

# TRACE FOSSILS FROM THE FOSSIL BLUFF SERIES OF ALEXANDER ISLAND

By BRIAN J. TAYLOR

ABSTRACT. The Upper Aptian Fossil Bluff Series of the central east coast of Alexander Island contains an interesting variety of well-preserved trace fossils. These include abundant *Zoophycus*, tubular burrows, *Chondrites* and (?) *Cylindrites*. Many of the siltstones are characteristically mottled by numerous small vermicular structures. Much of the sedimentary succession has been extensively re-worked.

THE Fossil Bluff Series (Adie, 1962) on the central east coast of Alexander Island, which has been examined between Pluto and Mercury Glaciers (lat.  $71^{\circ}07'$  to  $71^{\circ}34'S.$ ) (Fig. 1) forms

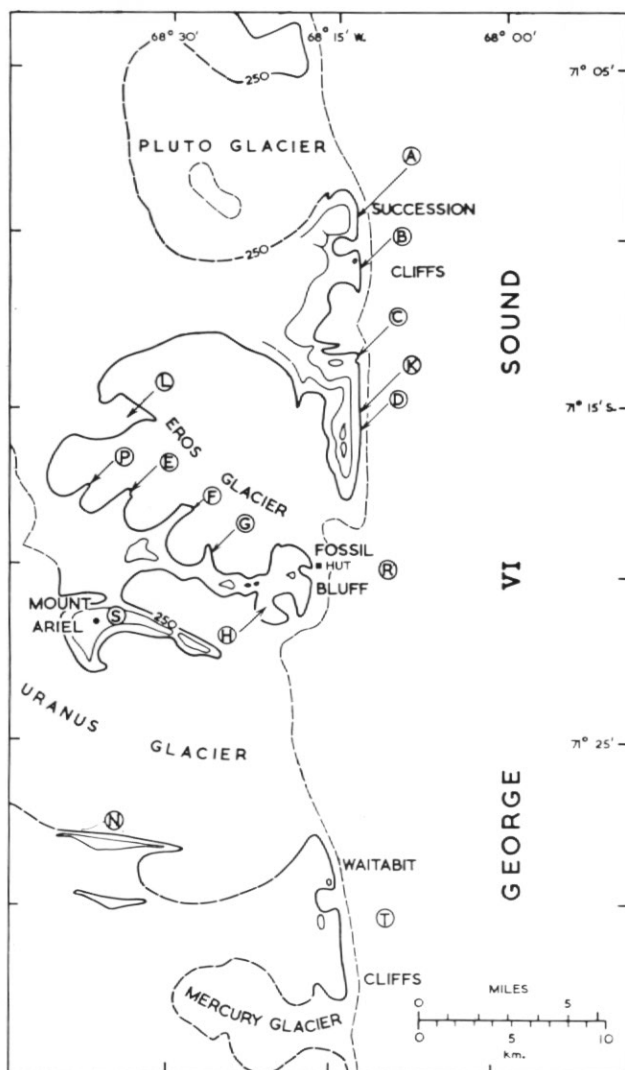


Fig. 1. Sketch map of part of the central east coast of Alexander Island, showing the localities where trace fossils have been collected.

part of a thick, well-exposed and relatively undisturbed succession composed predominantly of richly fossiliferous argillaceous sediments together with generally unfossiliferous sandstones, conglomerates and pebbly siltstones of Upper Aptian age. In parts of the succession a regular alternation of shales and siltstones with mainly flaggy bedded (3–10 cm.) sandstones indicates a flysch facies. South of Venus Glacier (lat. 71°38'S.) the sediments pass into a molasse-like succession of cross-bedded sandstones in which fossilized wood is comparatively common. The thickness of 8,050 ft. (2,455 m.) so far calculated for the Fossil Bluff Series and the visual estimates for the remainder of the succession and for the Belemnite Point and Ablation Point Beds (30,000–40,000 ft.; 9,140–12,190 m.) suggest that the sedimentary succession of Alexander Island forms part of a thick geosynclinal sequence.

Although there is usually no macroscopic indication that the Fossil Bluff Series has been metamorphosed, the sediments have been affected by two stages of low-grade load metamorphism which are intermediate between lithification and regional metamorphism, i.e. the quartz-prehnite stage of the prehnite-pumpellyite metagreywacke facies (Coombs, 1960, p. 342) and the laumontite stage of the zeolite facies (Coombs and others, 1959). However, the fossils are generally unaffected by these metamorphisms.

The depositional environment of the Fossil Bluff Series was probably that of an unstable shelf marginal to a deep trough which lay to the west of the present eastern coastal cliffs of Alexander Island. The presence of crystal lapilli, unweathered pellets of devitrified glass and horizons composed of abundant devitrified glass shards points to volcanic activity in the area surrounding the basin of deposition. The proximity of a hinterland is indicated by large quantities of plants, beach or offshore bar conglomerates and several belemnite shell banks similar to those described from the Jurassic and Cretaceous of New Zealand (Stevens, 1965) and the Middle Bajocian of Canada (Frebold, 1957). According to Frebold (1957), belemnite shell banks (or "belemnite battlefields") are the result of wave sorting in shallow water.

Although some current or wave sorting evidently took place, the discovery of comparatively large numbers of burrowing and other sedentary lamellibranchs, such as (?) *Pholadomya* and *Pinna*, in their living positions suggests that at times sedimentation rates exceeded those of penecontemporaneous erosion. The presence of numerous nodules of iron pyrites and the almost total absence of bedded limestones, apart from large numbers of calcareous concretions, point to a moderately reducing environment unfavourable to the deposition of calcium carbonate (Weeks, 1953).

These sediments were re-worked and the initial stratification was partly destroyed by detritus-feeding organisms which lived in abundance either on or just beneath the sea floor. Some of these organisms may have been suspension-feeders, extruding muddy faeces and pseudo-faeces, and although they are not preserved, they left numerous trails and burrow structures.

In the Fossil Bluff Series, trace fossils (or *Lebensspuren*), consisting of the tracks, trails and burrows of organisms, are abundant and include *Zoophycus laminatus*,\* tubular burrows, *Chondrites* sp. and (?) *Cylindrites*, and many of the siltstones are characteristically mottled by numerous small vermicular structures. The trace fossil *Zoophycus* is a sheet-like laminated burrow composed of a series of horizontally arranged curved lamellae resembling gutters which are crescentic in sections perpendicular to the bedding. Although *Zoophycus* is virtually confined to three stratigraphical horizons, it occurs at ten localities and is often particularly well displayed. It is occasionally associated with *Chondrites* but it is not clear whether the relationship is casual or causal. Another trace fossil is represented by tubular burrows composed of crescentic laminae a fraction of 1 mm. thick. These simple tubes are similar to burrows tunnelled by the anemone *Cerianthus*. *Chondrites* occurs as simple- and multiple-branched burrow systems, and as a radial or stellate structure which S. Simpson (personal communication) has suggested represents the occupation of an abandoned burrow by *Chondrites*. Associated with *Chondrites* are larger tunnels which are interrupted by circular and kidney-shaped swellings (or *Perlenkette*), which are similar to *Cylindrites*. At Fossil Bluff, Mount Ariel and locality H (Fig. 1), *Chondrites* is particularly common at three horizons which have proved useful in correlating the stratigraphy between the three localities.

\* A new type species proposed by S. Simpson (personal communication).

The argillaceous sediments are richly fossiliferous with numerous molluscs, annelids and echinoderms, but no trace fossils were found directly associated with a specific shell or group of shells. The only possible correlation is between a number of distinctive branched trails composed of a cream-coloured sandstone and the occurrence of large numbers of high-spined digitate gastropods similar to *Aporrhais* (*Tessarolax*) *antarctica* Cox. Both the trails and the gastropods occur in the same sequence of beds at Fossil Bluff, Mount Ariel and locality H. Although spirally coiled serpulids, such as *Rotularia callosa* Stoliczka and *Rotularia australis* Cox, together with smaller numbers of open-coiled forms occur in many of the beds, they were probably sessile or semi-sessile organisms. Several of the lamellibranchs were found in burrows but they are quite different from the burrows described in this paper, and it therefore seems probable that most of the trace fossils in the Fossil Bluff Series were produced by soft-bodied mud-feeders and burrowers tunnelling some distance beneath the sea bed.

Trace fossils are relatively common in sediments in South Georgia and South America, and in sediments of Carboniferous age in the Antarctic Peninsula and of Cretaceous age in the James Ross Island group.

When D. Ferguson visited South Georgia in 1911–12, he collected several trace fossils from the Cumberland Bay Series (? Permian—? Triassic) of Stromness Bay (Gregory, 1915). Because these specimens were regularly branched and often reticulate, Gregory (1915) thought they represented a colonial organism and he made comparisons with the monticuliporoid bryozoans, the sponge *Camarocladia* and fucoids. A relatively large plant-like specimen with branches 3–5 mm. across was so similar to the fucoid *Buthotrephis succulens* Hall from the Ordovician Trenton Limestone of New York State, U.S.A., that the sediments in which it occurred (referred to by him as the lower division of the Cumberland Bay Series) were given an Ordovician to Silurian age. However, Høltedahl (1929) and Wilckens (1930, 1932) considered these sediments were Mesozoic in age. *Buthotrephis* has since been recognized as a synonym of *Chondrites* and many of the trace fossils collected by Ferguson can therefore be identified as *Chondrites* sp.

In 1928–29 L. Kohl-Larsen collected from the Cumberland Bay Series several trace fossils which Wilckens (1947) identified as *Taenidium lusitanicum* Heer, *Chondrites palaeozoicus* Richter, *Palaeophycus arthropycoides* Wilckens, *Helminthopsis labyrinthica* Heer, *Gyrochorda* sp., *Chondrites* (?) *simplex* Hall and *Eophyton* sp.

In the same sediments, Trendall (1959) found *Chondrites* was very common in the upper parts of several graded greywacke sandstones and he observed two sizes of branch structure, the smaller type frequently occurring in radiating clusters. He also noted that the branches of *Chondrites* were composed of a sediment which was lighter in colour than the surrounding rock.

In the Upper Cretaceous of the James Ross Island area, numerous calcareous nodules have been found to be extensively marked by trace fossils similar to *Chondrites* (Ball, 1960, p. 2). *Chondrites* is also abundant in the Cretaceous (? Upper Campanian—Santonian) flysch of Chile and it covers the bedding planes at certain horizons (Cecioni, 1957).

Several interesting trace fossils have been found in the Carboniferous Trinity Peninsula Series at Crystal Hill, View Point and Panhard Nunatak in north-east Graham Land. These include flattened cylindrical worm burrows, zig-zagging ribbon-like trails (probably the creep trails of some bottom-dwelling animal), tiny siliceous coils arranged in a mesh-like structure and the traces of segmented worms (Aitkenhead, 1965, p. 38).

Trace fossils are difficult to classify and interpret, because the animal or plant responsible for the structure can rarely be positively identified, and, as recent work in the North Sea (Schäfer, 1962) and in The Wash (Evans, 1965) has emphasized, an almost infinite variety of traces can be made by such diverse organisms as the alga *Enteromorpha* and the burrowing crustacean *Corophium*. In the first half of the nineteenth century many trace fossils were regarded as marine algae and they were classified mainly on the shape of the "thallus" (Häntzschel, 1962, p. 180). Even as recently as 1951 the well-known trace fossil *Chondrites* was identified as a Rhodophyceae (Venzo, 1951). When it generally became recognized that many trace fossils represented the tracks, trails or resting places of invertebrate animals, other classifications were established on the basis of morphological or assumed genetic criteria.

A somewhat different classification was established by Seilacher (1953a), who observed that

different animals with similar habits often produce comparable traces even though their body shapes may be different. For example, outwardly similar burrows or creep trails characterized by C-shaped bands are made by the semi-burrowing anemone *Cerianthus*, the echinoid *Echinocardium cordatum* (Reineck, 1963) and the worm *Nereis*. Seilacher (1953a) classified trace fossils into five major ecological groups: Domichnia (dwelling burrows or *Wohnbauten*); Fodinichnia (feeding burrows or *Fressbauten*); Pascichnia (feeding trails or *Weidespuren*); Cubichnia (resting trails or *Ruhespuren*) and Repichnia (crawling trails or *Kriechspuren*). At least two of the trace fossils described from Alexander Island belong to the Fodinichnia.

Although Seilacher's classification satisfactorily groups ecologically similar trace fossils, it is often very difficult to distinguish a dwelling burrow from a feeding burrow, or a feeding trail from a resting or crawling trail, and some prior knowledge of the animal's probable behaviour is usually necessary. Moreover, when a particular trace fossil such as *Palaeodictyon* is interpreted in several ways by different authors, it is difficult to classify. For example, *Palaeodictyon* may either represent a network of feeding trails, i.e. Pascichnia (Seilacher, 1953b), or the traces of strings of gastropod eggs, i.e. probably Cubichnia (Wanner, 1949).

#### SYSTEMATIC DESCRIPTIONS OF *Zoophycus* AND *Chondrites*

##### FODINICHNIA SEILACHER

##### Genus *Zoophycus* Massalongo

Type species: *Zoophycus laminatus* Simpson

Figs. 7a-h, 8a-d, g

##### *Occurrences of Zoophycus*

The more important occurrences of *Zoophycus*, including their time range and geographical distribution, are:

*Ordovician*. Flat non-spiral form; Dershish Sandstone of Sinat, northern Iraq (Seilacher, 1964).

*Devonian*. *Spirophyton* or *Fucoides*; Lower or Middle Esopus Grit, Genesee Formation, Hamilton Group and Ithaca Shales of New York State (Vanuxem, 1842; Hall, 1863).

*Carboniferous*. Carboniferous Limestone of Linlithgowshire (Howell and Geikie, 1861). *Spirophyton cauda-galli*; Lower Limestone Group at Chapel Point and the Aberlady Limestones near Dunbar (Clough and others, 1910). "Cauda-galli"; Richmond Chert Series of north Yorkshire (Wells, 1955). "Cauda-galli"; *Dibunophyllum* zone of the Carboniferous Limestone near Carnforth, Lancashire (Donaldson and Simpson, 1962). *Spirophyton*; Hannibal Shale (Mississippian) of the upper Mississippi valley (Williams, 1957). "*Taonurus colletti*"; Morrow and Atoka Series (Pennsylvanian) of Arkansas (Henbest, 1960). *Taonurus uedai*; Upper Carboniferous Taiyuan Series of China (Yabe, 1950b).

*Permian*. "*Zoophycus*"; (?) Middle or Lower Permian of western Canada (McGugan, 1963).

*Triassic*. Alpine Upper Triassic (Seilacher, 1953b).

*Jurassic*. *Cancellophycus* and *Zoophycus*; Toarcian, Bajocian and Bathonian of Switzerland (Gross, 1965; Spicher, 1965). *Cancellophycus*; Upper Flags (Aalenian-? Lower Bajocian) of the Cuzieu Beds, southern French Jura (Ager, Evamy and Ramsey, 1963). *Cancellophycus*; Lower and Middle Toarcian of North Africa (Arkell, 1956, p. 265).

*Cretaceous*. *Zoophycus* (probably *Zoophycus insignis* Squinabol); Cerro Toro Formation (? Upper Campanian-Santonian) of Chile (Cecioni, 1957). *Zoophycus insignis* Squinabol and *Zoophycus brianteus* Massalongo; Cenomanian and Lower Turonian of Italy (Venzo, 1951). Upper Aptian Fossil Bluff Series of Alexander Island, Antarctica.

The problematical trace fossil *Zoophycus*, which ranges from the Ordovician to the Pliocene, is found in Europe, North and South America, Africa and the Middle and Far East. It is particularly common in the Devonian of the United States, the Carboniferous of the British Isles, the Permian of Canada and the Jurassic and Cretaceous of Europe. Häntzschel (1962)



has recognized 16 synonyms for *Zoophycus*, including *Taonurus*, *Spirophyton* (Fig. 2a-c, e, f) and *Cancellophycus* (Fig. 2d). When Vanuxem first described *Zoophycus*, he compared the distinctive markings left by the trace fossil with the feathers of a cock's tail and hence *Zoophycus* was originally referred to as "*cauda-galli*" (Vanuxem, 1842, p. 128) (Fig. 3a, b). Later, in the same paper, he referred to other forms of the trace fossil as "*curtain furoid*" (*Fucoides velum*) and "*retort furoid*" (Fig. 3c). The term "*cauda-galli*" has been used recently by Donaldson and Simpson (1962), although when Hall (1863) made *cauda-galli* the genotype of *Spirophyton*, the term "*cauda-galli*" became a specific name.

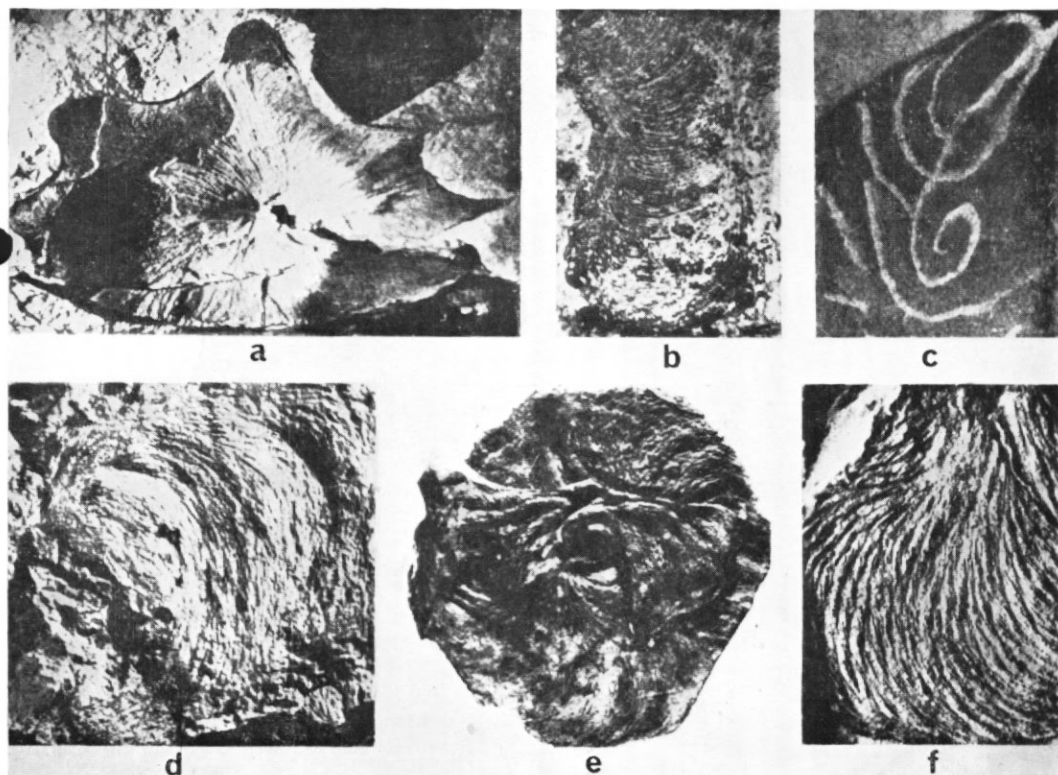


Fig. 2. a. *Spirophyton*, in situ. Plage de Bidart (lower Pyrenees);  $\times 0.11$ .  
 b. Detail of a fringe of *Spirophyton* showing the structure of the limb and border;  $\times 0.27$ .  
 c. Sectional view of *Spirophyton* showing the possibility of limbs crossing without changing direction;  $\times 0.2$ .  
 d. *Cancellophycus marioni* Saporta. Jurassic from the French Alps;  $\times 0.32$ .  
 e. *Spirophyton typum* Hall. Devonian sandstone from Tibesti;  $\times 0.4$ .  
 f. Detail of the limb of a *Spirophyton*. Devonian of Hellena (Ennedi);  $\times 0.8$ .  
 (Reproduced by permission of the Société Géologique de France and J. Lessertisseur from *Mem. Soc. géol. Fr.*, N.S., No. 74, 1955, pl. X.)

*Zoophycus* is common in the Upper Triassic, Miocene and Pliocene of Italy (Seilacher, 1953b), and in the Alpine Rhaetic and Jurassic, tongue-shaped burrows of *Rhizocorallium* are replaced by "*wedelförmige Typen*" such as *Zoophycus* (Seilacher, 1958, p. 1076). In the Toarcian, Bajocian and Bathonian of Switzerland, *Zoophycus* (= *Cancellophycus*) is very common and at certain horizons the trace fossil covers the bedding planes (Gross, 1965; Spicher, 1965). In the upper part of the Cerro Toro formation (? Upper Campanian to Santonian) of Ultima Esperanza, Chile, a few specimens of *Zoophycus* similar to *Zoophycus insignis* Squinabol have been found at one horizon (Cecioni, 1957).

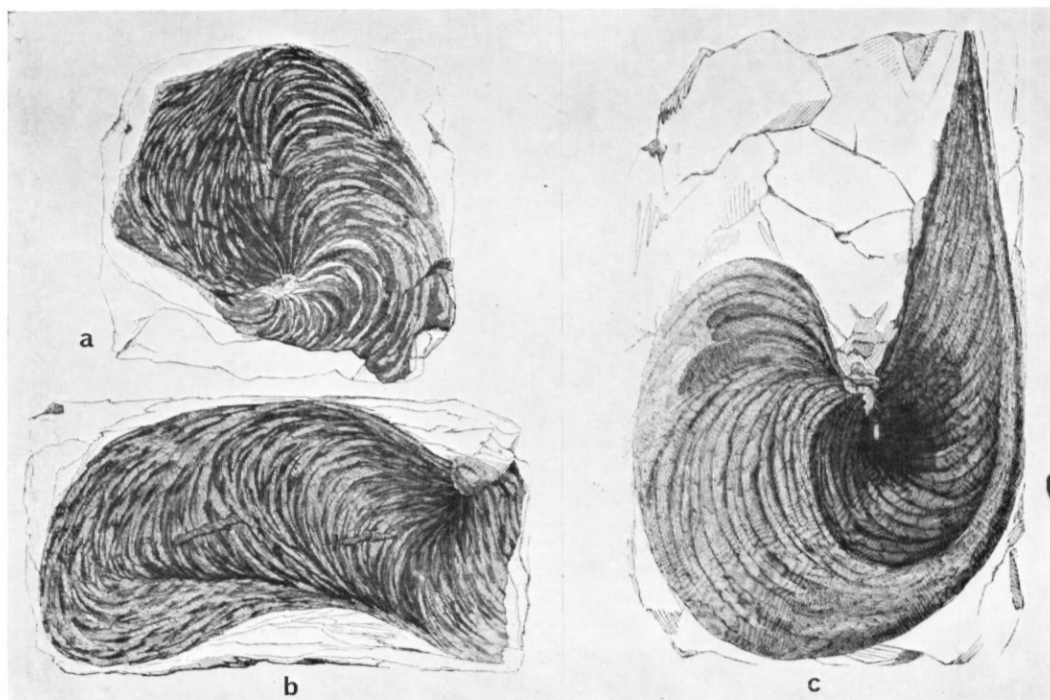


Fig. 3. a, b. "*Cauda-galli*" from the Lower or Middle Devonian Esopus Grit (formerly the *Cauda-galli* or Cocktail Grit), New York State (Vanuxem, 1842, p. 128);  $\times 0.55$ .  
 c. "*Retort fucoid*" from Burdick's quarry in the town of De Ruyter, Madison County, New York State (Vanuxem, 1842, p. 177);  $\times 0.55$ .  
 (Reproduced by courtesy of the New York State Museum and Science Service.)

Two facies are named after *Zoophycus*. In the Dogger of the Pre-Alps of Switzerland there are two facies, the *Mytilus* and the *Zoophycus* facies, the former representing a neritic environment and the latter a deeper-water environment (Heim, 1922). In northern Iraq, the Ordovician of Sinat can be divided into three ichno-facies, the *Cruziana*, *Zoophycus* and *Nereites* facies (Seilacher, 1964), which are thought to represent three distinct bathymetric zones of increasing depth. In the Dershish Sandstone of Sinat *Zoophycus* is associated with *Chondrites* and *Teichichnus* (Seilacher, 1963, p. 533).

Although there is evidence to suggest that *Zoophycus* and other flysch trace fossils represent a deep-water environment, *Zoophycus* is found occasionally in sediments which were deposited in a neritic or even an estuarine environment. In the Pennsylvanian Morrow and Atoka Series of Arkansas, *Zoophycus* (= "*Taonurus colletti*") is commonly associated with *Scalarituba* in a sequence of shallow-water(?) estuarine sediments (Henbest, 1960, p. 383). In the Cenomanian-Turonian of the Caprino area of northern Italy, *Zoophycus* occurs together with *Chondrites* in sediments of neritic facies. Recently, an X-ray radiographic study was made by the Scripps Institute of Oceanography of some sediments sampled from the Gulf of California and north-west of Mexico at depths of 1,416 and 670 fathoms (2,590 and 1,225 m.), respectively. A number of more or less horizontal burrows were found which, according to Ericson (Bouma, 1964, p. 306), may represent *Taonurus* or *Zoophycus*. These burrows are also alleged to be similar to those made by the echinoid *Echinocardium* sp.

#### *Previous descriptions of Zoophycus*

*Zoophycus* was first described from the Lower or Middle Devonian Esopus Grit (formerly the *Cauda-galli* or Cocktail Grit), the Middle and Upper Devonian Genesee Formation, the Middle Devonian Hamilton Group and the Upper Devonian Ithaca Shales of New York

State by Vanuxem (1842). Similar trace fossils in the Waverly Group (Mississippian-Devonian) of Ohio were referred to as *Fucoides velum* (Vanuxem, 1842, p. 176). The descriptive term "*cauda-galli*" was first used to describe several horizontal sections which showed alternating laminae arranged concentrically about a common centre (Fig. 3a). Vanuxem's specimens were between 4 in. and 1 ft. (10 and 30 cm.) wide. Some of them were in the form of a low cone or pagoda similar to those in the Cenomanian and Turonian of Italy (Venzo, 1951), whereas one was a U-shaped burrow similar to *Rhizocorallium* with definite legs or limbs (Vanuxem, 1842, p. 160, fig. 39). The State Geologist of New Jersey described the *Zoophycus* fossil as "a circular disc, often a foot in diameter, of radiating arched fibres, curving outwards from the centre, always in the same direction, like the hair parting on the crown of a man's head". Vanuxem (1842, p. 129) suggested that the "force" which produced the laminae "was excentric, returning upon itself in parallels like the movements of a comet". He hesitantly concluded that these markings were the remains of marine vegetation.

Massalongo, the author of the genus *Zoophycus*, found it difficult to decide to which kingdom the trace fossil properly belonged. In 1850 he referred this trace fossil to *Zonarites ? caput-medusae* and placed it amongst the cellular aquatic plants. However, in 1851 when he first proposed the name *Zoophycus*, he considered it to be intermediate in position between the Algae and the Zoophyta (a group term which formerly collectively described the coelenterates, sponges and bryozoans). In 1852 Massalongo included *Zoophycus* in the Zoophyta calcifera (Anthozoa) and suggested that the trace fossil resembled the Actiniais (probably equivalent to the Actiniaria) and was manifestly vegetable and not animal (Massalongo, 1855, p. 45).

In 1854 he met Milne-Edwards who proposed the new genus *Algarum* for these plant-like trace fossils but this name has not been accepted. Massalongo named four species: *Zoophycus caput-medusae*, *Z. villae*, *Z. brianteus* (Fig. 5a) and *Z. scarabelli*, which were described using botanical terminology. *Z. caput-medusae* was divided into a number of filiform stipes, whereas in the other species the stipes were confluent and the complete fossil resembled a transversely laminated cone.

In 1854 Koechlin-Schlumberger described several specimens of *Zoophycus* from Mende in southern France as "irregular circular and concentric striae forming an assemblage in the form of a leaf between 8 and 10 cm. in diameter". He counted between six and seven striae for every centimetre measured across the "leaf" and in sections which were probably perpendicular to the bedding he described the "fucoid" as forming a "hemi-cylindrical surface" (probably the "gutters" referred to here). Koechlin-Schlumberger was unable to discover any "trace of organization".

In 1861 Dumortier, who also worked in the Rhone basin, found *Zoophycus* (described as tuft-like marine vegetation of the family Algae) was very common on the upper bedding planes of several grey and light-yellowish limestones of Liassic age. These limestones were known locally as the "Fucoid beds or limestones with brush marks" (*coups de balai*), the latter term being particularly appropriate because it graphically described the rough surface on which *Zoophycus* occurred, the curved laminae or striae simulating the marks left by a broom when dragged over a muddy surface.

The trace fossil was represented by a number of thin slabs or sheets measuring up to 9 cm. in width and 12 cm. in length which were occasionally superimposed on one another. The weathered uppermost surface of each sheet or plane lamina was ornamented by a series of closely spaced arcuate laminae (the "gutters" referred to here), which were curved either to the left or to the right. Dumortier counted between four and six laminae for every 1 cm. across the "leaf". The two specimens of *Zoophycus* figured by Dumortier (1861, pl. XII, figs. 1, 2) are very similar to Fig. 8b and to material from the Carboniferous of the British Isles which has been shown to the author by Professor S. Simpson. In comparing the trace fossil with analogous living plants, Dumortier maintained that it was not similar to *Fucus* but belonged to the non-articulate algae, pointing out that the rod-like laminae ("gutters") must have withstood considerable pressure to leave an imprint in the limestone at least 2 mm. thick (Dumortier, 1861, p. 581). Clearly, Dumortier imagined that the *Zoophycus* plant lay first on top of the sediment like washed-up strands of sea-weed and was then compressed. He did not find any signs of fructification.

According to Dumortier, limestones containing *Zoophycus* could not be used as a building

stone because the brush-like markings which covered virtually every exposed surface made the stone too rough. Many of the surfaces covered with *Zoophycus* were usually planar but occasionally they were gently curved or inclined a few degrees to the general stratification (Dumortier, 1861, p. 582).

Hall (1863) was able to distinguish four species of *Zoophycus* from the Upper Palaeozoic of New York and Ohio States, i.e. *Spirophyton cauda-galli* (the genotype), *S. typum*, *S. velum* and *S. crassum* (Fig. 5d). *S. cauda-galli* and *S. velum* had been originally described by Vanuxem as *Fucoides cauda-galli* and *Fucoides velum*, respectively. All the species, especially those coiled about an axis or stem were considered by Hall (1863, p. 83) to be the remains of a natural but "very peculiar group amongst the numerous forms of marine vegetation". A photograph of the type *Spirophyton* Hall (McGugan, 1963) shows a rounded structure with laminae arranged concentrically about a centre and there is a possible stalk of attachment which may have supported a plant-like organism (Fig. 4). In the Hannibal Shale (Mississippian) of the upper Mississippi valley, *Zoophycus* (= *Spirophyton*) which is associated with *Scalarituba missouriensis* is thought to have been formed by currents moving over a shallow, muddy sea bottom (Williams, 1957).



Fig. 4. *Spirophyton* (*Taonurus*) *typum* Hall sp. from the Hamilton Group (Devonian), South New Berlin, New York State (McGugan, 1963, pl. II);  $\times 0.35$ .  
(Reproduced by permission from *The Annals and Magazine of Natural History*.)

*Zoophycus* was first described from a "thin bed of coarse calcareous grit" in the Carboniferous Limestone of Linlithgowshire (Howell and Geikie, 1861, p. 62) and later from the Lower Limestone group at Chapel Point and the Aberlady Limestones near Dunbar, where it was described as *Spirophyton cauda-galli* (Clough and others, 1910). Howell and Geikie thought that *Zoophycus* was the remains of sea-weed.

*Zoophycus* characterizes the bedding planes of many of the limestone units in the Richmond Chert Series of north Yorkshire (Wells, 1955). The trace fossil, which is planar and preserved in a siliceous limestone, comprises layers 1–4 mm. thick composed of alternating light and dark crescentic bands which vary in direction in different layers. The layers cross one another obliquely and some are clearly later in origin than others (Wells, 1955, p. 189). In horizontal sections, the alternating crescentic bands are arranged concentrically but no pagoda-like structure is indicated. Because the structures cross one another, Wells concluded that the trace fossils were post-depositional in origin and had formed beneath the surface when the sediments were still unconsolidated. He was unable to decide on their origin, although he considered several possibilities including small-scale current-bedding, slumping, unilateral shearing, injection of mud into cracks and the traces of an alga. No fossils were found on the same bedding surfaces as the *Zoophycus*.

In the *Dibunophyllum* zone near Carnforth, Lancashire, the trace fossil is planar and parallel to the bedding. The largest specimens are at least 15 cm. wide and 5 mm. thick. In plan view, the alternating bands of sediment tend to radiate from a centre and form a spiral pattern (Donaldson and Simpson, 1962). These markings are present immediately beneath two *Chomatichnus* mounds (interpreted as worm-casts) and they also occur within cylindrical structures in the "Stick Bed". The "sticks", which also represent burrows, contain undamaged foraminiferal tests (Donaldson and Simpson, 1962, p. 76). The *Zoophycus* markings have been interpreted as the "lateral migration" of an animal burrow, the "generating tube" rotating to produce the characteristic spiral pattern on the surface of the bed. *Zoophycus* has also been found in the C zone of South Wales (personal communication from S. Simpson) and in the D<sub>2</sub> zone at Wick. According to Goldring (1964), *Zoophycus* represents the trace of a sediment-eating organism which migrated through the sediment close to the sea floor.

In the Permian of western Canada, "*Zoophycus*" occurs extensively, ranging from the Northwest Territories to the border with the United States, and it is a useful index fossil. It is particularly abundant in the basal (?) Middle or Lower Permian sandstones of the Ishbel Formation (McGugan, 1963).

These "*Zoophycus*" structures are between 4 in. and 1 ft. (10 and 30 cm.) in diameter, and they comprise a large number of filaments or bands between 0.5 and 5.0 mm. thick. Although the majority of the structures exposed in sections parallel to the bedding are planar, a number form low cones and the filaments of these are arranged concentrically about a central point, rod or stalk which may be slightly raised. Many of the conical specimens are formed of several superimposed cones which may be spirally coiled. Distally, the filaments are curved either dextrally or sinistrally to give the "*Zoophycus*" a swirled appearance.

In sections perpendicular to "*Zoophycus*", McGugan observed a number of problematical crescentic laminae (or "tubes") forming a sheet-like trace which was roughly parallel to the bedding. Although he cut 168 sections perpendicular to "*Zoophycus*", only 17 of them showed any crescentic tubes, i.e. laminae, and McGugan (1963, p. 110) therefore concluded that they may have been "formed by a burrowing organism unrelated or (only) indirectly related to the filamental structures". Where the crescentic laminae met the horizontal filament pattern they formed tube-like traces (probably the major laminae referred to here), "which cut across the finer zoophycid filaments" (the minor laminae). McGugan also stated that he had not seen any illustration which satisfactorily demonstrated a direct relationship between the bedding-plane filaments and the crescentic laminae. However, it should be pointed out that he does not seem to have made many sections in the horizontal plane through the burrows.

McGugan has suggested that *Zoophycus* superficially resembles a hydromedusoid or mounds of algae which, when desiccated, shrink and rotate to produce structures similar to *Zoophycus*. Algal mounds can be similarly moulded by current action. However, McGugan virtually dismissed these analogies, although he contended that currents may have produced the curved filaments. He concluded that *Zoophycus* might embody a number of different structures which may include both animals and plants. In the Permian of western Canada "*Zoophycus*" is abundant in shallow-water shelf (or miogeosynclinal) sediments.

In the Upper Carboniferous Taiyuan Series of China, *Zoophycus* (= *Taonurus*) is abundant in a calcareous sandstone and it also occurs in a fusulinid limestone (Yabe, 1950b, p. 36). In horizontal sections parallel to the bedding, the trace fossil (described as *Taonurus uedai* Yabe)



consists of a number of laminae (or "tubes") arranged concentrically, and some of the laminae overlap one another. In sections perpendicular to the structure the laminae are crescentic or V-shaped. None of these *Zoophycus* specimens are spirally coiled, although all are incomplete.

In the (?) Jurassic Fengning Formation of China, several fossils similar to *Sewardiella verrucana* Fucini may represent *Zoophycus*. The specimens are conical with a central node and numerous radiating laminae, and most of the central nodes are convex downwards (Yabe, 1950a, p. 30). The specimens, which are approximately 11 cm. in diameter, were considered by Yabe to represent pseudomorphs after some unknown mineral.

In the Cenomanian and Lower Turonian sediments of the Caprino area of northern Italy, *Zoophycus* and *Chondrites* are very common in approximately 100 ft. (30.5 m.) of shallow-water sediments composed mainly of shales with alternating bands of marly and arenaceous rocks (Venzo, 1951). These sediments represent a gradual shallowing of the sea from semi-bathyal conditions in the Cenomanian to a neritic environment in the Lower Turonian. Both the sedimentary environment and the two trace fossils have been described in detail by Venzo.

*Zoophycus* and *Chondrites* commonly occur together and in large numbers. Both genera are classified as algae, *Chondrites* being included in the Rhodophyceae (red algae). Many of the *Zoophycus* specimens are 40 cm. in diameter and comprise what Venzo has described as veritable beds of algae. According to him, *Zoophycus* may either have been planktonic or it may have represented fragments of a large plant similar to the sea-weed *Sargassum* which multiplies by simple fragmentation of the thallus.

There are at least 12 forms of *Chondrites*, each of which is represented by a large number of examples. Venzo has suggested that, because *Chondrites* is a form of red alga, the trace fossil was fixed on the bottom in a zone between 50 and 90 m. where there would be optimum light-energy conditions for photosynthesis. Because the intensity of light available for photosynthesis is different in different latitudes, Venzo's bathymetric estimations are of doubtful practical value.

*Zoophycus*, which is generally well preserved, is common in the base of the Roncaletti Series (Lower Turonian) but rather rare in the underlying Upper Cenomanian. Two species have been described: *Zoophycus insignis* Squinabol and *Zoophycus brianteus* Massalongo.

*Z. insignis*, which includes a number of very large specimens with a diameter between 30 and 40 cm., is in the form of a low spiral. The outline of each whorl is "amoeboid" with six lobes for every single whorl of the spiral and a corresponding number of deep re-entrants or embayments. The exposed surface is ornamented with laminae sub-parallel to the margin and there is a well-developed radial rib for every lobe. However, the specimens are without a distinct peripheral ridge which some authors have regarded as a definitive character of *Zoophycus* (Venzo, 1951, p. 229). The *Zoophycus* specimens described by Venzo (1951) were orientated with their apices downwards so that in each case the last whorl is the broadest. He did not state how many whorls compose a complete spiral but in at least one specimen the second whorl is half the diameter (20 cm.) and more deeply embayed than the upper whorl.

*Zoophycus brianteus* is generally smaller than *Z. insignis* and the outer margin is less deeply embayed. The lobes are therefore correspondingly broader, the specimens are less "amoeboid" in appearance and they are spirally coiled with four whorls to each spiral. The laminae are arcuate.

A number of planar forms of *Zoophycus* have been recorded from Italy and some authors have therefore suggested that the spiral form may be a secondary feature of the genus *Zoophycus*. Venzo has considered *Taonurus brianteus* as a synonym of *Z. insignis*.

So far as is known, no sections of *Z. insignis* or *Z. brianteus* were made either parallel to or perpendicular to the bedding and Venzo did not mention the occurrence of crescentic bands similar to those described by McGugan (1963) from the spirally coiled "*Zoophycus*" specimens of Alberta.

#### *Forms of Zoophycus*

There are at least two main forms of *Zoophycus* and a number of variations on them. The commonest form, which has been described from the Cretaceous of Italy, the Permian of western Canada and the Devonian of the United States, is spirally coiled (Fig. 5a-d) and



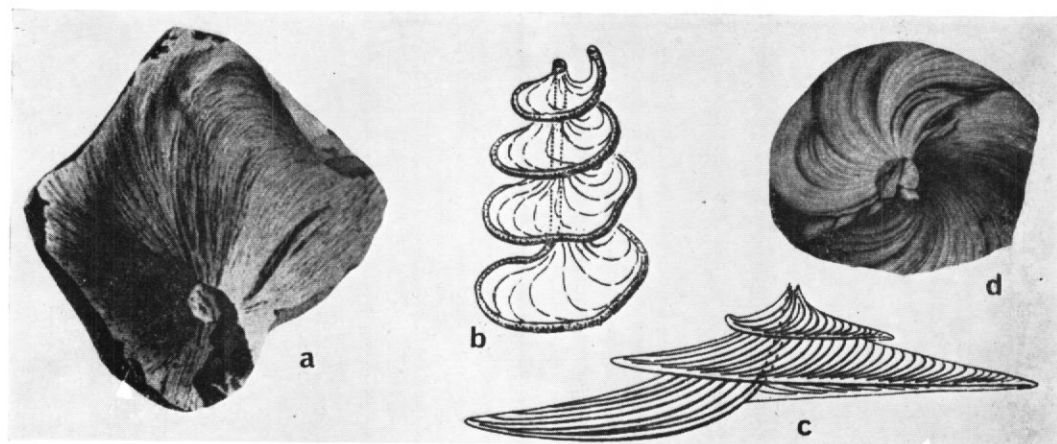


Fig. 5. *Zoophycus*, showing the spiral coiling of some forms.

- a. *Zoophycus brianteus* (Villa) from the Eocene of Italy (Massalongo, 1855, pl. III, fig. 3);  $\times 0.34$ .
- b. Schematic drawing after a Tertiary Italian specimen. The vertical scale is exaggerated (Häntzschel, 1962, fig. 137, 1b).
- c. A drawing showing the spiral form of *Taonurus* (Sarle, 1906, p. 213, fig. 2).
- d. *Zoophycus crassus* (Hall) [*Spirophyton crassum* Hall] from the Upper Devonian of the United States of America (Hall, 1863);  $\times 0.26$ .

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its outer margin may be embayed. The successive whorls increase in size downwards. In horizontal section, a series of laminae or concentric "swirls" radiate outwards from a central rod or stalk which is raised above the main part of the trace fossil. The vertical scale of the model in Fig. 5b has been exaggerated and in reality the whorls are more tightly coiled. Occasionally, the trace fossil is U-shaped or antler-like (Seilacher, 1958, p. 1070, fig. 38) and, as in some spiral forms, a distinct tube or cylinder can be seen. In the Medina Sandstone (Lower Silurian) of the United States, *Zoophycus* (= *Taonurus*) consists of a vertical pipe against which a number of J-shaped lamellae lie to form what is virtually a U-in-U structure (Abel, 1935, fig. 365). The second form (described here) is found mainly in the Carboniferous of Lancashire and Yorkshire. The burrow is planar and in sections cut in the horizontal plane the laminae or gutters may be arranged either in concentric swirls or divided into major and minor, the major ones being remarkably straight. This form is similar to that of a closed spiral *Spreite* (Seilacher, 1958, fig. 39).

The origin of *Zoophycus* is not properly understood and no single interpretation has yet found general acceptance, although most authors consider these unusual markings to be organic and either the feeding trails of a worm or the traces of large marine algae. Many of the trace fossils in the flysch of Europe, including *Zoophycus*, have been compared with the rhizoids of Laminariaceae (brown algae) but there is no general agreement on this (Hirmer, 1927, p. 94).

#### *Material from Alexander Island*

In the Fossil Bluff Series of Alexander Island, *Zoophycus* is confined to three stratigraphical horizons which have proved useful in correlating the stratigraphy between localities D, E, F, G, H, L, Fossil Bluff and Mount Ariel (Figs. 1 and 6). These horizons are:

- i. Approximately 173 ft. (53 m.) of siltstones and thin-bedded sandstones below the upper sandstone cliff at locality L and at equivalent horizons at localities E and F.
- ii. Between 92 and 98 ft. (28 and 30 m.) of siltstones and thin-bedded sandstones above the upper sandstone cliff at locality E and at equivalent horizons at localities F, G and Mount Ariel.

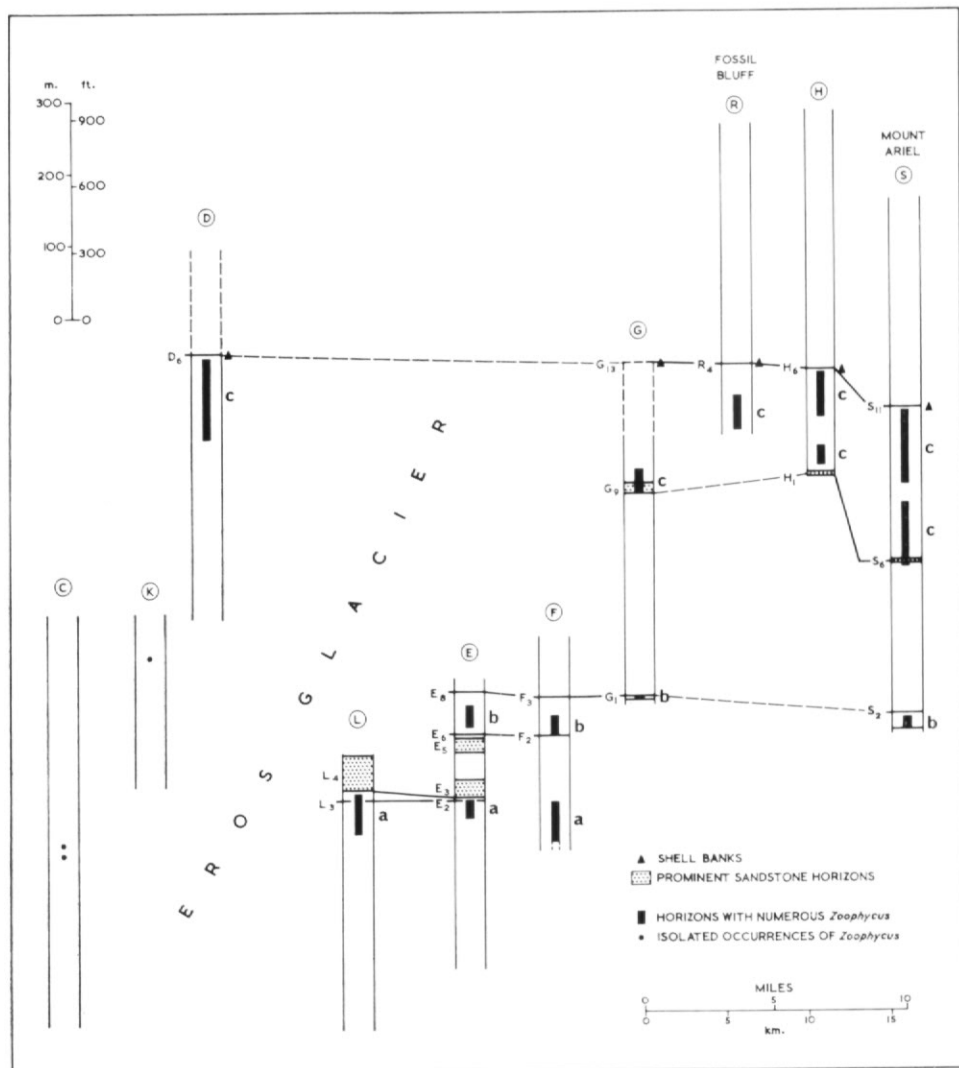
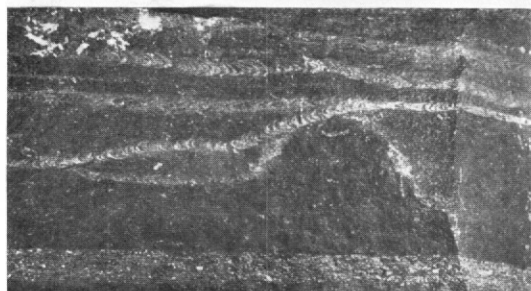


Fig. 6. Diagrammatic representation of the lateral and vertical distributions of marker horizons used in correlating the Upper Aptian succession on the central east coast of Alexander Island. The three *Zoophycus laminatus* marker horizons are indicated in black and by the letters a, b and c.

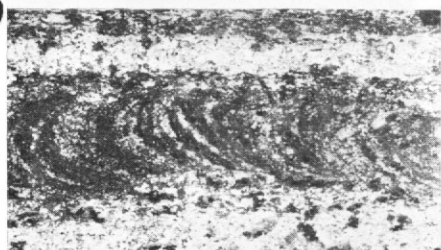
- c. Sheet-like laminated burrows of *Zoophycus laminatus* in a laumontitized and prehnitized vitric tuff. The upper burrows intersect one another;  $\times 0.75$ . (KG.19.5)
- d. A thin section cut perpendicular to a burrow of *Zoophycus laminatus* to show the concentric laminae. The light areas are composed of calcite and prehnite, and the dark areas are composed of siltstone; ordinary light;  $\times 3.5$ . (KG.12.14)
- e. Smaller sub-vertical burrows of *Zoophycus laminatus* in a laumontitized and prehnitized vitric tuff. The burrow in the upper right is very similar to *Teichichnus*;  $\times 1.7$ . (KG.19.3)
- f. A section through *Zoophycus laminatus* cut in the horizontal plane to emphasize the breadth of the burrows (see Fig. 7a). The crescentic bands are represented by a series of cross-cutting laminae. The broader crescentic bands form a number of sub-parallel major laminae from which minor laminae (corresponding to the thinner crescentic bands) are given off at an acute angle;  $\times 1.15$ . (KG.3.63)
- g. A vertical section through a calcareous arkose showing two burrows of *Zoophycus laminatus* intersecting at right-angles;  $\times 0.85$ . (KG.15.1)
- h. A thin section cut perpendicular to the bedding, showing a burrow of *Zoophycus laminatus* associated with lenticular vermicular structures; ordinary light;  $\times 2.6$ . (KG.1.187)



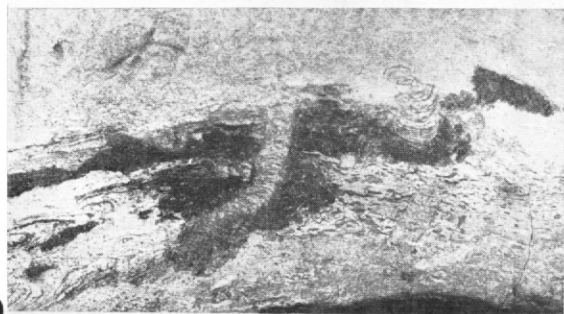
a



b



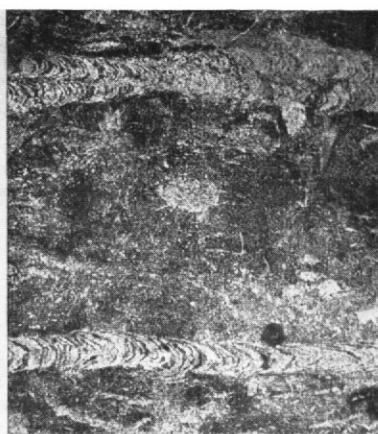
d



e



g



c



f



h

Fig. 7. a. A section through *Zoophycus laminatus* perpendicular to the bedding, showing a series of buff-coloured and slightly asymmetrical crescentic bands separated by sediment;  $\times 1.1$ . (KG.3.63)  
b. Sheet-like laminated burrows of *Zoophycus laminatus*. The uppermost burrows are almost parallel to the bedding, although the crescentic laminae point in opposite directions, but the lower two burrows are sinuous and transgress the bedding planes;  $\times 0.5$ . (KG.3.62)

- iii. Between 170 and 700 ft. (52 and 213 m.) of siltstones and thin-bedded sandstones below a shell bank (composed mainly of the compacted shells of *Aucellina* and *Inoceramus*) at locality D and at equivalent horizons at localities G, H, Fossil Bluff and Mount Ariel.

*Zoophycus* also occurs at localities C, K and P.

The trace fossil is best seen on weathered surfaces where the difference in colour between the crescentic bands representing the gutters and the surrounding rock is accentuated. In several of the light grey, friable laumontitized vitric tuffs at locality D, the alternating series of C-shaped bands of *Zoophycus* are particularly easy to distinguish from the sediment which is composed almost entirely of devitrified glass shards. Most probably the tuffs were originally airborne.

Most of the specimens collected were seen in sections perpendicular to the bedding but occasionally a few sections in the horizontal plane were observed. In the argillaceous sediments, where *Zoophycus* is particularly common, the larger burrows are usually parallel to the bedding although a few are inclined (KG.1.187; Fig. 7h), whereas in the sandstones and in several of the laumontitized tuffs the burrows are usually perpendicular to the bedding (KG.19.3; Fig. 7e). All the burrows are planar and they are never spirally coiled. The majority of the specimens were collected from a dark grey siltstone or greywacke-sandstone at Mount Ariel and Fossil Bluff but others were obtained from localities C, D, E, F, G, H, L and P (Fig. 1). Many of the beds containing *Zoophycus* display convolute lamination but this association is not invariable. Because the few sections that were examined in the horizontal plane are incomplete, both the shape and size of the *Zoophycus* burrow are not known although specimens at least 4 in. (10 cm.) wide have been recorded (KG.19.5; Fig. 7c). Most of the specimens of *Zoophycus* which have been described by other authors have been roughly circular in outline.

The *Zoophycus* burrows of Alexander Island are transversely laminated sheet structures between 3 and 7 mm. thick, 7 and 10 cm. wide and up to 56 cm. long (KG.3.63, 19.5; Fig. 7a, c, f). Definite branching does not occur but intersections are fairly frequent, often at right-angles (KG.15.1, 12.15a, b, 19.1; Figs. 7g, 8a, g). In several rock specimens the laminations cut by *Zoophycus* are completely destroyed and they are distorted at their junctions with the burrow. The crescentic banding of burrows lying one above the other frequently trends in opposite directions and some burrows are sinuous in a vertical plane (KG.3.62; Fig. 7b). The *Zoophycus* burrow, which is usually constant in thickness, terminates either by merging into the general mass of the rock or by coming to a rounded or tapering end.

- b. A polished section through *Zoophycus laminatus*, cut in the horizontal plane and showing the arrangement of the cross-cutting laminae as concentric swirls simulating festoon-bedding. It was this view that originally gave rise to the descriptive terms "cauda-galli" and "coups de balai";  $\times 1.8$ . (KG.10.74)
- c. A section cut in the horizontal plane, showing two burrows of *Zoophycus laminatus*, one of which transgresses a mass of vermicular structures. The crescentic banding has virtually disappeared and the outline of the burrow is rather diffuse. A few vermicular structures occur within the *Zoophycus laminatus* burrow;  $\times 1.8$ . (KG.19.4)
- d. A field photograph of *Zoophycus laminatus* showing the apparent "U" form of the burrow. Sections cut perpendicular to the plane of the photograph show that these burrows are sheet-like and not simple tubes;  $\times 0.1$ .
- e. *Chondrites* associated with a (?) *Cylindrites* burrow, which is interrupted by several circular swellings (*Perlenkette*). Several of the multiple-branched types of *Chondrites* are also interrupted by swellings. These necklace-like burrows may represent the movements of the whole *Chondrites* organism, the swellings corresponding to halting stages when the organism's body rested on the surface;  $\times 0.55$ . (KG.1.842)
- f. A relatively large branched specimen of *Chondrites* with a tunnel diameter between 3 and 5 mm.;  $\times 0.65$ . (KG.2.133)
- g. A section cut in the horizontal plane through *Zoophycus laminatus* to show the right-angle junction between two burrows. The cross-cutting laminae cannot be divided into major and minor ones as in some other specimens;  $\times 0.75$ . (KG.19.1)
- h. A multiple-branched *Fucus*-like *Chondrites* burrow system with individual branches 0.25–1.25 mm. in diameter;  $\times 2.6$ . (KG.19.42)
- i. A horizontal section of one of several stellate structures which probably represent the re-occupation of an abandoned burrow by *Chondrites*. There are three separate stratigraphical horizons which contain these structures, although not all of the structures are stellate in horizontal section;  $\times 1.15$  (KG.11.3)

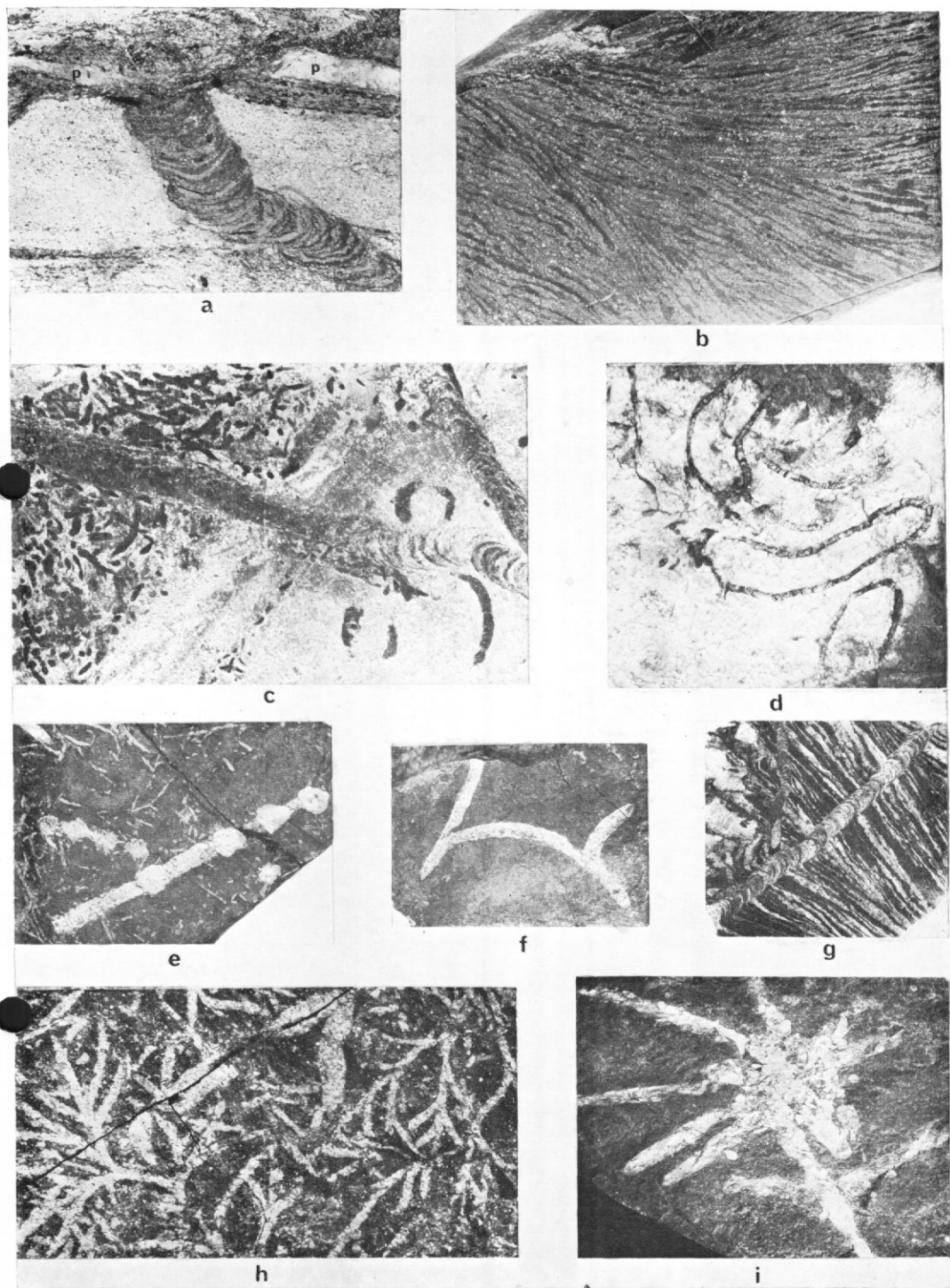


Fig. 8. a. A thin section cut perpendicular to the bedding of a prehnitized siltstone, showing the right-angle junction between two burrows of *Zoophycus laminatus*. A prehnite vein (p) cuts through the upper part of the specimen; ordinary light;  $\times 3.25$ . (KG.12.15b)



In a section cut perpendicular to the bedding and parallel to the length of the burrow, *Zoophycus* is composed of a series of buff-coloured and slightly asymmetrical crescentic laminae which represent the outlines of hemi-cylinders or gutters. These arcuate laminae are usually between 0.5 and 1.0 mm. at their widest part but broader ones 3–7 mm. wide occur at irregular intervals (KG.3.63; Fig. 7a). In sections cut in the horizontal plane parallel to the burrow, the crescentic bands are represented by a series of cross-cutting laminae (the junctions of the upper surfaces of the gutters with any horizontal plane) which are arranged in one of two ways. In specimens KG.3.63 (Fig. 7f) and 19.5, the broader crescentic bands form a number of sub-parallel major laminae from which minor laminae (corresponding to the thinner crescentic bands) are given off at an acute angle (Fig. 7f). With the aid of the major laminae it is possible to match the broader arcuate bands on one side of a 4 in. (10 cm.) wide burrow with those on the opposite side. If these specimens are orientated so that the crescentic bands are convex towards the observer, the branching is left-handed. In specimen KG.3.63 (Fig. 7f) there are usually nine minor laminae for every 2.5 cm. of a major lamina. In a few of the other burrows the laminae are arranged in a series of concentric "swirls" simulating festoon bedding (KG.10.74; Fig. 8b). This arrangement in planar forms of *Zoophycus* is similar to that described by Donaldson and Simpson (1962) and Wells (1955) from the Carboniferous Limestone of Lancashire and Yorkshire.

There are a large number of *Zoophycus* in a massive-bedded cliff at locality P. This cliff is composed mainly of slab-bedded (10–30 cm.) sandstones and subordinate interbedded siltstones which display convolute lamination and downward-intruded sandstone dykes. At the junction between a siltstone and an underlying sandstone, a number of burrows trend obliquely and vertically downwards into the sandstone. Elsewhere in the cliff section many of the burrows are almost parallel to the bedding and a vertical view (Fig. 8d) shows how these structures can be confused with U-tubes. However, sections cut in the horizontal plane parallel to the length of these burrows (KG.15.3) prove that they are sheet-like and not simple U-shaped tubular burrows.

At locality P the burrows are between 3 and 9 mm. wide and 35 cm. long, and they are composed of a series of crescentic laminae which are darker in colour, finer-grained and more argillaceous than the surrounding prehnitized sandstone (KG.15.1; Fig. 7g).

At a height of 800 ft. (244 m.) in the stratigraphical section at Waitabit Cliffs similar burrows occur in a finely banded, cream-coloured calcareous sandstone (personal communication from M. R. A. Thomson). The sandstone, which is 100 ft. (30.5 m.) thick, is divided into a number of smaller units by several thin intercalations of mudstone. The burrows are vertical or sub-vertical transversely laminated sheets several inches deep. In one specimen (KG.102.2) the laminae are arranged obliquely to what is assumed to be the base of the burrow. In sections perpendicular to the bedding these burrows are characterized by a series of crescentic laminae which are concave upwards.

The crescentic laminae of *Zoophycus* resemble stacks of roof gutters arranged horizontally, the minor laminae corresponding to a subsidiary set of gutters. In specimens KG.1.128 and 10.74 (Fig. 8b) several intersecting sets of laminae present an overall spiral pattern of concentric swirls. Because the burrows are rarely seen in horizontal section in Alexander Island the width of many of them is not known.

In thin sections cut perpendicular to the bedding and parallel to the length of the burrow, *Zoophycus* is composed of a series of crescentic mudstone bands which are finer-grained and darker in colour than the surrounding sediment which separates them (Fig. 7d). The mudstone is identical with that typical of the numerous vermicular structures (p. 24). The sediment between the laminae is identical in colour and texture to the general mass of the rock. In several specimens of the prehnitized sediments, the darker mudstone laminae are separated by layers composed mainly of prehnite and calcite (KG.12.14, 15a, b; Figs. 7d, 8a), and prehnite veins transgress them (KG.12.15b; Fig. 8a).

#### *Origin of Zoophycus*

Although the *Zoophycus* of Alexander Island are probably more numerous and better exposed than any of those described previously, their origin is still not clearly understood. The



writer agrees with Wells that they are post-depositional structures which were formed when the sediments were in an unlithified state. The occurrence of load-casts, convolute lamination and sandstone dykes in the stratigraphical succession suggests that the sediments were probably water-saturated, and they could have been subjected to load deformation and temporary liquifaction.

The trace fossil may therefore represent a form of planar squeeze structure or a muddy dyke that has been compacted. Structures of this kind could have attained a width of 7–10 cm. The Upper Limestone Group exposed in the United Kingdom Geological Survey's bore hole at Rashiehill in Stirlingshire has been disturbed by worm borings and "neptunian" dykes, one of which (Anderson, 1963, pl. VIII, fig. 4) is characterized by a series of partly overlapping crescentic bands similar to those associated with the *Zoophycus* of Alexander Island (Fig. 8a, g). However, the margins of the "neptunian" dyke are more irregular than those of *Zoophycus* and it is not known whether the dyke forms a tube or a transversely laminated sheet. According to Anderson (1963), the crescentic bands were formed by rising jets of water which carried up mud from an underlying source bed. Somewhat similar banded sandstone "plugged pipes" have been described from the lower Old Red Sandstone of Shropshire (Allen, 1961) and from the Upper Aptian of Alexander Island (Taylor, 1968). Alternatively, *Zoophycus* may have been formed by running or swirling water moving over a muddy surface (Williams, 1957).

However, at least two features of *Zoophycus* suggest it is organic and represents either an animal burrow or a marine plant. There is certainly a superficial resemblance between the shape of some marine algae and the more "amoeboid" specimens of *Zoophycus*, and in the Devonian of New York State *Zoophycus* has been found with "well defined stems, a foot or more in length at one end" (Vanuxem, 1842, p. 130).

Several authors have suggested that the trace fossil represents the surface markings made by the tentacles or branchial filaments of some organism, either an alga or a sabellid worm. It is difficult to agree with the latter interpretation for a number of reasons. First, the sabellid worms live in burrows which are usually found in a vertical or almost vertical position with at least their upper parts above the sediment so that when the branchial crown is extended for feeding all the filaments are above the muddy sea bottom. It is therefore difficult to imagine how they could have made the peculiar brush-like markings of *Zoophycus*. Secondly, the radius of the branchial crown of most living sabellid worms is usually no more than 2 in. (5 cm.), far smaller than most of the *Zoophycus* specimens which may have a radius of up to 12 in. (30.5 cm.). Lastly, if *Zoophycus* represents the impressions of gill markings, it is most likely that the more resistant mucus-lined burrow would have been preserved in a few specimens if not in all of them.

Probably more significant than the so-called stems is the occurrence of alternating light- and dark-coloured cusp-shaped bands arranged as a series of C's which have been interpreted in a number of ways. Seilacher (1962) has referred to the C-shaped bands in *Muensteria hoessii* Heer as mud and faecal layers, and Richter (Wilckens, 1947) has described similar banding in *Keckia* Glocker as a form of rhythmic defaecation phenomenon or "a pulsating emptying of the intestine". Other authors have suggested that these C-shaped bands were formed by animals such as gastropods creeping over a muddy bottom. In *Rhizocorallium* the C-shaped bands or septa form a compound U-in-U structure which may indicate the gradual progression of an animal downwards through the sediment, each septum representing either a halting stage or a thin layer of defaecated material which the animal has transferred from the outside of the U-shaped tube towards the middle, thus giving rise to the U-in-U form (Veevers, 1962). Crescentic banding within cylindrical structures ("sticks") in the "Stick Bed" may be due to sediment accumulating under gravity when the animal vacated its burrow. Because the "sticks" contain undamaged foraminiferal tests, it is improbable that the material composing these structures passed through an animal's gut (Donaldson and Simpson, 1962).

*Zoophycus* differs from most other laminated burrows in being either a planar or spirally coiled band extending over an area of 1 sq. ft. (0.09 m.<sup>2</sup>) or more (Wells, 1955, p. 189), whereas many of the other burrows are tubular, the C-shaped bands in the simple U-tubes being suspended between two limbs. So far as is known only one specimen of *Zoophycus* has been described which resembles a U-in-U structure (Vanuxem, 1842, fig. 39). Although *Dictyodora* Weiss is a spirally coiled transversely laminated sheet, the coiling is not in regular whorls and

the sheet itself is sinuous in both the vertical and the horizontal planes. The degree of coiling and the sinuosity both increase outwards away from the point of origin (Schindewolf and Seilacher, 1955, p. 379). Both *Scalarituba* Weller and *Taenidium* Heer are tubular, and *Teichichnus* represents the vertical (mostly upward) movements of an originally horizontal burrow.

Because no animal shell has been found associated with *Zoophycus*, it has been suggested that these trace fossils were probably made by a soft-bodied animal such as a worm. However, it is difficult to imagine any known organism burrowing a sheet-like structure between 4 in. and 1 ft. (10 and 30 cm.) wide. Although the Platyhelminthes are strap-like, most of them are only a couple of centimetres in length, whereas a larger organism is indicated by the trace fossil. If the organism was a worm, it was either a narrow vacillating form (to leave matching crescentic bands on either side of a 4 in. (10 cm.) block) or it was ribbon-like with an excretory system similar to that of most Platyhelminthes, i.e. a series of canals arranged on either side of the body. The worm may have crept over the surface by means of cilia or it may have moved more rapidly by producing a series of muscular undulations that passed backwards along the body, thus urging the animal forward. Alternatively, the trace fossil may represent the forward tunnelling in a horizontal plane by *Arenicolites* Salter or *Teichichnus* Seilacher. According to Donaldson and Simpson (1962), *Zoophycus* possessed a "generating tube" which it rotated to produce the characteristic spiral pattern on the surface of the bed.

*Zoophycus* has also been classified by several authors with the Renillidae, a family of pennatulids which includes the living sea-pen, *Renilla*, and a Silurian form, *Alectorurus* (Bayer, 1956). In some forms of *Zoophycus* the imbricately arranged crescentic gutters are joined to one another by trabeculae (Abel, 1935, fig. 368a) and together these form walls in a reticulate mesh structure composed of a number of lozenge-shaped areas which are thought to have contained the individual polyps. According to Alloiteau (1952) the under-surface of the folia of certain living renellids is characterized by a similar reticulate pattern, which represents the arrangement of the polyp canals and not the polyps themselves.

In several thin sections cut across the gutters (i.e. the polyp walls), French palaeontologists have found trifoliate spicule-like structures of calcite between 15 and 40  $\mu$  in diameter and about 1 mm. in length which appear to be identical to those found in pennatulids. Like most pennatulids, the *Zoophycus* organism may have been borne on a muscular and fleshy foot, which, because it was not strengthened by spicules, left no trace (Alloiteau, 1952, p. 415).

There are several objections to the suggestion that *Zoophycus* represents a form of pennatulid. Although the pennatulid lives in a type of burrow made by its stalk and some forms such as *Renilla* can move horizontally over the sea bottom to leave a pattern of concentric whorls on the surface (personal communication from Dr. J. A. C. Nicol), their movements are strictly limited and the burrow simply anchors the organism in the sediment. Normally, the leafy rachis is extended vertically above the substratum. It is highly unlikely that such an organism would tunnel vertically downwards and then horizontally some time after the sediments had been deposited. The occurrence of spicules within the gutters may be entirely fortuitous for they could have been ingested by some organism other than a pennatulid. In this connection, it is interesting to note that in some well-preserved Tertiary sea-pens from Trinidad no spicules were found (Bayer, 1955, p. 295). A few specimens of *Zoophycus* from the Fossil Bluff Series of Alexander Island contain undamaged foraminiferal tests and small spheres which may represent Radiolaria.

In Alexander Island the *Zoophycus* burrows are clearly later in origin than the vermicular structures which they cut, a feature well shown in specimen KG.19.3 (Fig. 8c). Where the *Zoophycus* burrow cuts through the vermicules, the crescentic banding virtually disappears and the outline of the burrow becomes diffuse, a few vermicules remaining within the burrow.

### Conclusions

*Zoophycus* represents an assemblage of trace fossils which have been described under a number of separate generic names by different authors from rocks ranging in age from Ordovician to Pliocene. Those found in the Jurassic have usually been described as *Cancellophycus*, whereas Devonian and Carboniferous forms have been referred to as *Spirophyton* or *cauda-galli*.

Although the various synonyms of *Zoophycus* are similar in form, there are important differences which are usually evident in the derivation of the generic or specific names. Most if not all of the species of *Spirophyton* are spirally coiled and resemble a screw, whereas the upper surface of *Cancellophycus* is usually reticulate and may be covered by rows of elliptical, linear or rhomboidal openings similar to those found in living Laminariaceae such as *Agarum* and *Thalassiphyllum clathrus* (Saporta, 1873, p. 131). Some specimens of *Taonurus* also have a reticulate pattern on their upper surfaces (Abel, 1935, p. 442, fig. 368a).

There are at least two forms of *Zoophycus*. The commoner form, which is spirally coiled, has been described from the Cretaceous of Italy, the Permian of western Canada, the Unterkreide of Czechoslovakia and the Devonian of the United States. Several spirals are arranged around a central axis, and a tube which determines the outer margin of the spiral is thought to have rotated about a variable radius of curvature. In most specimens, the tube rotated in ever increasing circles downwards thus expanding the spiral, but in the Upper Carboniferous of China (where the apex of *Zoophycus* is occasionally convex downwards) the direction of coiling was reversed. The rotation and drag of the tube across the sediment produced the concentric "swirls". In some specimens the upper whorls of the spiral are truncated by the lower ones, indicating that the organism moved downwards as a general rule (Sarle, 1906, p. 213).

According to Toots (1963), some helical burrows such as *Daimonelix* Barbour may be interpreted in terms of two components of movement—a horizontal one of circular motion caused by the asymmetrical burrowing of a bilaterally symmetrical animal with paired appendages, and a second component inclined to the horizontal plane resulting from an oblique orientation to gravity. Toots has further suggested that helical burrows are unlikely to represent feeding burrows, because they are not back-filled, lack faecal material and are unbranched, whereas Häntzschel (1962, p. 218) has stated that *all* forms of *Zoophycus* are feeding burrows.

Because the height of the spirally coiled zoophycids is small (measured from the apex to the broadest whorl), the organism probably rested on or near the surface and tunnelled into the sediments, increasing its radius of curvature as it did so. The rotating tube must have been anchored in some way to the central rod or stalk.

The second form of *Zoophycus*, which has been described mainly from the Carboniferous of Lancashire and Yorkshire and from the Upper Aptian of Alexander Island, is a planar lamina. These traces clearly intrude the sediments and the *Zoophycus* organism burrowed either by pushing aside the sediment in its path (without necessarily introducing material from outside) or by eating its way through the sediment. It is therefore highly unlikely that these structures were produced by algae which would be capable only of trapping the sediment and rotating in response to currents. No interpretation for these structures has found general acceptance although many have been invoked. It is an interesting fact that all the planar forms of *Zoophycus* are between 1 and 7 mm. thick.

It is evident that the genus *Zoophycus* must be re-diagnosed and a number of clearly defined ichnospecies established. The "species" *Zoophycus laminatus* proposed by Professor S. Simpson will, perhaps, include all the planar forms such as those previously described as *Chondrites scoparius*, *Physophycus* and the "cauda-galli" of the British Isles. Another ichnospecies should be established for the spirally coiled forms such as *Spirophyton*, *Taonurus* and some, if not all, of the so-called species of *Cancellophycus*. Because many specimens belonging to this genus have a reticulate pattern of curved lamellae, *Cancellophycus* may constitute a separate ichnogenus.

#### Genus *Chondrites*

Figs. 8e, f, h, i, 9b, c

The trace fossil *Chondrites* is well known from the Ordovician of New York State, the Devonian of north Devon, the Carboniferous of the British Isles, the Jurassic of Europe and the Cretaceous of England (Simpson, 1957). In the Ultima Esperanza area of Chile, black flysch and flysch with *Chondrites* have been recognized (Cecioni, 1957, p. 545). The flysch with

*Chondrites* was probably deposited in an oxygen-deficient environment. In some localities, such as in the Dingle Beds (Devonian) of County Kerry, Ireland, *Chondrites* is preserved in strong relief and strikingly resembles thick strands of sea-weed.

#### *Material from Alexander Island*

In the Fossil Bluff Series, simple- and multiple-branched tunnel systems of *Chondrites* occur either as solitary burrow networks or more abundantly in several of the mottled siltstones and mudstones, the mottling resulting from the piping down of a pale-coloured calcareous "tunnel sediment" into a number of excavated *Chondrites* burrows. At Fossil Bluff and at equivalent horizons at Mount Ariel and locality H there are three mottled siltstones which can be used for correlating the stratigraphy between the three localities. These siltstones are characterized by convolute lamination and other "soft-sediment" deformation structures.

There are four types of tunnel system. The commonest is a multiple-branched *Fucus*-like structure with individual branches 0.25–1.25 mm. in diameter (KG.19.42; Fig. 8h). Some of the second- and third-order branching is of capillary fineness. A larger branched structure (KG.2.133, 3.136; Fig. 8f) with a tunnel diameter between 3 and 5 mm. wide is similar to *Chondrites affinis* Brongniart. Associated with the *Fucus*-like *Chondrites* are very much larger tunnels 3–10 mm. in diameter which are interrupted by circular and kidney-shaped swellings or *Perlenkette* (KG.1.842, 844; Fig. 8e). Several of the multiple-branched types are also interrupted by swellings. At Fossil Bluff and at localities H and N, there are three horizons composed of buff-coloured mottles and devitrified glass pellets. The sediments have been re-worked, and spherical and elliptical calcareous mud clots enclose rotated pellets and crystal grains, which represent the fall-out products of an ash shower. In horizontal sections approximately parallel to the bedding, many of the mottles are radial or stellate and these form a fourth tunnel system (Fig. 8i). S. Simpson (personal communication) has suggested that these radial structures represent the occupation of an abandoned burrow by *Chondrites*. Horizontal and vertical views of *Chondrites*, both in the hand specimen and in thin section, reveal crescentic or less regularly shaped banding. At several horizons *Chondrites* is associated with *Zoophycus laminatus*, but it is not clear whether there is any connection between the two trace fossils. Horizons containing *Chondrites* have been re-worked.

The mottled siltstones in the Fossil Bluff Series are comparable with the "mottled marls" of the Dorset coast (Simpson, 1957, p. 492). At a height of 400 ft. (122 m.) at Succession Cliffs (locality B), a 1 in. (2.5 cm.) thick band of cream-coloured sandstone has been tunnelled by *Chondrites* which has piped down the sandstone into the underlying siltstone. A similar mottled siltstone has been described from the Lynton Beds of north Devon (Simpson, 1957, pl. XXII, fig. 4).

Many of the characteristic features of *Chondrites* observed by Simpson (1957) are also present in the Alexander Island material. The branching, which is frequently multiple, is lateral and never equally dichotomous, and the angle of branching (usually between 30 and 50°) is fairly constant along any one part of the tunnel system. The main tunnel is slightly wavy and constricted beyond the point where a side branch diverges from it in a smooth curve, and at the axial angle it is broader than the main tunnel. The tunnels, which are circular in cross-section, rarely cross one another. *Chondrites* is best developed in the upper parts of several siltstone units. At a locality in south-east Alexander Island (lat. 71°38'S., long. 68°17'W.) it is associated with larger tubular burrows, and the rock specimen which represents part of an alternating series of dark siltstones and grey-weathering calcareous sandstones has been extensively re-worked (Fig. 9a). The bed-junction preservation of *Chondrites* is clearly seen.

In thin and polished sections cut parallel and perpendicular to the multiple-branched tunnels, the *Chondrites* branch system is composed of a mudstone which is finer-grained and darker in colour than the surrounding rock (KG.19.42a, b, c). Many of the individual branches are crossed by a series of crescentic bands (Fig. 9b, c).

At Crabeater Point (lat. 68°41'S., long. 64°08'W.) on the east coast of the Antarctic Peninsula, *Chondrites* has been found in a scree fragment (E.2129.4) of probable Cretaceous age. In a thin section cut approximately perpendicular to the bedding, some of the more elliptical



mottles representing sections through the burrow system are characterized by a series of crescentic bands similar to those described from Alexander Island. The mottles are composed almost entirely of calcite, the larger crystals forming well-rounded spheres. Vermicular structures (p. 24) are present in the same thin section.

Wilckens (1932, p. 7) has described and figured a number of problematical umbrella-shaped structures from Prince Olav Harbour, South Georgia, which probably represent random sections through a *Chondrites* burrow. One of his illustrations (Wilckens, 1932, fig. 3a) shows a series of C-shaped bands which are separated by ordinary sediment.

### *Origin of Chondrites*

Simpson (1957) has shown that the typical form of *Chondrites* is a root-like system of tunnels radiating downwards and outwards from a fixed point on the surface. As such, the multiple-branched tunnels represent only the distal parts of the burrows. He has further suggested that the branched burrow system may have been produced by a siphunculoid and phobotactic worm feeding and excavating by means of an extendible proboscis. Because only a few root-like tunnel systems were found in Alexander Island, it is inferred that *Chondrites* tunnelled horizontally and only burrowed deeper when the food supplies were exhausted.

Although Simpson's (1957) account of *Chondrites* is ingenious, he had unsatisfactorily explained how a series of branched tubes with a length often 20 or 40 times their diameter became filled with sediment, even assuming that the tunnels were lined with mucus and were therefore relatively rigid. King (Simpson, 1957) has suggested that the *Chondrites* organism might have assisted the emplacement of the sediment, whereas Ferguson (1965) has postulated that sediment lying around the mouth of the tunnel system was sucked into the tunnels immediately after the withdrawal of the proboscis. The Alexander Island occurrences of *Chondrites* with crescentic laminae (KG.3.120) support King's suggestion that it may have assisted the emplacement of sediment, probably by repeatedly partially withdrawing its proboscis and thus allowing small amounts of sediment to filter down into the tunnel.

It is concluded that the four forms of *Chondrites* that occur in the Upper Aptian of Alexander Island are related to each other. The frequent association of *Chondrites* with *Cylindrites* in the Upper Emsian of north Devon and in the Lower Lias of Dorset led Simpson (1957) to tentatively suggest that *Cylindrites* might represent the progression of the whole *Chondrites* organism through the sediment. In the Upper Aptian of the central east coast of Alexander Island, *Chondrites* is often found with larger tunnels interrupted by circular and kidney-shaped swellings. Several of the multiple-branched *Chondrites* structures terminate in a swelling. From field observations, the writer concluded that these larger markings represented the movements of the whole *Chondrites* structure, the swellings corresponding to halting stages when the organism's body rested on the surface.

The behaviour pattern of phobotaxis, whereby an organism in its search for food stops short and retreats when it encounters (through some chemical stimulus) a second tunnel made either by itself or by another individual, was applied by Simpson (1957) to *Chondrites*, which he thought progressively withdrew its single proboscis along the various side branches towards the surface when it had successfully exploited the surrounding sediment. However, it is difficult to imagine why an organism should go to such lengths to avoid an empty tunnel unless that tunnel was simultaneously occupied by another part of itself. It is therefore suggested that radiating *Chondrites* tunnel systems may have been excavated by an animal with many tentacles rather than by one with a single extendible proboscis. Nevertheless, the writer agrees with Simpson that the *Chondrites* tunnels are in no way comparable with those of the tubicolous polychaete *Sabellaria*, which forms honeycomb-like banks of permanent living burrows composed of coarse sand near to low-water mark. The burrows of *Lanice* are also different from those of *Chondrites*.

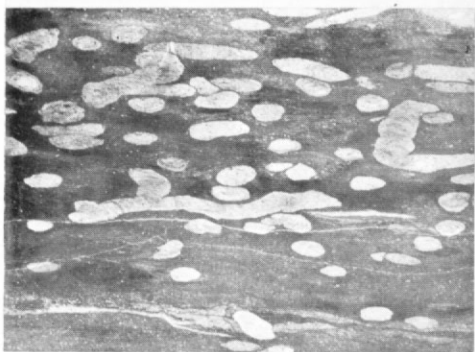
Horizons with numerous *Chondrites* branch structures probably represent extensive mud substrates. According to Venzo (1951), *Chondrites* is indicative of a neritic environment. Although the *Chondrites* organism occasionally descended deeply, its movements were mainly horizontal.



a



b



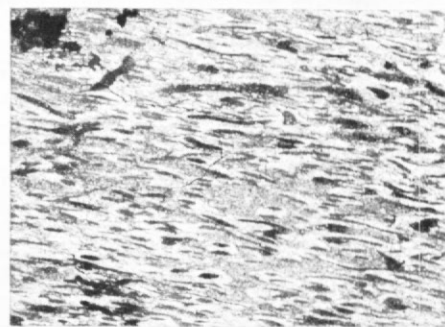
c



d



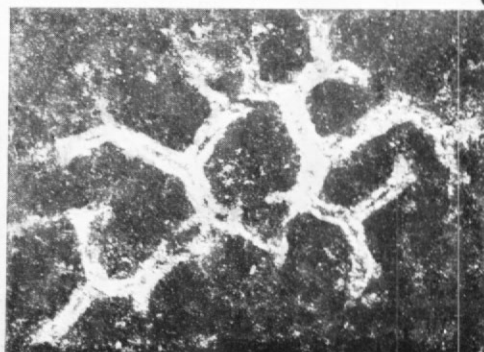
e



f



g



h



## TUBULAR BURROWS IN MOTTLED SANDSTONES

In many localities where sedimentary rocks occur extensive re-working by burrowing organisms has given rise to mottles or mottled structures. The mottles, which are usually different in colour and texture from the surrounding sediment, may have distinct or indistinct boundaries. Many mottled structures are formed either by the filling of open animal burrows with sand or mud after a period of non-deposition or by the sifting and ingestion of sediment by burrowing organisms such as worms or molluscs. Extensive bioturbation is common in the Jurassic of the Yorkshire coast (Farrow, 1966).

Mottled structures in sandstones have been described from the Upper Carboniferous of north and central Derbyshire (Greensmith, 1956), the Cretaceous (Lower Barremian) of Westphalia, Germany (Kuenen, 1961, p. 73), the Cretaceous of Colorado (Fentress, 1955; Lane, 1963) and the Cretaceous of Wyoming (Moore and Scruton, 1957). Mottled sandstones occur extensively at a locality in south-east Alexander Island (lat.  $71^{\circ}38'S$ , long.  $68^{\circ}17'W$ ) (personal communication from R. R. Horne). One of the specimens (KG.72.9; Fig. 9a) represents part of a cliff of alternating dark siltstones and grey-weathering mottled calcareous sandstones. Some of the sandstones are finely laminated, whereas the siltstones are mottled by the infilling of open animal burrows with sand. The colour difference between the sand forming the mottles and the surrounding siltstone is sharp and well defined.

There are two sizes of burrow, i.e. small branched tubes of *Chondrites* representing downward extensions from the base of a sandstone bed (bed-junction preservation) and larger tubular burrows 6–11 mm. in diameter, some of which were also excavated downwards from an overlying sandstone. These structures are circular or elliptical in cross-section. The larger burrows, which destroy laminations in their path, are either obliquely or sub-vertically inclined to the bedding and many of them are characterized by a series of dark-coloured crescentic laminations which in the hand specimen are similar in composition to the surrounding siltstone. They resemble a polished section of *Chondrites* described and figured from the southern block of Succession Cliffs (p. 20; Fig. 9c). In the same rock there are numerous vermicular structures (p. 24).

Tubular burrows, similar to those described here, are abundant in the marsh, tidal-flat and lagoonal deposits of the Dakota Sandstone of north-western Colorado (Lane, 1963) and in the shallow-water Upper Carboniferous sediments of Derbyshire (Greensmith, 1956).

Greensmith (1956, p. 352) has described two sizes of burrow: small tubular ones between 1 and 4 mm. in diameter and up to 20 mm. in length, and larger ones with a maximum

- Fig. 9. a. *Chondrites*, representing downward extensions from the base of a sandstone (top left), associated with larger tubular burrows 6–11 mm. in diameter which are crossed by crescentic bands. The larger burrows, which are also tunnelled down from the overlying sandstone, destroy all laminations in their path;  $\times 0.63$ . (KG.72.9)
- b. A view in the horizontal plane of (?) *Chondrites* showing crescentic banding, which may indicate that the organism filled the abandoned parts of its burrow system by repeatedly partially withdrawing its proboscis and thus allowing small amounts of sediment to filter down into the burrows;  $\times 0.7$ . (KG.3.120)
- c. A polished section of a mottled siltstone, cut perpendicular to the bedding and showing the mottling which has resulted from the piping-down of a pale-coloured calcareous "tunnel sediment" into a number of abandoned *Chondrites* burrows. Many of the mottles are characterized by crescentic banding;  $\times 1.15$ . (KG.8.46)
- d. Worm-like markings on the upper bedding plane of a prehnitized siltstone. The vermicular structures have a slightly higher relief than the surrounding sediment;  $\times 0.85$ . (KG.2.11)
- e. Two sizes of vermicular structure which can be clearly seen in a hand specimen of a siltstone from the Fossil Bluff Series of Alexander Island. The smaller vermicular structures are ovate, lensoid or hook-like, whereas the larger ones are more irregular and elongated;  $\times 0.75$ . (KG.14.3)
- f. A thin section cut perpendicular to the bedding of a mottled siltstone, which is composed of compacted "lenticules" of brownish silt surrounded by lighter-coloured aureoles of calcite and quartz or prehnite; ordinary light;  $\times 3.5$ . (KG.3.49)
- g. A thin section cut in the horizontal plane and parallel to the bedding of a prehnitized mottled siltstone, showing the darker cores and lighter-coloured surrounding sheaths or tubes. Many of the cores are traversed by fine cracks; ordinary light;  $\times 4.2$ . (KG.1.392f)
- h. A hand specimen of a honeycomb-like network similar to the regular hexagonal structures of *Palaeodictyon*. In sections perpendicular to the bedding the branches are elliptical in cross-section;  $\times 4.35$ . (KG.19.17)

diameter of 11 mm. and a maximum length of 44 mm. The angle of the smaller burrows varies between vertical and horizontal, although all the tubes are initially vertical. The burrows were probably tunnelled in the more argillaceous sediment during periods of comparative quiescence before the onset of more turbulent conditions when the intercalated sandstones were deposited. The transverse laminations are interpreted as infillings and the burrows themselves are attributed to annelids. The larger structures, usually vertical tubes, may have been formed by boring molluscs. Similar structures with somewhat diffuse lateral margins are made by the burrowing lamellibranch *Mya arenaria* and by various siphunculoid worms.

Laboratory studies by Moore and Scruton (1957) have indicated that the re-working of a sediment and the resultant mottling take place within the uppermost 6 in. (15 cm.) of sediment and usually before the sediment has been buried more than 2 ft. (0.6 m.) below the sea floor.

#### VERMICULAR STRUCTURES IN MOTTLED SILTSTONES

Throughout the Fossil Bluff Series of Alexander Island the siltstones and fine-grained mudstones are characteristically mottled by numerous small, lenticular and cusped structures resembling vermicelli (Fig. 9e, f). These structures are best seen in some of the grey-weathering laumontitized tuffs and brownish weathering siltstones where there is a marked colour difference between the surrounding rock and the vermicular structures, which occasionally have a higher relief than the ordinary sediment and resemble aggregations of worm casts. The upper bedding planes of several siltstones in the section at Fossil Bluff are covered by these vermicular structures, which may represent the almost complete bioturbation of the sediment by burrowing organisms. In some horizons there are between 100 and 200 of these structures in every square inch of sediment and therefore very little material has not been re-worked. Dense patches of the vermicular structures are crossed by traces of *Zoophycus laminatus* (Fig. 8c) and thin beds composed of compacted vermicules are often more resistant to weathering than the surrounding sediment. Where the siltstones are banded or laminated, the stratification is undisturbed even though the vermicular structures may be abundant. There are at least two sizes of vermicular structure, which are frequently found together in the siltstones and mudstones of Alexander Island, and both can be clearly seen in the hand specimen (KG.14.3; Fig. 9e). The larger marking, which is between 1 and 3 mm. wide and elliptical in cross-section, probably represents either the trace of a soft-bodied worm or the faecal pellet of a worm (KG.2.11; Fig. 9d). The smaller vermicular structures, which are between 0.25 and 0.50 mm. wide, are similar to worm casts. They are lenticular or cusped in outline and, in thin sections cut perpendicular to the bedding, these worm-like structures are surrounded by lighter-coloured aureoles of coarser-grained material composed mainly of calcite and quartz or prehnite (Fig. 9f). These small structures may represent the infilled burrows of a worm, faecal pellets or thin flakes of mud. Flakes of mud resulting from the stripping of a surface lamina by tidal waters may have been incorporated into the normal sediment.

In thin sections cut in the horizontal plane parallel to the bedding, both the large and small vermicular structures appear as oval or elongated pellets composed of a brownish silt, which is finer-grained and darker in colour than the surrounding rock that forms a narrow sheath or "tube" separating the structures from the ordinary sediment. Because these tubes are approximately twice as wide as the vermicular structures and longitudinally more extensive, the structures occupy only a small part of each tube. Several vermicular structures may occur within the same tube which is occasionally branched. Some of the branched structures are similar to a small form of *Chondrites*. There is usually a sharp and striking colour and compositional difference between the structures and the surrounding tube, and between the tube and the ordinary sediment. The vermicular structures are occasionally crossed by fine cracks (KG.1.392f; Fig. 9g) and the more ovate forms are enclosed by sediment which "flows" around them. In rocks which are prehnitized the darker pellets are either unaffected or only partly affected by prehnitization, whereas the surrounding tubes are almost completely prehnitized, as can be seen under crossed nicols.

In thin sections cut perpendicular to the bedding these structures are ovate, lensoid or hook-like, up to 7 mm. long and 0.125 mm. thick, and many of the more elongated forms are orientated parallel to the bedding (Fig. 9f). Because the surrounding tubes of light-coloured

sediment are represented by aureoles in these sections, many of the structures resemble "eyes". In this respect, the vermicular structures are very similar to the trace fossil *Planolites ophthalmoides* Jessen, which may represent the infillings of annelid burrows, the walls of which may have been strengthened by a secretion of mucus (Heide, 1955).

Although *Planolites* occurs in rocks ranging in age from Precambrian to Mesozoic, the trace fossil is commonest in the Carboniferous, particularly in some of the more brackish water sediments. In the lower Coal Measures of South Wales there are several sizes of *Planolites*, a small form between 1 and 2 mm. in diameter, an intermediate form with a diameter between 5 and 8 mm. and a large form with a diameter between 12 and 15 mm. (Woodland and others, 1957). In the Palaeozoic of Portugal there are trace fossils similar to the large and small vermicular structures of Alexander Island but, although they have been figured by Delgado (1910, pl. XIIa, fig. 9; pl. XXI, fig. 2), they have not been described. Delgado's pl. XIIa, fig. 9 is almost identical to specimen KG.2.11 (Fig. 9d).

Outwardly similar mottled siltstones composed of lenticular vermicular structures have been described from the Silurian graptolitic mudstones of the Howgill Fells in north-west Yorkshire and Westmorland (Rickards, 1964), the Wenlockian Brathay Flags of the Lake District (Llewellyn, 1965) and the Wenlockian-Ludlovian Nantglyn Flags of north and central Wales (Cummins, 1959). According to Cummins (1959), the "lenticules" may have been originally almost equidimensional structures produced by some benthonic organism and which have since become compacted and distorted. Llewellyn (1965, p. 277) has described the discoidal "lenticules" as compressed faecal pellets produced by some soft-bodied organism. In his correspondence with Llewellyn, Rickards (1965, p. 559) has described graded-bedding in some of the "lenticules", therefore suggesting that they were mud flakes transported by turbidity currents.

Because the vermicular structures have smooth outlines rather than the more ragged outlines of rafted material, they are probably organic but it is difficult to decide whether they represent faecal pellets or the infilled burrows of worms. The occurrence of definite trails or tubes surrounding these structures indicates that they were probably burrows (made by some soft-bodied organism), which became partly filled with "cleaner" sediment, some perhaps passing undigested through the organism's body. The darker vermicular structures may represent the finer material which was defaecated after the nutriment had been extracted. There may or may not be a connection between these vermicular structures and *Zoophycus laminatus* and *Chondrites*, which are frequently associated with them. The vermicular structures and surrounding tubes are evidently similar to *Planolites* and they may therefore represent burrows of organisms.

#### OCCURRENCES OF (?) *Palaeodictyon*

Honeycomb-like networks composed of a large number of regular hexagonal structures are commonly found on or a few millimetres below the upper bedding planes of siltstones throughout the Fossil Bluff Series. Where the hexagons are found singly, they are usually open at one end and only two or three sides are preserved but where the structures are locally concentrated on the bedding planes, as at locality K, the hexagonal form is evident (Fig. 9h). The angle of branching is constant and individual branches maintain a regular width (0.7 mm.) from one dichotomy to another. There is no attenuation of a branch at the point of bifurcation.

In a thin section (KG.18.2) cut perpendicular to the bedding, the branches are elliptical in cross-section and flattened parallel to the bedding. They are approximately 0.8 mm. across the long axis and 0.3 mm. across the short axis and have a well-defined outer rim which is entire. Each ellipse is composed of a distinct core of dark sediment which is surrounded by a broader layer of coarser-grained clear quartz. The sediment filling the cores is identical in colour and composition to that surrounding the individual branches. A few of the elliptical sections and other areas in the same thin section are characterized by framboidal iron pyrites, which in some other siltstones from Alexander Island is associated with micro-organisms. It probably formed diagenetically in shallow water under reducing conditions. Individual spherical grains of the iron pyrites are approximately 0.012 mm. in diameter.

## PASCICHNIA SEILACHER

Genus *Palaeodictyon*Type species: *Palaeodictyon strozzii* Meneghini

*Palaeodictyon*, a trace fossil which has been described by some authors as organic and by others as inorganic, is very similar to the network structures of Alexander Island. *Palaeodictyon* has been interpreted either as a form of interference ripple-marking or as an infilling of fine mud cracks in a colloidal mud, but Wanner (1949) has concluded that an inorganic origin is highly improbable. Several forms of organic origin have been invoked; *Palaeodictyon* has been compared with the alga *Hydrodictyon*, but *Hydrodictyon* is a paludal form whereas *Palaeodictyon* is always found in marine sediments. *Palaeodictyon* has also been compared with a calcareous sponge similar to *Euplectella*, fossil tadpole nests or strings of gastropod eggs preserved in semi-relief. Wanner (1949, p. 185) has concluded that *Palaeodictyon* probably represents strings of gastropod eggs, although Seilacher (1953b) has suggested that the trace fossil represents feeding trails made on the surface (*Weidespuren*).

The main difference between *Palaeodictyon* and the structures from Alexander Island is one of relief. *Palaeodictyon*, which is usually found on the lower bedding plane of a stratum, has a higher relief than the ordinary sediment, whereas the structures from Alexander Island have no relief and they are usually preserved on the upper bedding plane. However, when *Palaeodictyon* occurs in argillaceous rocks it is preserved as a network of flattened tube fillings without any apparent relief (Seilacher, 1962). *Palaeodictyon* ranges from the Ordovician to the Tertiary (Häntzschel, 1962, p. 208) and it occurs mainly in the Upper Cretaceous and Lower Tertiary flysch deposits of the Alps, the Apennines and the Carpathians. In the (?) Rhaetic of Austria, *Palaeodictyon* has been found together with *Zoophycus* (= *Spirophyton*) and *Chondrites* (Wanner, 1949, p. 185).

## CONCLUSIONS

The Fossil Bluff Series represents part of a thick succession of flysch sediments which have been intensively re-worked over a wide area by several unknown but probably soft-bodied organisms. Although there is a rich shelly fauna associated with the trace fossils, no shells (apart from *Aporrhais*) were found in such a position as to suggest that they are related in any way to the trails and burrows, and neither was an organism found which could conceivably have been responsible for some of the structures. Many of the trace fossils represent the feeding burrows (Fodinichnia) of several semi-sessile sediment-eaters which simultaneously ate their way through the sediment and excavated their own tunnel systems.

Numerically, the commonest trace fossil is a vermicular structure similar to *Planolites*. Virtually every siltstone and mudstone bed contains numerous vermicular structures which are interpreted either as faecal pellets or worm burrows. Because these structures are surrounded by a distinct tube, the latter explanation is preferred. These *Planolites*-like vermicular structures probably represent intensive bioturbation. The upper bedding planes of many of the siltstones are covered by a large number of hexagonal networks similar to *Palaeodictyon*. Although they probably represent feeding trails, it is difficult to imagine an organism producing a closed system of feeding trails which have such a geometrical pattern.

*Chondrites* is also found either as single-burrow systems or more abundantly in several of the mottled siltstones. Four types of burrow system are described and the phenomenon of phototaxis is discussed. Several of the massive-bedded sandstones are mottled, the mottling resulting from the piping-down of a pale-coloured calcareous "tunnel sediment" into the abandoned tubular burrows.

Of particular interest is the occurrence of *Zoophycus*, a transversely laminated sheet-like burrow which is planar and never spirally coiled. The varying forms of *Zoophycus* are described and the interpretations given by other authors regarding its origin are discussed. However, it has not been possible to satisfactorily compare *Zoophycus* with any known organism or even to postulate its mode of locomotion through the sediments.

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## APPENDIX

Locality (see Fig. 1)	Specimen number	Identification
A	KG.10.74	<i>Zoophycus laminatus</i> Simpson. Not <i>in situ</i>
B	KG.8.46	Mottles in a siltstone resulting from the filling of abandoned burrows by <i>Chondrites</i> sp.
K	KG.18.2	Thin section cut perpendicular to a branch structure of <i>Palaeodictyon</i>
D	KG.19.1 KG.19.3 KG.19.4 KG.19.5 KG.19.17 KG.19.42a, b, c	<i>Zoophycus laminatus</i> Simpson. Not <i>in situ</i> <i>Z. laminatus</i> Simpson. Not <i>in situ</i> <i>Z. laminatus</i> Simpson. Not <i>in situ</i> <i>Z. laminatus</i> Simpson. Not <i>in situ</i> <i>Palaeodictyon</i> <i>Chondrites</i> sp.
L	KG.12.14 KG.12.15a, b	<i>Z. laminatus</i> Simpson <i>Z. laminatus</i> Simpson
P	KG.15.1 KG.15.3 Field photograph	<i>Z. laminatus</i> Simpson <i>Z. laminatus</i> Simpson <i>Z. laminatus</i> Simpson simulating tubular U-burrows
E	KG.14.3	Vermicular structures in a siltstone
Fossil Bluff	KG.1.128 KG.1.187 KG.1.392f KG.1.842 KG.1.844	<i>Z. laminatus</i> Simpson <i>Z. laminatus</i> Simpson Vermicular structures <i>Chondrites</i> sp. and ? <i>Cylindrites</i> sp. Not <i>in situ</i> <i>Chondrites</i> sp. Not <i>in situ</i>
H	KG.2.11 KG.2.133	Vermicular structures <i>Chondrites</i> sp. Not <i>in situ</i>
Mount Ariel	KG.3.49 KG.3.62 KG.3.63 KG.3.120 KG.3.136	Vermicular structures <i>Z. laminatus</i> Simpson <i>Z. laminatus</i> Simpson (?) <i>Chondrites</i> sp. <i>Chondrites</i> sp.
N	KG.11.3	Stellate structure representing the occupation of an abandoned burrow by <i>Chondrites</i> sp.
Waitabit Cliffs	KG.102.2	<i>Z. laminatus</i> Simpson
Lat. 71°38'S., long. 68°17'W.	KG.72.9	Tubular burrows in mottled sandstones
Crabeater Point, Wilkins Coast, Palmer Land	E.2129.4	<i>Chondrites</i> sp.