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-*

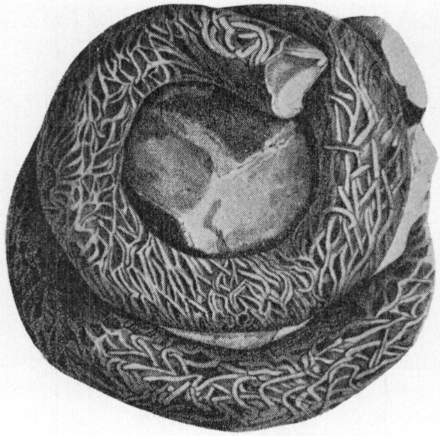

Fig. 1. Saporta, 1884, pl. 5, fig. 3: lectotype of *Gyrolithes davreuxi*. ×1.

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

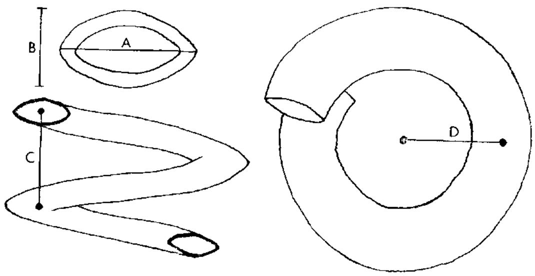

Fig. 2. Dimensions of *Gyrolithes davreuxi* used in this paper. A, width and B, height of the burrow; C, height of whorl and D, radius of spiral.

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

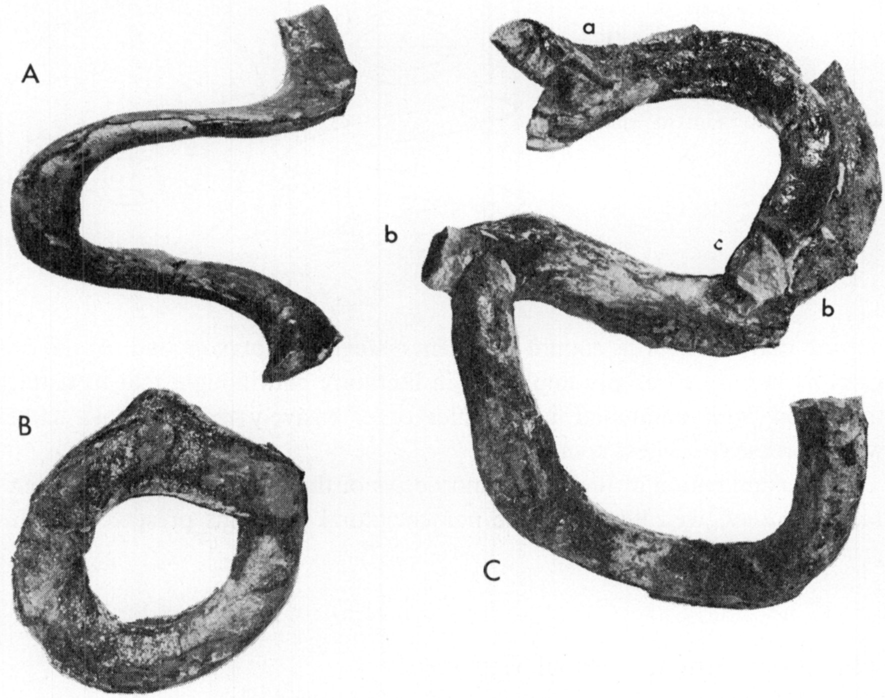

Fig. 3. Three fragments of *Gyrolithes davreuxi.* A: lateral view of dextral spiral. B: axial view of a sinistral whorl with a swollen elbow. C: oblique view of a branched specimen showing reversal of coiling; a genuine branch (a, cf. fig. 6a); change of course or partial re-excavation of older fills (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

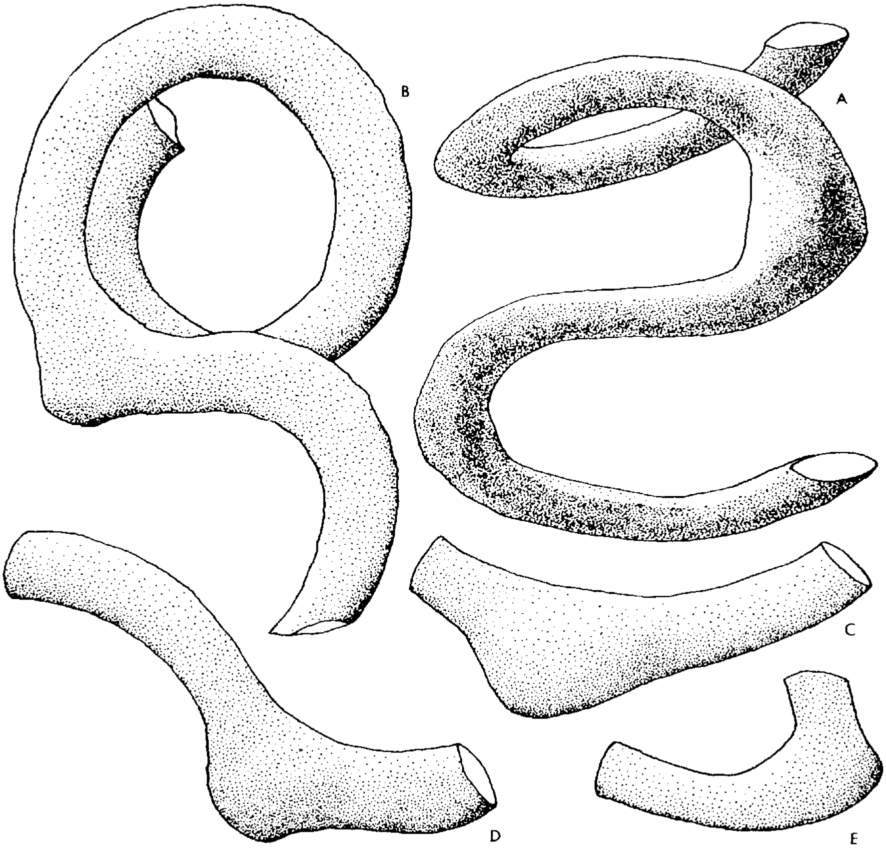

Fig. 4. Elbows in *Gyrolithes davreuxi*. A: View from slightly below lateral, showing a vertical loop including a swelling, where coiling reverses from dextral (below) to sinistral. The swelling, unlike the rest of the burrow, has a circular section. B-E: axial views of fragments of burrows with various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

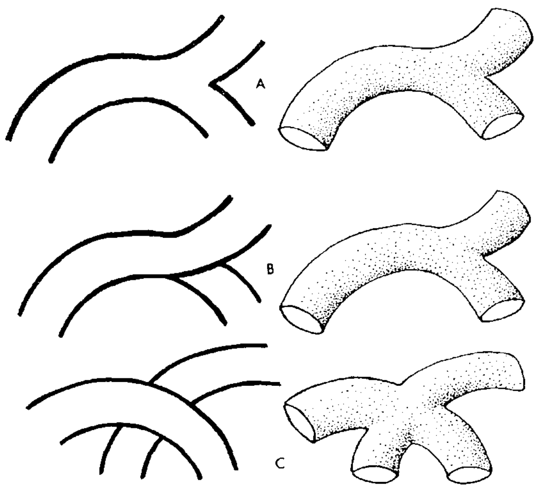

Fig. 6. The internal structure (left) reveals the nature of branches in *Gyrolithes davreuxi*. Few represent true branches of the original burrow (A). The majority are places where an older fill has been partly re-excavated (B) or simple intersections of burrows with older fills (C).

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