REDESCRIPTION OF THE TRACE FOSSIL *GYROLITHES* AND TAXONOMIC EVALUATION OF *THALASSINOIDES*, *OPHIOMORPHA* AND *SPONGELIOMORPHA*

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The branching burrow systems *Thalassinoides* and *Ophiomorpha* vary widely in morphological detail. Individual burrow components otherwise characteristic of these two genera may in fact occur together in the same system, and may further intergrade with the spiral burrow *Gyrolithes* (redescribed herein).

Nevertheless, the predominant morphological traits within each ichnogenus tend to be distinctive, and most specimens can be identified ichnogenerically with relative ease. Thus, despite a recent suggestion to the contrary, these ichnogenera are not strict synonyms; such variations are to be expected among trace fossil taxa. Furthermore, extensive taxonomic revision would undermine the present stability and proven usefullness of these ichnogeneric concepts in field application and environmental reconstruction.

The ichnogenus *Spongeliomorpha* is so ill-defined that the name should be abandoned, regardless of whether one wishes to "split" or "lump" the related burrow ichnogenera.

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In 1818 Thomas Say described the shrimp *Callianassa major*, and commented on recent and fossil burrows of this species. Since then a voluminous literature has accumulated on the burrows of fossorial shrimp or shrimp-like crustaceans, fossil and recent. Various trace fossil names are now used to designate ancient burrows, including *Gyrolithes* Saporta, 1884 (=*Xenohelix* Mansfield, 1927), a vertically spiralled burrow; *Spongeliomorpha* Saporta, 1887, originally interpreted as a sponge but bearing a network of ridges that were convincingly interpreted by Kennedy (1967, p. 150) as scratch patterns made on the burrow wall by a digging animal; *Ophiomorpha* Lundgren, 1891, ramose burrows having a prominently nodose exterior; and *Thal-*

Fig. 1. Saporta, 1884, pl. 5, fig. 3: lectotype of *Gyrolithes davreuxi*. ×1.

assinoides Ehrenberg, 1944, a branching burrow having no special wall lining (Häntzschel, 1962; 1965). These names are now well known to most palaeontologists, sedimentologists and stratigraphers because various occurrences of these trace fossils have yielded valuable palaeoenvironmental information.

Recently another distinctive branching burrow has been described from the Permian of Utah under the name *Ardelia* (Chamberlain & Baer, 1973). This is a *Thalassinoides*-like burrow the wall of which is highly perforated in places, giving off profuse small bifurcations that radiate from the wall of the main galleries.

In spite of their overall distinctiveness, however, these burrows exhibit considerable morphological variation, including broad intergradations among the different burrow forms. For this last reason, Fürsich (1973) concluded that *Spongeliomorpha, Thalassinoides* and *Ophiomorpha* are synonymous (*Spongeliomorpha* being the senior synonym), and he proposed some correspondingly new criteria for recognizing ichnospecies within his redefined ichnogenus.

Although we agree with the basic sentiments underlying Fürsich's move, we hope to show here that: (1) any such "lumped" ichnogenus would also have to include *Gyrolithes* and *Ardelia*; (2) *Gyrolithes*, the ichnogenus having priority within this "group", would be inappropriate (or at least a glaring misnomer) as a broadly conceived name for branching burrow systems that normally lack any spiral elements; and (3) in final analysis, *Spongeliomorpha* is a nomen dubium. Furthermore, and more importantly, (4) Fürsich's revised taxa are equally as arbitrary and intergradational as the original ones, so that the problem is merely transferred from ichnogenus to ichnospecies level; (5) the occurrence of combinations of *Ophiomorpha, Thalassinoides* and *Gyrolithes* as interconnected parts of a single burrow system does not

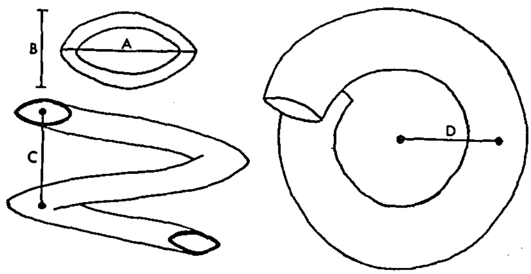


Fig. 2. Dimensions of *Gyrolithes davreuxi* used in this paper. A, width and B, height of the burrow; C, height of whorl and D, radius of spiral.

require that these forms should represent a single ichnotaxon; and (6) the original names are so deeply implanted in literature and thought that to replace them now with unfamiliar new names or extensively redefined old names would produce needless confusion.

A re-examination of the type ichnospecies of the oldest of these ichnogenera, *Gyrolithes*, well illustrates the nomenclatural problems presented by this group of trace fossils.

The type ichnospecies of *Gyrolithes*

There has been no detailed description of *Gyrolithes davreuxi* since Saporta (1884) originally designated the name for what he considered to be an unusually well preserved siphonate alga. The conspicuous spiral fossils were well known by that time (earlier literature in Saporta, 1884) and had been loosely termed "Gyrolithen" by Debey (1849, p. 279). The stratum typicum of Saporta's material is well exposed today in the type area in Belgium and numerous topotypes have been collected by one of us (RGB); these correspond closely to Saporta's excellent description and illustrations. A lectotype has been chosen from among Saporta's illustrations (fig. 1) and a redescription of the trace fossil in ichnological terms follows. A redescription is necessary because, although Saporta's illustrations are of high quality, he included two distinct trace fossils under this name: the spiral burrow and a small branching burrow within its wall lining. *Thalassinoides* networks interconnect with the spiral burrows, but the name *Gyrolithes davreuxi* undoubtedly should apply only to the spiral part of the burrow.

Morphology

The geometry of *Gyrolithes davreuxi* shows a very high degree of irregularity, even within individual burrows. Among the measurable parameters (fig. 2), the height and width of the burrow cross section and the radius of the whorl show the least variation. The cross section of the tunnel is oval, the

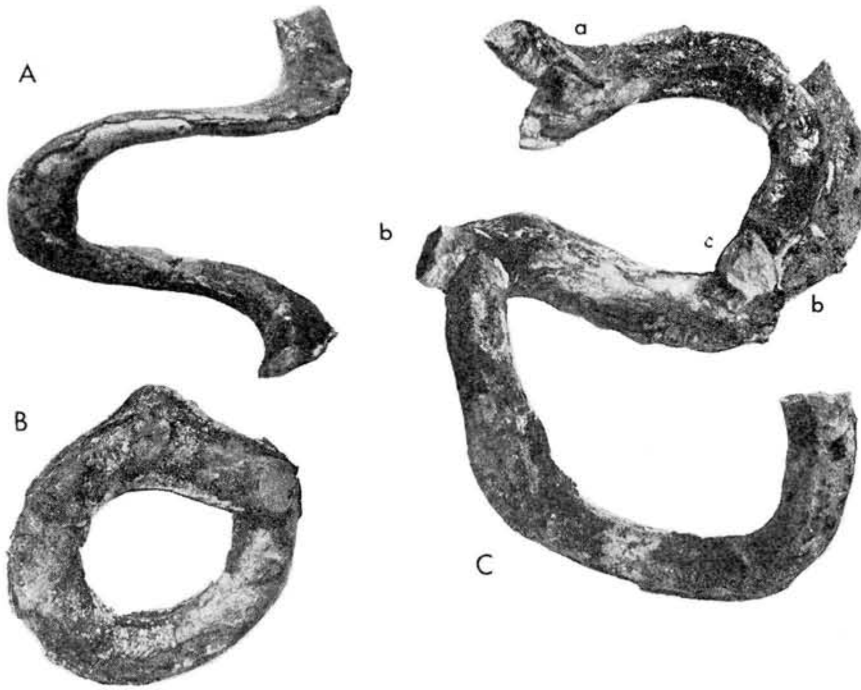


Fig. 3. Three fragments of *Gyrolithes davreuxi*. A: lateral view of dextral spiral. B: axial view of a sinistral whorl with a swollen elbow. C: oblique view of a branched specimen showing reversal of coiling; a genuine branch (a, cf. fig. 6a); change of course or partial re-excavation of older fills (b, cf. fig. 6b); and a later intersection by another burrow (c, cf. fig. 6c). Mineralogical Museum, Copenhagen, MMH 13053–5. Natural size.

larger diameter lying more or less horizontally. The oval has been exaggerated somewhat by compaction of the sediment, but it is quite clear that the burrow section was originally elliptical since, in its irregular path through the sediment, the widest diameter deviates from the horizontal in places, while vertical lengths are also oval in section (fig. 3). The width of any one burrow remains very constant at 9 or 10 mm (observed range 7.5–10.5 mm) whereas the height is more variable owing to compaction, typically 4–5 mm but up to 7.5 mm. The radius of arc of the spiral averages 15mm (12–21 mm).

On the other hand, the spirals are very irregularly coiled. Individual whorls show variable deviation from the horizontal plane so that the distance between consecutive whorls is very inconsistent (pl. 1). Further irregularity is caused by alternation between dextral and sinistral coiling, the change-over involving either a U-turn or a swollen "elbow" (figs. 3 & 4). Except

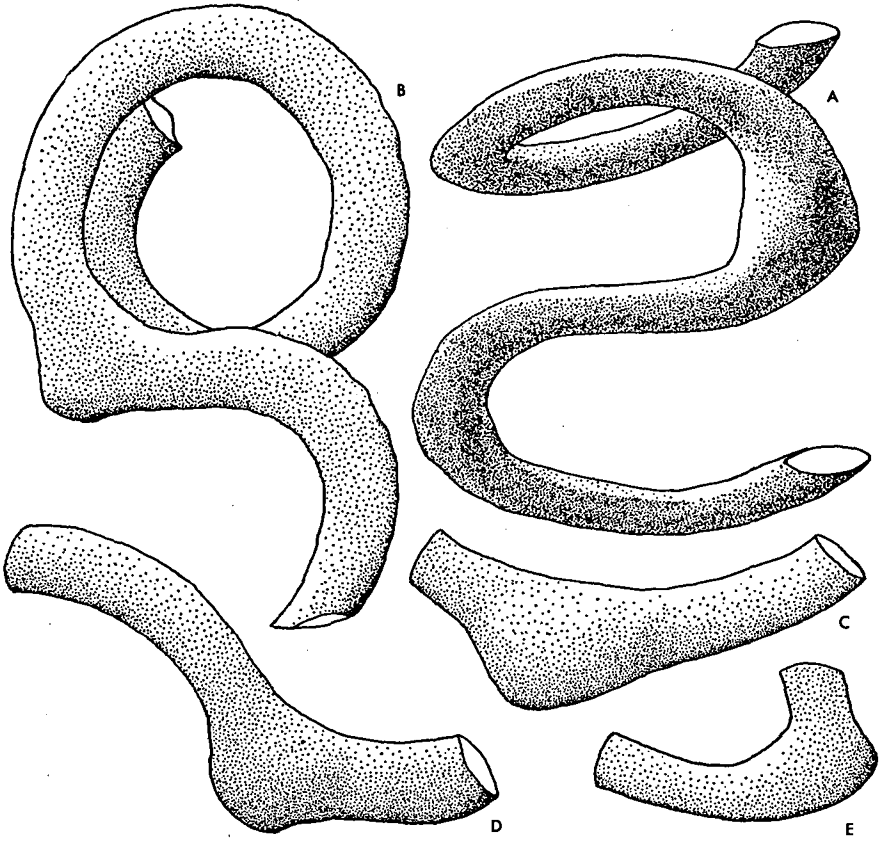


Fig. 4. Elbows in *Gyrolithes davreuxi.* A: View from slightly below lateral, showing a vertical loop including a swelling, where coiling reverses from dextral (below) to sinistral. The swelling, unlike the rest of the burrow, has a circular section. B-E: axial views of fragments of burrows with various forms of elbows each, except C, occurring at a reversal of coiling. Natural size.

in such cases where the U-bend lies in a vertical plane, the reversal from sinistral to dextral involves a lateral displacement of the spiral axis. Where coiling reversals occur repeatedly, within the distance of less than one whorl, the burrow morphology breaks down into a series of loops and arcs which nevertheless retain a more or less constant radius (fig. 3).

A further complication is the development of swellings, which increase the width of the tunnel by a factor of c. 1.5 and in some cases have a circular cross section. In most specimens these swellings cause an "elbow" and occur at points of coiling reversal (fig. 4).

Upper and lower terminations of the burrows have not been observed, which indicates that the structures have a considerable length. The longest

Fig. 5. *Chondrites* in the wall of *Gyrolithes davreuxi*. MMH 13056.

observed spiral measured 12.5 cm. However, it is difficult to trace individual burrows over such distances owing to intersections with other burrows and to the friable nature of the calcsiltite in which they occur. The fill of the burrows consists of the same sediment as surrounds them. No body fossils have been detected in the fill.

The most consistent and characteristic feature of *Gyrolithes davreuxi* is the wall material, which consists of a layer of dark green glauconite about 1 mm thick. Within this layer, in about 80 % of specimens, there is a closely branched system of small burrows 0.5–1.0 mm wide, filled with unglauconitized siltstone and therefore very clearly visible within the dark glauconite (fig. 5). Saporta (1884, p. 31) compared these wall burrows to *Chondrites* (which at that time was also considered to be an alga), and Häntzschel (1962, p. 200) identified them as *Chondrites* from Saporta's illustrations. The small burrows do not show the constant branching angle or the straightness of course diagnostic of idiomorphic *Chondrites*, but these differences may be attributed to the spacial restrictions imposed by the curved thin wall of the *Gyrolithes* within which they are confined. Spreads of idiomorphic *Chondrites* are detectable in places in the sediment outside and having no connection with the *Gyrolithes*, so the wall burrows may thus be considered tentatively to be stenomorphic *Chondrites*.

Many of the spiral burrows display branches. In almost all cases, however, these can be shown to be either intersections of two separate burrows or re-excavation of a new burrow along an old fill (fig. 6). Only a small minority of burrows appear to have existed as open branched galleries. The first two types of apparent branches demonstrate that the burrows were filled rapidly with sediment, a conclusion that is supported by the extreme rarity of completely collapsed burrows.

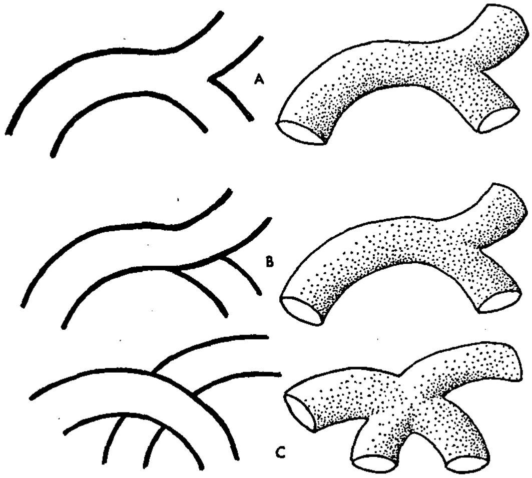


Fig. 6. The internal structure (left) reveals the nature of branches in *Gyrolithes davreuxi.* Few represent true branches of the original burrow (A). The majority are places where an older fill has been partly re-excavated (B) or simple intersections of burrows with older fills (C).

Three specimens have been observed in which more or less straight burrows having *Thalassinoides* branching pattern are associated with the spiral burrows (fig. 7). In only one of these cases has a direct connection with spiral tunnels been observed, but there can be little doubt that these branched burrows were excavated by the same organism since the width and height of the oval burrows, and the glauconite wall containing *Chondrites,* are precisely the same as in the *Gyrolithes.* The dichotomous branching nodes are widened, and there is nothing to hinder the application of the name *Thalassinoides* to these parts of the burrows. They contrast strongly to the poorly preserved mazes of *Thalassinoides* that accompany them in the sediment, but these have a smectite fill 2 cm in diameter locally floored by fish scales. These, in turn, are not to be confused with the postomission suite of unbranched tunnels that descend from the overlying glauconitic chalk and intersect the smectite burrows (Bromley, in press, fig. 4).

Ichnogenus *Gyrolithes* Saporta 1884

The spiral part of the burrow described above represents the type ichnospecies of *Gyrolithes.* It was on the basis of Saporta's description that Häntzschel (1962; 1965) phrased his diagnosis of the ichnogenus. However, it cannot be denied that, among the ichnospecies of *Gyrolithes* now recognized, *G. davreuxi* is a very aberrant form, and that the ichnogenus should be defined in rather broader terms than those used by Häntzschel. The following emended diagnosis is offered.

Diagnosis: burrows more or less describing a dextral or sinistral circular helix more or less upright in the sediment; surface with or without wall

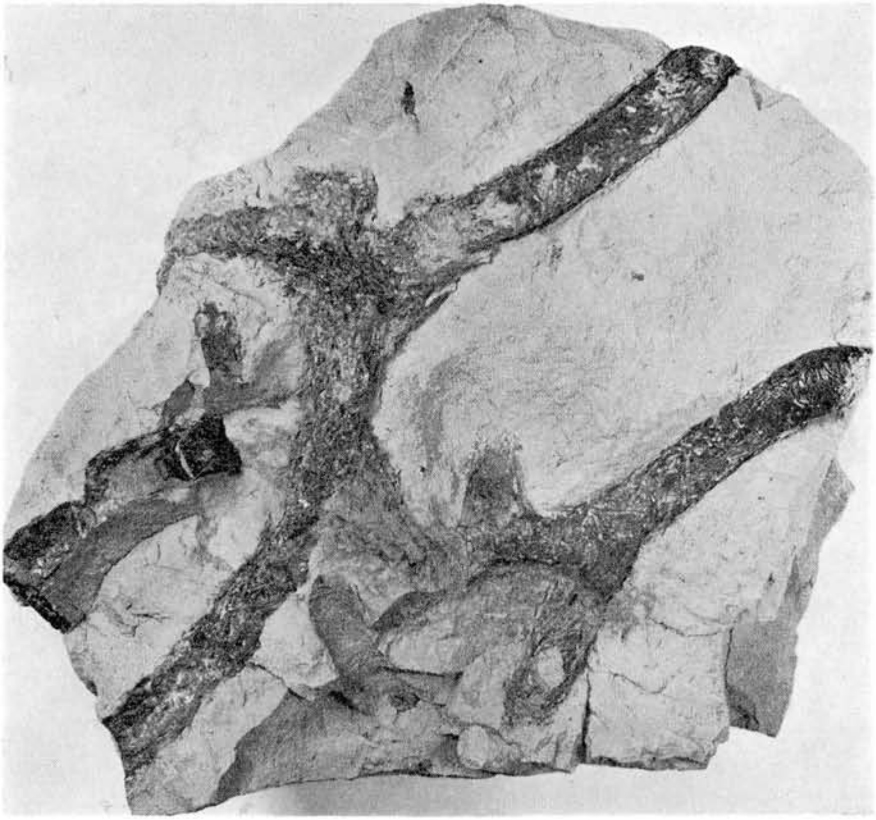


Fig. 7. Branching *Thalassinoides* that connect with *Gyrolithes davreuxi*. Burrow width (1 cm) is the same as that of the spiral burrows, and the glauconite walls likewise contain *Chondrites*. MMH 13057. ×0.8.

structure or scratch traces; radius of whorls and diameter of tunnel rather constant; may branch and interconnect with *Thalassinoides* or *Ophiomorpha* networks.

Gyrolithes davreuxi Saporta 1884

Lectotype: Saporta 1884, pl. 5, fig. 3. Paralectotypes: Saporta 1884, pl. 5, figs. 1, 2, 4; pl. 6, figs. 1, 2.
Locus typicus: Province de Liége, Belgium.
Stratum typicum: Smectite (Campanian, U. Cretaceous). The material illustrating this paper was collected from the top 5 m of smectite exposed in the great quarry at Hallembaye and from the loop-line cutting at the east side of Bon Espérance quarry (now incorporated in Carrière North), west of the River Meuse near Visé, Belgium.

Diagnosis: *Gyrolithes* with an oval cross section c. 5 × 10 mm, coiling alternately dextrally and sinistrally with a radius of c. 15–20 mm. Distance between whorls variable, from 7 to 33 mm in the same burrow. Swellings occur at some points of reversal of coiling direction. Branches rare. Well developed wall structure consisting, in the type material, of a 1 mm thick layer of glauconite.

Taxonomy and morphology of crustacean burrows

Except for *Ardelia*, the trace fossils discussed here are popularly known in Mesozoic and Cainozoic strata and are widespread geographically. *Gyrolithes* occurs as far back as the Jurassic (Gernant, 1972). *Thalassinoides* has been recorded in the Triassic (Fiege, 1944) but very similar burrows are also known from the Pennsylvanian (Warme & Olson, 1971; Chamberlain & Clark, 1973). *Ophiomorpha* and *Ardelia* occur in the Permian of Utah (Chamberlain & Baer, 1973). Increased antiquity diminishes the accuracy of detailed ichnological interpretations, of course, but these long-ranging ichnogenera have proven themselves as distinct entities and as valuable facies indicators in the sedimentary record.

The basic morphology of most of the above burrows is generally well known (Häntzschel, 1952; Weimer & Hoyt, 1964; Kennedy, 1967; Kennedy & MacDougall, 1969; Frey, 1970; Gernant, 1972; Chamberlain & Baer, 1973). Intergradations among these burrow types within the same burrow system are perhaps less well known but the recent literature has tended to draw increased attention to them. The major intergradations are summarized in table 1.

Morphological variation among these branching burrow systems results from several factors, especially (1) the wide variety of organisms responsible for such burrows, (2) the diversity of environments in which the burrows are excavated, (3) differences in behaviour patterns regulating the burrowing activity and (4) differences in the processes or circumstances of preservation. These factors and their implications are summarized in the following discussions.

Nature of the burrower

Virtually all workers have attributed *Thalassinoides, Ophiomorpha* and *Gyrolithes* to decapod crustaceans, especially to callianassid or thalassinidean shrimp. In rare cases the remains of such shrimp have in fact been found within, or in close association with, the burrows (Ehrenberg, 1938; Mertin, 1941; Glaessner, 1947; Waage, 1968; Shinn, 1968; Pickett, Kraft & Smith, 1971). This attribution has been supported by work in modern environments (Weimer & Hoyt, 1964; Shinn, 1968; Farrow, 1971; Frey & Mayou, 1971; Hertweck, 1972), which has shown that several callianassids produce burrows that exhibit the branching patterns and wall structure of *Ophiomorpha* and *Thalassinoides*.

However, the numerous species within these families cover a wide range in form, function and habitat. For example, Biffar (1971) reported 10 extant species of *Callianassa* from south Florida alone, and about 20 from the western Atlantic, ranging from the well known *C. major* to species that construct shallow tunnels or bore or nestle in coral heads, from the intertidal zone to depths of about 700 m. Neither can *Callianassa* be claimed to be an exclusively marine genus. In Africa, *C. kraussi* tolerates a salinity range of about 1 to 60‰ (Day, 1951) and *C. turnerana* periodically migrates up freshwater rivers to mate (Monod, 1927).

Also in modern seas, brachyuran crabs have been shown to excavate spiral burrows corresponding to *Gyrolithes* (Hogue & Bright, 1971; Braithwaite & Talbot, 1972). Among heterochelate crabs the burrows coil sinistral-

Table 1. Intergradational morphologies among crustacean burrows (see also Fürsich, 1973).

Between *Thalassinoides* and *Ophiomorpha:*	
Doust (in Bromley, 1967)	Kennedy & Sellwood (1970)
Kennedy (1967)	Müller (1970; 1971)
Groetzner (1968)	Martini & Mentzel (1971)
Kemper (1968)	Schloz (1972)
Kennedy & MacDougall (1969)	
Ager & Wallace (1970)	
Between *Gyrolithes* and *Ophiomorpha:*	
Kilpper (1962)	Hester & Pryor (1972)
Keij (1965)	
Between *Gyrolithes* and *Thalassinoides:*	
Kennedy (1967)	Stanton & Warme (1971)
Gernant (1972)	Braithwaite & Talbot (1972)
Between *Spongeliomorpha,** *Thalassinoides* and *Ophiomorpha:*	
Kennedy (1967)	Kennedy & MacDougall (1969)
Thalassinoides having *Teichichnus*-like spreiten:	
Siemers (1971)	
Ophiomorpha having *Teichichnus*-like spreiten:	
Hester & Pryor (1972)	

* *Spongeliomorpha* sensu Kennedy (1967) is characterized by having scratched walls. Similar scratches have been found on walls of other ichnogenera, including *Rhizocorallium, Diplocraterion, Trichophycus* and even *Tisoa* (Frey & Cowles, 1969, pl. 2, fig. 5).

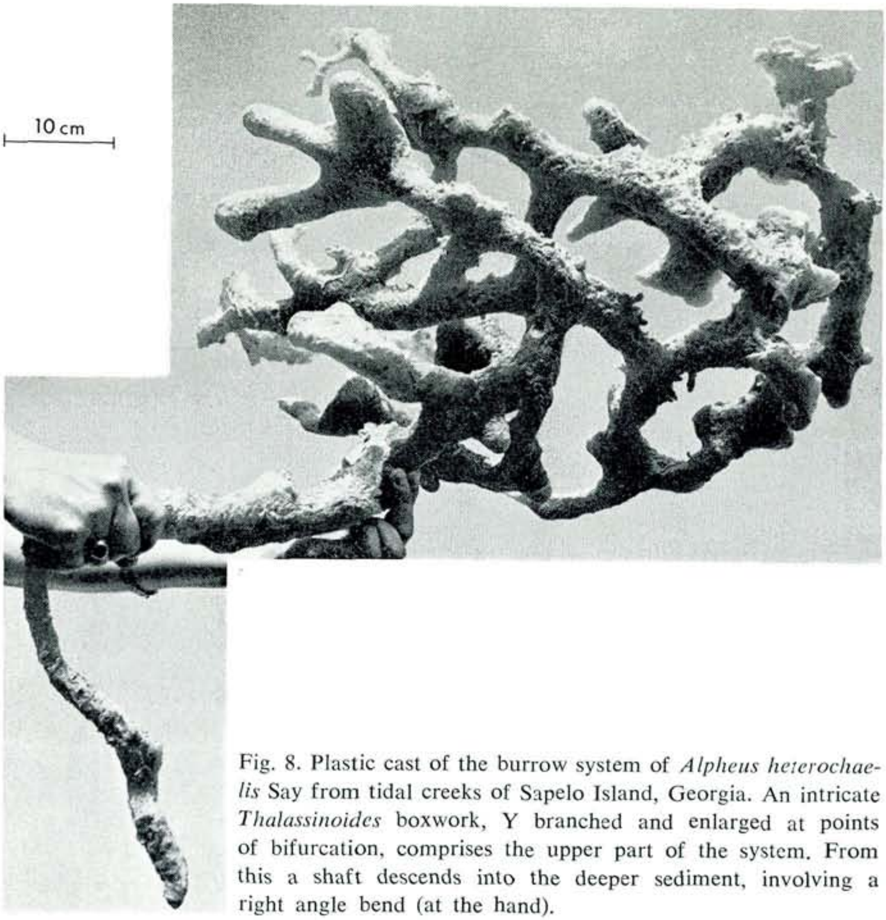


Fig. 8. Plastic cast of the burrow system of *Alpheus heterochaelis* Say from tidal creeks of Sapelo Island, Georgia. An intricate *Thalassinoides* boxwork, Y branched and enlarged at points of bifurcation, comprises the upper part of the system. From this a shaft descends into the deeper sediment, involving a right angle bend (at the hand).

ly or dextrally according to which of the two claws is the larger (Farrow, 1971). However, spiral parts have also been reported as extensions of modern branched burrow systems of the *Thalassinoides* type, possibly excavated by *Callianassa* (Braithwaite & Talbot, 1972).

Other crustaceans have been found to construct *Thalassinoides* systems. Sellwood (1971) and Bromley & Asgaard (1972) found glypheoid shrimp preserved in Jurassic *Thalassinoides*, whereas the work of Shinn (1968) and Farrow (1971) suggests that recent alpheid shrimp might equally well produce burrows of this type (see also fig. 8). Other candidates as *Thalassinoides* and *Ophiomorpha* architects include stomatopods (Frey & Howard, 1969; Hertweck, 1972; Braithwaite & Talbot, 1972), astacid lobsters and crayfish, and even brachyuran crabs (Rice & Chapman, 1971; Chamberlain, in press).

From these studies it is clear that *Spongeliomorpha suevica* and *S. pa-*

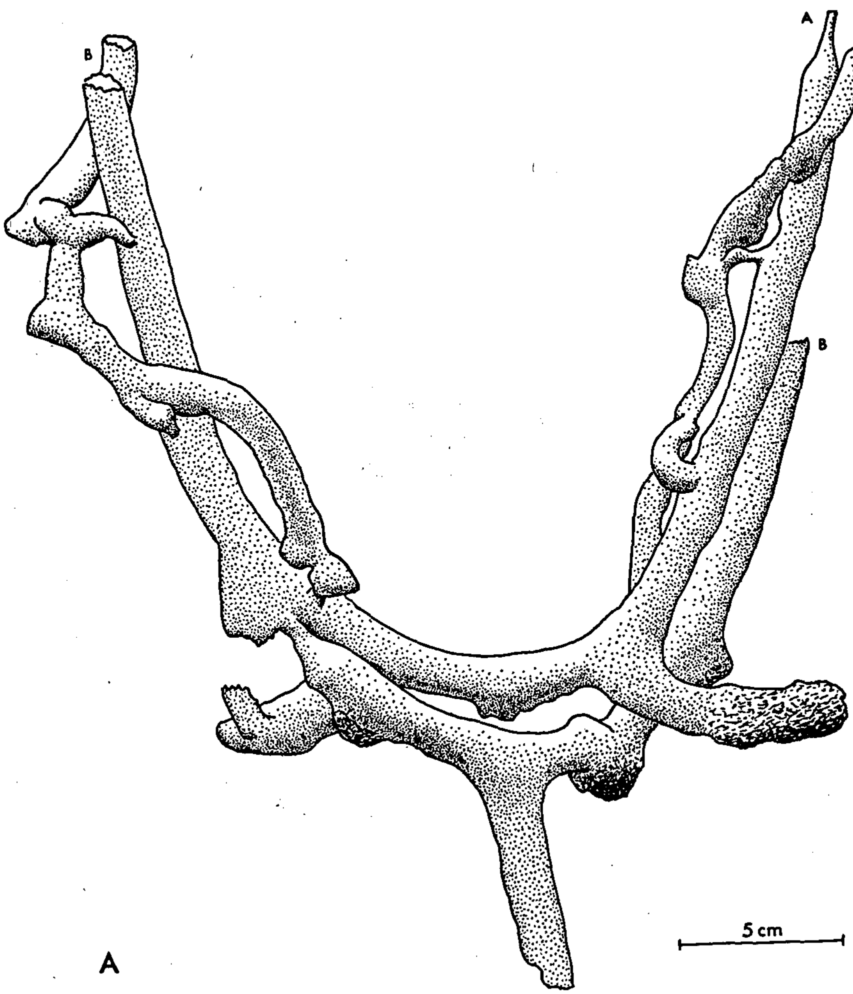
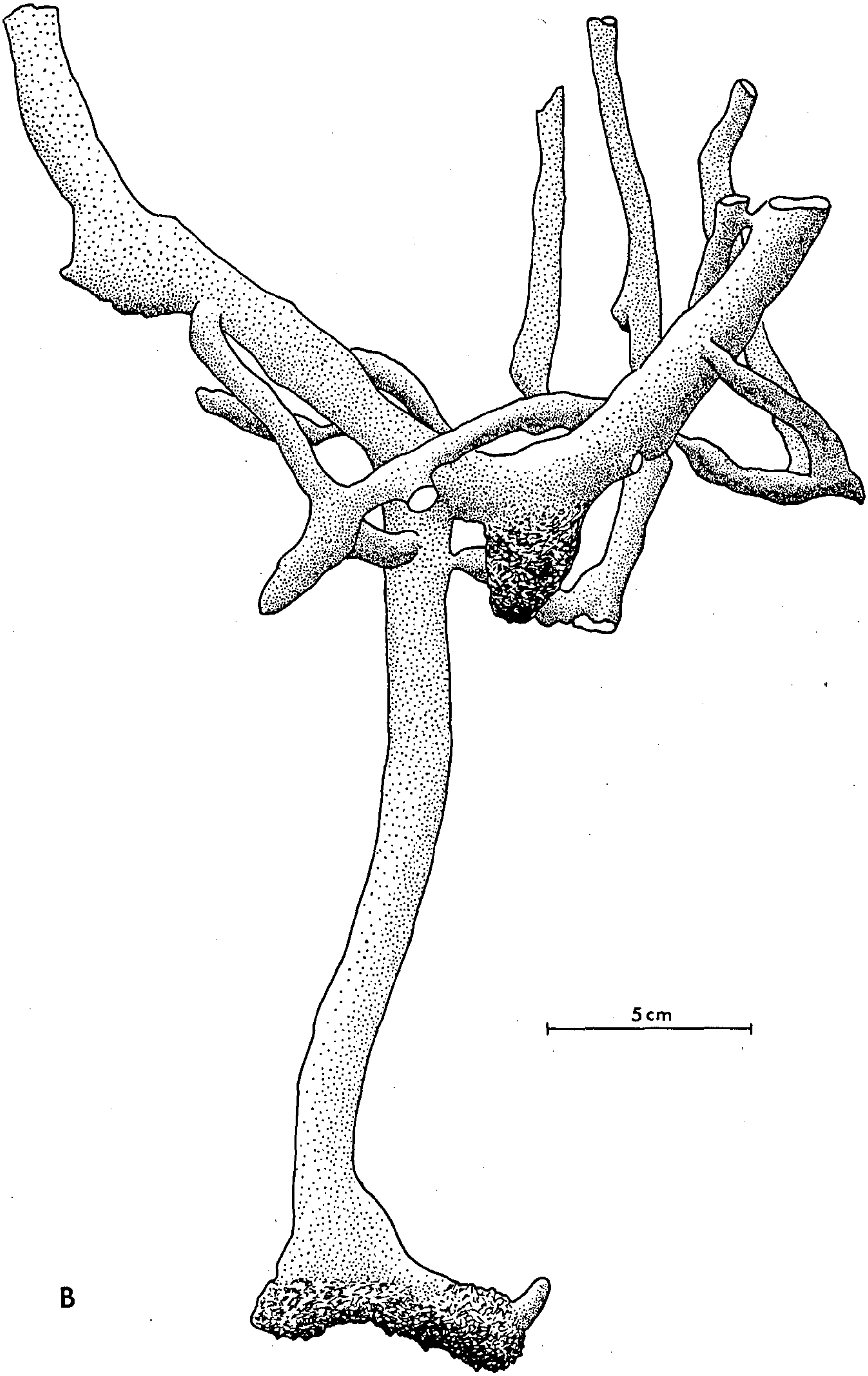


Fig. 9. Plastic casts of two heterogeneous burrow systems of *Upogebia affinis* (Say) (Sapelo Island tidal creeks). The surface of the casts is smooth, indicating that the burrows were lined. Special stippling indicates parts having rough surfaces, but interpretation of these abnormal parts is difficult. They may represent special chambers (cf. fig. 10), local lack of lining, or places where the burrow has been constructed through locally peaty sediments. **A:** The basic burrow shape is a Y with two apertures, but in this case an extra Y element is connected. Two upper extremities are broken (B) but one is intact and shows a constriction at the sea floor (A). Entwined around this double-Y is a narrower, irregular burrow. Points of interconnection with the larger burrow are markedly constricted, as is also the intact apertural neck. The connections are too narrow to admit the passage of adult shrimp but would allow water to circulate freely. **B:** In this case the surface apertures are broken but the stem of the Y is intact. Here, too, a smaller, irregular system entangles the arms of the Y, and most of the interconnections are constricted.



B

radoxica, as depicted by Fürsich (1973, fig. 6), are merely "ideal end points" in a continuum of interrelated burrow forms (see also Chamberlain & Baer, 1973, fig. 4). Thus, the wonder is not that branched crustacean burrows exhibit intergradational morphologies but rather that the three essentially distinct burrow forms, *Thalassinoides, Ophiomorpha* and *Gyrolithes,* can still be differentiated so consistently in diverse, widespread occurrences.

Heterogeneous burrow systems

A more confusing problem for the taxonomist is the not uncommon mingling of two or more of these burrow forms within a single, continuous burrow system. Examples from the literature are listed in table 1, to which we may now add *Gyrolithes davreuxi* and the burrows of *Upogebia affinis* shown in figs. 9 and 10. But even here the problem is easily solved by commonsense analysis. The situation is analogous to the palaeobotanical concept of form or organ taxa. We may find a fossil leaf attached directly to a fossil stem, in which case we would know that they were parts of the same plant. But where we find only isolated leaves and stems, it is more practical and explicit to refer each leaf and stem to its respective form genus rather than to the supposed parent plant (cf. Sarjeant & Kennedy, 1973). In short, if we find *Gyrolithes* attached to another type of burrow we can simply say so; if it occurs in isolation we cannot say with certainty that it originated as an actual extension of *Thalassinoides* or *Ophiomorpha.* In ichnology, as in palaeontology, our taxonomic distinctions should be concerned more with descriptive morphology than with interpretations on origins or interrelationships (Simpson, in press).

Animal behaviour reflected in burrow morphology

Variations such as those mentioned above stem not only from phylogeny and major habitat adaptations (obligate behaviour) but also from differences in burrowing technique in relation to changes in the immediate environment (facultative behaviour). As noted by Schäfer (1956), for example, the prominence and construction of crustacean burrow walls are commonly influenced by the coherence of the substrate. *Ophiomorpha* that lose their distinctive knobbiness with depth may be indicative of increasingly stable sediments at greater depths of burial (Kennedy & Sellwood, 1970; Frey, 1971); in other cases, however, these may represent merely the unfinished newer parts of the ever expanding burrow system (Asgaard & Bromley, 1974, fig. 2). Irregularly knobbed horizontal *Ophiomorpha* from the Cretaceous of Utah (Frey & Howard, 1970, fig. 8i) have relatively thicker roofs than floors. In the quiet waters and stable substrates of aquaria, *Callianassa major* – the best known analogue for the *Ophiomorpha* animal – does not construct thick knobby walls (Frey & Howard, 1972).

In the Miocene of Denmark (Asgaard & Bromley, 1974), unlined burrows project through the wall of *Ophiomorpha* systems and extend into the surrounding sediment. These naked, almost invisible burrows have the same diameter as the *Ophiomorpha* and probably represent briefly occupied feeding burrows in contrast to the permanently occupied, well maintained living burrows from which they emerge. An example of a comparable situation in Cretaceous *Thalassinoides* was recorded by Bromley (1967, p. 163, fig. 3) in which unfinished or feeding galleries bore scratches on their walls.

Seilacher (1953, fig. 2) described a similar phenomenon in burrows of the modern polychaete *Nereis diversicolor*. This worm, under certain conditions, constructs a semipermanent U-burrow in which to live and respire, but extends this structure downward by means of ephemeral, branched feeding burrows having a substantially different morphology.

Likewise, *Gyrolithes* is clearly a dwelling, not a feeding burrow (Toots, 1962; Gernant, 1972); in contrast, *Thalassinoides*, in most cases at least, is excavated in the process of feeding although ultimately the open tunnels are maintained as a dwelling burrow. Thus, where *Gyrolithes* is connected as an integral part of a *Thalassinoides* system, it may reflect once again a specialization of different parts of the same burrow complex for different life activities of the inhabitant.

Further striking examples of environmental control over burrow construction are found in hardgrounds (Bromley, 1967; 1968; in press) and reef flats (Farrow, 1971).

Preservational problems

Equally troublesome at the ichnospecies level are differences in preservation, as when the upper parts of a given assemblage of burrows are removed by erosion or destroyed by shallower bioturbation, leaving the burrows conspicuously but superfluously different from their counterparts in neighbouring assemblages. The *Ophiomorpha* figured by Pickett, Kraft & Smith (1971), for example, are seemingly unusual in that they consist of an irregular maze of horizontal tunnels, yet they probably represent only the basal parts of a normal system having almost equally prominent vertical and horizontal components (cf. fig. 11). This kind of situation could easily account for the difference between *Spongeliomorpha nodosa* and *S. saxonica*, as depicted by Fürsich (1973, fig. 6). Erosional modification is also observed commonly in *Thalassinoides*, which ordinarily does not extend nearly as deeply into the substrate as certain forms of *Ophiomorpha*.

Differential preservation of trace fossils in leached or mineralized sedi-

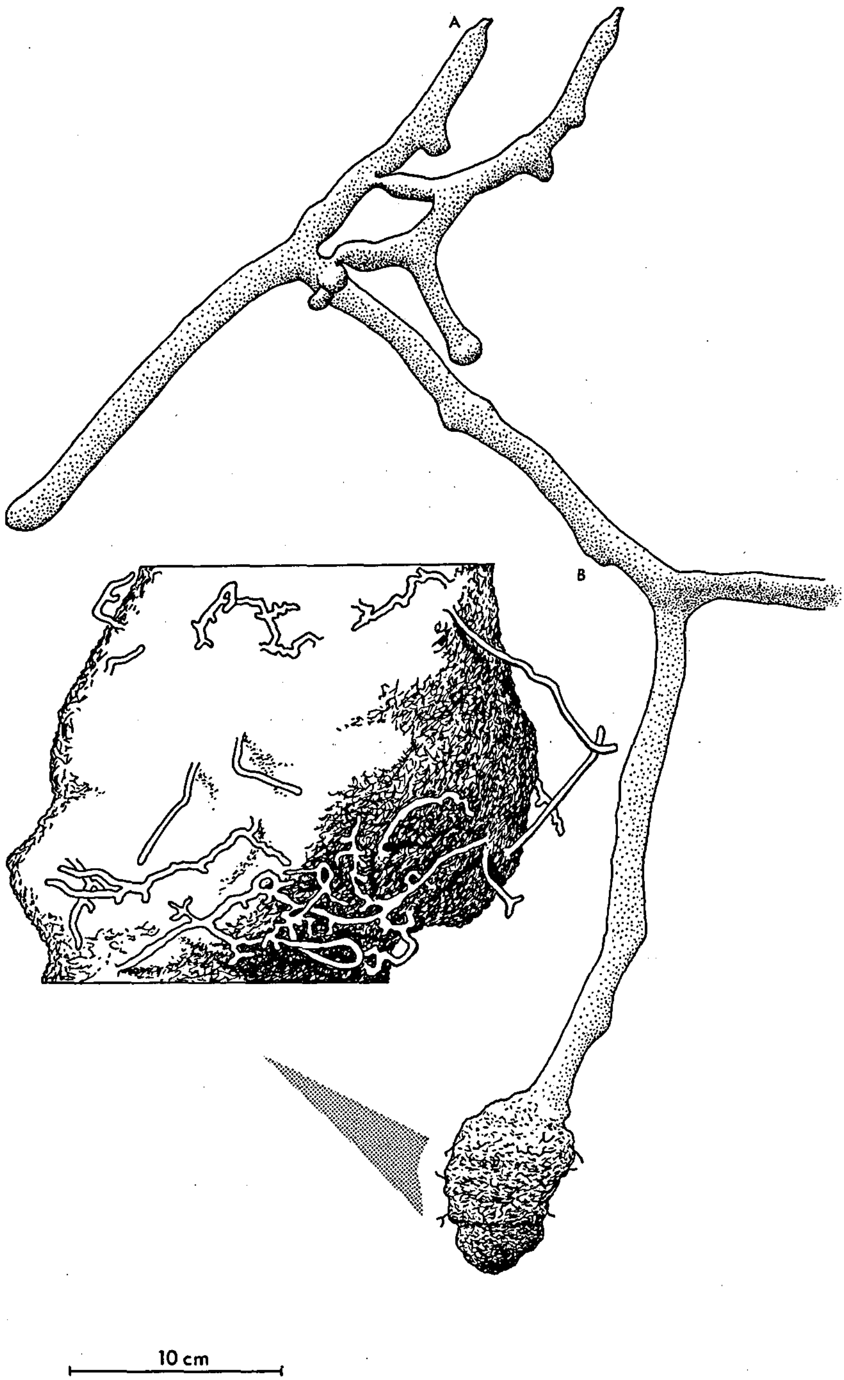
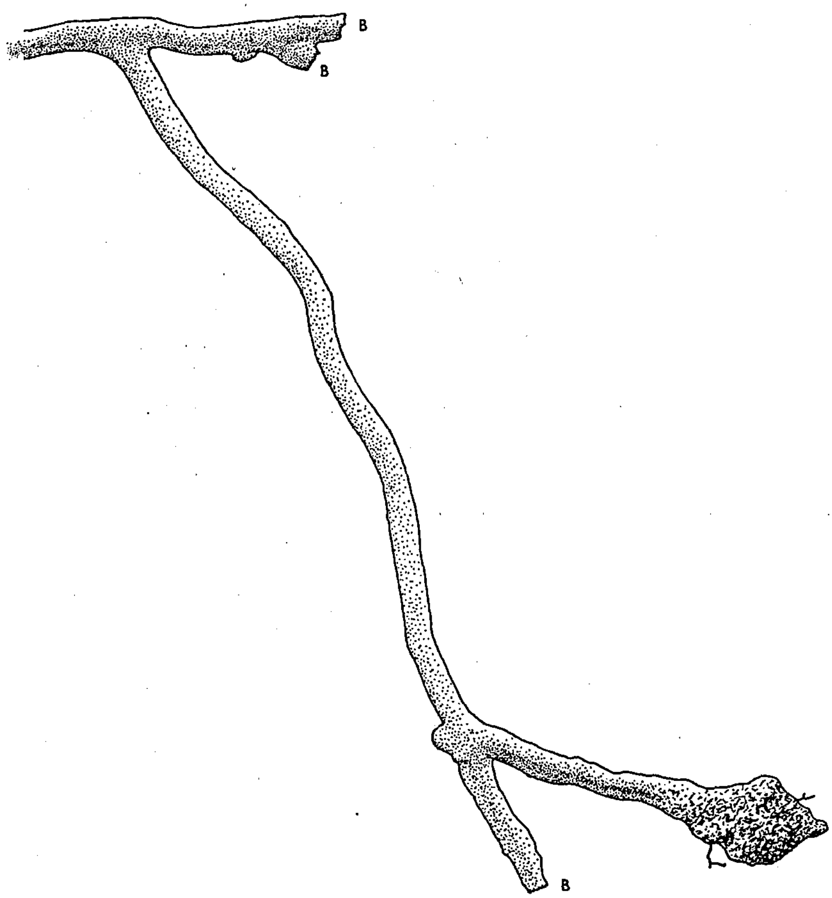

A
B
10 cm

Fig. 10. Plastic cast of a heterogeneous burrow of *Upogebia affinis* (tidal creeks, Sapelo Island, Georgia). Several side branches and the deepest extremity broke during recovery (B). Unlike fig. 9, the Y-shape is not apparent, but a short, secondary, irregular burrow communicates with the main burrow via constricted interconnections and both burrows have constricted apertures (A). However, bifurcations within the two parts of the system show the characteristic slight widening so commonly seen in fossil *Thalassinoides* and *Ophiomorpha*.

Two of the three recovered terminations of the cast are swollen chambers, the rough surfaces of which indicate that they were not lined in the same way as the rest of the burrow. Numerous minute burrows emerge from the walls of the chambers (enlargement). Some of these show Y-branching whereas others are simple; their diameter is uniform at 1 mm and most are connected at several points with the chamber wall. The similarity of morphology to the main burrow invites the thought that these minute burrows are the first excavations of juvenile *Upogebia* and that the swellings are breeding chambers. Forbes (1973) has indeed described burrows of juveniles emerging from those of adults in the case of *Callianassa kraussi*, in which species the planktonic larval stage is correspondingly eliminated. However, in *U. affinis* the larvae are abundant elements of the oceanic plankton (Sandifer, 1974). Thus the interpretation of the chambers and their minute burrows must await further research on the life history of *U. affinis*.



ments also produces morphologically or compositionally different trace fossils, as does sediment compaction and deformation.

Cumulative biogenic structures

A further problem is caused by the "fossilization barrier" (Seilacher, 1964), whereby the biogenic structure that is preserved as a fossil may not be directly comparable with extant burrows observable in modern environments. This is because the trace fossil does not always represent the burrow of an organism; in most cases it represents instead organic activity over a certain period of time. This is particularly the case with the highly mobile burrows that have produced spreiten as trace fossils, but is also significant in the interpretation of branched feeding burrows that are constructed continuously over long periods of time. Seilacher (1953, fig. 2) illustrated this clearly with the temporary branched burrow of the worm *Nereis diversicolor*, which produces in time a complex cumulative structure in the sediment. Likewise, several sediment-eating species of *Callianassa* are highly active burrowers and within a short time a population will cause 100 % bioturbation of the sediment (e.g. MacGinitie, 1934; Warme, 1967). At any one moment the inhabited burrow may be cast by pouring plastic into it, which will reveal a branching system of tunnels (fig. 8). However, this cast may give a falsely simple impression of the incipient trace fossil, for the system may be under continuous enlargement with construction of new tunnels while old tunnels are allowed to collapse or are actively filled up by the inhabitants (MacGinitie, 1934) (fig. 11). In many cases it is impossible for the geologist to disentangle the "standard burrow" morphology from the final pattern of bioturbation in the rock. The superimposition of several simple systems will nearly always lead him to interpret the burrow morphology to have been more complicated than it originally was. In some cases, textural differences of fill allow successive systems to be distinguished (e. g. Bromley, 1967, fig. 1; Bromley & Asgaard, 1972, fig. 7), but in many cases the complexity of a *Thalassinoides* network reflects a bioturbation pattern rather than the original morphological characteristics of the burrow.

Conclusions

The complexities illustrated by the foregoing examples have led many workers to adopt the ichnogenus rather than the ichnospecies as the basic unit in ichnology, assuming of course that the ichnogenera themselves are sufficiently distinctive. The voluminous literature on *Thalassinoides, Ophiomorpha* and *Gyrolithes* is itself a viable testimony to the distinctiveness and usefulness of these taxa in diverse geological settings, or to say it another way, a testiment to the fact that scores of workers in numerous different countries can consistently recognize these genera and can easily communicate their ideas to other workers. And all of this would essentially be lost if the ichnogenera were to be lumped together. Thus, although we laud Fürsich's conservative approach to trace fossil taxonomy, we contend that his ichnogenus *Spongeliomorpha* (1973) is too broadly conceived to be meaningful. Indeed, his concept is more in keeping with the familial taxa proposed by Richter (1924), e.g. the Rhizocorallidae.

The diagnostic features of the ichnogenera discussed in this paper are summarized as follows.

Spongeliomorpha. This ichnogenus is based on an ichnospecies, *S. iberica,* that is unrecognizable (Fürsich, 1973, p. 731). Although Kennedy (1967) made a reasonable attempt at interpreting Saporta's (1887) original description and illustrations as a burrow fill moulding a scratched wall, this remains but a second author's interpretation. On the basis of the original description, *Spongeliomorpha* must be considered a nomen dubium and should be abandoned.

Gyrolithes. In contrast to *Spongeliomorpha,* Saporta's (1884) description and illustrations of *Gyrolithes* are of high quality; a redescription of the type ichnospecies, *G. davreuxi,* comprises a section of the present paper. The ichnogenus includes spiral burrows having a vertical axis. The "devil's corkscrew", *Daimonelix,* is usually excluded as a separate ichnogenus on account of its extreme size (Häntzschel, 1962). Ichnospecies may be differentiated on the basis of wall structure, helical angle, dimensions, etc.

Ophiomorpha and *Thalassinoides.* We would recommend that these taxa be kept separate, although the only distinguishing character is that of wall construction: the wall of *Ophiomorpha* consists of pellets of sediment pressed into the surrounding sediment and smoothed off internally (Häntzschel, 1952). The two ichnogenera share all other features of morphology, i.e., dominance of shafts, maze or boxwork, all dimensions and types of fill, branching with Y and T junctions, with turn-arounds (swellings) especially at nodal points. Likewise, *Ardelia* appears to be distinct from these two ichnogenera on the basis of its complex wall structure alone.

Despite great variation in *Ophiomorpha,* only two ichnospecies appear to be consistently recognizable: *O. nodosa* Lundgren, 1891, having single pellets in the wall and *O. borneensis* Keij, 1965, having double pellets. As suggested by Fürsich (1973), one might also employ geometrical criteria in order to define additional species; but we prefer the use of simple descriptive terms (e.g., Chamberlain & Baer's (1973) boxwork, maze, etc.,) in conjunction with the formal diagnoses of *O. nodosa* and *O. borneensis.*

A potential problem here is that in certain kinds of substrates the knobby walls of *Ophiomorpha* may not be distinguishable from the surrounding sediment; one might almost say that inside every *Ophiomorpha* there is a *Thalassinoides* in the guise of a burrow cast. In practise, however, this situation does not promise to pose a serious problem. In most cases there is a striking contrast between the wall and surrounding sediments, usually enhanced by diagenesis (fig. 11), and *Ophiomorpha* consequently tends to be a conspicuous trace fossil.

The ichnospecies of *Thalassinoides* are based on several criteria, such as regularity of branching and smoothness of walls. Several burrows of this type may have special wall linings, such as fish scales or shell fragments, but these linings usually are distributed only patchily, commonly as ceilings or floors only. They do not compare with the extensive sediment facing of *Ophiomorpha* walls, which is an essential feature of the burrow. In this respect *Ophiomorpha* is set apart from other burrows, representing a special response by an animal to a particular environment and substrate, and as such its generic identity should be preserved if it is to continue to be of service to sedimentary geology.

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Dansk sammendrag

De grenede gravegangsystemer *Ophiomorpha* og *Thalassinoides* er nu velkendte af sedimentologer og palæontologer, og har vist sig værdifulde i tolkningen af palæomiljøer i talrige tilfælde. I en recent artikel (Fürsich, 1973) blev det foreslået at disse to navne smeltes sammen med *Spongeliomorpha,* af hvilke den sidstnævnte havde prioritet. Men et sådant skridt vil kun overføre de taxonomiske problemer af disse gravegange fra slægts- til artsniveau. Hvis imidlertid Fürsichs taxonomiske procedure fulgtes helt ud skulle et fjerde spornavn, *Gyrolithes,* naturligt smeltes sammen med de andre; og *Gyrolithes* ville have prioritet.

For at belyse problemet er typearten af *Gyrolithes, G. davreuxi* Saporta, 1884, genbeskrevet. De spirale *G. davreuxi* fortsætter nogle steder i grenede *Thalassinoides* netsystemer, ligesom mange andre eksempler af recente og fossile heterogene gravegangsystemer er kendte. Kombinationer kendes mellem *Ophiomorpha* og *Thalassinoides, Ophiomorpha* og *Gyrolithes,* o. s. v. Men eksistensen af sådanne heterogene systemer anses ikke for grund nok til at slå de nævnte slægter sammen til een. I dette forhold ligner sporfossil taxa botaniske formtaxa i modsætning til zoologiske taxa.

Spongeliomorpha er et nomen dubium. Det anbefales derfor at slægtsnavnene *Gyrolithes, Ophiomorpha* og *Thalassinoides* opretholdes i modsætning til *Spongeliomorpha.* At slå disse navne sammen under *Gyrolithes* vil skabe forvirring og vil, på grund af de i forvejen dårligt definerede arter, reducere denne sporfossil-gruppes effektive anvendelse i tolkningen af palæomiljøer.

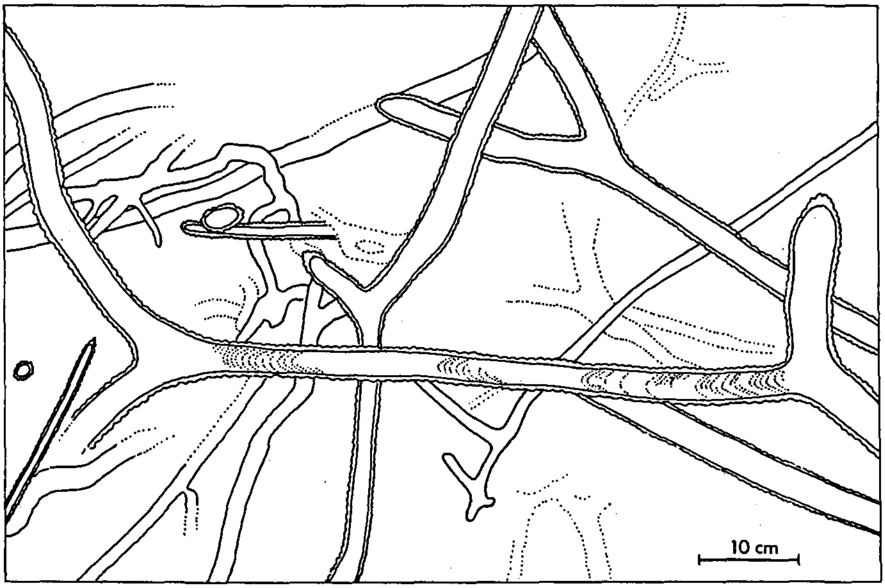

Fig. 11. Horizontal section of a bioturbation pattern composed of *Ophiomorpha nodosa* in chalk. Despite uniform filling material, successive mazes of burrows are distinguishable on account of their well developed wall lining, which consists of less ferruginous chalk than the remaining sediment. Some fills exhibit meniscus structure. Basal 2 m of Lower Globigerina Limestone (Miocene), Dwejra Point, Gozo (Malta).

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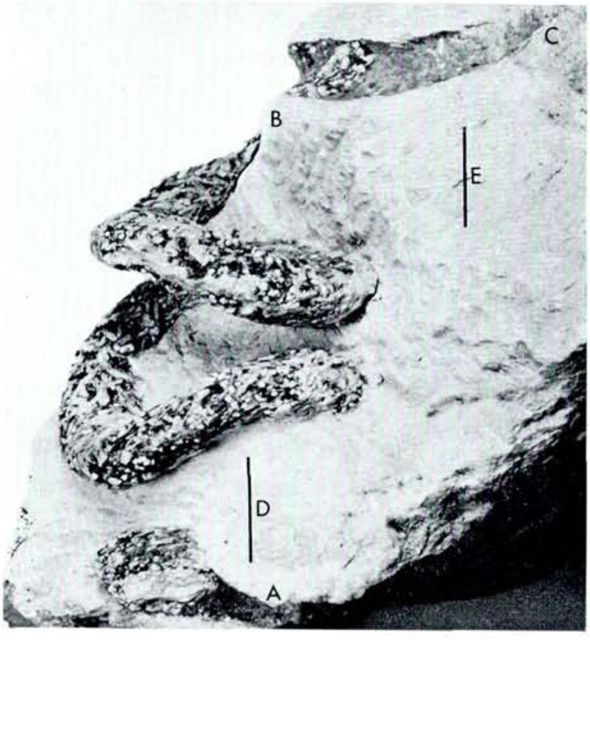
Plate 1

Two views of a specimen of *Gyrolithes davreuxi* from Lower Campanian smectite, Bon Espérance quarry, near Visé, Belgium; no MMH 13052 in Mineralogical Museum, Copenhagen. Slightly enlarged. The upper figure views the burrow obliquely from above; the lower shows a lateral view. From the broken end A the burrow climbs sinistrally through two and a half whorls to B, where an oblique loop reverses coiling into a dextral spiral from B to C. A considerable lateral shift of the spiral axis has been involved in reversal of coiling from sinistral (D) to dextral (E).


C
B
A


C
B
E
D
A

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