. Seel House Press, Liverpool.
- Crimes, T. P. 1977: Trace fossils of an Eocene deep-sea sand fan, northern Spain. In Crimes, T. P. & Harper, J. C. (eds.): *Trace Fossils 2. Geol. J. Spec. Issue* 9, 71–90. Seel House Press, Liverpool.
- Delgado, J. F. N. 1910: Terrains paléozoïques du Portugal. Étude sur les fossiles des schistes à néréites de San Domingos et des schistes à néréites et à graptolites de Barrancos. *Commis. Serv. Geol. Portugal* 56, 1–68.
- Doughty, P. 1980: Some trace fossils from the Silurian rocks of Co. Down. *Ir. Nat. J.* 20, 98–104.
- Emmons, E. 1844. *The Tuconic System*. 68 pp. Albany, New York.
- Freyberg, B. 1923: Die Fauna und Gliederung des Thüringer Untersilurs. *Z. Deusch. Geol. Ges.* 74, 237–276.
- Geinitz, H. B. 1853: *Die Versteinerungen der Grauwackenformation in Sachsen und den angrenzenden Länder-Abtheilungen*, 2. 95 pp. Engelmann, Leipzig.
- Geinitz, H. B. 1864: Über organische Überreste in dem Dachschiefer von Wurzbach bei Lobenstein. *Neues Jahrb. Miner. Geol. Paläont.* 1864, 1–9.
- Geinitz, H. B. 1867a: Beiträge zur älteren Flora und Fauna. *Neues Jahrb. Miner. Geol. Paläont.* 1867, 273–290.
- Geinitz, H. B. 1867b: Die organischen Überreste im Dachschiefer von Wurzbach bei Lobenstein. *Nova Acta Acad. Caes. Carol.-Leop. Natur. Curios* 33 (3), 1–24.
- Göppert, H. R. 1852: Die fossile Flora des Uebergangsgebirges. *Nova Acta Acad. Caes. Carol.-Leop. Natur. Curios.* 22, *Suppl.*, 1–299.
- Goldring, R. 1962: The trace fossils of the Baggy Beds (Upper Devonian) of North Devon, England. *Paläont. Z.* 36, 232–251.
- Gräbe, R. 1974: Dinant. In Hoppe, W. & Seidel, G. (eds.): *Geologie von Thüringen*, 256–290. VEB Hermann Haack, Gotha/Leipzig.
- Gumbel, C. W. 1879: *Geognostische Beschreibung des Fichtelgebirges mit dem Frankenwalde und dem westlichen Vorlande*. 698 pp. Perthes, Gotha.
- Häntzschel, W. 1958: Oktokoralle oder Lebensspur? *Mitt. Geol. Staatsinst. Hamburg* 27, 77–87.
- Häntzschel, W. 1975: Trace fossils and problematica. In Teichert, C. (ed.): *Treatise on Invertebrate Paleontology W, Misc., Suppl. 1*, W1–W269. Univ. Kansas, Geol. Soc. Am.
- Hoppe, W. & Seidel, G. 1974: *Geologie von Thüringen*. 1000 pp. VEB Hermann Haack, Gotha/Leipzig.
- Hundt, R. 1912: Organische Reste aus dem Untersilur des Hüttchenberges bei Wünschendorf an der Elster. *Zentralbl. Min. Geol. Paläont.* 1912, 91–95.
- Hundt, R. 1913: Eine Ergänzung zu 'Organische Reste aus dem Untersilur des Hüttchenberges bei Wünschendorf an der Elster'. *Zentralbl. Min. Geol. Paläont.* 1913, 180–181.
- Hundt, R. 1928: *Das Untersilur thüringens mit besonderer Berücksichtigung des nördlichen Ostthüringens*. 48 pp. Kanitzsch, Gera.
- Hundt, R. 1931a: Neues von *Phycodes circinnatum* Richt., *Dictyodora zimmermanni* Hundt und einem neuen Problematikum aus dem untersten Silur Ostthüringens. *Zentralbl. Min. Geol. Paläont.* 1931, 181–186.
- Hundt, R. 1931b: *Eine Monographie der Lebensspuren des Unteren Mitteldevons Thüringens*. 69 pp. Max Weg, Leipzig.
- Hundt, R. 1940: Neue Lebensspuren aus dem ostthüringer Paläozoikum. *Zentralbl. Min. Geol. Paläont.* 1940, 210–216.

- Hundt, R. 1941a: Neue Fundstellen der *Dictyodora zimmermanni* Hundt in Ostthüringer Schiefergebirge. *Beitr. Geol. Thüringen* 6, 150–151.
- Hundt, R. 1941b: *Das Mitteldeutsche Phycodesmeer*. 136 pp. Fischer, Jena.
- Hundt, R. 1943: Zur Kenntnis der Frankenstein-Paläozoikums. *Beitr. Geol. Thür.* 7, 120–123.
- Kayser, E. 1894: Über das Alter der thüringer Tentaculiten- und Nereiten-Schichten. *Z. deutsch. Geol. Ges.* 46, 823–827.
- Knüpfer, J. 1967: Zur Fauna und Biostratigraphie des Ordoviziums (Grafitenthaler Schichten) in Thüringen. *Freiberger ForschHft. C* 220, 1–119.
- Korn, H. 1929: Fossile Gasblasen aus dem Thüringer Paläozoikum. *Z. Naturwiss.* 89, 25–46.
- Książkiewicz, M. 1970: Observations on the ichnofaunas of the Polish Carpathians. In Crimes, T. P. & Harper, J. C. (eds.): *Trace Fossils. Geol. J. Spec. Issue* 3, 283–322. Seel House Press, Liverpool.
- Ludwig, R. 1869: Fossile Pflanzenreste aus der paläolithischen Formation der Umgebung von Dillenberg, Biedenkopf, und Friedberg und aus dem Saalfeldischen. *Palaeontographica* 17, 105–128, 137–140.
- Marr, J. E. 1889: Notes on the Lower Palaeozoic rocks of the Fichtelgebirge, Frankenstein, and Thüringerwald. *Geol. Mag.* (3) 6, 411–415.
- Müller, A. H. 1962: Zur Ichnologie, Taxologie, und Ökologie fossiler Tiere. I. *Freiberger ForschHft. C* 151, 7–18.
- Müller, A. H. 1971: Über *Dictyodora liebeana* (Ichnia invertibratorum), ein Beitrag zur Taxologie und Ökologie sedimentfressender Endobionten. *Deutsch. Akad. Wiss. Berlin, Monatsber.* 13, 136–151.
- Murchison, R. I. & Morris, J. 1855: On the Palaeozoic and their associated rocks of the Thüringerwald and the Harz. *Q. J. Geol. Soc. Lond.* 11, 409–450.
- Osgood, R. G., Jr. 1970: Trace fossils of the Cincinnati area. *Palaeont. Americana* 6, 281–444.
- Papentin, F. 1973: A Darwinian evolutionary system. III. Experiments on the evolution of feeding patterns. *J. Theoretical Biol.* 39, 431–445.
- Papentin, F. & Röder, H. 1975: Feeding patterns: the evolution of a problem and a problem of evolution. *Neues Jahrb. Geol. Pal., Mh.* 1975, 184–191.
- Pfeiffer, H. 1954: Der Bohlen bei Saalfeld. *Geologie Beih.* 11, 1–105.
- Pfeiffer, H. 1959: Über *Dictyodora liebeana*. *Geologie* 8, 425–439.
- Pfeiffer, H. 1960: Über Lebensspuren im allgemeinen und aus dem Ostthüringischen Schiefergebirge im besonderen. *Der Aufschluss* 9, 33–42.
- Pfeiffer, H. 1968: Die Spurenfossilien des Kulms (Dinant) und Devons der Frankenthaler Querzone (Thüringen). *Jh. Geol.* 2, 651–717.
- Pickering, R. K. 1980: Phanerozoic flysch trace fossil diversity – observations based on an Ordovician flysch ichnofauna from the Aroostock–Matapedia carbonate belt of northern New Brunswick. *Can. J. Earth Sci.* 17, 1259–1270.
- Rauff, H. 1892: Über Pseudoorganismen, besonders über *Dictyodora* und *Crossopodia*. *Z. Deutsch. Geol. Ges.* 44, 561–564.
- Raup, D. M. & Seilacher, A. 1969: Fossil foraging behavior: computer simulation. *Science* 166, 994–995.
- Rhoads, D. C. & Morse, J. W. 1971: Evolutionary and ecological significance of oxygen-deficient marine basins. *Lethaia* 4, 413–428.
- Richter, R. 1849: Silurische Versteinerungen des Thüringer Waldes. *Z. Deutsch. Geol. Ges.* 1, 456–461.
- Richter, R. 1850: Aus der Thüringischen Grauwacke. *Z. Deutsch. Geol. Ges.* 2, 198–206.
- Richter, R. 1853: Thüringer Graptolithen. *Z. Deutsch. Geol. Ges.* 5, 439–464.
- Richter, R. 1865: Aus dem Thüringer Schiefergebirge. II. *Z. Deutsch. Geol. Ges.* 17, 361–376.
- Richter, R. 1869: Das thüringische Schiefergebirge. *Z. Deutsch. Geol. Ges.* 21, 341–443.
- Richter, R. & Unger, F. 1856: Beitrag zur Palaontologie des thüringer Waldes. *Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl.* 11, 87–138.
- Röder, H. 1971: Gangsystem von *Paraonis fulgens* Levinsen 1883 (Polychaeta) in ökologischer, ethologischer und aktuell-paläontologischer Sicht. *Senck. Maritima* 3, 3–51.
- Ruchholz, K. 1967: Zur Ichnologie und Fazies des Devons und Unterkarbons im Harz. *Geologie* 16, 503–527.
- Seilacher, A. 1967: Fossil behavior. *Scient. Am.* 217(2), 72–80.
- Seilacher, A. 1974: Flysch trace fossils: evolution of behavioural diversity in the deep-sea. *Neues Jahrb. Geol. Paläont. Mh.* 1974, 233–245.
- Seilacher, A. 1977a: Evolution of trace fossil communities. In Hallam, A. (ed.): *Patterns of Evolution*, 358–376. Elsevier, Amsterdam.
- Seilacher, A. 1977b: Pattern analysis of *Paleodictyon* and related trace fossils. In Crimes, T. P. & Harper, J. C. (eds.): *Trace Fossils 2. Geol. J. Spec. Issue* 9, 289–334. Seel House Press, Liverpool.
- Seilacher, A. 1978: Use of trace fossil assemblages for recognizing depositional environments. In Basan, P. B. (ed.): *Trace Fossil Concepts*, 167–181. S.E.P.M., Oklahoma City.
- Steinbach, W. 1974: Devon. In Hoppe, W. & Seidel, G. (eds.): *Geologie von Thüringen*, 208–256. VEB Hermann Haack, Gotha/Leipzig.
- Volk, M. 1961: *Protovirgularia nereitarum* (Reinhard Richter), eine Lebensspur aus dem Devon Thüringens. *Senck. Leth.* 42, 69–75.
- Volk, M. 1964a: Über *Chondrites* aus dem Devon und Kulm am Schwarzburger Sattel. *Senck. Leth.* 45, 285–297.
- Volk, M. 1964b: Die Spurengemeinschaften im Paläozoikum am Schwarzburger Sattel (Thüringen). *Abh. Deutsch. Akad. Wiss., Kl. Bergbau, Hüttenw. Montangeol.* 2, 163–179.
- Weiss, E. 1884a: Vorlegung des *Dictyophytum Liebeanum* Gein. aus der Gegend von Gera. *Sitz.-Ber. Ges. Naturf. Freunde, Berlin* 1884, 17.
- Weiss, E. 1884b: Beitrag zur Culm-Flora von Thüringen. *Jahrb. Preuss. Geol. Landesanst.* 1883, 81–100.
- Wiefel, H. 1974: Ordovizium. In Hoppe, W. & Seidel, G. (eds.): *Geologie von Thüringen*, 165–194. VEB Hermann Haack, Gotha/Leipzig.
- Ziegler, A. M. & McKerrow, W. S. 1975: Silurian marine red beds. *Am. J. Sci.* 275, 31–56.
- Ziegler, A. M., Scotese, C. R., McKerrow, W. S., Johnson, M. E. & Bambach, R. K. 1979: Palaeozoic paleogeography. *Ann. Rev. Earth Planet. Sci.* 7, 473–502.
- Zimmermann, E. 1889: Über die Gattung *Dictyodora*. *Z. Deutsch. Geol. Ges.* 41, 165–167.
- Zimmermann, E. 1891: Neue Beobachtungen an *Dictyodora*. *Z. Deutsch. Geol. Ges.* 43, 551–555.
- Zimmermann, E. 1892: *Dictyodora liebeana* (Weiss) und ihre Beziehungen zu *Vexillum* (Rouault), *Palaeochorda marina* (Geinitz) und *Crossopodia henrici* (Geinitz). *Jahrb. Ges. Freunde Naturwiss. Gera* 32–35, 28–63.
- Zimmermann, E. 1893: *Dictyodora liebeana* Weiss, eine rätselhafte Versteinerung. *Naturwiss. Wochenschr.* 8(16), 155–158.
- Zimmermann, E. 1910: *Blatt Lehesten. Erläuterungen zur geologischen Spezialkarte von Preussen*. 110 pp. Berlin.
- Zimmermann, E. 1911: *Blatt Lobenstein. Erläuterungen zur geologischen Spezialkarte von Preussen*, Berlin.