THALLOPHYTE BORINGS IN PHOSPHATIC FOSSILS FROM THE LOWER CRETACEOUS OF SOUTH-EAST ALEXANDER ISLAND, ANTARCTICA

by BRIAN J. TAYLOR

ABSTRACT. Numerous unbranched fungal borings penetrate the phosphatic cuticles and shells of decapods and discinid brachiopods from the Lower Cretaceous (? Upper Neocomian–Upper Aptian) of south-east Alexander Island, Antarctica. Comparable borings probably made by a similar saprotrophic, endogenous, and host-specific fungus occur in other phosphatic fossils in the geological record. A high host specificity is particularly characteristic of aquatic phycomycetous zoospores, many of which are chitinophilic. Spherules of iron pyrites and hydrated iron oxide at the blind ends of many of the borings were probably deposited in a suitable micro-environment generated by a decaying part of the thallophyte.

IN the Lower Cretaceous sedimentary succession exposed in south-east Alexander Island (lat. 71° S., long. 70° W.), Antarctica, between Pluto and Mercury Glaciers (lat. 71° 07′ to 71° 34′ S.), macrurous decapods and discinid brachiopods are quite common, particularly at certain localities. Although most of the specimens are natural moulds, a few have black or more commonly bluish white shells. From amongst the latter, five decapods and two discinids were examined by means of thin sections and cellulose peels. Additional specimens studied by X-ray diffraction indicate that the fossil decapod cuticles and the shells of *Discinisca variabilis* Thomson are composed of either calcium phosphate or hydroxyapatite and that both are practically identical in composition with modern *Lingula*. The composition and micro-structure of the fossil decapod cuticles will be described elsewhere.

The five decapod specimens, comprising four species from at least three different horizons, were found in dark indurated mudstones at the northern end of Waitabit Cliffs and three other localities (D, K, and N) in south-east Alexander Island (text-fig. 1). Three of the species, *Glyphea alexandri* Taylor, *Palaeastacus foersteri* Taylor, and *Palaeastacus* cf. *sussexiensis* Mantell are represented by almost complete carapaces, whereas the fourth consists of only a glypheid cheliped. The cheliped is preserved in a concretion. The cuticles of the articulated specimens and small areas of the cheliped cuticle (all remarkably well preserved) contain numerous tubiform borings which are not visible in the hand specimen. Practically identical borings also occur in two discinid shells from Mount Ariel and the northern part of Waitabit Cliffs. The similarity of the borings in size and general morphology throughout all the affected shell and cuticular fragments suggest that they were probably made by the same type of organism. The borings are best developed in the thicker parts of the cuticle and are rare only in the cheliped, which may have been effectively protected by the syngenetic formation of the concretion. Most of the other decapods and discinids in the succession were probably affected by the same 'mycosis'.

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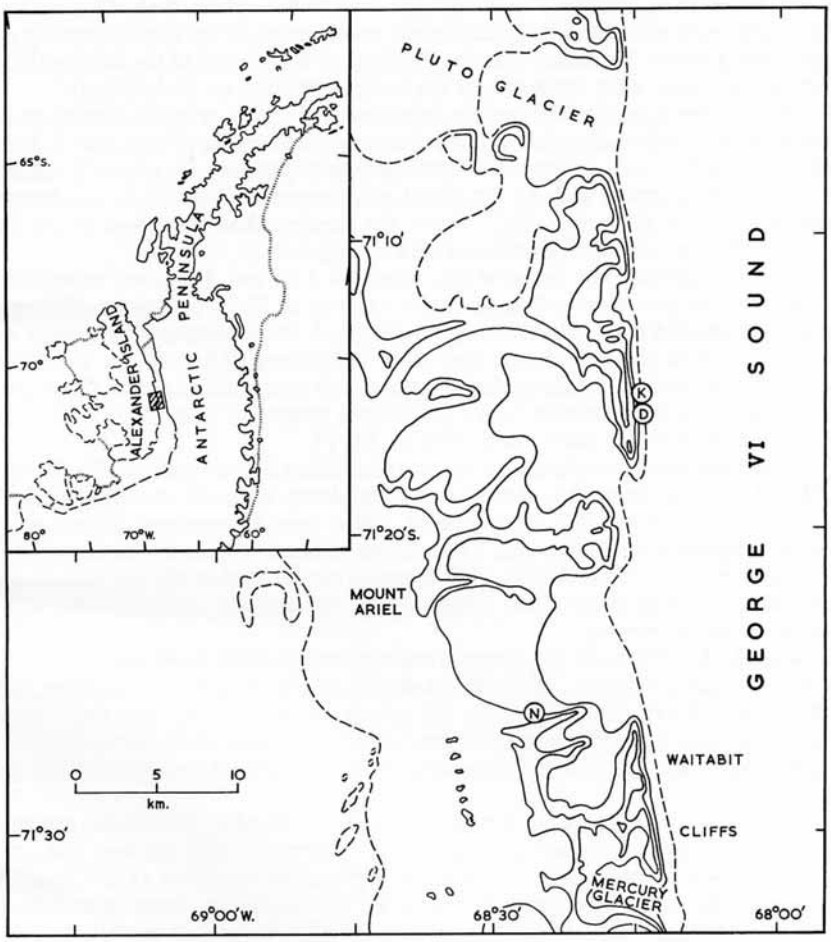

TEXT-FIG. 1. Map of part of south-east Alexander Island showing localities where bored decapods and discinid brachiopods were collected. Inset: location of field area (cross-hatched) in relation to Alexander Island and Antarctic Peninsula.

GENERAL MORPHOLOGY

The borings, which are vermiform, occur as straight, filiform, or sigmoidal tubules, planicurves, planispirals or as open sinistral and dextral helices comprising 4–7 coils (Pl. 52). They are circular in cross-section, of constant diameter, aseptate, and frequently intertwined. In both ordinary light and under crossed nicols, the white or pale brown borings contrast with the darker amber of the cuticle. With one possible exception (in

specimen KG.3.56 of *Discinisca variabilis*), the tubules are unbranched, although branching is frequently simulated by intersections, coalescence, or by tubules passing over or under one another. Thin dark margins defining the boundaries of the tubules (Pl. 52) may either represent walls deposited by the boring organism or Becke effects.

Many of the blind ends of the borings terminate in a round or bullet-shaped granule of iron pyrites or hydrated pyrites which is black or red in colour (Pl. 52, figs. 2, 3, 5, 7). Most of the red forms are translucent. Although these spherules are relatively common in the matrix, they appear to be concentrated either around the outside of the decapods or they fill voids in the cuticle. Spherules in the tubules other than those at the blind ends invariably represent the junction of intersecting borings.

The normal diameter size range of the tubules is 3–15 μm. However, exceptionally fine borings 0·60 μm wide and much larger tubules of 30–50 μm occur. The pyrite granules at the blind ends of the latter are aggregated. Small tubules within larger ones probably represent more than one period of 'infestation'. Most of the tubules are perpendicular or oblique to the cuticular surface and many extend across the whole of the procuticle and the epicuticle where the latter is preserved. Several are deflected on approaching the inner or outer margin (Pl. 52, fig. 1).

Where the tubules are in clusters or sheaves resembling fibrous tumours (Pl. 52, fig. 3; Pl. 53, fig. 1), the cuticle has almost been completely removed or assimilated. The location of these tumour-like developments, which seem to represent centres of proliferation, appears to be haphazard. There are no indications that the boring organism utilized any microstructural feature of the decapod cuticle, such as the lamellae or pore-canal fibrils. Although many of the tubules appear to be empty, some are filled with an as yet unidentified mineral.

In general, the tubules in the decapod cuticles and discinid shells cannot be traced into the surrounding matrix. However, in several of the decapod thin sections, a few tubules seem to lie fractionally outside the cuticle, and in one specimen there appears to be a small area of completely dissociated tubules. Unfortunately, in the absence of any colour contrast such as in the decapod cuticles, it is difficult to detect tubules in the matrices.

By comparison, the borings in the two discinids examined in thin section are poorly developed. The shells are much thinner (120 μm compared with 480 μm) and one of them (KG.3.56) is fragmentary. In the better-preserved specimen (KG.103.81), the outer, colourless cross-fibred layer is not bored but the thicker inner layer (which is brown in colour and sub-horizontally laminated) contains several small borings 0·6–4·5 μm in diameter, some of which terminate in a particle of iron pyrites.

PRESERVATION AND SEDIMENTARY ENVIRONMENT OF THE BORED DECAPODS AND DISCINIDS

The bored decapods and discinids probably lived and died within the photic zone (living *Discinisca* commonly occurs in less than 16·5 m (Stenzel 1965; Thomson, in press). The almost complete preservation of many of the decapods and of other articulated fossils in the same succession (ophiuroids and stemmed crinoids), the rarity of epizoans, and the frequent occurrence of burrowing bivalves in life positions suggest quiet, non-turbulent conditions occasionally coupled with rapid sedimentation. There were few

scavengers. At one locality (K), the decapods may have lived and died in the lee of an offshore bar where abnormally large amounts of plant debris and bored wood fragments accumulated.

On the assumption that the borer was not completely heterotrophic and that the decapod cuticles were secondarily phosphatized in a way analogous to that reported from the Pacific Ocean (Goldberg and Parker 1960), it is probable that the dead decapods or their exuviae and the discinids lay uncovered long enough for the former to be recrystallized and for the spores of some thallophyte to settle and proliferate.

Although the seawater probably had a normal pH value, the non-occurrence in Alexander Island of bedded limestones (other than calcareous concretions) and the large amounts of disseminated and nodular iron pyrites suggest that toxic conditions may have existed below the water/sediment interface. The occurrence of *Lingula*, which can tolerate such conditions, and the phosphatization of the decapod cuticles support this view. The associated fossil flora suggests that the climate was humid and temperate. The sea temperatures may also have been relatively warm since *Trigonia*, which occurs at localities K and D in the same strata as the decapods, is today restricted to the warm waters around Australia (Arkell 1956, p. 616). Deltaic or fluviatile conditions may also have existed periodically.

DISCUSSION

The vermiform tubules in the decapods and discinids are too small and complex for solution cavities. Similarly, because of the high host specificity of the tubules and their absence in the matrices and more richly pyritized shells at the same localities, they are unlikely to have been formed inorganically by 'ambient' pyrites (Tyler and Barghoorn 1963). Therefore, it seems probable that the tubules represent the borings of a microscopic organism.

Like most other trace fossils, fossil borings (particularly the tubiform type) are difficult to interpret. Different organisms with similar habits frequently produce practically identical borings, whereas the same organism penetrating various substrata for one or more purposes (shelter, nutrition, or anchorage) may produce a number of dissimilar cavities. [Here, *substratum* refers to the medium penetrated by the boring organism and *substrate* the chemical compound acted upon by the borer's enzymes.] With some notable exceptions, few fossil borings are morphologically diagnostic and the body fossils are rarely preserved. However, if particular borings can only be grouped in the broadest sense (as Algae, Fungi, or Bacteria), they may contribute towards an understanding of the sedimentary environment in which the host lived or was buried.

The type of vermiform boring discussed here has not previously been recorded in fossil decapod cuticles. However, similar borings are known from the Precambrian (Gruner 1923; Tyler and Barghoorn 1963) and from several Palaeozoic fossils. Occasionally, living lower plants penetrating mainly calcareous substrata produce borings which are comparable in their general morphology (Peyer 1945, fig. 19, p. 515; Schmidt 1962, fig. 2*a*, p. 247). Because the Antarctic borings are better developed in the decapods than in *Discinisca variabilis*, the following comments are concerned mainly with their occurrence in the arthropods.

Although certain Sporozoa, Ciliophora, Cestoda, and Copepoda are parasitic or

symbiotic on decapods, they only inhabit living or dead soft tissues and do not penetrate the cuticle. Similarly, because of their small size, the vermiform tubules are unlikely to have been made by boring trematodes, annelids, bryozoans, cirripedes, and most sponges, the cavities of which are commonly macroscopic. Although the tumour-like growth of *Sacculina* and *Thompsonia* (two parasitic cirripedes) are similar to the bunched tubules in the decapods, the cirripedes only produce a straight hole in the decapod cuticle and the rhizoidal systems are restricted to the soft parts (Borradaile *et al.* 1959). Despite their dubious nature, the origin of the vermiform tubules can be discussed in terms of four groups of parasitic or saprotrophic thallophytes, i.e. Actinomycetes, Bacteria, Algae, and Fungi.

Although the Actinomycetes (which occupy a position between the filamentous Fungi and the true Bacteria) are much smaller than the tubules and are usually branched (Waksman 1959, p. 71), there is at least a superficial resemblance between the coiled sporogenous hyphae of some Actinomycetes and the helical tubules. Moreover, the Actinomycetes attack chitin by secreting chitinase and, more than any other group of micro-organism, they are particularly active at decomposing proteins which they convert to amino acids and ammonia (Waksman 1959). However, the borings are too wide for Actinomycetes (pers. comm., H. Lechevalier), and for Bacteria which are usually less than 2 μm in diameter.

Although parasitic or saprotrophic Fungi on arthropods (usually entomophilous forms) can pierce through unbroken cuticle from the outside and are both chitinivorous (e.g. Laboulbeniaceae) and pathogenic, they penetrate the cuticle only to reach the host's soft parts where the hyphae proliferate (Atkins 1929, 1954; Lefebvre 1934; Takahashi 1958). Nevertheless, the hyphae of the many-branched *Leptolegnia marina*, which bores through the cuticle and soft tissues of live pea-crabs, are approximately the same order of size as the vermiform tubules.

Because many living boring Algae and Fungi are similar morphologically and have comparable pH ranges and size ranges (fungal and algal borings with diameters between 4 and 30 μm overlap one another), the affinities of several fossil forms are uncertain or disputed (Seward 1898; Pia 1927). However, observations based on the morphology, substrate, specificity, and palaeobathymetry may indicate a likely origin for a particular type of boring.

From amongst the many occurrences of essentially unbranched fossil 'algal' and

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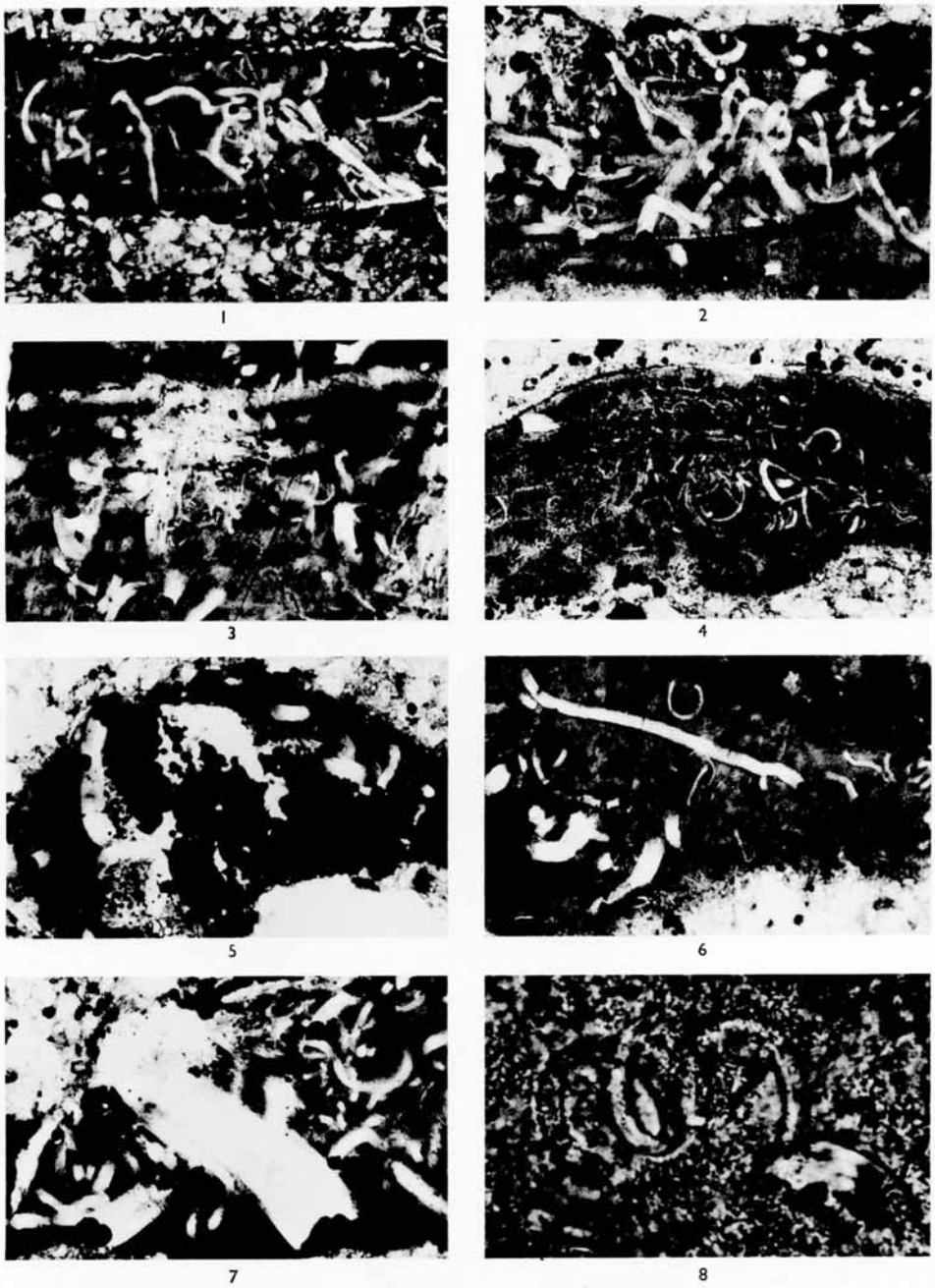
EXPLANATION OF PLATE 52

Figs. 1–8. Thin sections through parts of the cuticle of a specimen of *Glyphea alexandri* Taylor (KG.18.43) showing numerous borings attributed to a saprotrophic fungus. The sections are shown in ordinary light and all but one (Fig. 8) are approximately normal to the cuticular surface. 1, (slide KG.18.43a), ×90. 2, (KG.18.43a), ×230. 3, (KG.18.43a), ×240. 4, (KG.18.43e), ×230. 5, (KG.18.43e), ×270. 6, (KG.18.43b), ×230. 7, (KG.18.43e), ×230. 8, (KG.18.43f), ×1000.

EXPLANATION OF PLATE 53

Figs. 1–3. Thin sections through the cuticle of *Gl. alexandri* Taylor (specimen KG.18.43) showing borings attributed to a saprotrophic fungus. 1, (slide KG.18.43a), ×420. 2, (KG.18.43b), ×300 and in X-nicols. 3, (KG.18.43c), ×300; the cuticle in the right-hand corner in fig. 3 has been virtually assimilated by the boring organism. 4, 5, 'Vermiform tubules' in the cuticle of *Ceratiocaris papilio* Salter (slide 291, carapace 1), both ×300. Figs. 4, 5, by kind permission of Dr. W. D. I. Rolfe.



TAYLOR, Thallophyte borings in phosphatic fossils

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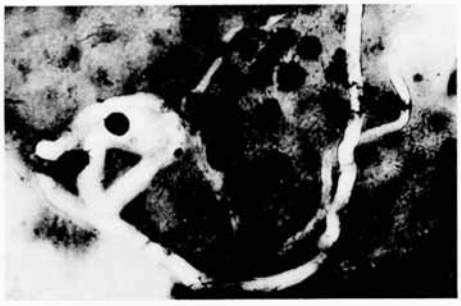

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5

TAYLOR, Thallophyte borings in phosphatic fossils

'fungal' borings without apophyses (i.e. excluding practically all forms of *Mycelites* Roux), the vermiform tubules most resemble those in phosphatic substrata, some of which are relatively rich in iron salts, e.g. the decapod epicuticle and exocuticle, and the periostracum of *Lingula*, which contains up to 10% by weight of ferric hydroxide (Jope 1965). The earliest known vermiform tubules occur in the Precambrian cherts of Minnesota. They are similar in size, have *in situ* grains of pyrite, and are practically identical morphologically to those discussed here. They were originally identified as blue-green Algae (Gruner 1923) but subsequently re-described as inorganic trails produced by ambient pyrite and the authigenic growth of associated quartz, or carbonate trails (Tyler and Barghoorn 1963). Observations based mainly on the Alexander Island material suggest that all the vermiform borings discussed here (including most of the Precambrian examples) are organic structures, some of which have been recrystallized following the death and decay of the organism.

In the iron-bearing Ordovician Wabana Series of Newfoundland, tubular borings 0·20–4 μm in diameter occur within fragments of iron-enriched *Lingula*, spherules of haematite and chamosite, and in phosphatic nodules (Hayes 1915; Clarke 1921). The borings, attributed to a parasitic or saprotrophic Cyanophyceae (*Hayesia hematitica*), are superfically similar to those in the Antarctic decapods and discinids although they are commonly traceable beyond the shell walls into the matrix. However, the morphology and affinities of *H. hematitica* require re-examination.

A more satisfactory comparison can be made with borings in several Devonian fish. In the estuarine placoderm *Phyllolepis orvini* Heintz from the Upper Devonian of East Greenland, there are numerous tubiform borings which, although said to be branched (Stensiö 1936, p. 19), are similar in size and morphology to those described here. Some reach the outer margin, whereas others end blindly in dark blebs which may represent particles of iron pyrites.

In other fish from the lower part of the Upper Devonian of Wildungen (Germany), comparable borings have completely destroyed the minute structure of practically all the bone tissue (pers. comm., E. Stensiö). Similar borings (described as hyphae of the saprotrophic fungus *Odontomycelites lucasi*) occur in a Lower Devonian freshwater psammosteiform from Poland (Tarlo 1964, pl. 13, figs. 4, 5, 6).

Borings practically identical with those in the Devonian fish and Cretaceous decapods also occur in the cuticle of the Silurian phyllocarid *Ceratiocaris papilio* (Rolfe 1962). A re-examination of Rolfe's material has shown that whereas most of these 'vermiform tubules' end blindly, some terminate in a black sphere, probably of iron pyrites. Rolfe compared his structures with the borings of *Clionolithes reptans* Clarke, which has been interpreted as a boring bryozoan or thallophyte (Elias 1957, pp. 380–1).

The spherules of iron pyrites and hydrous iron oxide, which partly surround the decapod cuticles and occupy the blind ends of many of the borings, have not been studied in detail. Nevertheless, they are evidently very similar both in size and general morphology to those described from other 'black shale' successions and sapropelic sediments ranging in age from Precambrian to Recent (Love 1962, 1965; Neves and Sullivan 1964). Except in the larger borings (30–50 μm) where the spherules are aggregated, the diameters of those associated with the tubules exactly match the blind ends. This suggests that the pyrite may have grown *in situ* and that the two structures are related in some way. In Upper Palaeozoic spore exines (Neves and Sullivan 1964) and

in recent invertebrates (Love and Murray 1963) pyrite spherules have grown *in situ* as a result of bacterial activity. There is much in common between the spherules and those of the saprotrophic thallophyte *Polymorphyces* Moore which occurs in the cuticle of *Gigantoscorpio willsi* Størmer (Moore 1963). *Polymorphyces* may be equally affiliated to the Algae, Fungi, or Actinomycetes (pers. comm., L. R. Moore).

In the Alexander Island material, it is probable that the saprotrophic filaments which excavated the tubules posthumously provided foci for iron sulphide precipitation. The putrefaction of these filaments could have released hydrogen sulphide which reacted with iron in the cuticle (mainly in the epicuticle and exocuticle) or in the surrounding sediment.

CONCLUSIONS

Periodically throughout the Lower Cretaceous of Alexander Island, phosphatic decapod cuticles and discinid brachiopod shells from different horizons were bored by an organism with a high host specificity and a high inoculum potential. The extensive development of these vermiform tubules, the large-scale assimilation of parts of the cuticle and the virtual restriction of known arthropod parasites to the soft tissues suggest that the borings were made by a saprophyte after the death or moult of the hosts. Infection of the body tissues may have preceded penetration.

The borings were made either by mechanical pressure exerted by the growing tips (as in some insect exuviae) or by the secretion of acids and/or proteolytic enzymes. The similarity between the helical borings and the Pascichnia of other trace fossils, and the obvious reluctance of the organism to vacate the decapod cuticle, indicate that it was saprotrophic. Its food may have been phosphate, protein, chitin, iron, or some combination of these as all four potential nutrients are relatively common in both the decapods and discinids. In the decapods, the borer may either have been attracted by a small amount of primary phosphate or the cuticles were secondarily phosphatized before, or concomitant with, the boring process. The tumour-like growths in the decapods and the progressive increase in size of uncoiling tubules in *Ceratiocaris papilio* suggest that in both instances, the borer developed *within* the cuticle like certain ciliate Protozoa in modern crab tissues (Chatton and Lwoff 1935).

Algologists have compared *H. hematitica* and the Precambrian tubules with living Cyanophyceae, some of which have a chemotactic affinity for iron (Ellis 1915, p. 121), but the vermiform tubules are unlikely to be algal because most penetrating Algae bore for protection. Furthermore, those which compare with the tubiform borings, i.e. the heterotrophic Oscillatoriaceae, coil only in the free-swimming state (Fritsch 1952) and are usually neither saprotrophic nor holozoic.

The vermiform tubules are probably fungal, since Fungi (although rarely coiled and less commonly marine than Algae) are usually saprotrophic, bore for food, and some forms are stimulated by phosphates. The chitin in the decapods and discinids may also have been important, as this often occurs in the cell walls of many Fungi. Of more doubtful significance is the superficial resemblance between the bullet-shaped apical ends of many of the borings and those of undifferentiated hyphal tips (Robertson 1965, p. 615).

Amongst the aquatic Fungi, the borings resemble an unbranched chytrid type with an exogenous chytrid reproductive system and an endogenous rhizoidal system

(Johnson and Sparrow 1961, p. 330). A high host specificity is particularly characteristic of aquatic phycomycetous zoospores, many of which are chitinophilic.

No borings similar to the vermiform tubules have been found in live crab cuticles (derived from normal marine habitats), dead cuticles, or various calcareous invertebrate shells collected from stagnant pools. The patchy distribution of the vermiform tubules, particularly in the fossil fish, suggests that the corpses were buried and then partly re-exposed long enough for the spores to settle.

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Repository. The specimens are in the Lapworth Museum, Department of Geology, University of Birmingham, and will ultimately be deposited in the British Museum (Nat. Hist.).

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BRIAN J. TAYLOR
British Antarctic Survey
Department of Geology
The University of Birmingham
P.O. Box 363
Birmingham 15

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