INTRODUCTION

Bifungites was an ichnogenus established by Desio in 1940 for certain dumb-bell shaped trace fossils found in Late Devonian rocks in Libya. Since its original diagnosis it has been reported in rocks ranging in age from (?) Cambrian to Upper Devonian (Dubois and Lessertisseur 1964, Hantzschel 1975) and is particularly conspicuous in Devonian strata, where it has been reported and, or described by Gutschick et al 1962, Dubois and Lessertisseur 1964, Rodriguez and Gutschick 1970, Gutschick and Lamborn 1975, and Melou and Plusquellec 1975. Indeed, some of its supposed pre-Devonian occurrences are questionable as many of the original specimens described for example by Hall (1852) and Zenger (1971) from the Silurian Clinton Group of New York have been destroyed, can no longer be located or are not illustrated. Furthermore, detailed descriptions of the trace fossils were incomplete and the traces could easily have been synonymous with the morphologically similar ichnogenera Arthraria, Corophioides or Diplocraterion. One of the purposes of this paper is, therefore, to record in some detail a definitive Ordovician occurrence of Bifungites.

In ichnology it is extremely rare when the producer of a trace can be identified with confidence as unrelated groups are sometimes morphologically very similar and can therefore produce similar traces, or groups are morphologically very different but behave in a similar manner due to physical and biological parameters and again produce similar traces (Osgood 1970). This is particularly true when the producer of a particular trace is a soft-bodied organism as the preservation potential for such organisms is extremely low. In spite of these inherent difficulties an assessment of the zoological affinities of the Bifungites trace is also attempted in this paper and comment is made on its palaeoecology.

LOCATION AND GEOLOGIC BACKGROUND

The Middle Ordovician (Caradocian) Trenton limestone northeast of the Quebec City area consists of a number of small autochthonous outliers that sit with pronounced unconformity on an undulating surface of Precambrian Grenville Gneiss (Riva 1972). The rocks are abundantly fossiliferous and consist of a combined thickness of at least 160 m of Trenton Limestone (Raymond 1912) with a few centimetres to as many as 33 m of basal sandstone (Riva 1972). Lithologically the limestones are composed of fossiliferous calcarenites and calcisiltites, biosparites and bio- micrites with thin shale and calcareous shale interbeds. They represent a Middle Ordovician transgressive platformal sequence which is extremely shallow-water in origin near its base then progressively deepens to subtidal shallow shelf and deeper water shelf towards the top of the sequence until finally it is overlain by the greywacke flysch succession of the Utica shales (Riva et al 1977). In addition to being a richly fossiliferous sequence the Trenton limestone here contains a moderately abundant and diverse ichnocoassembly consisting of Crusiana, Rusophycus, Bifungites, Diplocraterion, Planolites, Tomaxium, Chondrites, cf. Chevrotia, cf. Gyroehorte, cf. Teiohiohnus and horizontal annelid-produced surface trails (Pickerill and Forbes, in press). The Bifungites trace fossils are located in a series of small quarries sited in one of the outliers in the Chateau Richer area some 22 km northeast of Quebec City (Fig. 1).

DESCRIPTION

(i) Mode of Occurrence

The Bifungites traces are found in convex hyporelief on lower surfaces of thinly bedded (3-10 cm) delicately laminated or occasionally cross-laminated extremely bioturbated fine grained calcisiltites. Arms associated with the dumb-bell shaped trace fossils (see below) extend upwards into these calcisiltites. Specimen outlines are usually well-defined and the dark colouration of the silt-filled burrows is in marked contrast to the lighter grey-brown calcisiltites.
Bifungites of halli Desio 1940

The trace consists of a U-shaped or, strictly speaking, an inverted pi-shaped burrow in which two vertical or subvertical cylindrical tubes extend upwards from a horizontal basal chamber. The horizontal basal chamber is cylindrical in cross-section and is typically smooth and unornamented though rare specimens do in fact exhibit closely spaced transverse annulations (Fig. 4A). Typically the basal chamber width (d) is consistent.

(i) Systematic Description

Ichnogenus Bifungites Desio 1940

Hall 1852, Pl. 10, Fig. 6; Desio, 1940, pp. 78-79, Pl. 8, Fig. 3; Gutschick et al. 1962, pp. 79-89, Pl. 2, Figs. 13, 19-20; Hántzschel 1962, p. 186, Fig. 113.1; Dubois and Lessertisseur 1964, pp. 626-634, 7 Figs, Pl.1; Osgood 1970, pp. 314-325, Figs. 7-8, Pl. 60, figs. 3-4, Pl. 61, figs. 1-3, 7; Rodriguez and Gutschick 1970, pp. 418-419, Pl. 5, figs. a-f; Knox 1973, p. 172; Fursich 1974, pp. 957, 959-960; Hántzschel 1975, p. W46, Fig. 21.1; Gutschick
Throughout its length, thus giving the basal chamber parallel sides. In occasional specimens, however, maximum width is located centrally within the chamber, which then decreases slightly in size towards both lateral terminations (Fig. 4B). The lateral terminations of the basal chamber are consistently spherical in shape and always project beyond the vertical tubes, thus giving the burrow the typical inverted pi-shape. The spherical terminations are consistently wider than the connecting basal chamber, thus giving the trace a characteristic dumb-bell appearance. Polished sections reveal that sediment between the vertical paired tubes is undisturbed and clearly lacks spreiten structures. Significant dimensions of the Trenton specimens are illustrated in Figure 2.

(iii) Discussion

When Desio (1940) originally defined the ichnogenus *Bifungites* as a dumb-bell shaped expression on bedding surfaces he unfortunately failed to mention any associated vertical tube structures. Desio distinguished two ichnospecies each based on the shape of the dumb-bell terminations. The Libyan representatives he referred to as *Bifungites fessanensis*, these being characterized by hemispherical terminations. His second ichnospecies, *Bifungites halli*, was based on descriptions given by Hall (1852) of dumb-bell shaped trace fossils from the Silurian Clinton Group of New York and these possessed spherical terminations. At a later date Dubois and Lessertisseur (1964) also described *Bifungites fessanensis* from the Devonian of the Sahara. Though no detailed descriptions were given they interpreted the traces as molds of U-tube openings of spreiten-bearing *Rhiaconoclonium*. The general absence of the complete and detailed descriptions subsequently led Osgood (1970) and later Know (1973) to include species of *Bifungites* within the ichnogenus *Corophioides*, in particular *Corophioides bivacatum*. Later Fürsich (1974) placed *Corophioides*, and hence *Bifungites*, into synonymy with *Diplocraterion*, particularly *Diplocraterion bivalvatum*. *Diplocraterion* spp. is indeed a U-shaped burrow morphologically very similar to *Bifungites*. However, *Diplocraterion* and its synonyms (*Corophioides*, *Arthraria* and *Polypagastia*) are characterized by spreiten patterns between the U-shaped arms. As spreite are regarded as significant ichnogeneric features (Fürsich 1974) *Bifungites* cannot be regarded as a synonym of *Diplocraterion* as spreite are always absent. The ichnogenus *Bifungites* must therefore remain a distinctive form (cf. Gutschick and Lamborn 1975, Mélou and Plusquellec 1975).

Gutschick and Lamborn (1975) erected three new ichnospecies of *Bifungites*: *B. bisagitta*, *B. bisagittula* and *B. bisagittatula*, from Devonian–Mississippian rocks of Pennsylvania and Montana. The three ichnospecies were separated on 'markedly different size and shape of the fossil traces in three stratigraphic zones' (Gutschick and Lamborn 1974, p. 193). However, examination of the size data indicates that there is considerable overlap between the three ichnospecies (Fig. 3) and, in addition, the ichnospecies each exhibit many gradations in burrow shape. Whether or not these three ichnospecies are meaningful and realistic is therefore open to question. Specimens of *Bifungites* from the Trenton limestone exhibit little variation in size or shape and are particularly characterized by their spherical terminations. In this respect they closely resemble *B. halli*. Unfortunately no type specimens of *B. halli* are available in Hall's collections at the New York State Museum (Gutschick and Lamborn 1975, p. 194) and therefore the Trenton specimens are referred to as *Bifungites of Bifungites halli*.

At this point it is also worthwhile commenting on the size of *Bifungites of halli* from the Trenton limestone as recently Mélou and Plusquellec (1975) concluded that Ordovician forms of *Bifungites* were bigger than Devonian forms. Clearly, the data in Figure 3 indicates that this is an oversimplification as the Trenton forms described here are equally as small, if not smaller, than the majority of Devonian forms.

**The Producer and Its Palaeoecology**

In general it is impossible to assign U-shaped burrows to any single group of organisms, as such burrows have been observed to be constructed by polychaete annelids, amphipods, echinurodids, hemichordates and freshwater insect larvae in modern marine and freshwater environments (Osgood 1970, Häntzschel 1975). With the possible exception of the hemichordate *Balanoglossus*, however, the majority of these organisms are sedentary filter-feeders, which feed by setting up currents with the aid of moving parapodia or equivalent mechanisms and drawing in organic detritus. The exception is the case of the freshwater insect larvae which can obviously be immediately dismissed as possible producers of *Bifungites* as the latter is restricted to marine sediments. *Bifungites* can therefore be interpreted as a trace fossil produced by some form of filter-feeder(s). When Desio (1940) first described *Bifungites* he interpreted it as a 'fucoid' or 'colonial animal'. Subsequent examination of his material led Dubois and Lessertisseur (1964) to interpret the burrows as dwelling structures (domichnia) of small trilobites. Gutschick and Lamborn (1975) interpreted the burrows as domichnia of sedentary soft-bodied infaunal filter-feeders. A similar interpretation is adopted here and, furthermore, it is suggested that the most likely producing organism was some form of errant polychaete annelid. This conclusion is based on the following:

1. Though a variety of organisms have been suggested to possess the ability of constructing U-shaped burrows (see above) the majority of such burrows, for example *Arenicola*, *Arthraria*, *Corophioides*, and *Diplocraterion* are usually attributed to polychaete annelids (Osgood 1970, Häntzschel 1975, Hakes, 1976) and only rarely to amphipods, echinurodids or hemichordates.

2. Rare specimens of *Bifungites of halli* (Fig. 4A) actually preserve detail of transverse segmentation or annuli, this segmentation presumably reflecting the detailed anatomy of the producer. This immediately dispossesses echinurodids as potential producers, as the phylum echinurodids are unsegmented, thus suggesting that the potential producers were amphipods, hemichordates or annelids.
3. Amphipods are malacostracan crustaceans and as such are distinctly segmented. However, it is generally accepted that arthropod (crustacean) burrows are particularly characterized by spreite and scratch markings (Osgood 1970). Indeed, other crustacean-produced ichnogenera (e.g. Thalassinoides, Isopodichnus, Spongeliomorpha, Ophiomorpha, etc.) are all characterized by scratch markings preserved particularly on the walls of the burrows. The obvious absence of both spreite and scratch markings therefore suggests that amphipods did not produce Bifungites.

4. If the potential producer of Bifungites was a hemichordate then only the vermiform class enteropneusta would be capable of producing such burrows as other classes live in aggregates or colonies enclosed within a secreted encasement. Some enteropneusts, such as Balanoglossus and Saccoglossus, do in fact live in U-shaped burrows but the majority of genera, such as Ptychodera, Spengelia, and Glandiceps do not make definitive burrows but live buried immediately below the sediment-water interface. Balanoglossus and Saccoglossus live in sand substrates with burrows usually in the order of 10 to 30 cm in diameter (Hyman 1959). Thus the observed substrate type and burrow diameter contrasts strongly with those observed for Bifungites. In addition, enteropneust hemichordates are sluggish and inactive animals, rarely, if ever, venturing from their burrows and never crawling on or below the surface (Hyman 1959 p. 141). In the Trenton limestone, specimens have been observed (Fig. 4D) where trails enter and leave the typical Bifungites trace. Detailed slabbing indicates that these trails were obviously constructed by the Bifungites-producer. Thus it is apparent that the producer was in fact vagile and utilized the U-shaped burrows merely for feeding purposes. The evidence suggests that hemichordates were therefore not responsible for producing the burrows.

5. The most commonly associated trace fossils with Bifungites are simple, straight to meandering crawling trails. These trails are identical in width to the Bifungites traces suggesting that similar sized organisms produced both types of trace and, furthermore, as stated above, rare specimens demonstrate that the producer responsible for the trails was also probably responsible for Bifungites. It was recently demonstrated by Pickrell and Forbes (in press) that morphologically similar trails were produced by earrant polychaete annelids, as a single example of one of these trails actually preserved its producing annelid Valoottiia rugosa. Thus there is good evidence to suggest that Bifungites was produced by errant polychaete annelids.

Based on these observations it therefore appears that the organism responsible for the Bifungites trace was in all probability an errant polychaete annelid. The annelid lived in the uppermost few centimetres in silt substrates and employed its constructed Bifungites trace as a means of protection from predation and as an aid in filter-feeding. In terms of palaeoenvironment, the infaunal annelids most probably lived in 'shallow' areas where current energy and sedimentation rates were low but where there was an adequate supply of oxygen and food for the benthos. Low sedimentation rates are indicated by extensive associated bioturbation and low current energy by the absence of erosive structures and the general absence of bedforms such as ripples and cross-bedding. Associated ichnofaunas with Bifungites and the simple trails described previously include Crustana, Aasophyana, Planolites, cf. Chevrionichnus and cf. Gyrochorte, a Crustana-ichnofacies assemblage (Seilacher 1964) indicative of 'shallow' marine conditions. Associated biota includes a variety of linguloid, orbiculoi, dalmanellid, orthid and strophomenid brachiopods; trinucloid, calyemid and encrinurid trilobites and crinoids, an assemblage similarly indicative of 'shallow' marine conditions. Thus it appears likely that the producing infaunal polychaete annelids lived in 'shallow' marine conditions, which is in agreement with Gutschick and Lamborn (1975), who recently suggested that Bifungites are most likely to be found in tidal flat environments, delta and bar margins and very shallow basinal areas. Unfortunately specific details of sub-environments or related physical environmental parameters such as temperature, salinity and water depth must remain obscure as there is no positive evidence with which to assess them.

CONCLUSIONS

This study of Bifungites of. halli from the Trenton limestone of the Quebec City area has indicated that:

1. Bifungites as a distinctive ichnogenus must be retained and must not be placed into synonymy with the related ichnogenera Arthronia, Cornichnus and Diplocraterion; as suggested by Knox (1973) and Fürsich (1974).

2. Ordovician forms of Bifungites are not necessarily bigger than Devonian forms, as suggested by Mélou and Plusquellec (1975).

3. The most likely producer of Bifungites was some unknown errant polychaete annelid which utilized the burrows as domicinia and adopted a filter-feeding mode of life.

4. The organism responsible for the burrows was probably also responsible for the trails commonly found in association with Bifungites. Thus the polychaete annelid did not adopt a strictly sedentary mode of life as recently suggested by Gutschick and Lamborn (1975).

5. The Bifungites organism inhabited 'shallow' marine environments, though the exact nature of these environments in terms of water depth and other physical environmental parameters, such as temperature and salinity, are indeterminate.

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