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Corallian (Upper Jurassic) trace fossils from England and Normandy

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With 2 tables and 36 figures

Summary

Middle and Upper Oxfordian shallow-water trace fossil assemblages from Normandy, Dorset, Yorkshire, and the Oxford region are described in their morphology (including *Arenicolites variabilis* n. sp.). A regional, stratigraphical and facies distribution of the various ichnospecies is given, and preservational aspects as well as ecological observations and the nature of the trace fossil producers are discussed.

Zusammenfassung

Flachwasser-Spurengemeinschaften des mittleren und oberen Oxfordiums der Normandie, von Dorset, Yorkshire und der Gegend um Oxford werden taxonomisch erfaßt (darunter *Arenicolites variabilis* n. sp.). Die regionale, stratigraphische und Fazies-Verteilung der einzelnen Ichnospezies wird gegeben, und Erhaltungszustand, ökologische Beobachtungen, sowie Urheberschaft der Spuren werden diskutiert.

Content

Introduction

The Corallian (Middle and Upper Oxfordian) of Normandy and England has been the subject of numerous stratigraphical (e. g. Guyader 1968 in the case of Normandy; Blake & Hudleston 1877, Hudleston 1878, Arkell 1927, 1933, 1936, Wilson 1933, 1949, Callomon 1960, Wright 1972 for England) and sedimentological studies (e. g. Twombley 1964, Guyader 1968, Wilson 1968a, b, Lee 1971, Talbot 1973). Palaeontological investigations have confined themselves to taxonomy (e. g. Arkell 1929—37, 1935—48) and no palaeoecological studies have yet been undertaken.

The shallow-water sediments of the Corallian comprise a variable sequence of clays, sands and limestones and are intercalated between the dominantly argillaceous sediments of the Oxford Clay and those of the Kimmeridge Clay (for generalized sections see Fig. 1). In the area under investigation, the Corallian sediments stretch from the Yorkshire coast down to the Dorset coast and are found again on the other side of the Channel on the Normandy coast southwest of Le Havre (Fig. 2). They contain a rich invertebrate (mainly bivalve and gastropod) and trace fossil fauna. This paper treats of the latter, whereby emphasis is laid upon the taxonomy of the ichnofauna, as a basis for a palaeoecological analysis (FÜRSICH, in prep.).

Three main areas have been investigated: 1. Yorkshire coast, near Filey, 2. Dorset coast between Ringstead Bay and East Fleet, and 3. Normandy coast between Houlgate and Villerville. Fallen blocks at beach level, or exposures in the intertidal zone usually provide extensive surfaces for examination of bedding planes, whereas the cliffs themselves provide vertical sections in the same strata. Further observations were made in the Oxford region as well as in quarries on both sides of the Vale of Pickering, Yorkshire.

The material will be deposited in the Staatliches Museum für Naturkunde in Stuttgart.

Systematics

1. Cubichnia (resting traces)

Ichnogenus *Bergaueria* PRANTL 1946

Type species: *Bergaueria perata* PRANTL 1946, p. 52.

Diagnosis: Broad, unlined vertical cylinders; U-shaped in cross-section.

Ichnospecies *Bergaueria perata* PRANTL 1946

Fig. 3

Diagnosis: Broad, unlined vertical cylinders; U-shaped in cross-section.

Description: Broad vertical cylinders, lower end rounded with shallow trough. Diameter of cylindrical structure 4.5 cm, depth 6 cm; burrow walls smooth, without lining.

Preservation: Positive hyporelief; fill identical with the overlying sediment (poorly sorted oolite).

Facies: Well-sorted, fine-grained sands with herringbone cross-bedding.

Regional and stratigraphic distribution: Known only from Shellingford Cross-Roads Quarry, Berkshire (Berkshire Oolite Group).

Associations: Found together with entrance funnels of *Spongeliomorpha nodosa*.

Discussion and interpretation: The Corallian specimens do not possess any lining: a feature which distinguishes them from the heavily lined *Kulindrichnus* HALLAM 1960. They are, however, comparable to forms from the Ordovician of Bohemia which PRANTL (1946) described as *Bergaueria perata*. PRANTL (1946) suggested that they might represent the burrows of some anthozoans or allied forms. Whilst SEILACHER (1956) regarded them as domichnia of partly burrowed actinians HÄNTZSCHEL (1962, 1965) thought it likely that they are resting traces of „burrowing“ actinians.

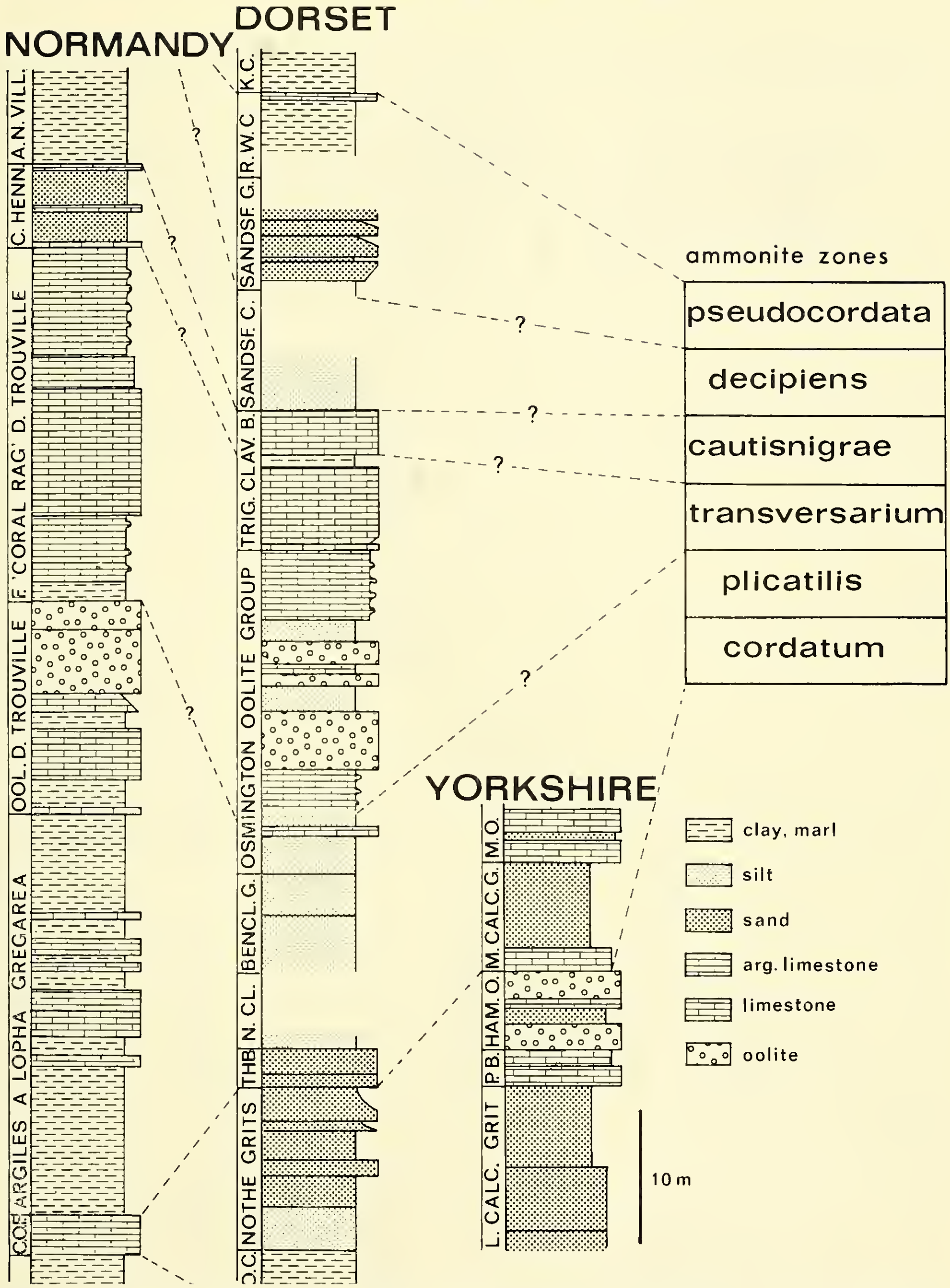


Fig. 1 Generalized sections of the Corallian outcrops examined in Normandy, Dorset, and Yorkshire. C. O. F. = Calcaire à oolithes ferrugineuses; OOL. D. TROUVILLE = Oolithe de Trouville à *Nucleolites scutatus*; F. ,CORAL RAG' D. TROUVILLE = Facies ,Coral Rag' de Trouville; C. HENN. = Calcaire de Hennequeville; A. N. VILL. = Argiles noires de Villerville; O. C. = Oxford Clay; THB = ,*Trigonia*' *hudlestoni* Bed; BENCL. G. = Bencliff Grit; TRIG. CLAV. B. = ,*Trigonia*' *clavellata* Beds; SANDSF. C. = Sandsfoot Clay; SANDSF. G. = Sandsfoot Grit; R. W. C. = Ringstead Waxy Clays; K. C. = Kimmeridge Clay; L. CALC. GRIT = Lower Calcareous Grit; P. B. = Passage Beds; HAM. O. = Hambleton Oolite; M. CALC. GRIT = Middle Calcareous Grit; M. O. = Malton Oolite.

Fig. 2. Outcrop of Upper Jurassic rocks in England and Normandy.

The lack of any lining suggests that *B. perata* might belong to the cubichnia rather than to the domichnia. Here, therefore, in agreement with HÄNTZSCHEL (1962, 1965), they are interpreted as the resting traces of actinians.

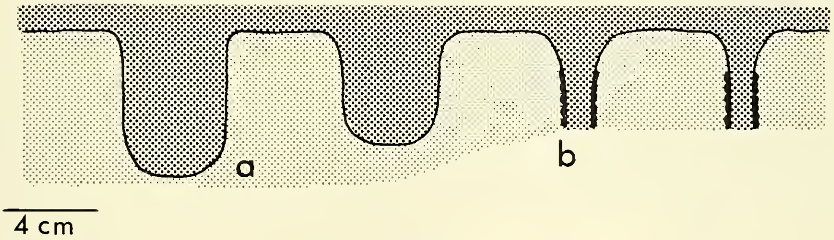


Fig. 3. *Bergaueria* sp. (a) and entrance funnels of *Spongeliomorpha nodosa* (LUNDGREN) (b) at the junction of fine-sand/oolite. — Berkshire Oolite Group, Shellingford Cross-Roads Quarry, Berkshire.

2. Domichnia (dwelling burrows)

Ichnogenus *Arenicolites* SALTER 1857

Type species: *Arenicola carbonaria* BINNEY 1852, p. 192 (designated by RICHTER 1924, p. 137).

Diagnosis: Vertical U-tubes without spreite.

Ichnospecies *Arenicolites variabilis* n. sp.

Figs. 4, 5 b, c

Diagnosis: Variable, narrow or wide, vertical or slightly oblique, mainly straight circular U-tubes without spreite; tube diameter 0.7—1.0 cm; floor deposits occur.

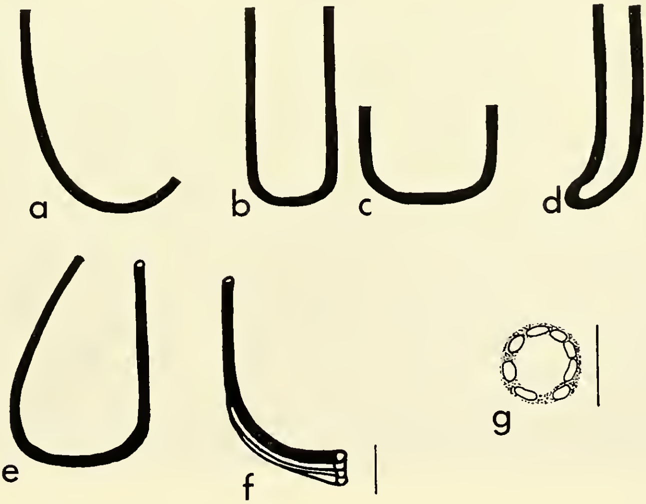


Fig. 4. *Arenicolites variabilis* n. sp.
a—f: morphological varieties within a population (scale: 5 cm); g: cross-section through a tube, showing the burrow wall stabilized by ooliths (scale: 1 cm).
Osmington Oolite Group, Bran Point, Dorset.

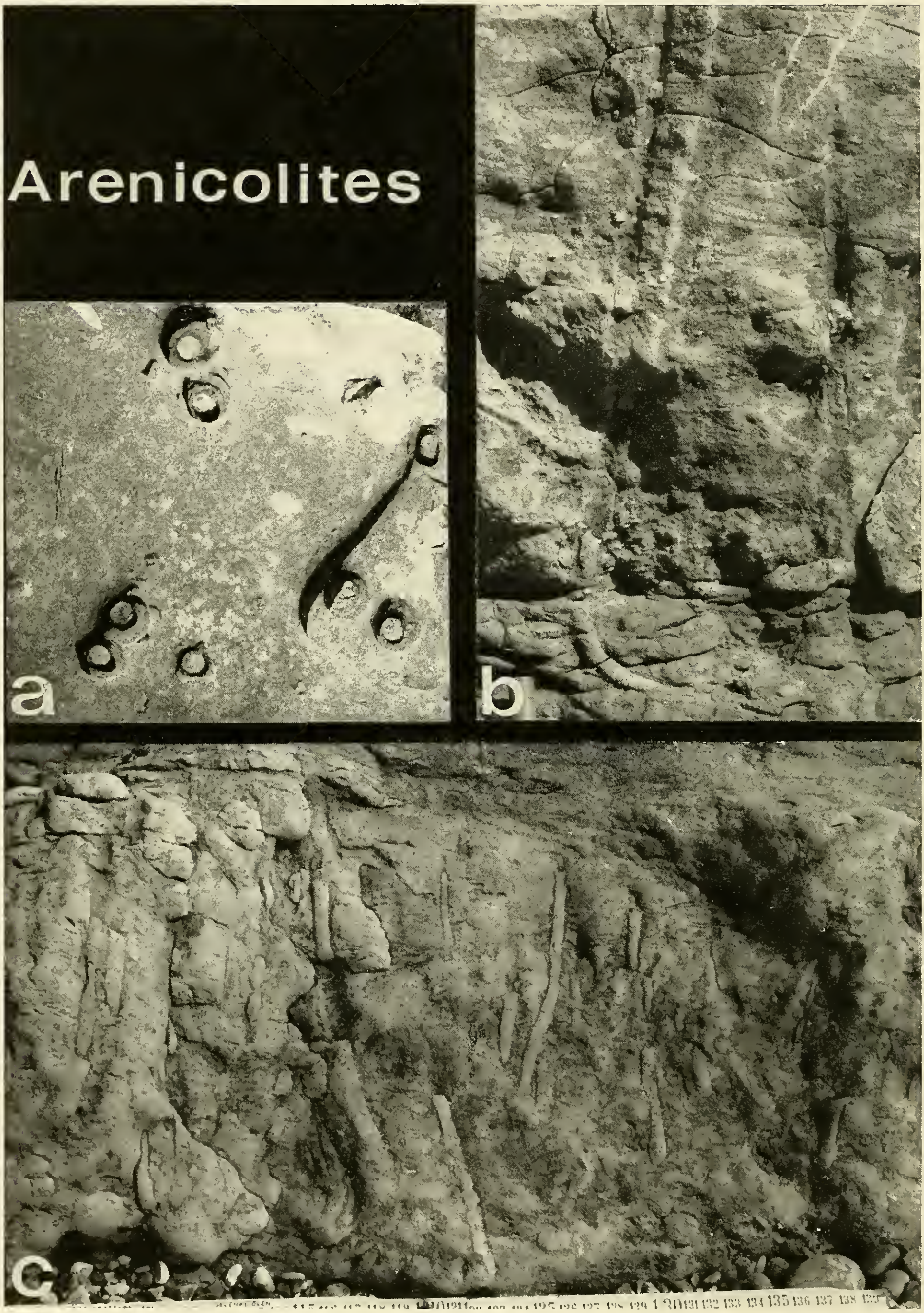


Fig. 5. a: paired openings of *Arenicolites statheri* BATHER in oolitic sandy limestone. — Osmington Oolite Group, Bowleaze Cove, Dorset (x 0,4); b: *Arenicolites variabilis* n. sp. (holotype) in fine-sandy oolitic limestone. — Osmington Oolite Group, Bran Point, Dorset (x 0,3); c: *Arenicolites variabilis* n. sp. in oosparite. — Osmington Oolite Group, Shortlake, Dorset.

Holotype: Fig. 5 b from the Osmington Oolite Group, Middle Oxfordian, at Bran Point (SY 742813), Dorset (type locality).

Description: Vertical or slightly oblique tubes (maximum deviation from the vertical 35 °) occasionally exhibiting a U-turn; the tube diameter varies from 0.7—1.0 cm, and the distance between both shafts from 2.3—10 cm; maximum depth observed was 34 cm. The two shafts of the U-tube are commonly not in the same plane (Fig. 4 e) and this is also true of the U-turn (Fig. 4 d); the latter frequently displays retrusive features (Fig. 4 f). Crossing over of burrows is a common feature. A burrow lining is usually present and consists of dark calcareous clay, sometimes with ooliths. The ooliths are arranged parallel to the tube wall (Fig. 4 g) indicating that the walls have been purposely stabilized by the inhabitant („Bauauskleidung", Reineck 1957). Internal structures in the infilling are absent except in a few cases where a meniscus-like structure has been observed.

Preservation: Full relief; fill identical with the matrix.

Facies: A. *variabilis* occurs in ooliths (sometimes with large-scale planar cross-bedding) and oolitic limestones.

Regional and stratigraphic distribution: Occurs in the Osmington Oolite Group at Bran Point and Black Head (Dorset coast) only.

Associations: *Diplocraterion parallelum, Planolites, Spongeliomorpha suevica* and *Chondrites.*

Discussion and interpretation: A. *variabilis* occurs only at a few levels in the Corallian of the Dorset coast, but usually in great numbers (Fig. 5 c). The proliferation in the same bed of morphologically sligthly different burrows next to each other as well as numerous intervening forms favour the assumption that the same animal was responsible for their formation. The lining of the burrows and their stabilization by the regular arrangement of ooliths indicate that the burrows were inhabited by suspension-feeders rather than by deposit-feeders.

The retrusive feature, so often seen in the U-turn, seems to contradict the assignation of A. *variabilis* to the ichnogenus *Arenicolites* (U-tube without spreite). Seilacher (1967, p. 419) defines spreite as „the product of a transverse shift of a tube through the sediment" and explains this transverse shift by the following three biological purposes (p. 421):

a. growth of the animal
b. feeding
c. response to sedimentation/erosion.

The first two reasons for building a spreite are purely biological and independent of the physical environment, whereas the third motive is a response of the inhabitant to this environment (see also Schäfer 1962, p. 406). The first two motives (a) and (b) result in a protrusive spreite, whereas (c) can result in a protrusive or retrusive spreite. The retrusive feature in A. *variabilis* cannot be explained by either of Seilacher's biological motives.

As the retrusive part is relatively short, compared with the depth of the whole burrow, the amount of sediment reworked is far too small for a deposit-feeder. (The construction of a tube wall in A. *variabilis* also contradicts a deposit-feeding mode of life of the inhabitant.) The spreite resulting from the growth of the animal will be protrusive and not retrusive as is always the case in A. *variabilis*. Similary, the shortness of the retrusive part casts doubt on its being a response to sedimentation.

However, there is a further explanation for retrusive structures. In the basal part of an U-burrow, those can be interpreted as floor deposits (see also under *Spongeliomorpha*, p. 26). The animals removed unwanted sediment, which fell into the burrows, by pressing it to the burrow floor („einseitige Räumauskleidung", Reineck 1957, Schäfer 1962, p. 331). If this process is a recurring event, it will finally result in a slight retrusive shift of the U-turn. Floor deposits differ from a spreite in their shortness and in being strictly retrusive. In some cases, however, the difference between a floor deposit and a spreite may not be very clean cut; a detailed ethological analysis of the whole trace fossil concerned is, therefore, necessary to elucidate the origin of the retrusive structure.

Another feature seen in the vertical shafts of *A. variabilis* resembles meniscus fills, known for example from *Spongeliomorpha nodosa* (Kennedy & MacDougall 1969). However, an interpretation of this structure as active back-fill seems in this case very unlikely as it would mean that the animal blocked its own U-tube. It is suggested for *A. variabilis* that the structure was generated mechanically during the filling of the U-tube after the animal's death.

Comparisons: *A. curvatus* Goldring 1962, *A.* (?) *compressus* (Sowerby 1829) and *A. subcompressus* (Eichwald 1860) differ from *A. variabilis* mainly in having an elliptical cross-section which is, at least in the case of *A. curvatus*, not the product of unidirectional deformation during compaction or tectonic stress conditions (Dr. R. Goldring, pers. comm.). *A. carbonaria* (Binney 1852) is far smaller than *A. variabilis*, and *A. statheri* Bather 1925 is strictly vertical and the tubes are always strictly parallel. Finally, *A. kahlaensis* Kolesch 1922 (U-turn not observed), *A. frankonicus* Trusheim 1934 (branching U-tubes occur), *A. graptolithiformis* Hundt 1931 (no U-tubes) and *A. sparsus* Salter 1857 (only paired openings seen; could, therefore, equally represent *Diplocraterion*) do not or only partly (in the case of *A. sparsus*) belong to the ichnogenus *Arenicolites*.

Arenicolites has often been compared with the burrows of modern *Arenicola marina* (e. g. Binney 1852, Bather 1925, Trusheim 1934), but already Richter (1924) and later Wells (1945) pointed out, that *Arenicola* usually does not build a simple U-tube. Wells (1945) demonstrated that the burrows of *Arenicola marina* is usually L-shaped, except in rapidly drying sand, where an open U-tube is constructed although the second shaft lacks a mucus-lining. An open U-tube is also required by *Arenicola* when it burrows in consolidated fine-grained sediment (Schäfer 1962, p. 341). However in the Corallian, most burrows are found in oolites where *Arenicola* does not require a second shaft in order to maintain water circulation through the burrow.

Rieth (1931) drew a parallel between his U-tubes and the burrows of the enteropneust *Balanoglossus clavigerus*, which, however, constructs a complex U-tube with several side-branches. Goldring (1962, p. 247) interpreted *A. curvatus* as the result of the burrowing activity of annelid- or crustacean-like organisms secreting a thick mucus-lining.

A. variabilis is considered to belong to the domichnia and to have been formed by a suspension-feeding polychaete rather than a crustacean as in no case have scratch marks, typical for crustaceans, been recorded. Moreover Rieth (1931) noticed an annulation in one of his Rhetian U-tubes which he explained as the impressions of the muscular activity of the animal on the burrow wall (see also HÄNTZSCHEL 1938).

Ichnospecies *Arenicolites statheri* BATHER 1925

Figs. 5 a, 6

1859 *Scolithus linearis.* — MURCHISON, p. 14; *non* HALDEMAN 1840.
? 1885 *Scolithus linearis.* — DELGADO, p. 82, pl. 39, fig. 1; *non* HALDEMAN 1840.
* 1925 *Arenicolithes statheri* BATHER, p. 198, pl. 14—16.

Diagnosis: Straight, symmetrical Arenicolites.

Description: Simple U-tubes without spreite, commonly preserved as paired funnel-shaped openings on bedding planes showing a distinct annulation (Fig. 5 a). A lining (0.1—0.25 cm in thickness) is present consisting of a soft ferruginous marl (Fig. 6). Floor deposits, similar to those found in *A. variabilis* though not as thick are common. The tube diameter ranges from 0.4 to 0.9 cm and the distance between the two arms varies from 3.3 to 6.0 cm, greatest depth recorded being 7.6 cm (table 1).

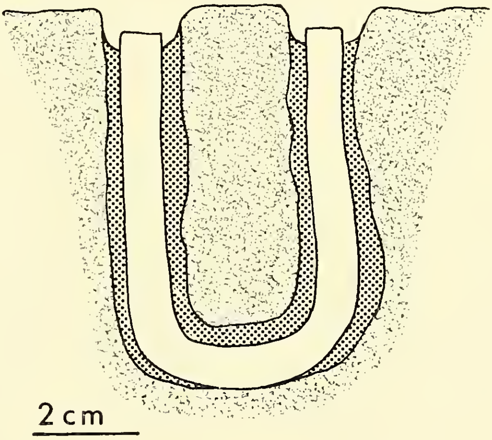


Fig. 6. *Arenicolites statheri* BATHER in oolitic sandstone. Note heavy lining (dark) surrounding the plugged tubes (light). — Fallen block from the Osmington Oolite Group, Bowleaze Cove, Dorset.

Preservation: Full relief; fill identical with the matrix.

Facies: Sandy limestone with abundant immature ooliths.

Regional and stratigraphic distribution: Osmington Oolite Group at Bowleaze Cove, Dorset.

Associations: *Spongeliomorpha saxonica* and rarely *Rhizocorallium* sp.

Discussion and interpretation: This second Corallian *Arenicolites* has been identified as *A. statheri* despite the fact that BATHER's specimens burrow down to a depth of 30 cm (whereas the Corallian *Arenicolites* does not exceed 6.8 cm in depth), and never exhibit funnel-shaped apertures. But FÜRSICH (in press) argued that funnel-shaped apertures and burrow depth cannot be used as ichnospecific features: the former are often purely the result of the weathering of the softer burrow lining (see also WESTERGÅRD 1931, p. 6); and the burrow depth, as preserved, depends on the degree of erosion after the animal vacated its burrow. As the degree of erosion usually cannot be established, and on the other hand the tube diameter and width of the burrow as well as the general morphology are well within the range of *A. statheri*, the Corallian specimens have been included within the latter.

Interpretation: see under *A. variabilis*.

w_1	w_2	observed depth
4.9	4.0	— —
— —	3.3	6.5
4.0	3.0	— —
4.1	3.2	— —
6.0	5.0	— —
5.3	3.9	— —
3.3	2.7	7.6

Table 1

Dimensions of *Arenitolites statheri* (measurements taken from one population). w_1: distance between the outer rim of the funnels; w_2: distance between the tubes.

Crustacean burrow

Fig. 7

At the top of the Berkshire Oolite Group, Middle Oxfordian, between Osmington Mills and Bran Point (Dorset coast), sections of large burrows are seen which originate at the unconformity with the overlying Osmington Oolite Group.

The burrows are rounded angular or subcircular in cross-section, but also squashed burrows occur (Fig. 7 b, c). The burrow diameter varies between 4.5 and 7 cm. In one case the entrance of a burrow could be seen: an oblique burrow, inclined at an angle of about 40 °, could be followed down 40 cm below the unconformity surface (Fig. 7 a). The burrow walls are smooth and show a distinctive lining consisting of a sheet of plant debris. The sediment in which these burrows occur consists of highly carbonaceous and bituminous fine-sand, with small-scale cross-bedding, which grades downwards into large-scale trough cross-bedding (channels) with impersistent bands of clay.

Fig. 7. Crustacean burrow.
a: burrow entrance; b—c: cross-section through burrows (partly squashed) exhibiting a lining of plant debris. — Top of the Bencliff Grit, Berkshire Oolite Group, Osmington Mills, Dorset (scale: 5 cm).

No branching could be observed, which might be due to the fact that only the vertical cliff-face was exposed. The diameter is larger than that of *Spongeliomorpha saxonica* burrows found associated with them. This, and the characteristic lining make it likely that the structures represent a new burrow type. As the three-dimensional form of the burrows could not be established with certainty, it does not seem suitable to erect a new ichnogenus or ichnospecies.

The burrows are most likely of crustacean origin. *Callianassa* burrows stuffed with eel-grass blades have been observed by FARROW (1971) and a lining consisting of finely macerated eel-grass was found by the same author in burrows of the anomuran *Neaxius*, both from the Aldabra atoll, Indian Ocean. In all likelyhood, the Corallian burrows are similar in shape and function to those of *Ocypode* (broad U- or L-shaped), *Cardisoma, Sesarma, Pseudosquilla* or even *Uca, Macrophthalma* or *Neaxius*. (For literature on these burrow types see HAYASAKA 1935, FREY & MAYOU 1971, FARROW 1971, BRAITHWAITE & TALBOT 1972, and HILL & HUNTER 1973.) The inhabitant might have been a scavenger like *Ocypode* (TAKAHASI 1935, FREY & MAYOU 1971), *Macrophthalma* or *Uca* (MILLER 1961). The burrows served most certainly as a refuge and dwelling and were occupied only intermittently.

Ichnogenus *Diplocraterion* TORELL 1870

Typespecies: *Diplocraterion parallelum* TORELL 1870, p. 13 (designated by RICHTER 1926, p. 214).

Diagnosis: Vertical U-shaped spreiten-burrows; dwelling burrows of suspension-feeders.

Ichnospecies *Diplocraterion habichi* (LISSON 1904)

Figs. 8, 9

For synonymy see FÜRSICH (in press).

Diagnosis: *Diplocraterion* in which arms of the U-tube diverge upwards (adapted from FÜRSICH in press).

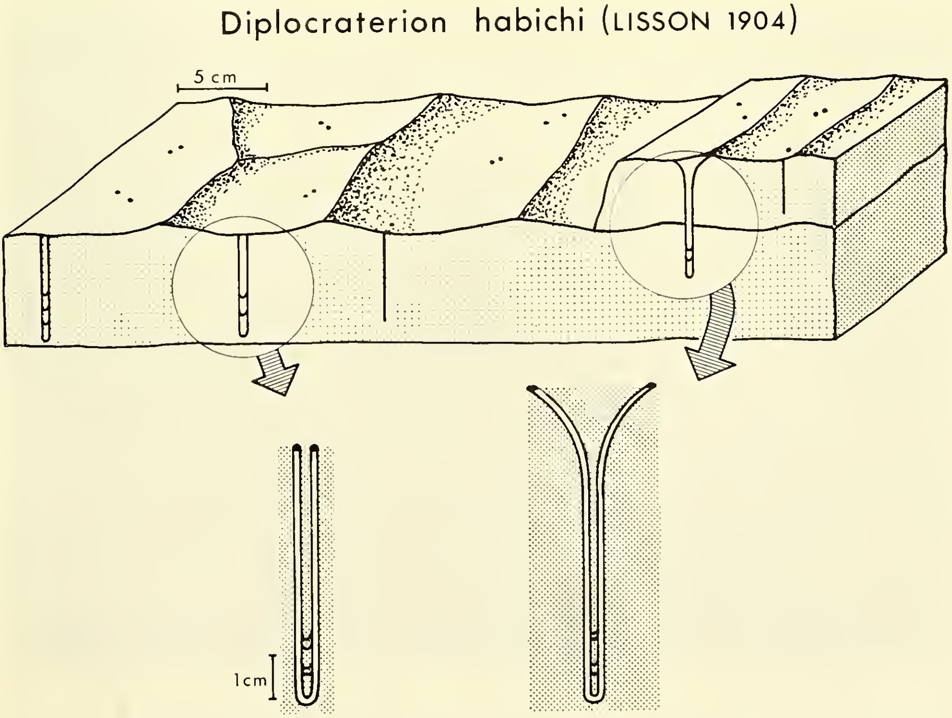


Fig. 8. *Diplocraterion habichi* (LISSON) associated with oscillation ripples. — Bencliff Grit, Berkshire Oolite Group of Bowleaze Cove, Dorset.

Description: The Corallian specimens range in width from 0.6 cm (at the basal parallel part of the burrow) to 1.8 cm (distance of paired openings). The tube diameter varies from 0.15 to 0.3 cm. Between the two arms, a discontinuous protrusive spreite is usually found. Erosion sometimes capped the upper part of the U-tube; as a result, the diverging arms are not preserved in each specimen (Fig. 8). On bedding planes, only the paired openings are usually encountered. In the case of the Bencliff Grit specimens, these paired openings are surrounded by a raised rim (Fig. 9 b).

Preservation: Full relief; fill identical with the matrix. The raised rim of the openings indicates early cementation of the sediment in the vicinity of the U-tube. This was probably caused by organic-rich mucus with which the inhabitant lined its burrow.

Facies: *D. habichi* is a very good facies indicator. It is unvariably found in high-energy sediments: most commonly in trough cross-bedded, well sorted silts and fine-sands (e. g. in the Berkshire Oolite Group of Dorset and Oxfordshire), and rare in oosparites (e. g. in the Osmington Oolite Group at Black Head, Dorset). Associated with *D. habichi* are commonly ripples, abundant wood and plant fragments, as well as pebbles.

Regional and stratigraphic distribution: Common in parts of the Middle Oxfordian of Oxfordshire and Dorset only.

Associations (in order of decreasing abundance): *D. parallelum, Spongeliomorpha nodosa, Gyrochorte, Scolicia, Muensteria, Skolithos,* and *Gyrophyllites.*

Discussion and interpretation: Vertical spreiten-burrows are usually regared as the domichnia of suspension-feeders (Richter 1926, Goldring 1962, Seilacher 1963, 1967), the spreite being rather the result of the animal's intention to keep its burrow at a constant depth than the result of mining the sediment for food. The divergence of the arms in *D. habichi* offers an additional argu-

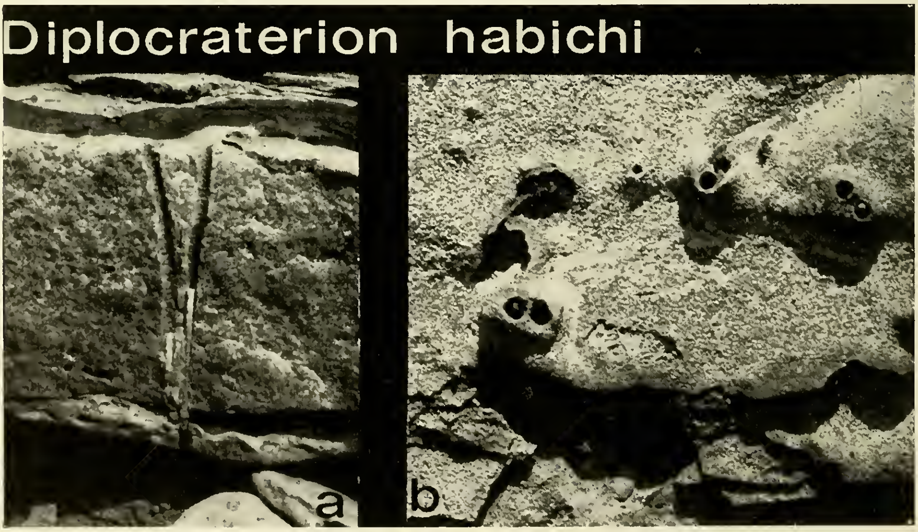


Fig. 9. *Diplocraterion habichi* (Lisson) in fine-grained sandstone. a: section showing the flared arms (x 0.5); b: paired openings. The raised rim indicates early cementation of the sediment in the vicinity of the burrows (x 1). Fallen blocks from the Bencliff Grit, Berkshire Oolite Group, of Bowleaze Cove, Dorset.

ment for its interpretation as the dwelling burrow of a suspension-feeder. Increasing the distance between the two apertures of a small U-tube guarantees a better separation of inhalent and exhalent currents. In larger burrows, e. g. *D. parallelum*, the distance between the apertures is wide enough to keep the two currents separate; and divergence of the arms is thus superfluous.

Howell (1957) regarded *D. habichi* as the burrow of a scoleciform annelid. The similarity of *D. habichi* with burrows of the Recent amphipod *Corophium volutator* is, however, surprising. Seilacher (1967 Pl. 1 A) figures a burrow of *Corophium volutator* which is not only very similar in size but also shows the divergence of the arms. Furthermore, the environmental range of the two forms is very similar. *C. volutator* is widespread on the tidal flats of northwestern European shelf seas, and *D. habichi* predominantly occurs in a similar setting, which is shown by its association with ripples, channels, flaser bedding and a high amount of wood fragments. The inhabitant of *D. habichi* is, therefore, more likely to be found amongst the crustaceans than the polychaetes.

Ichnospecies *Diplocraterion parallelum* Torell 1870

Figs. 10—13

For synonymy see Fürsich (in press).

Diagnosis: *Diplocraterion* having parallel burrow walls and an unidirectional spreite (adapted from Fürsich in press).

Description: *Fairly straight* U-tubes the arms of which are more or less

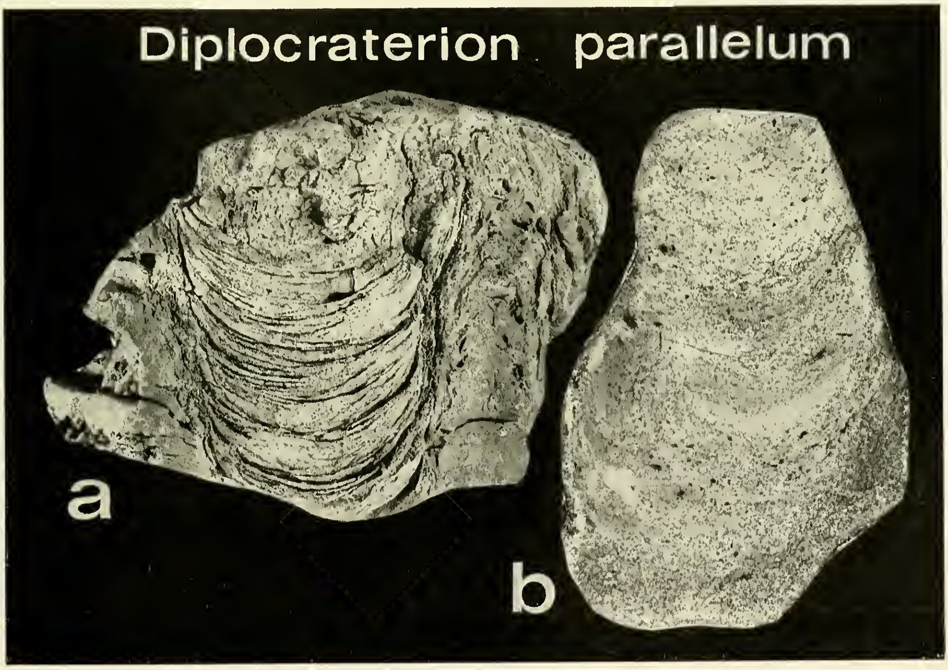


Fig. 10. Retrusive *Diplocraterion parallelum* Torell. a: in fine-grained sandstone showing spreite. — Fallen block from the Bencliff Grit, Bowleaze Cove, Dorset (x 0.2); b: cross-section through spreite in fine-sandy marl. Note the rhythmic alternations of pellet layers (light-grey) with those of fine-sand. — Osmington Oolite Group, Bran Point, Dorset (x 0.9).

parallel. The tube diameter varies between 0.9 and 1.8 cm, the width of the smallest burrow is 8 cm, that of the largest 18 cm. These U-tubes penetrate the rock down to 40 cm and have a well-developed spreite. Only in very few cases is this spreite protrusive; in some beds a retruso-protrusive spreite is found, whilst in the majority of the cases the spreite is of the retrusive type (Fig. 10). In thin-section, the structure of the spreite (where dug into fine-sandy biomicrite) has been found to consist

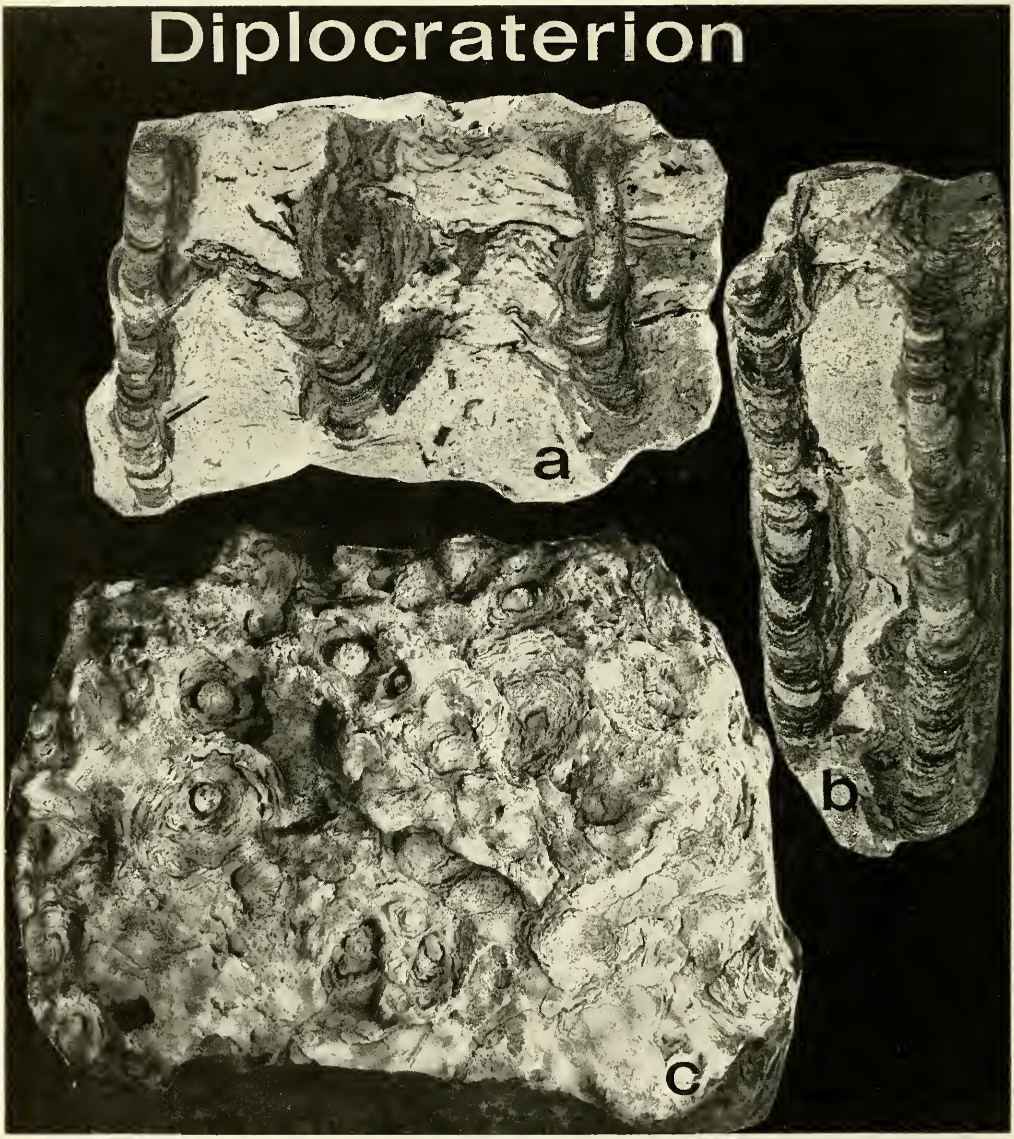


Fig. 11. *Diplocraterion parallelum* TORELL in fine-grained sandstone.
a—b: cross-section through retrusive spreiten showing the heavy burrow lining and the irregular nature of some spreiten. The spreite consists of alternating layers of faecal pellets (dark) and sand grains (light); (a: x 0.4, b: x 0.3);
c: top view, indicating the heavy lining which surrounds the plugged tubes (x 0.3).
a—c: fallen blocks from the Bencliff Grit, Bowleaze Cove, Dorset.

of layered alternations of quartz grains and faecal pellets (Fig. 10 b). The latter, up to 1 mm in diameter, consist of micrite, show no internal structure, and are closely packed in laminae up to 5 mm thick. In the case of *D. parallelum* from the Bencliff Grit, which were excavated in fine-grained sand, the spreite consists once again of concave layers (retrusive) of rod-shaped faecal pellets and plant debris alternating with layers of quartz grains (Fig. 11 a, b). The spreite is well-developed in all specimens and is either straight and vertical or else irregular or deflected (Fig. 11 a).

Concentric laminae surrounding the apertures of most *D. parallelum* as well as evidence from polished sections (Fig. 11 b) show that the tubes are heavily lined (Fig. 11 c). However, this lining is only seen in burrows which were excavated in arenaceous sediments, and consists of quartz grains and faecal pellets.

Crisscrossing of up to three superimposed burrows occurs occasionally, especially where a high burrow density indicates several phases of burrowing. Orientation of the U-tubes, probably to currents, could be observed in a few cases (Fig. 12 b).

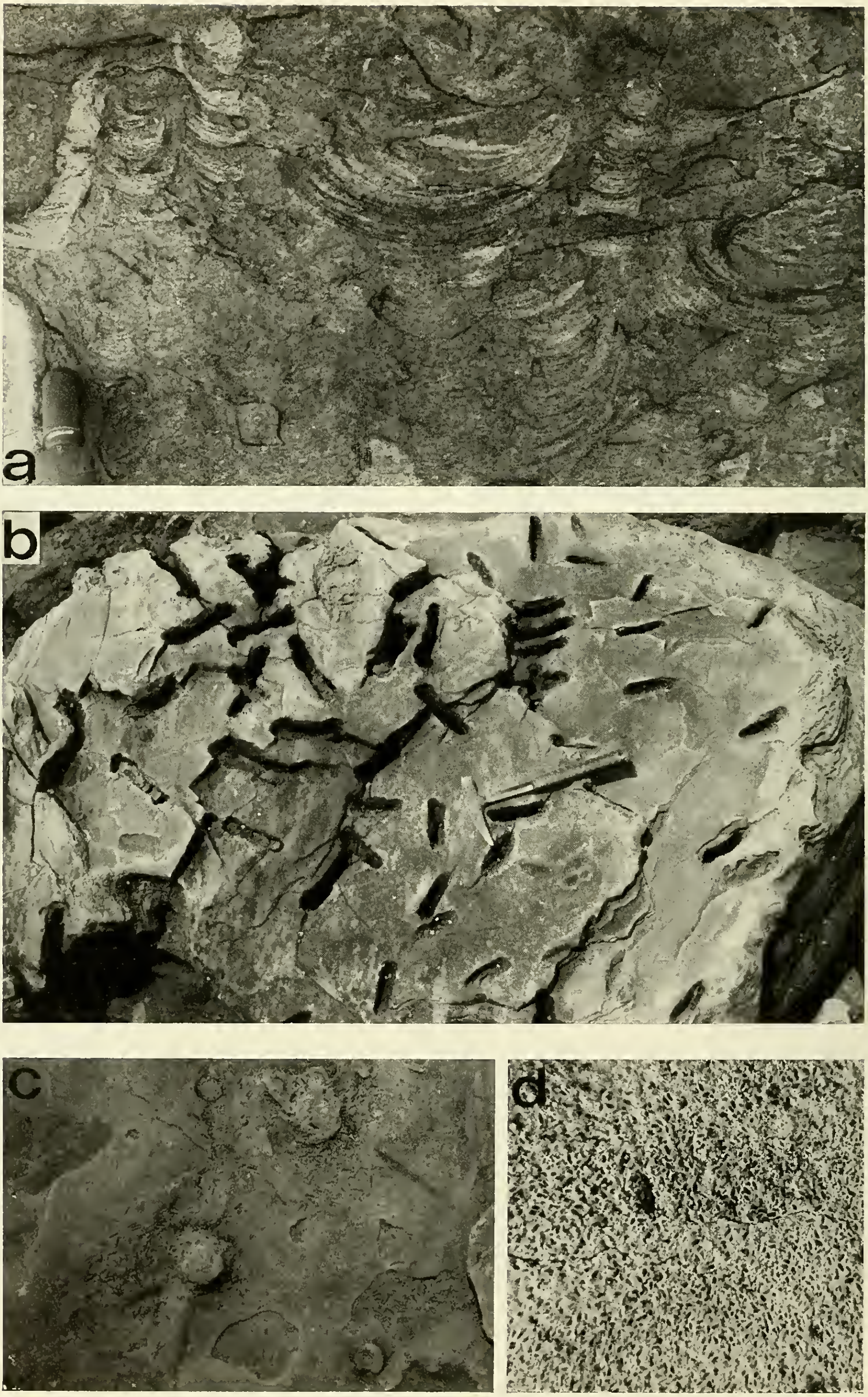
Preservation: Full relief; in argillaceous micrite, the burrows are sometimes preserved as limestone nodules in a similar way as described for „*Thalassinoides*“ (Fürsich 1973 a). In sandstones, the burrows may weather out and only casts are preserved (Fig. 12 b); alternatively they occur in sandstone-preservation. When found in oolites, horizontal cross-sections reveal concentric laminae of red-brown sideritic clay alternating with laminae of ooliths (Fig. 13).

Facies: Most common in marly fine-sand and oolitic limestones. In fine-grained sandstones this burrow is associated with large-scale trough cross-bedding, flaser bedding, asymmetric and oscillation ripples, occasionally also with abundant plant debris and pieces of lignite.

Regional and stratigraphic distribution: *D. parallelum* is very common in the Bencliff Grit of the Dorset coast and occurs also in some beds in the Osmington Oolite Group (e. g. Littlemore Clay Beds) at Bran Point and Black Head (Dorset).

Associations (in order of decreasing abundance): *Spongeliomorpha suevica, Diplocraterion habichi, Planolites, Muensteria, Gyrophyllites, Gyrochorte, Teichichnus, Rh. irregulare, Scolicia* and *Spongeliomorpha nodosa*. Faecal pellets are found abundantly both in the burrows and spreite, and around the apertures of the U-tubes (Fig. 12 c).

Discussion and interpretation: The abundance of faecal pellets in the spreite of most *D. parallelum* seems to contradict its interpretation as the domichnium of a suspension-feeder, as they are usually associated with deposit-feeders (e. g. most *Rhizocorallium*, Reis 1910). Seilacher (1963) noted the abundance of faecal pellets in the spreite of *Diplocraterion* and Goldring's (1962) specimens from the Devonian Baggy Beds show an association with faecal pellets very similar to that of the Corallian specimens. Alternations of densely packed layers of faecal pellets and of sediment, as found in some retrusive *D. parallelum* from the Bencliff Grit and in all specimens from the Littlemore Clay Beds suggest that the shifting of the burrows was a relatively slow process: periods during which the inhabitant shifted its burrow (indicated by the layer of sediment) up to one centimeter because of sedimentation alternated with periods during which the animal was feeding (indicated by the layers of faecal pellets). These rhythmic alternations of periods of relatively little sedimentation and non-deposition may be related to a tidal environment. There, periods of sedimentation during slack water alternate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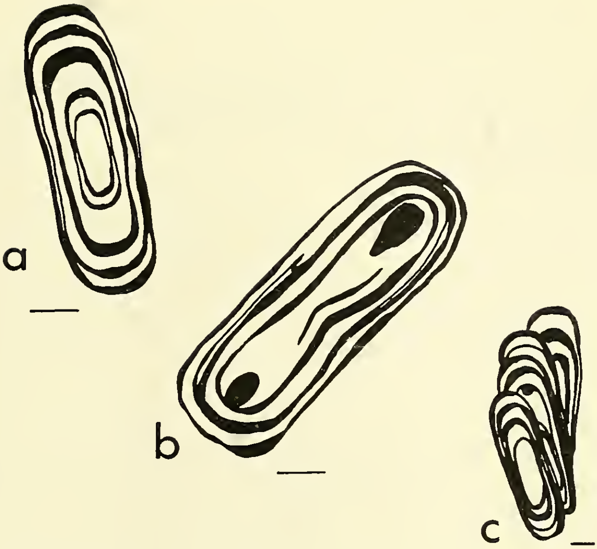

Fig. 13. Horizontal sections through the basal parts of *Diplocraterion parallelum* TORELL in siderite preservation showing retrusive spreiten, in (b) with plugged tubes, and in (c) with sidewards migration of the burrows. — Osmington Oolite Group, Black Head, Dorset (scale: 2 cm).

with those of non-deposition when tidal currents are active. More conspicuous events like rapid sedimentation or erosion (e. g. in connection with storms) might in most cases have either killed off the inhabitant or forced it to excavate a new burrow. Erosion was a common phenomenon in this habitat: only rarely are free tubes present in *D. parallelum* from the Corallian.

ARKELL (1939) who first described *D. parallelum* from the Corallian as U-shaped burrows, interpreted them as having been formed by a burrowing polychaete. HERTWECK (1970, p. 240, pl. 1) figures bioturbation structures produced by the Recent *Echiurus echiurus* from the German Bay, which are very similar to bioturbation structures of *D. parallelum* (Fig. 12 a). Again, burrows of the Recent *Corophium* can be very similar except for their smaller size (SCHÄFER 1962 fig. 179). Thus it seems not justified to exclude either polychaetes or crustaceans as possible producers of *D. parallelum*, though the presence of scratch marks in some burrows (e. g. from the Middle Jurassic Ellerbeck Formation of Yorkshire) may favour a crustacean origin. Moreover, there is no doubt that *D. parallelum* has been produced by a variety of forms as it is already known from the Cambrian (SEILACHER 1957, p. 377, TORELL 1870, ÖPIK 1929). However, what is far more important is that it clearly represents the burrow of a suspension-feeder.

Fig. 12. a: bioturbation in fine-sandy marl, caused by retrusive *Diplocraterion parallelum*. — Osmington Oolite Group, Bran Point, Dorset (x 0.5);
b: orientated *Diplocraterion parallelum* preserved as casts in fine-grained sandstone;
c: rod-shaped faecal pellets surrounding the apertures of *D. parallelum* (x 0.35);
d: bedding plane covered with faecal pellets (x 0.8);
b—d: fallen blocks from the Bencliff Grit, Berkshire Oolite Group, of Bowleaze Cove, Dorset.

Ichnogenus *Rhizocorallium* ZENKER 1836

Type species: *Rhizocorallium jenense* ZENKER 1836, p. 219.

Diagnosis: U-shaped spreiten-burrows, parallel or oblique to bedding plane; limbs more or less parallel and distinct; tube diameter: diameter of spreite > 1 : 5 (adapted from FÜRSICH 1974).

Ichnospecies *Rhizocorallium jenense* ZENKER 1836

Fig. 14 a

Diagnosis: More or less straight, short U-shaped spreiten-burrows, commonly oblique to bedding plane and sometimes vertically retrusive (adapted from FÜRSICH 1974).

Description: Tube diameter 1—1.7 cm, width of spreite 4—4.6 cm; vertically retrusive structures, up to 3 cm high, are present (Fig. 14 a). The short burrows (maximum length 20 cm, usually not exceeding 15 cm) are slightly inclined towards the vertical and fairly straight. The spreite is well developed, but no ornamentation has been found on the tube walls.

Preservation: Full relief; fill identical with the matrix.

Facies: *Rh. jenense* has been found in intraclastic oolites only.

Regional and stratigraphic distribution: Known from the Middle Oxfordian southwest of Villers s.M./Normandy.

Associations: Found together with abundant *Spongeliomorpha suevica* type A.

Fig. 14. a: *Rhizocorallium jenense* ZENKER with vertically retrusive structures. — Oolithe de Trouville, Les Vaches Noires, southwest of Villers s. M./Normandy;
b: *Rhizocorallium irregulare* MAYER with scratch marks on the limbs. — ‚*Trigonia*' *hudlestoni* Bed, Berkshire Oolite Group, Bowleaze Cove, Dorset (scale: 5 cm).

Discussion and interpretation: The ichnogenus *Rhizocorallium* has been recently revised by FÜRSICH (1974). According to him, short oblique vertically retrusive forms (i. e. *Rh. jenense*) should be interpreted as the burrows of suspension-feeders, probably crustaceans. In the Corallian, *Rh. jenense* occurs only in intraclastic oolites which confirms this interpretation: oolite shoals are usually poor in organic matter and therefore void of deposit-feeders (PURDY 1964).

To distinguish between a deposit-feeding origin and a suspension-feeding origin in *Rhizocorallium* might not always be very easy, if only individual specimens are considered. In the case of a whole *Rhizocorallium* community, however, it should be fairly easy to assign it to one of the two feeding types.

Ichnogenus *Skolithos* HALDEMAN 1840

Type species: *Fucoides ? linearis* HALDEMAN 1840, p. 3.

Diagnosis: Unbranching, straight vertical burrows.

Remarks: The taxonomy of simple vertical burrows is in urgent need of revision. Morphological features such as funnel-shaped apertures in *Monocraterion* TORELL 1870 or less crowding of the tubes as in *Tigillites* ROUAULT 1850 do not justify separation at the ichnospecific and certainly not at the ichnogeneric level. All straight and unbranching vertical burrows are, therefore, regarded as synonyms of *Skolithos* HALDEMAN 1840 which has priority. It is not the aim of this paper to revise the numerous ichnospecies belonging to these ‚ichnogenera'. As it seems not suitable to designate the Corallian specimens to an ichnospecies the synonymy of which has not yet been investigated, they are described solely as *Skolithos* sp.

Skolithos sp.

Description: Straight, unbranching vertical burrows with a diameter ranging from 0.3 to 1.0 cm. The walls of the burrows are smooth and lack ornamentation. No lining or funnel-shaped apertures have been found. Observed maximum length of the un-crowded tubes is 25 cm.

Preservation: Full relief; fill identical with the matrix.

Facies: *Skolithos* sp. occurs in fine-grained sandstones as well as in intraclastic or shelly limestones and in oolites.

Regional and stratigraphic distribution: Occasionally found in the Middle Oxfordian (Berkshire Oolite Group, Osmington Oolite Group) of the Dorset coast (Bowleaze Cove, East Fleet) and in Normandy (Falaises des Vaches Noires); rare in Yorkshire.

Associations: *Asterosoma, Scolicia, Chondrites, Muensteria, Spongeliomorpha suevica, Teichichnus, Cylindrichnus, Diplocraterion habichi* and *Gyrochorte.*

Discussion and interpretation: *Skolithos* and *Monocraterion* have been discussed in detail, e. g. by RICHTER (1920, 1921), WESTERGÅRD (1931), HOWELL (1943), and HALLAM & SWETT (1966). It is difficult to add to the last account according to which SKOLITHOS represent the domichnia of suspension-feeding worms (RICHTER 1920, HOWELL 1943) or phoronids (FENTON & FENTON 1934).

Ichnogenus *Spongeliomorpha* SAPORTA 1887

Type species: *Spongeliomorpha iberica* SAPORTA 1887, p. 299.

Diagnosis: Cylindrical branching burrow systems with both vertical and horizontal elements; branching Y- or T-shaped; burrow walls unlined, with pelletal or smooth lining, or covered with longitudinal ridges (scratch marks); dwelling burrows of crustaceans (adapted from FÜRSICH 1973 b).

Remarks: *Spongeliomorpha* and other similar crustacean burrows (*Ophiomorpha, Thalassinoides*) have recently been revised by FÜRSICH (1973 b). No features worthy of ichnogeneric separation could be found in these three ichnogenera; consequently, *Ophiomorpha* LUNDGREN 1891 and *Thalassinoides* EHRENBERG 1944 have been declared to be junior synonyms of *Spongeliomorpha.*

Ichnospecies *Spongeliomorpha nodosa* (LUNDGREN 1891)

Figs. 3 b, 15

For synonymy see FÜRSICH (1973b).

Diagnosis: Three-dimensional, cylindrical branching burrow systems; vertical elements very common; predominantly with pelletal lining (adapted from Fürsich 1973 b).

Description: Predominantly vertical burrow systems, bifurcating at irregular intervals. At bifurcations and at ‚turn-arounds' the burrows are enlarged. The burrows are cylindrical, range from 0.4 cm to 1.2 cm in diameter and are characterized by a mammillated outer surface (Fig. 15). This wart-like exterior is formed by cemented pellets of sediment; the pellets range in size from less than 1 mm to 1.2 mm. When found in uncemented sands, the burrow lining is often cemented by Fe-hydroxid and therefore more resistent to weathering. Internally, the lining which accounts for up to one-third of the burrow diameter, is smooth. Funnel-shaped entrance shafts have been found in one case (Fig. 3 b).

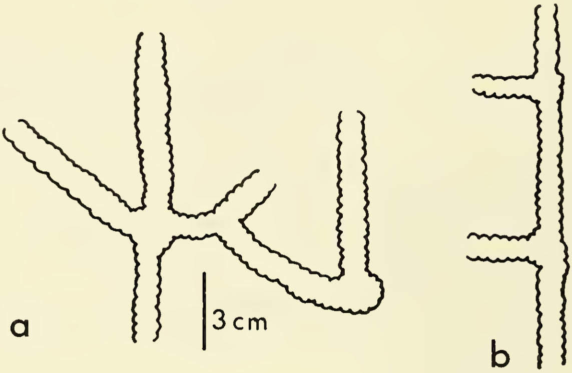

Fig. 15. *Spongeliomorpha nodosa* (Lundgren). — Berkshire Oolite Group, Shellingford Cross-Roads Quarry, Berkshire.

Preservation: Full relief; fill identical with the matrix.

Facies: *Sp. nodosa* occurs preferably in well-sorted, fine-grained sands, associated with small-scale cross-bedding, flaser-bedding, clay drapes and channels. It is also common in intraclastic, fine-sandy oolitic limestones. *Sp. nodosa* is a very good facies indicator.

Regional and stratigraphic distribution: *Sp. nodosa* is abundant in the Berkshire Oolite Group (Middle Oxfordian) of Berkshire (Shellingford Cross-Roads Quarry, SU 32694, and Amey's Quarry, SU 457992) and occurs occasionally in the Osmington Oolite Group of Normandy.

Associations: *Diplocraterion habichi*; rarely *Sp. suevica*, *Planolites*, *Bergaueria* and *Cylindrichnus*.

Discussion and interpretation: The origin and significance of the morphological features in the ichnospecies of *Spongeliomorpha* has been discussed in detail by Fürsich (1973 b). *Sp. nodosa* is usually recorded from fine-grained, well-sorted sands and sandstones, often associated with features typical of the littoral or sublittoral environment (e. g. Kanes 1963, Hoyt & Weimer 1963, Weimer & Hoyt 1964). The occurrence of *Sp. nodosa* in the Corallian confirms this observation.

The pelletal lining served to stabilize the burrow walls in the unconsolidated sands. Thus the burrow system was kept open while inhabited, and served as a dwelling burrow.

The inhabitant of modern *Sp. nodosa* systems is the shrimp *Callianassa major* SAY (WEIMER & HOYT 1964). The identical shape of fossil and recent systems and records of *Callianassa* debris in the burrows (WAAGE 1968) make it seem reasonable to interprete the Corallian burrows as domichnia of callianassids. *Callianassa major* is a suspension-feeder/scavenger: it feeds on detritus which it obtains by sifting sand (POHL 1946). A continuous water current through the burrow system, created by hair-like structures which cover the body of the crustacean (MACGINITIE 1934), aids the feeding and facilitates the removal of waste. Thus, *Sp. nodosa* can be interpreted as the burrow of an endobenthonic suspension-feeder/scavenger which is specially adapted to a life in sands and sandy muds.

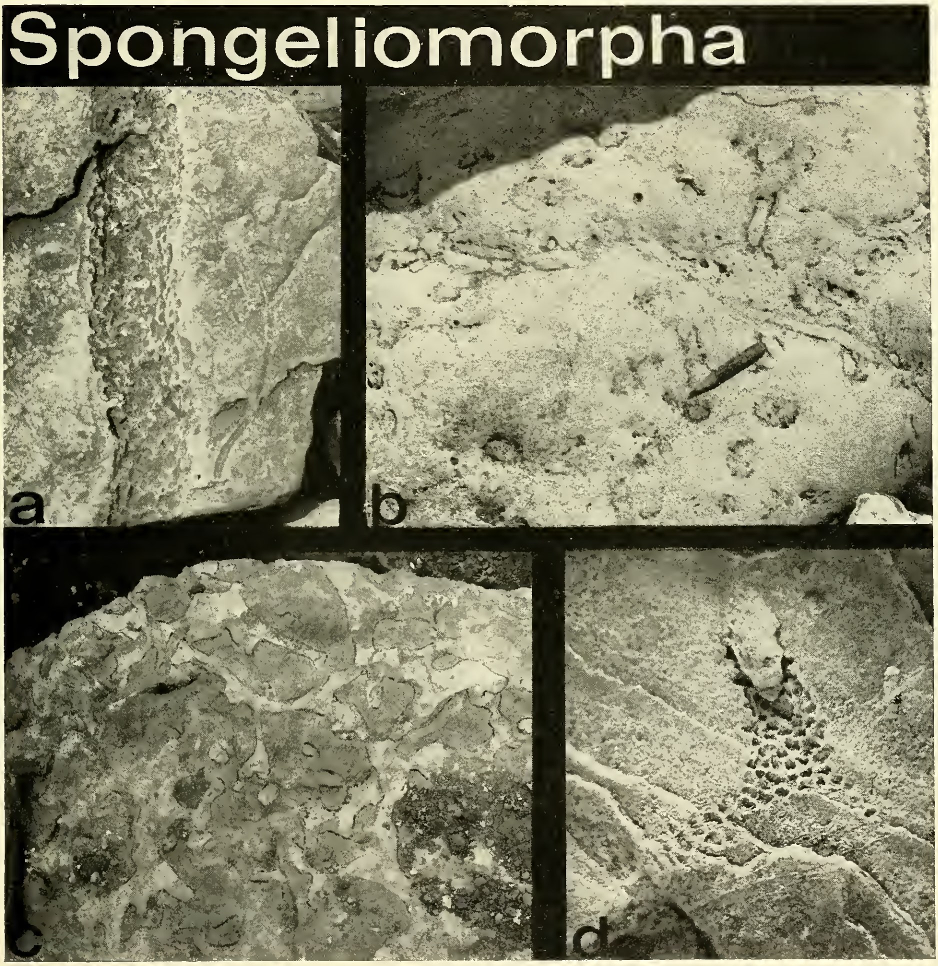

Fig. 16. a: *Spongeliomorpha saxonica* (GEINITZ) type B in fine-grained sandstone. — Slab from the top of the Berkshire Oolite Group, east of Osmington Mills, Dorset (x 0.25);
b, d: *Spongeliomorpha saxonica* (GEINITZ) type A. — Osmington Oolite Group, Black Head, Dorset (x 0.3) (b) and Berkshire Oolite Group, Osmington Mills, Dorset (x 0.7) (d);
c: *Spongeliomorpha paradoxica* (WOODWARD) in fine-grained silicious sandstone. — Spaunton Sandstone, Upper Calcareous Grit, Spaunton Quarry (SE 722868), Yorkshire.

Ichnospecies *Spongeliomorpha saxonica* (GEINITZ 1842)

Figs. 16 a, b, d.

For synonymy see FÜRSICH (1973b).

Diagnosis: Cylindrical branching burrow systems; vertical elements rare; predominantly with pelletal lining (adapted from FÜRSICH 1973 b).

Description: Predominantly horizontal and oblique burrow systems with only few vertical elements. The burrows branch frequently and are enlarged at bifurcation points. Two size classes occur ranging from 0.9 to 1.5 cm and from 3 to 4 cm in diameter respectively. The cylindrical burrows show a pelletal lining with a mammillated exterior and smooth interior (Fig. 16 d). The pellets range from 0.8 mm in diameter (in the small systems) to 4 mm (in the large systems), and can merge to form a clay lining with an irregular surface.

Preservation: Full relief; fill identical with the matrix.

Facies: *Sp. saxonica* is found in oosparites, sometimes associated with large-scale planar cross-bedding; in fine-grained sandstones with shallow trough cross-bedding; and in fine-sandy limestones.

Regional and stratigraphic distribution: Found in the Berkshire Oolite Group and Osmington Oolite Group of the Dorset coast.

Associations: *Diplocraterion habichi* (common), *D. parallelum, Skolithos* and *Gyrochorte* (rare).

Discussion and interpretation: *Sp. saxonica* characterizes burrow systems with pelletal lining and mainly horizontal elements. That it does not just represent the erosional relict of *Sp. nodosa* systems can be shown by the rare vertical elements which are present. It is thought to be more likely that the preference for horizontal arrangement of the burrows reflects a somewhat different environment than the littoral environment of *Sp. nodosa*. Thus FARROW (1971, p. 480) observed that horizontal systems are characteristic of strongly current-swept areas with relatively thin sediment cover.

FÜRSICH (1973 b) demonstrated in a review of Recent and fossil *Spongeliomorpha* that size cannot be used as an ichnospecific feature. The two distinctly different size classes are therefore called *Sp. saxonica* type A (small systems; Fig. 16 b) and *Sp. saxonica* type B (larger systems; Fig. 16 a).

The same can be said concerning the nature of the producer of *Sp. saxonica* as for *Sp. nodosa*. Fragments of *Protocallianassa antiqua* have been found associated with *Sp. saxonica* in the Upper Cenomanian of Saxony (MÜLLER 1970). *Sp. saxonica* is, therefore, interpreted as the dwelling burrow of a suspension-feeding/scavenging callianassid with a slightly different behaviour than the inhabitant of *Sp. nodosa* (perhaps reflecting different environmental conditions).

Ichnospecies *Spongeliomorpha paradoxica* (WOODWARD 1830)

Figs. 16 c, 17 a

For synonymy see FÜRSICH (1973b).

Diagnosis: Cylindrical, irregularly branching burrow system; burrow diameter very variable; horizontal elements dominate, but vertical elements may also be common; burrow walls unlined, with smooth lining, or covered with scratch marks (adapted from FÜRSICH 1973 b).

Description: Irregular branching burrow systems with both vertical and horizontal elements; burrows elliptical, cylindrical or rounded angular in cross-section. The burrow diameter varies considerably, usually between 1 and 7 cm. Side branches have commonly a smaller diameter than the main trunk, and often terminate after a short distance. Small protruberances (representing unfinished tunnels) are present everywhere in the system. The individual burrow systems are joined and thus form extensive networks (Fig. 16 c), which are connected to the surface by short vertical shafts. The burrow walls are smooth.

Preservation: Full relief; the burrow fill (identical with the matrix) underwent early diagenetic lithification similar to the one described by Fürsich (1973 a) in ,*Thalassinoides*' systems. The difference lies in the matrix (silicified medium-grained sandstone) which resulted in the formation of a nodular sandstone. The nodules weather out readily (Fig. 17 a) as the surrounding sediment is often only poorly cemented.

Facies: *Sp. paradoxica* occurs in massive medium-grained silicious sandstones.

Regional and stratigraphic distribution: Spaunton Sandstone (Upper Oxfordian) of Yorkshire.

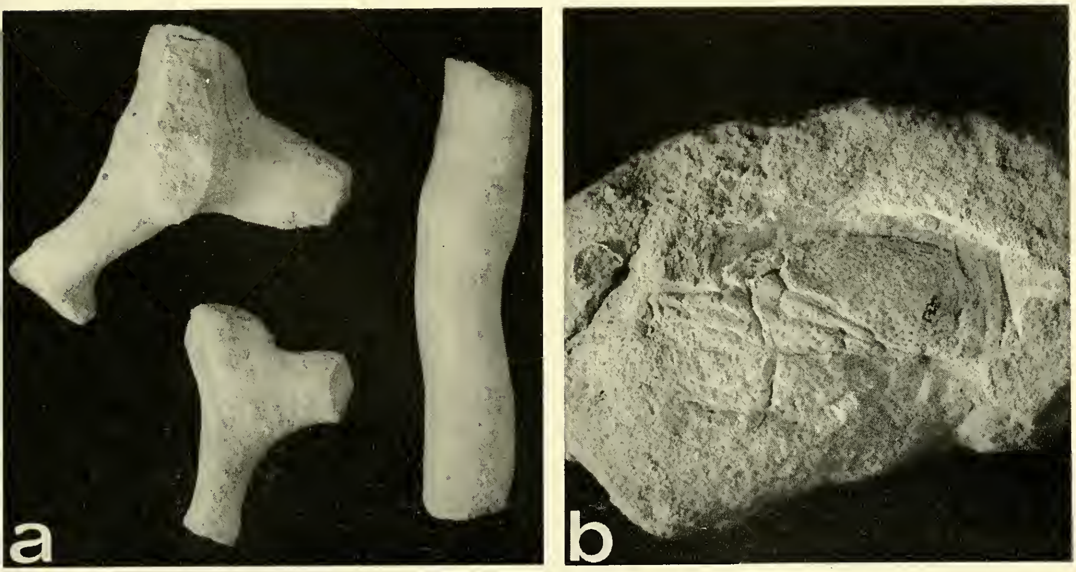

Fig. 17. a: *Spongeliomorpha paradoxica* (Woodward) in nodule preservation. — Spaunton Sandstone, Newbridge Quarry (SE 800860), Yorkshire (x 0.3);
b: *Glyphea rostrata* (Phillips) in *Spongeliomorpha suevica* type B. — ,*Trigonia*' *clavellata* Beds, Bran Point, Dorset (x 0.9).

Discussion and interpretation: *Sp. paradoxica* has been discussed in detail by Kennedy (1967). In chalk it is usually associated with hardgrounds and Kennedy (1967, p. 148) believed this association to be a valid one. The occurrence of *Sp. paradoxica* in the Upper Oxfordian of Yorkshire is not connected with hardgrounds. Moreover, as in the case of the ,*Thalassinoides*' systems from the Littlemore Clay Beds and the Nodular Rubble of the Dorset coast, it is the burrows which became lithified during early diagenesis whilst the matrix is only poorly cemented.

The irregular shape and branching of *Sp. paradoxica* makes it easily distinguishable from other forms of *Spongeliomorpha*. The producer is again most likely a decapod crustacean. Burrows of the Recent *Alpheus*, as figured by SHINN (1968, pl. 109), are very similar to those described here which might have been inhabited by a similar decapod. RASMUSSEN (1971) describes systems of *Sp. paradoxica* from the Maastrichtian-Danian boundary at Stevns Klint, Denmark, which he thinks are the work of the callianassid *Ctenocheles*, the only burrowing crustacean found in the lowermost Danian of Stevns Klint.

In view of the extensive burrow systems an endobenthonic suspension-feeding/scavenging or even deposit-feeding mode of life of the inhabitant seems likely.

Ichnospecies *Spongeliomorpha suevica* (RIETH 1932)

Figs. 17b, 18—24

For synonymy see FÜRSICH (1973 b).

Diagnosis: Mainly horizontal, cylindrical branching burrow systems; branching predominantly dichotomous; burrow walls unlined, with smooth lining, or covered with scratch marks; burrow diameter more or less constant except at branching points or turn-arounds (adapted from FÜRSICH 1973 b).

Description: Regularly, mainly dichotomously branching burrow systems with a circular, oval or, less often, rounded angular cross-section. The burrows are enlarged at the points of bifurcation which are either Y- or T-shaped (Fig. 18). The angle of bifurcation varies from 35 ° to 195 °, with its maximum between 90 ° and 160 ° (Fig. 19). Most burrows are oriented parallel or slightly oblique to the bedding plane; vertical shafts are extremely rare. The burrow walls are usually smooth; only in one case could scratch marks be observed on part of a burrow system (Fig. 20 d).

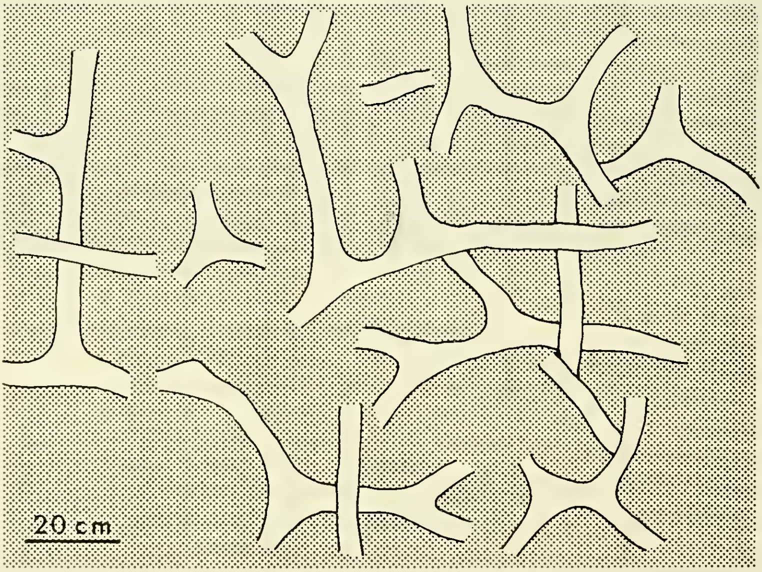

Fig. 18. Branching pattern of *Spongeliomorpha suevica* (RIETH) type B. — Sketched from fallen block, ‚*Trigonia*' *hudlestoni* Bed, Berkshire Oolite Group, of Bowleaze Cove, Dorset.

The burrows occur in two size classes: type A ranges from 0.9 to 2 cm (Fig. 20 a—c), type B from 2 to 5.5 cm; often, both types occur together. Extensive branching leads to formation of huge networks which consist of numerous burrow systems. In other cases, crossing over of burrows is quite common. Due to compaction, burrow systems are often superimposed one upon another (Fig. 21 a).

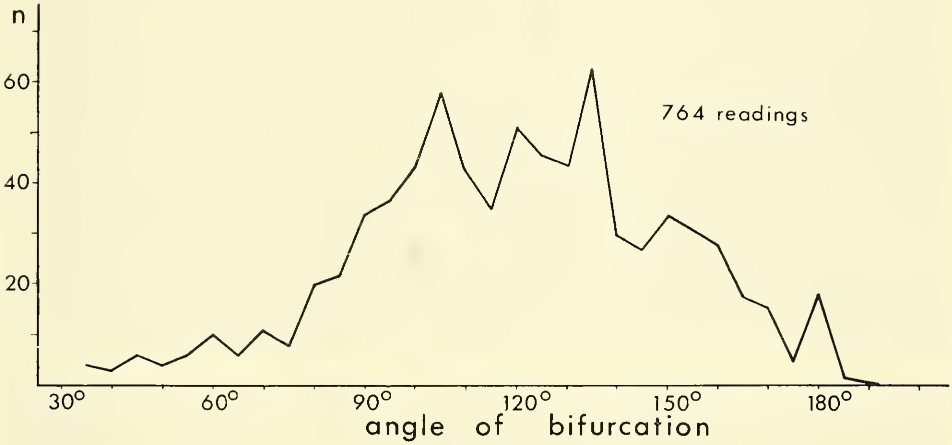

Fig. 19. Angles of bifurcation in *Spongeliomorpha suevica* type B.

In some systems, the burrows widen at certain points to form central chambers from which several tunnels originated (Fig. 22). Occasionally the roof of the burrows is highly irregular whilst the floor is smoothed by layers of lining (Fig. 23 a).

Preservation: Full relief; usually the fill is identical with the matrix (except where diagenetic changes occurred). Most burrows became infilled before compaction took place. Due to compaction, their cross-section is often elliptical except in cases, where lithification of the fill preceeded that of the matrix. The latter process, combined with a high burrow density, can lead to the formation of nodular limestone as in the case of the Nodular Rubble and the Littlemore Clay Beds from the Middle Oxfordian of the Dorset coast (Fürsich 1973 a). Diagenetic changes are also responsible for preservation of the burrows as chert nodules in a spiculitic fine-grained sandstone. Only rarely do primary differences in the fill occur, for instance the clay-filled burrows (diagenetically enriched with siderite) in some intraclastic limestones or coarse sandstones. In many burrows the fill is laminated (Figs. 21 b, 23).

Facies: *Sp. suevica* occurs in a wide range of facies, in intraclastic oolites as well as in fine-grained sandstones or in argillaceous fine-sand. Clay is the only facies type where *Sp. suevica* could not be found in the Corallian.

Regional and stratigraphic distribution: *Sp. suevica* is one of the commonest trace fossils in the Corallian and ranges from Normandy to Yorkshire. The only major section where it is absent are the Middle Oxfordian clays and argillaceous limestones of the Normandy coast.

Associations: Because of its wide distribution, *Sp. suevica* is found associated with most other trace fossils, notably *Cylindrichnus, Teichichnus, Chondrites, Rhizocorallium* etc.

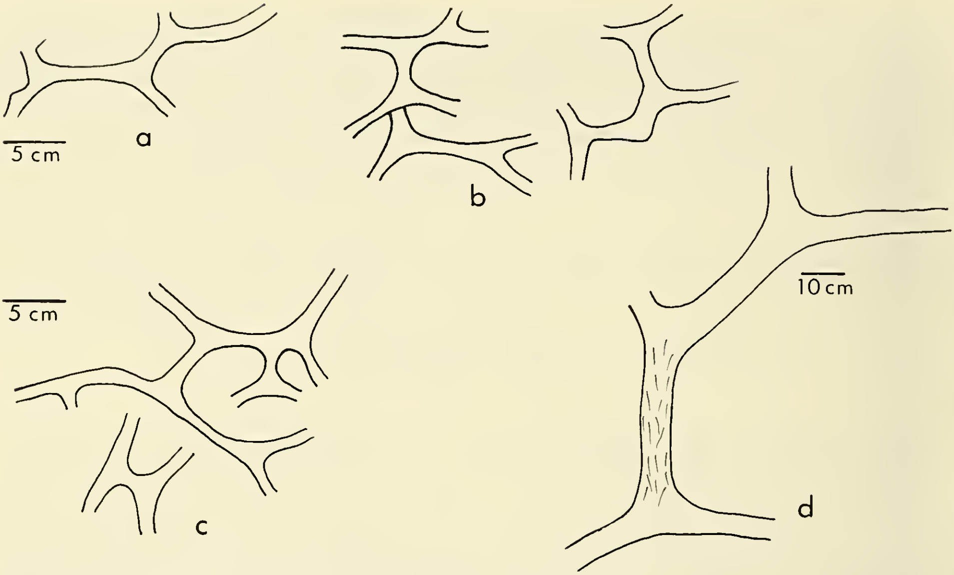

Fig. 20. a—c: branching pattern of *Spongeliomorpha suevica* type A; d: *Spongeliomorpha suevica* type B exhibiting scratch marks. — ,*Trigonia*' *hudlestoni* Bed, Berkshire Oolite Group, Bowleaze Cove, Dorset.

Discussion and interpretation: The branching pattern and burrow outline of most Corallian *Spongeliomorpha* identifies them as *Sp. suevica*. Attempts to subdivide this burrow type have not been successful, except for an informal subdivision on grounds of size. The angle of branching has been measured in numerous networks (Figs. 19, 24): the statistical maximum was found to be the same for all burrow systems.

A part of the burrow fill shows lamination which can, in some cases, be interpreted as floor deposits. These were actively produced by the crustacean in an attempt to cope with unwanted sediment which was loosened from the roof or fell into the burrow (see Shinn 1968, Fürsich 1973 a). Other laminations are the result of a passive infilling after the animal vacated its burrow. Sometimes, both types of infilling can be observed in one burrow (Fig. 23 a). Laminated fills of *Spongeliomorpha* may sometimes be similar to cross-bedding and give rise to misinterpretations (Fig. 21 b).

An irregular roof as opposed to a smooth floor has been recorded from burrows of the Recent *Alpheus floridanus* (Shinn 1968, fig. 4 b). Shinn's interpretation that

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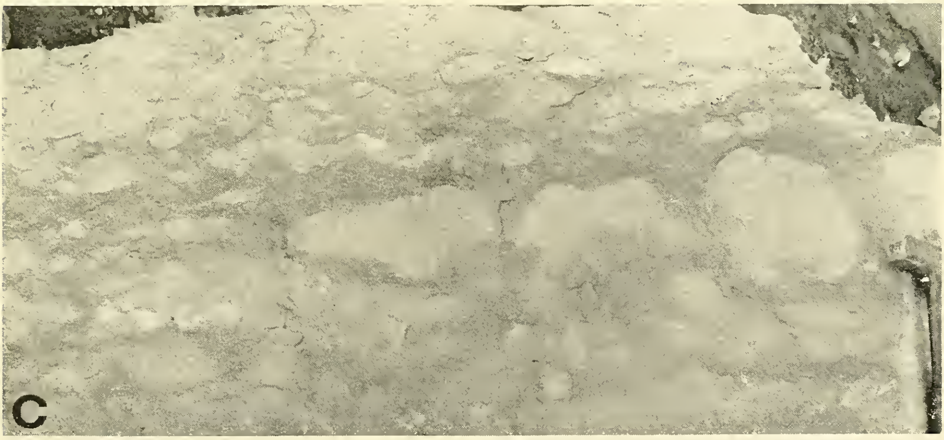
Fig. 21. a: crowded and diagenetically superimposed *Spongeliomorpha suevica* type B systems in intraclastic, oolitic limestone. — Facies ,Coral Rag' de Trouville à *Cidaris florigemma*, coast between Deauville and Hennequeville, Normandy (x 0.03);

b: laminated structures in medium-grained sandstone, representing floor deposits of *Spongeliomorpha suevica* type B. — Fallen block from the ,*Trigonia*' *hudlestoni* Bed, Berkshire Oolite Group, Bowleaze Cove, Dorset;

c: burrow-induced nodular limestone. The large nodules (lower half) indicate that cementation did not stop after lithification of the burrows, but affected the surrounding sediment as well. — Middle Calcareous Grit, Newbridge Quarry, near Pickering, Yorkshire (x 0.08).


a


b


c

both result from movements of the crustacean within its burrow (see above) is also thought to explain the same feature in some *Sp. suevica* burrows from the Corallian.

The absense of vertical shafts in *Sp. suevica* systems has been commented upon by Fürsich (1973 a). It is most likely, that in these burrow systems the entrance shafts were merely inclined, as is the case in the burrow systems of the Recent *Goneplax rhomboides* and *Nephrops norvegicus* (Rice & Champman 1971).

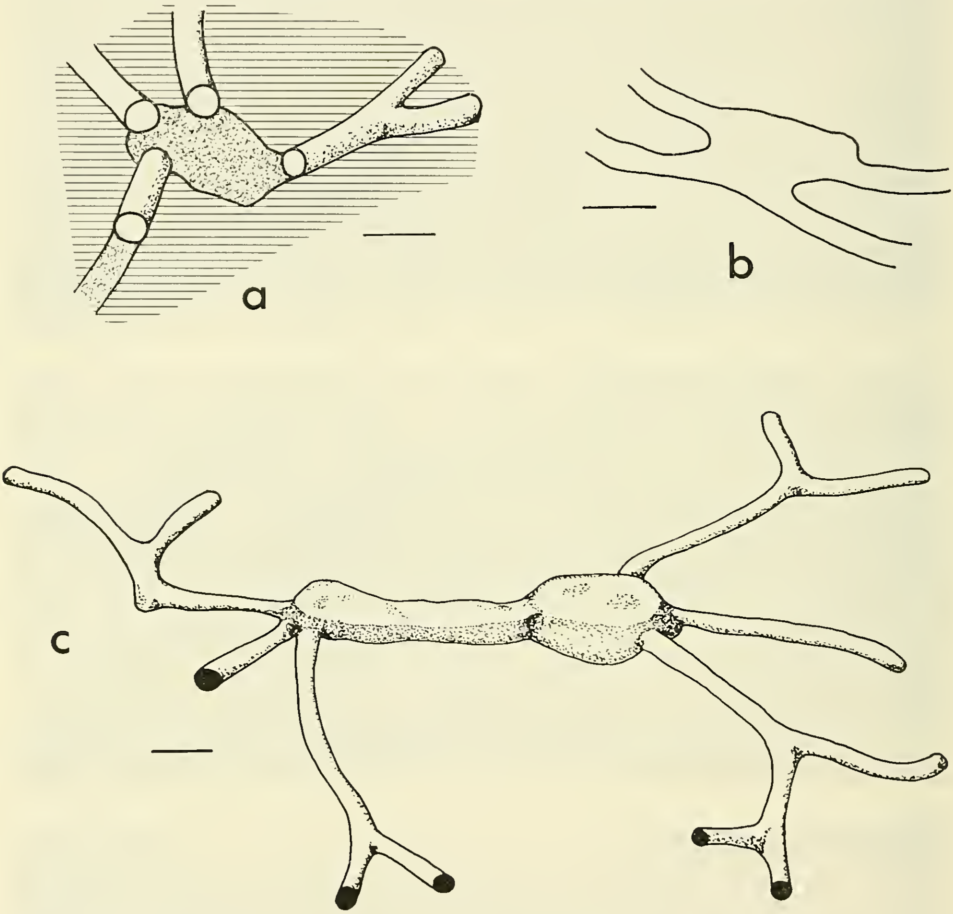


Fig. 22. Central rooms of *Spongeliomorpha suevica* type B. a. c: bedding plane view; b: cross-section; a: the central room has been removed (dark area). — Littlemore Clay Beds, Osmington Oolite Group, Bran Point, Dorset;
b, c: Calcaire de Hennequeville, coast between Deauville and Hennequeville (scale: 10 cm).

Thalassinoides-induced nodular limestone, so far recorded from the Middle Oxfordian of the Dorset and the Normandy coast, is also a common feature at the top of the Middle Calcareous Grit of Yorkshire (exposed e. g. at the base of Newbridge Quarry, Pickering, SE 800860). Whilst numerous nodules are of the diameter of large *Spongeliomorpha* burrows, many others are far larger, thus indicating that the cementation process did not stop after lithification of the infillings but affected the surrounding sediment as well (Fig. 21 c).

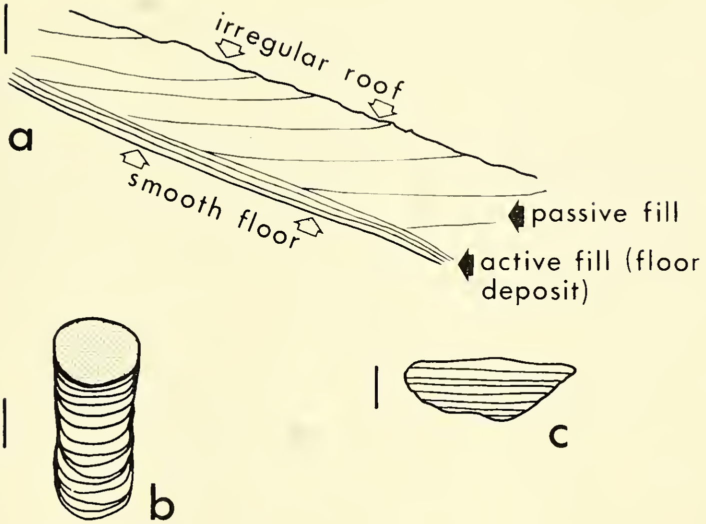


Fig. 23: Floor deposits in *Spongeliomorpha suevica* type B.
a: longitudinal section; b—c: cross-section. — ‚*Trigonia*' *hudlestoni* Bed, Berkshire Oolite Group, Bowleaze Cove, Dorset (scale: 2 cm).

Central rooms from which several tunnels branch off are usually only encountered where whole networks are exposed (Fig. 22). They are comparable to those figured by SHINN (1968 pl. 110), FARROW (1971, fig. 15), and BRAITHWAITE & TALBOT (1972 pl. 3). These Recent ones are produced by species of *Callianassa*. Remains of callianassids have been found in or associated with burrows of the *Sp. suevica*

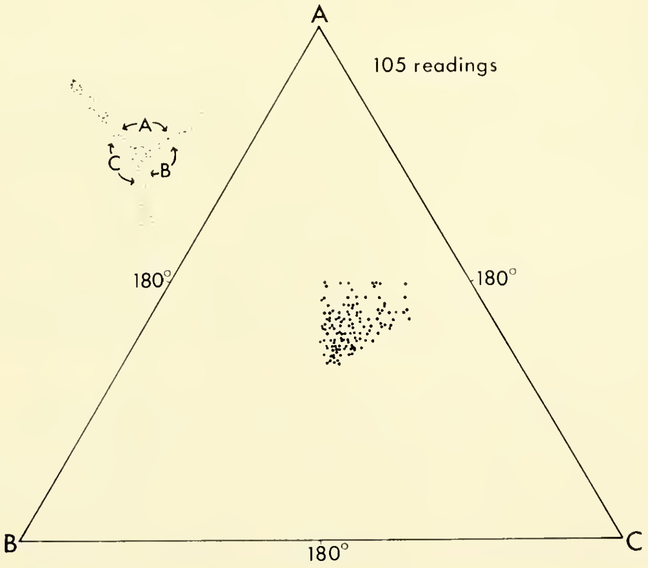


Fig. 24. Angles of bifurcation in *Spongeliomorpha suevica* type B from various horizons in the Corallian.

type by Ehrenberg (1938) in the Miocene of Austria, Mertin (1941) in the Upper Cretaceous of Northern Germany (*Protocallianassa antiqua*), and Glaessner (1947) in the Eocene of Victoria, Australia, (*Callianassa bakeri*).

There are two records of palinuran crustaceans occurring in *Sp. suevica* systems: Sellwood (1971) described *Glyphea udressieri* from the Bathonian of Oxfordshire, and Bromley & Asgaard (1972) found numerous *Glyphea rosenkrantzi* preserved in concretions within the burrow systems from the Lower Jurassic of Jameson Land (Greenland). A third record comes from the ,*Trigonia*' *clavellata* Beds, Upper Oxfordian, at Bran Point, Dorset: at the bottom of a burrow fill, the cephalothorax and one claw of *Glyphea rostrata* (Phillips) (Fig. 17 b) have been found, probably representing an exuvia. This new find confirms the assumption of Sellwood (1971) and Bromley & Asgaard (1972) that *Glyphea* was the producer of these burrows. Whilst in the Cretaceous and Tertiary callianassids were likely to be the producers of at least some *Sp. suevica* systems, their ecological niche was apparently occupied in the Triassic and Jurassic by palinuran crustaceans, namely glypheids. *Glyphea* does not possess any special adaptions for burrowing but neither do the Recent lobster *Nephrops norvegicus* or the crab *Goneplax rhomboides* (Rice & Chapman 1971), both of which construct fairly complex burrow systems. Furthermore, Bromley & Asgaard (1972, fig. 9) demonstrated that *Glyphea* fits its burrow even better than *Nephrops* (though still far less than the highly adapted shrimp *Callianassa*). There is little evidence as to the feeding habits of the *Sp. suevica* producer. The extensive burrow systems as well as the extensive retrusive structures found in some burrows (Fig. 23 b) may indicate that the crustaceans were endobenthonic filter-feeding scavengers, i. e. sifting sand for food within the burrows.

3. Fodinichnia (feeding traces)

Ichnogenus *Chondrites* Sternberg 1833

Type species: *Fucoides targionii* Brongniart 1828, p. 56, pl. 4, fig. 2—6 (designated by Andrews 1955, p. 130).

Diagnosis: Regularly branching tunnel systems consisting of a small number of mastershafts open to the surface which ramify at depth to form a dendritic network (adapted from Häntzschel 1962, p. W187 and Osgood 1970, p. 328).

For synonymy see Osgood 1970, p. 328.

Chondrites sp.

Fig. 25

Chondrites is very common in the Middle and Upper Oxfordian of north-western Europe, but not always easily detectable because of its poor preservation. The latter fact as well as the unsatisfactory taxonomic state of affairs makes it pointless to designate the Corallian specimens to any particular species.

However, on grounds of size two form types can be distinguished: type A, with a tube diameter of 0.1—0.3 cm, which is the common form; and type B, with a tube 0.5—0.7 cm in diameter, which is rare. The tube diameter is constant within one tunnel system. In cross-section, horizontal tubes are frequently elliptical, probably due to compaction (Fig. 25 b). Regular branching (Fig. 25 a) and phobotactic behaviour (Richter 1927) could be observed in the better preserved specimens.

Preservation: Full relief; tubes usually slightly squashed; fill in most cases darker than the surrounding sediment and highly argillaceous.

Facies: *Chondrites* occurs in a wide range of facies in the Corallian: in calcareous clays and lutites, silts and medium-grained sandstones, and even in calcarenites, though the maximum of its distribution clearly occurs in argillaceous and silty sediments.

Regional and stratigraphic distribution: Rarely found in Yorkshire, *Chondrites* is quite common in the Middle and Upper Oxfordian of Dorset and reaches its maximum in the argillaceous Middle Oxfordian of the Normandy coast where it is the dominant trace fossil.

Associations (in order of decreasing abundance): *Planolites, Teichichnus,* pyritic tubes, *Sp. suevica* type B, *Rhizocorallium irregulare,* and *Spongeliomorpha suevica* type A.

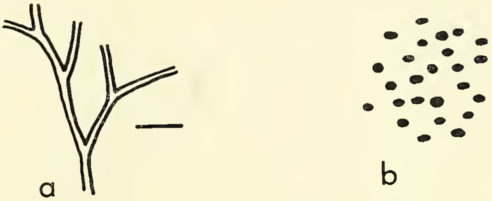


Fig. 25. *Chondrites* sp.
a: bedding plane view; b: cross-section. — ‚*Trigonia*' *clavellata* Beds, Black Head, Dorset (scale: 1 cm).

Discussion and interpretation: SIMPSON (1957) interpreted *Chondrites* as a system of lined tunnels excavated in the sediment by a deposit-feeding sipunculoid worm. The animal exploited particular organic-rich layers from a central point on the surface of the sediment by extending its proboscis and perhaps part of its body into the substrate. OSGOOD (1970, p. 335) could show by a mineralogical analysis of the infilling and the surrounding sediment, that *Chondrites* is not a stuffed burrow as suggested by TAUBER (1949), but that the filling is derived from the overlying sediment.

The filling of the extensive burrow systems with sediment seems at first hand a major problem. However, OSGOOD (1970, p. 338) showed in experiments that mechanical filling of the tunnels up to 87 % with clay is possible, provided slight currents moved across the burrow openings and the whole network was not a closed system. Alternatively, FERGUSON (1965) suggested that the filling of the individual branches of *Chondrites* took place when the animal withdrew its proboscis from part of the tunnel system thus creating a vacuum which sucked in sediment from the surface opening. Phobotaxis — according to OSGOOD (1970) not present in all *Chondrites* — has been observed in the Corallian specimens.

Ichnogenus *Cylindrichnus* HOWARD 1966

Type species: *Cylindrichnus concentricus* HOWARD 1966, p. 45, fig. 10.

Diagnosis: Simple cylindrical tubes with central or excentric core, surrounded by concentric layers.

Ichnospecies *Cylindrichnus concentricus* HOWARD 1966

Figs. 26, 27

1962 *Cylindrichnus concentricus.* — TOOTS, p. 64. — [nom. nud.]
* 1966 *Cylindrichnus concentricus* HOWARD, p. 45, fig. 10.

1970 *Asterosoma* form „*Cylindrichnus concentricus*"; FREY, p. 12, fig. 3 a; pl. 2, fig. 5.
1970 *Asterosoma form Cylindrichnus.* — FREY & HOWARD, p. 160, 162, figs. 2 a, 7 b.
non 1973 *Anemonichnus concentricus* (HOWARD). — CHAMBERLAIN & CLARK p. 677, fig. 2; pl. 3, fig. 8.

Diagnosis: Simple cylindrical tubes with central or excentric core, surrounded by concentric layers; without preferred orientation.

Description: Simple cylindrical tubes with an orientation ranging from horizontal to vertical; their core is 0.1—0.3 cm in diameter, surrounded by concentric layers up to 0.7 cm thick. The diameter of the whole tube ranges from 0.4—1.5 cm with a maximum frequency at 1 cm. The concentric structure consists of alternations of light and dark (e. g. argillaceous) layers. Commonly, the core is not in the centre but in the upper part of the tube (Fig. 26). Sometimes the tubes exhibit retrusive structures (Fig. 26).

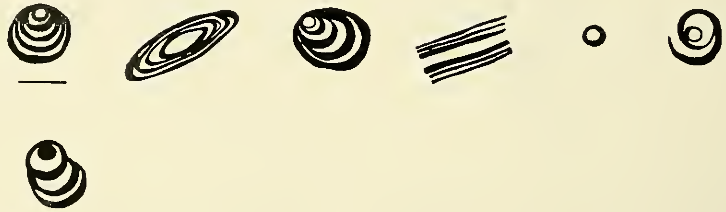


Fig. 26. Sections through *Cylindrichnus concentricus* HOWARD, showing central or excentric core and concentric layering, sometimes retrusive. — Nothe Grits, Lower Calcareous Grit, Bowleaze Cove, Dorset (scale: 1 cm).

Preservation: Full relief; fill of the core either identical with the matrix or consisting of dark clay.

Facies: C. *concentricus* is found in a wide range of facies, in oolites as well as in carbonaceous fine-sand or medium-grained sandstones. However, its main distribution is in fine-sands, argillaceous fine-sands and in spiculitic, oolitic or intraclastic limestones. Sometimes, it is associated with flat lamination or large-scale trough cross-bedding.

Regional and stratigraphic distribution: Common from Normandy to Yorkshire in the Middle and Upper Oxfordian.

Associations (in order of decreasing abundance): *Spongeliomorpha suevica, Teichichnus, Chondrites, Planolites, Rhizocorallium* sp., and *Muensteria.*

Discussion and interpretation: C. *concentricus* is a burrow with a relatively small diameter compared to the thick wall which surrounds it. That the concentric layers represent alternating coatings of pellets and sediment could be demonstrated in several cases. For example in some burrows the pelletal structure is still well preserved within the dark concentric layers, in others, evidence comes from the concentric arrangement of carbonaceous matter. Commonly, the burrow is not in the centre of the concentrically arranged layers but at their top, thus indicating a shift in a vertical (retrusive) direction.

C. *concentricus* represents most likely the burrow of a deposit-feeder. The inhabitant removed its faeces not by depositing it outside its burrow as do many other burrow-dwelling organisms (e. g. *Arenicola*, many crustaceans) but by pressing it into the walls of the burrows. In this way, together with undigested sediment, the alternating layers of the thick burrow wall were formed. As much of this material will be pressed onto the burrow floor the burrows frequently undergo a shift in a vertical direction, thus creating the retrusive features.

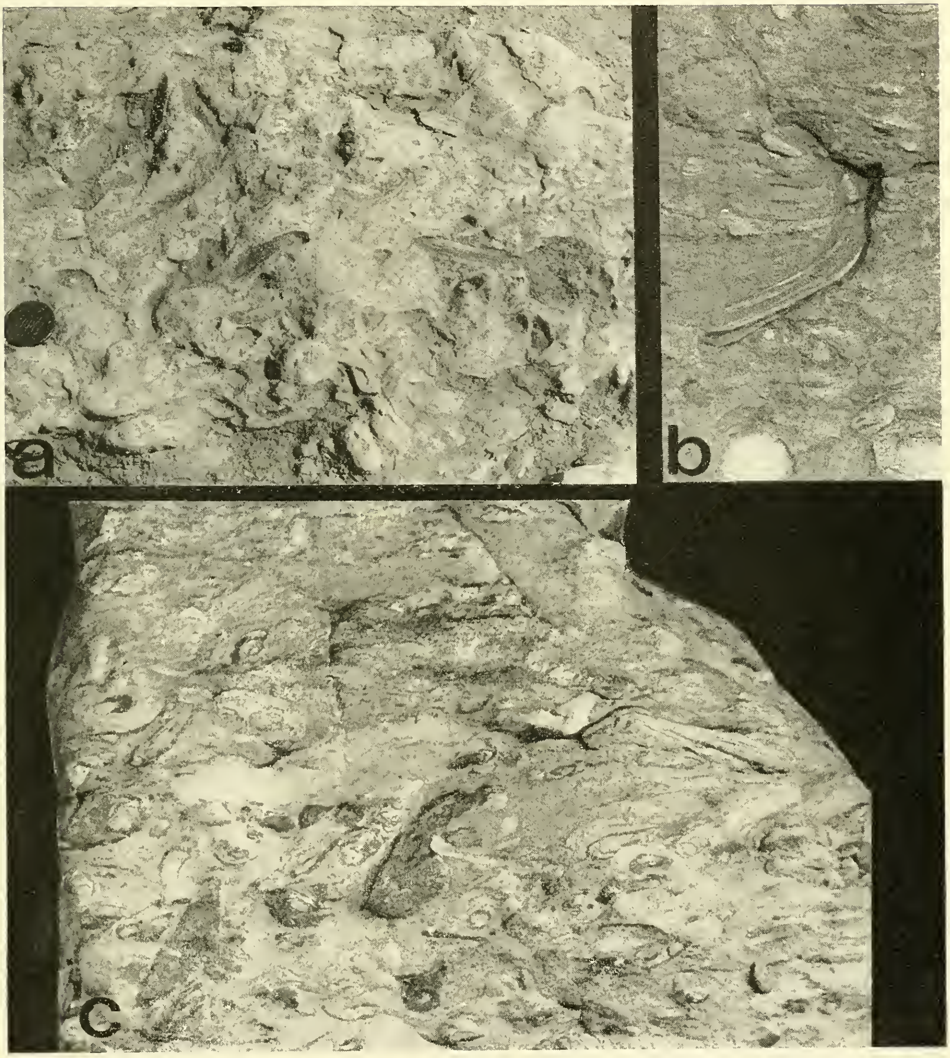


Fig. 27. a: *Cylindrichnus concentricus* HOWARD in sandy micritic limestone. — Basal ‚*Trigonia*' *clavellata* Beds, Black Head, Dorset (x 0.4);
b: *Teichichnus rectus* SEILACHER in fine-sandy marl. — Littlemore Clay Beds, Osmington Oolite Group, Bran Point, Dorset (x 0.4);
c: bioturbation in fine-sand, caused by *Teichichnus rectus* and *Cylindrichnus concentricus*. — Osmington Oolite Group, east of Sandsfoot Castle, Dorset (x 0.25).

HOWARD (in FREY 1970) records that *C. concentricus* in the Upper Cretaceous of Utah and Wyoming is fully gradational with *Asterosoma* and helicoid funnels (see also p. 38). In the Corallian, no such relationship has been observed, but *C. concentricus* forms alsways very distinctive burrows. Thus, there is no need to declare *C. concentricus* to be only one part of a more complex burrow system in

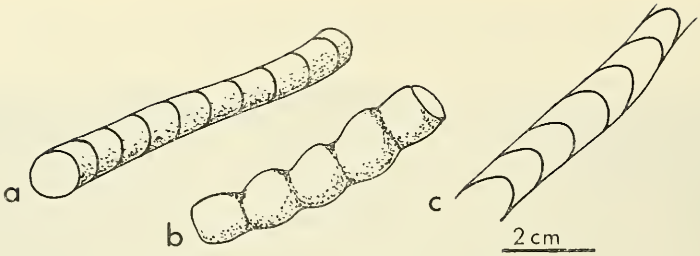


Fig. 28. *Muensteria* sp.
a: oblique view; b: lateral view of specimen with distinct annular constrictions; c: longitudinal section.
a—b: Bencliff Grit, Berkshire Oolite Group, Osmington Mills, Dorset; c: Osmington Oolite Group, Bran Point, Dorset.

the Corallian. *Anemonichnus concentricus* represents a different burrow type, having a far larger diameter and occurring usually in a vertical position.

Judging from its morphology, *C. concentricus* was produced by a worm-like animal, probably a deposit-feeder.

Ichnogenus *Muensteria* STERNBERG 1833

Type species: *Muensteria vermicularis* STERNBERG 1833, p. 32; pl. 1, fig. 3 (designated by ANDREWS 1955, p. 191).

Diagnosis: Cylindrical tubes with cup-shaped segments.

Remarks: Trace fossils with back-fill structures are either called *Planolites montanus* RICHTER 1937, *Taenidium* HEER 1877, *Keckia* GLOCKER 1843 or *Muensteria* STERNBERG 1833. There is no basic difference between these ichnogenera and the former are, therefore, regarded as synonyms to *Muensteria* which has priority.

Muensteria sp.

Figs. 28, 29 a

Description: The diameter of the usually horizontal or inclined simple tubes varies between 0.6 and 1.2 cm. A transverse section reveals an internal structure in the form of concavo-convex segments. The surface of the burrows hints at this segmentation either by concentric rings or annular constrictions (Fig. 28). The width of a segment varies between one and several millimeters.

Preservation: Full relief or positive hyporelief; fill more or less identical with the matrix.

Facies: *Muensteria* occurs in fine- to medium-grained sandstones and in fine-sandy marl.

Regional and stratigraphic distribution: Found in the Bencliff Grit and basal Osmington Oolite Group of the Dorset coast, and in the Middle Oxfordian of Yorkshire (Filey Brigg section).

Associations (in order of decreasing abundance): *Diplocraterion habichi, Cylindrichnus, Gyrochorte, Spongeliomorpha saxonica, Diplocraterion parallelum, Skolithos, Scolicia,* and *Asterosoma.*

Discussion and interpretation: In a detailed analysis of *Planolites montanus* and *Taenidium*, RICHTER (1937; and in WILCKENS 1947) interpreted the cup-shaped segments as back-fill structures made by a deposit-feeder. The probably worm-like animal was eating its way through the sediment and filled the thus created tunnel immediately in a backward direction by the periodic release of waste. These segments of waste were then pressed into each other by the animal, resulting in their cup-shaped arrangement.

Fig. 29. a: *Muensteria* sp. in fine-grained sandstone. — Top of the Bencliff Grit, Berkshire Oolite Group, Osmington Mills, Dorset (x 0.4);
b: *Rhizocorallium irregulare* MAYER in heavily churned argillaceous sandstone. — Nothe Grits, Lower Calcareous Grit, Bowleaze Cove, Dorset (x 0.3).

RICHTER's interpretation is well in agreement with the observations made on the Corallian specimens and *Muensteria* is therefore regarded as the fodinichnium of a deposit-feeder (probably a worm).

Ichnogenus *Planolites* NICHOLSON 1873

Type species: *Planolites vulgaris* NICHOLSON & HINDE 1875, p. 139 [teste HOWELL 1943, p. 17].

Diagnosis: Unbranching, slightly sinuous tubes.

Planolites sp.

Description: Unbranching slightly sinuous tubes which occupy a horizontal, oblique or vertical position in the rock. Tube diameter ranges from 0.2 to 2.8 cm, though in the majority of cases it varies between 0.8 and 1.2 cm. The tube walls are smooth, no ornamentation in the form of annulations or striae could be found. A clay lining, up to one millimeter thick is commonly present. When found in argillaceous limestones or marls, the tubes are surrounded with a yellow-brown oxidation zone with a sharp inner and a diffuse outer boundary.

Preservation: Full relief; fill is either identical with the matrix, or alternatively, there are differences in grain size and colour; the fill tends to be finer-grained, better sorted and darker than the matrix. Sideritic clay in the fill is especially common where the matrix consists of ooliths or intraclastic limestone. Sometimes the burrows are elliptical due to compaction.

Facies: *Planolites* sp. is not a facies indicator; it occurs in all types of sediment, ranging from oolites to argillaceous silts.

Regional and stratigraphic distribution: Ranging from Normandy to Yorkshire, *Planolites* sp. is widespread in the Middle Oxfordian of Normandy, but is somewhat commoner in the Upper Oxfordian.

Associations: *Planolites* sp. occurs together with all other elements of the Corallian trace fossil fauna, without any obvious preferences.

Discussion and interpretation: The uncharacteristic nature of the Corallian *Planolites* does not justify an ichnospecific designation. However, two types of burrows can be distinguished: Type A is without lining but the fill is reworked in the way described above, whereas type B possesses a lining or oxidation zone and is filled with material identical with the matrix.

There can be no doubt that *Planolites* represent the burrows of deposit-feeders. Already NICHOLSON (1873, p. 289) interpreted *Planolites* as tunnels excavated by worms in their search for food. Similar interpretations were given by RICHTER (1937) and REINECK (1955) who additionally observed back-fill structures. Type A may have been made by an organism eating its way through the sediment, filling the thus produced tunnel instantly with its waste. The lining and oxidation zone in type B indicate that this burrow type remained open for some time. It is suggested here that the animal, though deposit-feeding, did not refill the burrow with its waste, but removed it from the burrow, which thus remained open for some time (JESSEN 1949).

The irregular and usually oblique orientation of the burrows seems to indicate that their producers lacked geotaxis.

Pyritic tubes

Pyritic tubes are commonly found in argillaceous limestones and marls of the Middle Oxfordian of the Vaches Noires sections, west of Villers sur Mer, Normandy. The diameter of the usually simple burrows ranges from 0.1—0.5 cm. The burrows do not show any preferred orientation and are found in a vertical, oblique and horizontal position in the sediment. In some cases the pyritic fill weathered into Fe-hydroxid. Other trace fossils found with them are *Planolites* and *Chondrites*.

Pyritic tubes can be interpreted as the burrows of deposit-feeders (annelids, nuculid bivalves etc). A fairly high concentration of organic matter in the burrow fill is thought to be responsible for the formation, during early diagenetic stages, of pyrite in this microenvironment.

Ichnogenus *Rhizocorallium* ZENKER 1836

See also p. 18.

Ichnospecies *Rhizocorallium irregulare* MAYER 1954

Figs. 14 b, 29 b, 30

Diagnosis: Long sinuous bifurcating or planispiral U-shaped spreiten-burrows; in the main horizontal (adapted from FÜRSICH 1974).

Description: The tube diameter varies between 1.0 and 1.5 cm, the width of the spreite from 2 to 4 cm. The U-tube is always distinctly set off the spreite. The burrows are strictly horizontal and can reach up to 110 cm in length.

The burrow outline varies from sinuous, curved, planispiral to bifurcate (Fig. 30). The limbs ran closely parallel, except where the burrows bend or bifurcate. Most U-tubes are smooth; only rarely have elongate ridges — arranged at an acute angle to the long axis — been observed (Fig. 14 b). Orientation of a *Rhizocorallium* assemblage is rare, as is crossing over.

Preservation: Full relief; fill either identical with the matrix or consisting of sideritic clay.

Facies: Common in fine- or medium-grained sandstones and in oolitic limestones. Sometimes found on top of beds which display large-scale trough cross-bedding and symmetric or asymmetric ripples.

Regional and stratigraphic distribution: Middle and Upper Oxfordian, from Yorkshire to Normandy with a maximum in Dorset; abundant at the base and top of the Berkshire Oolite Group of the Dorset coast (e. g. the ‚*Trigonia*' *hudlestoni* Bed).

Associations (in order of decreasing abundance): *Sp. suevica* type A, *Sp. suevica* type B, *Chondrites*, *Cylindrichnus*, *Planolites*, and *Teichichnus*.

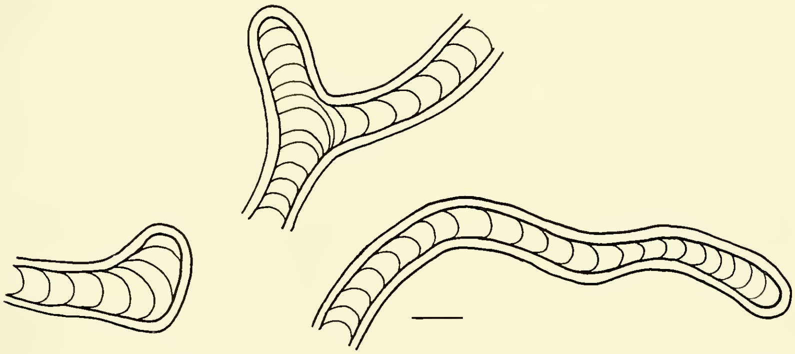


Fig. 30. *Rhizocorallium irregulare* MAYER. — Osmington Oolite Group, east of Osmington Mills, Dorset (scale: 5 cm).

Discussion and interpretation: *Rh. irregulare* represent burrows excavated by deposit-feeders (FÜRSICH 1974). The variable burrow outline of most of the Corallian specimens as well as their horizontal nature justify their assignation to *Rh. irregulare*. The animals searched the sediment for food using the spreiten-technique for efficient exploitation (SEILACHER 1967). The association of these forms with ripples and large-scale cross-bedding seems, at a first glance, to be somewhat anomalous. But *Rh. irregulare* occurs always at the top of these beds, probably burrowing downwards from above. Thus, the association is a spatial one, but not contemporaneous.

Star-shaped trace fossils

Remarks: The taxonomy of star-shaped trace fossils is, despite attempts made by GRUBIĆ (1970) and HÄNTZSCHEL (1970), still a very unsatisfactory state of affairs. Besides the large number of ichnogenera and ichnospecies (see VIALOV 1964 a, b, 1968, VIALOV et al. 1964), there is a wealth of described and / or figured star-shaped traces which have, however, not been named. It is beyond the scope of this paper to sort out the taxonomy of these traces; the Corallian specimens have, therefore, been included into already existing taxa without inquiring too much into the validity of the latter.

Ichnogenus *Asterosoma* v. OTTO 1854

Type species: *Asterosoma radiciforme* v. OTTO 1854, p. 15; pl. 2, fig. 4; pl. 3, fig. 1—2.

Diagnosis: Star-shaped positive hyporeliefs with bulbous rays which taper towards the ends; centre elevated (modified from HÄNTZSCHEL 1962, p. W184).

Remarks: The ichnogenus *Asterosoma* has been used to cover a number of fairly different trace fossils of various origin (e. g. ALTEVOGT 1968, FREY 1970, FREY & HOWARD 1970, CHAMBERLAIN 1971). For example, FREY (1970) and FREY & HOWARD (1970) use *Asterosoma* to describe concentric tubes and helicoid funnels. HOWARD (in FREY 1970, p. 11) maintains that both forms are fully gradational with *Asterosoma*. However, no evidence of this relationship has been published.

Asterosoma sp.

Fig. 31 b

Description: The Corallian specimen consists of elliptical club-shaped tubes originating from a central point. The tubes narrow towards the centre (which is not preserved), have a bulbous middle region, and a rounded distal termination. The four club-shaped tubes are arranged in a semi-circle; their internal structure consists of concentric laminae, often combined with retrusive structures. The radial tubes range from 5—5.5 cm in length and from 1.5—2.2 cm in diameter. Their external surface is smooth except for a few constrictions (a manifestation of the retrusive nature of some of the tubes).

Preservation: Positive hyporelief.

Facies: Fine-grained silty sandstone.

Regional and stratigraphic distribution: At the top of the Bencliff Grit (Middle Oxfordian) east of Osmington Mills (Dorset).

Associations: *Diplocraterion habichi, D. parallelum, Muensteria, Gyrochorte, Spongeliomorpha suevica* and *Sp. saxonica*.

Discussion and interpretation: The specimen from the Dorset coast is identical with *Asterosoma radiciforme* as described by CHAMBERLAIN (1971, p. 233, text-figs. 8H-I). CHAMBERLAIN interpreted his specimens as the feeding burrows of a worm exploiting the sediment in a radial direction starting from a central tube. In the Corallian specimen, only part of the burrow system is preserved and the existence of a central tube could not be established. It seems, however, safe to interpret *Asterosoma* sp. in a similar manner to CHAMBERLAIN's specimens as the fodinichnium of a deposit-feeder.

Ichnogenus *Gyrophyllites* GLOCKER 1841

Type species: *Gyrophyllites kwassizensis* GLOCKER 1841, p. 322, fig. on p. 322.

Diagnosis: Vertical shaft from which rosettes of short, simple (feeding) tunnels radiate at different levels, as in a mine (adapted from HÄNTZSCHEL 1962, p. W200).

Gyrophyllites sp.

Figs. 31 a, c, 32

Description: Rosette-like trace fossils, consisting of 5—16 flat, petalshaped radiating grooves narrowing towards the centre. In the centre, a plug of 0.4 to 0.6 cm in diameter is visible. The diameter of the whole structure varies between 3 and 8 cm. The radiating grooves are arranged fairly regulary and are separated from each other by a pronounced rim.

Preservation: Negative epirelief.

Fig. 31. a, c: *Gyrophyllites* sp. in fine-grained sandstone. — Bencliff Grit, Berkshire Oolite Group, Bowleaze Cove, Dorset (a: x 0.5 cm; c: x 0.35);
b: *Asterosoma* sp. in fine-grained sandstone. — Top of the Bencliff Grit, Berkshire Oolite Group, Osmington Mills, Dorset (x 0.5).

Facies: Fine-grained sandstone; in one case found associated with oscillation ripples.

Regional and stratigraphic distribution: *Gyrophyllites* occurs in the Bencliff Grit (Middle Oxfordian) of Bowleaze Cove (Dorset).

Associations: *Diplocraterion habichi, D. parallelum, Muensteria, Gyrochorte,* and *Spongeliomorpha suevica.*

Discussion and interpretation: HÄNTZSCHEL (1970, pl. 2) figured star-like trace fossils from the Lower Lias of Saxony which are of more or less the same shape as the Corallian forms.

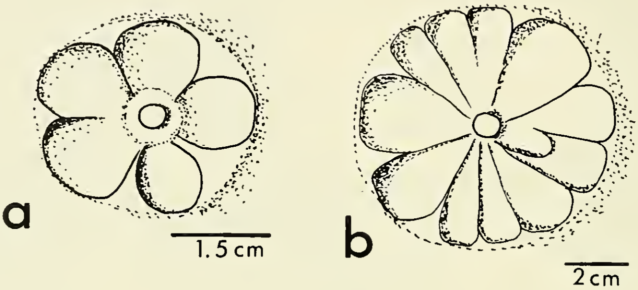


Fig. 32. *Gyrophyllites* sp.
Bencliff Grit, Berkshire Oolite Group, Bowleaze Cove, Dorset.

Similar trace fossils have, till recently, been described as fossil medusae as in the case of *Palaeosemaeostoma* (e. g. HARRINGTON & MOORE 1956). Their interpretation as trace fossils is, however, far more logical. The central plug is easier to explain as central shaft than as the pedicle of a medusa. This shaft was inhabited by an organism which was also responsible for the rosette pattern.

The Corallian specimens are endogenic traces. The sharp well defined grooves and the raised circular, sometimes even overhanging rim speaks against an origin at the depositional interface. It is very likely, that the rosettes form the only preserved part of a three-dimensional feeding system and have, therefore, been included into *Gyrophyllites* GLOCKER 1841.

Ichnogenus *Teichichnus* SEILACHER 1955

Type species: *Teichichnus rectus* SEILACHER 1955, p. 378; pl. 24, fig. 1.

Diagnosis: Long, wall-like burrows formed by vertical displacement of horizontal or oblique tubes (adapted from SEILACHER 1955, p. 378 and HÄNTZSCHEL 1962 p. W218).

Ichnospecies *Teichichnus rectus* SEILACHER 1955

Figs. 27 b, 33

Diagnosis: Simple, straight or sinuous Teichichnus.

Description: The tube diameter of the Corallian specimens ranges from 0.3 to 1.0 cm and is most commonly about 0.5 cm. The final tube is preserved in only a few cases. Unusually only the retrusive structure is seen (Fig. 33 a, b). The latter can reach a depth of 5 cm and a maximum length of 12 cm. The retrusive part is straight or somewhat sinuous and never shows any signs of branching. Lateral displacement in the vertical plane can be observed quite frequently (Fig. 33 b, d). *T. rectus* is commonly found lying at an angle (0°—60°) to the horizontal in the sediment. Darker, highly argillaceous material marks the individual laminae of the retrusive structure thereby making the internal structure more easily visible. The diameter of the final burrow on top of the retrusive part is often considerably smaller than the diameter of the basal part.

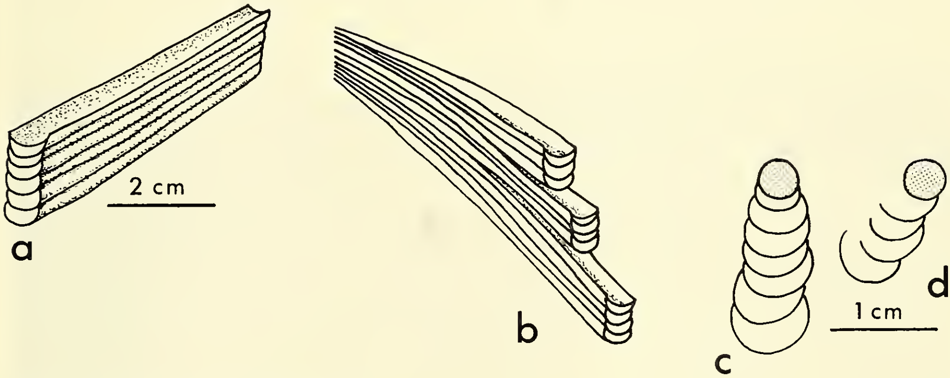


Fig. 33. Teichichnus rectus SEILACHER
a—b: oblique view; c—d: cross section. — Basal ,*Trigonia*' *clavellata* Beds, Shortlake, Dorset.

Preservation: Full relief; fill usually identical with the matrix, but better cemented than the latter.

Facies: *T. rectus* is common in silts, fine-sands, marls and fine-grained limestones with a varying amount of intraclasts, bioclasts and ooliths; rare in medium-grained sandstones.

Regional and stratigraphic distribution: Abundant in the Osmington Oolite Group and ,*Trigonia*' *clavellata* Beds of the Dorset area; rare in Yorkshire and Normandy.

Associations (in order of decreasing abundance): *Spongeliomorpha suevica* type B, *Cylindrichnus, Chondrites, Planolites, Sp. suevica* type A, and *Diplocraterion parallelum.*

Discussion and interpretation: SEILACHER (1955, p. 122) interpreted *Teichichnus* as the result of the upward shift of a more or less horizontal burrow which might be U-shaped. *Chisholm* (1970) described *Teichichnus,* some of them U-shaped, from the Carboniferous of Scotland and interpreted them as „dwelling (or feeding) burrows". MARTINSSON (1965) discussed ,Teichichnia' up to 135 cm in length from the Middle Cambrian of Öland and thought that ellipsocephalids or possibly solenopleurid trilobites might have been responsible for them.

The extensive reworking of sediment as shown by the retrusive part of the burrow justifies the interpretation of *Teichichnus* as a feeding burrow (see also HÄNTZSCHEL 1962, 1965) and of its inhabitant as a deposit-feeder. No morphological patterns as recorded by MARTINSSON (1965) from the Middle Cambrian have been found in the Corallian specimens: to say more about the nature of their producer is, consequently, scarcely possible. SEILACHER (1957, p. 203; pl. 23) figures structures comparable to *Teichichnus* made by the Recent *Nereis diversicolor* [though in this case the structure is a result of ‚Räumauskleidung' and not of ‚Freßumsatz' (Reineck 1958)].

The relationship of *Teichichnus* to other trace fossils: Chisholm (1970, p. 49) found forms intermediate between *Teichichnus* and *Rhizocorallium* and suggested that these two ichnogenera and *Diplocraterion* are closely related to each other. However, this ‚relationship' is purely a morphological one and need not indicate similar behaviour, or a related producer. Therefore the term ‚teichichnid' for sections of up- or downwards moving burrows should be avoided and replaced by the purely descriptive terms ‚retrusive' and ‚protrusive', respectively. Table 2 illustrates the different behaviour expressed by, and the environmental factors responsible for the construction of a retrusive and protrusive tube.

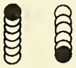
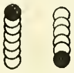
structure	trace fossil	feeding group	interpretation
	retrusive and protrusive Teichichnus	deposit-feeder	systematic explcitation of sediment for food
	retrusive Rhizocorallium	suspension-feeder	response to sedimentation
	retrusive and protrusive Diplocraterion	suspension-feeder	response to sedimentation or erosion
	retrusive Arenicolites	suspension-feeder	'einseitige Räumauskleidung' (floor deposits)
	retrusive Spongeliomorpha	deposit-feeder/ suspension-feeder/predator/ scavenger	'einseitige Räumauskleidung' (floor deposits)

Table 2. Similar structures in different trace fossils and their interpretation.

4. Repichnia (crawling traces)

Ichnogenus *Gyrochorte* Heer 1865

Type species: *Gyrochorte comosa* Heer 1865, p. 142; pl. 9, fig. 12 (designated by Häntzschel 1962, p. W 196).

Diagnosis: Ridges on bedding planes with biserially arranged, obliquely aligned transverse pads, both series separated by median furrow (adapted from Häntzschel 1962, p. W 196).

Ichnospecies *Gyrochorte comosa* Heer 1865

Fig. 34

Diagnosis: Ridges on bedding planes with biserially arranged obliquely aligned transverse pads, both series separated by median furrow.

Description: Long winding ridges on the upper surface of thick beds of sandstone, width of ridges 0.3—0.7 cm, maximum length observed 40 cm. The height of the relief is 0.1—0.25 cm. The angle between pads and median furrow varies from 45 ° to 55 °. The ridges may end abruptly. Crossing over occurs frequently, whereby the earlier ridge is not destroyed.

Preservation: Positive epirelief.

Facies: G. *comosa* occurs in highly carbonaceous fine-grained sandstone only; sometimes it is associated with asymmetric ripples or oscillation ripples.

Regional and stratigraphic distribution: Bowleaze Cove and coast east of Osmington Mills, Dorset (Berkshire Oolite Group).

Associations (in order of decreasing abundance): *Muensteria, Diplocraterion habichi, D. parallelum, Scolicia, Gyrophyllites* and *Skolithos.*

Fig. 34. *Gyrochorte comosa* HEER in fine-grained sandstone. — Fallen block from the Bencliff Grit, Berkshire Oolite Group, Bowleaze Cove, Dorset (x 0.3).

Discussion and interpretation: Most of the specimens have been found on fallen blocks at beach level and are consequently worn. As a result, the morphological features are not very distinct. Additionally, a relatively coarse overlying sediment (e. g. silt rather than clay) may have been responsible for inferior preservation in the first place. No grooves on undersurfaces — equivalent to the ridges on the upper surfaces — were observed, due to the fact that G. *comosa* occurs in thick-bedded sandstone units.

After early interpretations, such as impressions of ophiurids (QUENSTEDT 1858) or egg strings of molluscs (HEER 1865), *Gyrochorte* was later thought to represent tunnel structures, made by amphipods (FUCHS 1895, ABEL 1935). WEISS (1940, 1941) and SEILACHER (1955) however, interpreted *Gyrochorte* as produced by a polychaete or worm-like animal moving obliquely through the sediment. HALLAM (1970) discussed the origin of *Gyrochorte* at some length and concluded that the previous interpretation i. e. the ridges as the product of tunneling amphipods seems to be more likely than WEISS' model. Recently, HEINBERG (1973) was able to show in a detailed study, based on excellently preserved material from East Greenland, that WEISS' interpretation was correct and that *Gyrochorte* was in fact produced by an elongate organism moving obliquely through the sediment in search of food.

Ichnogenus *Scolicia* DE QUATREFAGES 1849

Type species: *Scolicia prisca* DE Quatrefages 1849, p. 265.

Diagnosis: Highly variable endogenic trails, usually of a flattened ribbonlike shape with transverse pads of sediment. Longitudinal furrows in varied arrangement may occur (modified from HÄNTZSCHEL 1962 p. W215).

For synonymy see SEILACHER 1955, p. 373.

Scolicia sp.

Figs. 35, 36

Description: The trails are straight or slightly curved, and sometimes taper towards both ends (Fig. 35 b); maximum length observed is 25 cm. The width of the trail varies between 1 and 4 cm. The median furrow is of varying diameter, usually narrow. The biserially arranged pads are often very distinct and symmetri-

Fig. 35. *Scolicia* sp. in fine-grained sandstone. — Upper surfaces of fallen blocks from the Bencliff Grit, Berkshire Oolite Group, Bowleaze Cove, Dorset (a: x 0.3; b: x 0.4; c: x 0.5).

cal, and opposing pads form highly obtuse angles. The pads are inclined towards the bedding plane at about 45 °; their thickness varies between 1 and 4 mm. In some specimens, the pads are arranged very irregularly; in these cases, the median furrow is not present (Fig. 35 c). The cross-section of the trail is heart-shaped, or somewhat compressed (Fig. 36 a, c).

Preservation: Positive epirelief; fill identical with the matrix.

Facies: Fine-grained sandstone with much plant debris.

Regional and stratigraphic distribution: *Scolicia* sp. is found in the Bencliff Grit (Middle Oxfordian) of Bowleaze Cove, Dorset coast.

Associations: *Skolithos, Diplocraterion habichi, D. parallelum, Gyrochorte* and *Muensteria.*

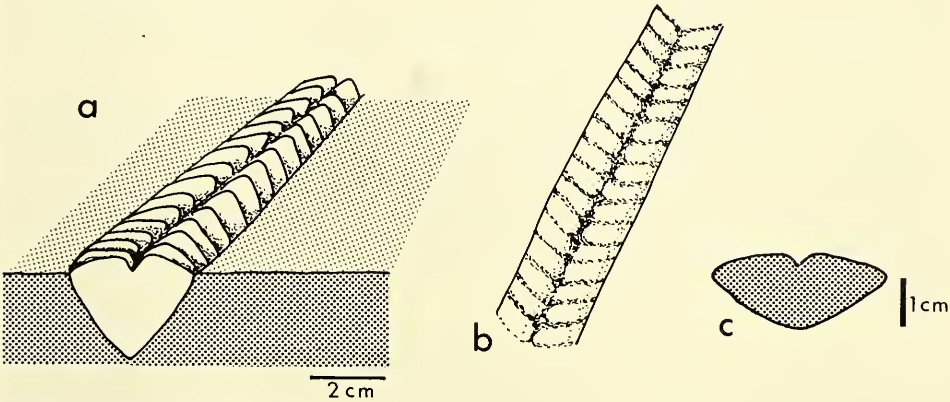


Fig. 36. *Scolicia* sp.
a: oblique view; b: viewed from above; c: cross-section. — Sketches based on observations from fallen blocks from the Bencliff Grit, Berkshire Oolite Group, Bowleaze Cove, Dorset.

Discussion and interpretation: *Scolicia* comprises a group of trace fossils with an extremely high variability. Whilst it was first thought that they represent trails made on the sediment surface (GÖTZINGER & BECKER 1932, 1934, ABEL 1935), it is now assumed that they represent endogenic traces (*Subphyllochorda*, GÖTZINGER & BECKER 1934; SEILACHER 1962, HANISCH 1972). ABEL (1929, 1935) by comparing them with the trails of the recent gastropod *Bullia rhodostoma* showed that they are most likely of gastropod origin. Their variability reflects mainly preservational aspects, for example whether they represent upper or lower surface forms (for extensive discussion see SEILACHER 1955, p. 373—376).

The validity and usefulness of specific names in *Scolicia* remains doubtful as long as no detailed analysis of the form group has been undertaken. For this reason, the Corallian specimens are referred to *Scolicia* sp. only. They are interpreted as the endogenic trails of scavenging gastropods.

5. Miscellaneous trace fossils

Escape structures

Escape structures can most easily be observed in finely laminated sands or sandstones. They indicate fairly rapid sedimentation which forced most endobenthonic organisms to move upwards in order to regain their original position relative to the depositional interface. Escape structures are also generated by epibenthonic animals as long as they are not killed by the sediment cover.

In the Corallian, numerous escape structures can be seen in a thinly laminated, shallow trough cross-bedded fine-sand unit in the Calcaire de Hennequeville on the coast between Deauville and Hennequeville, Normandy.

Faecal pellets

Figs. 12 c, d

Cylindrical, rod-shaped faecal pellets of 1—1.5 mm length and 0.3—0.5 mm in diameter are very common in some parts of the Corallian. In the Bencliff Grit of the Dorset coast, they form occasionally mm-thin layers in a large-scale trough cross-bedded sandstone unit (Fig. 12 d). Thin-sections reveal no internal structure which might be due to micritization.

The faecal pellets are usually encountered in septal laminae or around entrances of *Diplocraterion parallelum* (Fig. 12 c) (see also ARKELL 1939, and GOLDRING 1962, p. 240). This close association makes it very likely that they have been produced by the inhabitants of *D. parallelum*, probably crustaceans.

The radial arrangement of faecal pellets around the burrow entrances is also a feature well known from Recent crustacean burrows (e. g. WEIMER & HOYT 1964, pl. 123, fig. 2; CHAKRABARTI 1972).

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