IMPLICATIONS OF NORMAL AND ABNORMAL GROWTH STRUCTURES IN A SCOTTISH SILURIAN DENDROID GRAPTOLITE

by ELIZABETH E. BULL

ABSTRACT. Normal growth patterns and structure of one species of dendroid, *Dictyonema pentlandica*, from the North Esk Inlier, Pentland Hills, Lothian, UK, are described and considered to be the result of the secretory zooids adhering to a strict and characteristic growth pattern. Aberrant and abnormal structures include: stipe truncation and compensatory growth by neighbouring stipes; changes in growth pattern; abnormal bursts of growth; tearing or splitting; and abnormal thecal growth. The possible causes of these abnormalities are considered to be the result of mutation, injury or trauma, disease and/or parasites, environmental-change, and preservation. Dendroids could repair their rhabdosomes after damage, the nature of the repair being dependent on where the injury had taken place. It is suggested that more palaeoenvironmental and palaeoecological data could be obtained by the recognition of aberrant features in other animal groups.

DENDROIDS were marine invertebrate fossil organisms, that ranged from the Cambrian to the Carboniferous. They are thought to be ancestors of the widely studied, biostratigraphically important, graptoloids. Pterobranchs are considered to be their closest living relatives (Rigby and Dilly 1994).

They were colonial animals, with a complex skeleton (or rhabdosome). This consisted of stipes of overlapping thecae, made of collagen. Each theca was occupied by a zooid, that secreted the precisely determined shape of theca in which it lived. These thecae developed in a remarkably constant and regular pattern, with thecal size, shape, ornament, and orientation very accurately repeated and constant for each species. The zooids in each stipe, it is thought, were all linked in some way by living tissue. Each dendroid had an internal stolon system of connecting canals which at regular nodal points, divided into three (the triad bud); this produced two thecae (the bitheca and autotheca) which opened into the ocean, and a third stolotheca that continued the stipe. Each theca overlapped its neighbour by a predetermined amount, combining to form long chain- or rope-like stipes, which in turn split, bifurcated or terminated according to seemingly predetermined patterns. This built, throughout the dendroid's life, three dimensional structures that included fan, shrub, disc or conical forms, specific to the pattern (blueprint), of growth characteristic of each species. Each colony was highly integrated, the size and shape of each theca being independent of its position in the colony. Unlike the graptoloids, there is no proximal to distal thecal size gradient (Urbanek 1973). More details of dendroid growth patterns, including the form of holdfasts, extrathecal tissue, and sexual interaction can be found in Palmer and Rickards (1991).

Dendroid species are identified from the details of standard rhabdosome structure. Taxonomically important features include: thecal morphology and distribution; stipe width, separation and branching patterns (including the number of primary branches or stipes); presence, dimensions, and arrangement of dissepiments; gross rhabdosomal morphology and dimensions; and proximal growth (siculate or with a stem, root or holdfast structure). Measurement and description of these features can enable production of statistically reproducible data. During this study, a detailed examination of normal thecal and rhabdosome structure has been made. The blueprint of thecal

structure and rhabdosome shape of one species, *Dictyonema pentlandica* Bull, 1987, is described and illustrated, as are abnormal structures.

Studies of living colonial animals such as bryozoans have concentrated on two-dimensional encrusting colonies (Taylor 1988), where not only standard patterns of bryozoan colony growth have been identified, but also more complex histories of zooid mortality, colony fission, regrowth, repair, and fusion. For the dendroid discussed herein, a comparison with regenerative and reparative patterns described for bryozoams and other taxa is included below.

Recent work on the pterobranch *Rhabdopleura* (Rigby 1994), has shown that zooids are 'aware' of their spatial position in the tube that they are secreting. Even when successive generations of zooids are involved in the secretion of one tube, tube growth is a highly ordered process. The overall shape of the final tube is less ordered than that of dendroids, because of the encrusting nature of *Rhabdopleura*. The comparison of dendroids with these, their closest living relative, has not yet been attempted. Relationships between patterns of colony construction and ultrastructure of graptolites and pterobranchs were discussed by Rigby (1994) and Rigby and Dilly (1994).

Astogeny is not easy to study in three dimensional, complex, erect colonies such as dendroids. Controls on colony growth are dependent on both internal forces (such as the genetic design of colony with which each species is programmed, i.e. the normal structure), and external forces, such as competition for space with neighbouring dendroids or other taxa, and environmental parameters (temperature, food supply, predation, and mechanical damage).

Study of this species has revealed that a number of aberrant structures are present in the growth patterns of dendroids, similar to those described in bryozoans. Whilst it is difficult in fossil material to distinguish pre-mortem from post-mortem damage, certain forms of damage, and changes occurring during the life of the colony can be identified by their effect on surrounding stipes. The probable causes of these aberrant structures, including trauma, predation, mutation, and change in external conditions, are discussed below. While this study concentrates on the regrowth of the dendroid mesh, it also focuses attention on our understanding of the growth patterns of the whole rhabdosome.

Bulman (1950) described a single well-preserved specimen of *Dictyonema flabelliforme* cf. var. *anglica* (Text-fig. 1) from the Shineton Shales (Tremadoc) of Shropshire, which displayed an unusual discontinuity at the periphery of the rhabdosome. In Bulman's opinion, this showed the species to be capable either of regeneration after damage, or rejuvenated growth after a pause. He favoured the latter explanation. This specimen is doubly important as it was not only the first described indication of such renewed growth, but it is also used as the illustration of the zones of bifurcation characteristic of the species '*Dictyonema*' *flabelliforme* in the *Treatise* (Bulman 1970, p. 3); only part of the specimen is illustrated.

Whilst Bulman (1950) recognized the implications of the specimen he was describing, a number of other workers have figured, without comment, species with aberrant structures, such as *Reticulograptus snajdri* (Kraft 1982); *Dictonema delicatulum* (Kraft 1984); *D. desmoides* (Bassler 1909), and various species figured by Ruedemann (1947). However, only one other author (Bouček 1957, p. 22) mentioned the phenomenon directly. His statement on regeneration is as follows: 'It happens sometimes that one or several of the lateral branches finishes its growth prematurely. So a certain gap in the uniform network of the rhabdosome should arise. But such gaps did not form completely. The adjacent branchlets reacted namely very quickly to the space in the neighbourhood and began at once to furcate laterally into the gap, soon healing it'.

Bulman (1950) discussed the variation in dendroid thecal structure with time. He noted that increased thecal isolation is the only trend that has been proved, but the increase in the production of thecal spines also seems to indicate another line of development. The information obtained from the specimens described in this paper is therefore a quite important addition to the scant knowledge of any evolutionary patterns for Lower Palaeozoic dendroids.

Dictyonema is now considered to include only sessile dendroids, and *Rhabdinopora* has replaced *Dictyonema* as the generic name for the planktonic forms, although the phylogenetic differences between the two have not yet been clearly established. The response of *Rhabdinopora flabelliforme*
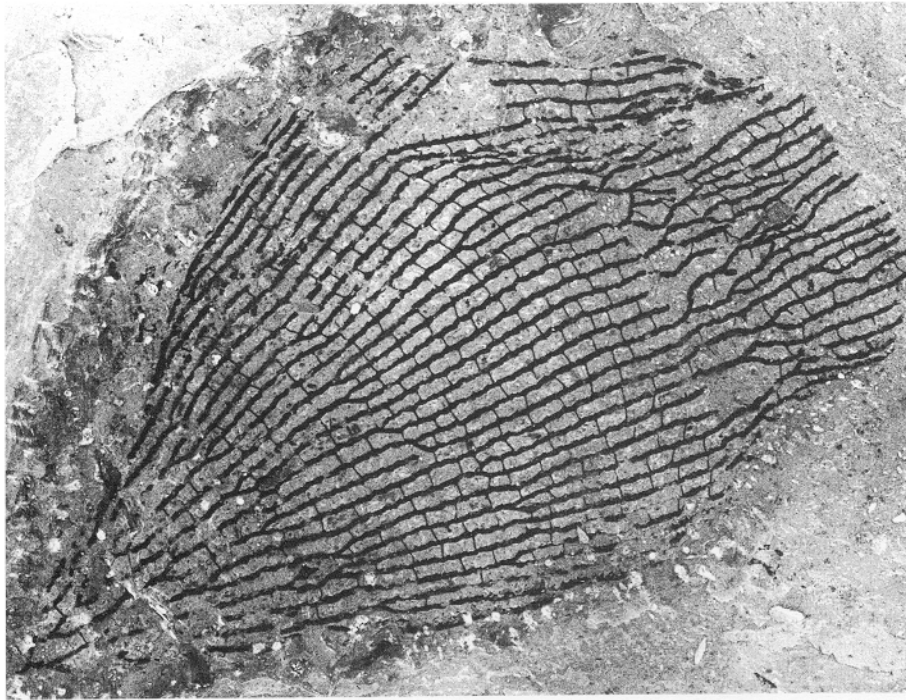
TEXT-FIG. 1. *Rhabdinopora flabelliformis anglica* (Bulman, 1950); Sedgwick Museum, Cambridge A23397; Shineton Shales, Tremadoc (Ordovician); Shropshire, UK; the original of Bulman (1950, pl. 17); also figured in Bulman (1970, fig. 26, this figure copied by Urbanek (1973, fig. 24)); in these last two figures the magnification is wrongly given as × 1; see also Palmer and Rickards (1991, fig. 126); eight zones of branching are apparent, five before the specimen reaches the normal adult proportions for this subspecies, and three in the zone of rejuvenation; × 2.

to environmental pressure was discussed by Erdtmann (1982); he suggested that some species were capable of 'gerontic astogeny' by thickening of stipes and addition of extra dissepiments, in response to exposure to high energy environments. This may be a record of ecophenotypic variation in dendroid species.

Both planktonic and benthonic dendroids are found only sporadically in the fossil record. It is thought however, that they were once widely distributed in shallow marine environments or perhaps throughout the oceans and the relative rarity of dendroids, particularly as completely articulated fossils, is a result of the low preservation potential of such fragile three dimensional colonies. As discussed below, it is possible that the benthonic forms were able to withstand quite rough conditions in life, but fairly exceptional conditions are required to preserve the biota from such environments.

The dendroid specimens described in this study were deposited in an active tectonic regime (Stone *et al.* 1987), in an environment possibly subject to frequent changes in conditions. The dendroids seem to have been able to cope with these changes, whereas those in other areas may not have been able to. This suggests that the amount of disruption that a species could withstand may have important implications for our understanding of the environment of deposition. Similarly, we may eventually be able to identify dendroid species that have evolved to inhabit different niches or colonize distinct environments.

Aberrant structures in dendroids are not of universal occurrence, and this survey is not exhaustive. In the material from the Pentland Hills here studied, there is usually at least one

'imperfection' per colony, which is a higher incidence compared with specimens from other areas; it is possible that it reflects high energy conditions at the time of deposition.

MATERIAL, LOCATION AND STRATIGRAPHY

Most of the dendroids studied for this paper are excellently preserved, some in partial relief, although no isolated material is yet available. *D. pentlandica* is known from more than 50 specimens. It is the most common species of a varied dendroid fauna from the *Oktavites spiralis* Biozone, late Llandovery (Telychian), of the North Esk Inlier, Pentland Hills, near Edinburgh, Scotland, (locality details are outlined in Bull 1987, and the stratigraphy in Bull and Loydell 1995). All of the specimens of *D. pentlandica* are from the Reservoir Formation, and most specimens were preserved within 15 m thick series of calcareous siltstones found at one locality, the site of the well known 'Gutterford Burn Limestone Beds' (Robertson 1990) and 'Gutterford Burn Eurypterid Bed' (Waterston 1979). The presence of these dendroids fills a gap in the fossil record of dendroids, and particularly of *Dictyonema* in Britain. *D. pentlandica* has not yet been identified from any other locality.

The North Esk Group (Robertson 1989) represents a continuous sequence of marine sediments recording a regression from outer shelf environments (BA 3–4), through lagoonal conditions, to terrestrial sediments. The tectonic history is complex. The depositional basin was restricted, separated from the remnant Iapetus Ocean by the emergent mass of the Southern Uplands. The sediments are now considered to have been deposited at the margins of the eastern end of a rapidly subsiding, elongate (Midland Valley), interarc basin, deepening to the west (Cope *et al.* 1992, fig. S7). The dendroid specimens are found mostly in the Reservoir Formation, the deepest water sediments preserved, which were previously thought to have been deep marine turbidites (Robertson 1989). My subsequent analysis and reinterpretation in the light of current models for the tectonic history of the south of Scotland has suggested that, although distal turbidites cannot be ruled out, there is some evidence for storm-generated deposits. Furthermore, faunal evidence (articulated dendroids, starfish and crinoids deposited *in situ*, along with articulated shallow water eurypterid specimens) is not consistent with a deep marine environment of deposition, and an outer shelf depositional environment is considered more likely.

High faunal diversity in the Pentlands Hills extends to other fossil groups (Robertson 1989). Some have been well documented, such as the crinoids (Brower 1975), trilobites (Clarkson and Howells 1981), eurypterids (Waterston 1979), echinoids (Kier 1973), and starfish (Spencer 1914–1940), whilst others require further revision, such as the brachiopods (Davidson 1868) and bivalves (Lamont 1954).

All specimens described, except for that figured in Text-figure 1 are housed in the collections of Royal Museum of Scotland (RMS), Chambers Street, Edinburgh, Scotland, or in the Grant Institute of Geology (EDCM), Edinburgh University, Scotland.

NORMAL STRUCTURE OF *DICTYONEMA PENTLANDICA*

In the course of this study of *D. pentlandica*, details of the gross morphology have been elucidated by the use of a Scanning Electron Microscope; in particular, the autothecae have now been observed in detail, and the bithecae are also described. This section is a description of the normal growth pattern, or the 'blueprint' for growth, which was adhered to as closely as possible by the zooids when constructing the thecae, and hence the rhabdosome. This normal growth pattern is remarkably regular, and is probably the result of genetically controlled processes, characteristic of each species. It is vital to the understanding of dendroids to ascertain a clear picture of normal growth patterns. Any abnormalities can then be considered independently in terms of variations in external, internal and environmental factors, as discussed below.

Whole rhabdosome. The rhabdosome forms a broad cone with opposing sides diverging at an angle of 30–50°. Most specimens are preserved with some relief. There may be some increase in the angle of divergence because of compression. The walls of the cone fall into gentle folds (Bull 1987, fig. 6). At the base of the cone is a short stem, up to 10 mm long, which was attached generally to a solid object such as a pebble or shell (Pl. 2, fig. 3) or has root fibres attached to secure the specimen to the substrate. The base of the cone is sometimes secondarily thickened (Bull 1987, text-fig. 7A), and usually consists of four primary branches.

The specimens include sections of rhabdosome up to 0·6 m long which represent portions of even larger specimens. Most species of *Dictyonema* previously described are 30–50 mm long, only exceptionally reaching 100 mm. The preservation of this species is remarkable since its constituent stipes are some of the most slender (0·22 mm wide and spaced 0·29 mm apart, or 17–22 in 10 mm). This is, to some extent, consistent with the graptoloid material from the Pentland Hills (Bull and Loydell 1995). Some of the more robust species, characteristic of the *Oktavites spiralis* Biozone, are rare or absent, but more slender forms are present (e.g. *Oktavites excentricus*, *Monoclimacis geinizti*).

The vast majority of the stipes of *D. pentlandica* attain remarkably even distribution, with constant positioning of thecae and dissepiments at standard spacing (Pl. 1, fig. 1) with zones of bifurcation evenly arranged, occurring every 20 mm (Pl. 2, fig. 3). Bulman (1950, p. 351), noted 'well-marked zones of branching', suggesting that these might become features of systematic importance. These zones are apparently present in other genera, and although clear enough in the published plates, they rarely feature in the descriptions. This was discussed by Urbanek (1973, p. 475) who noted how the branching pattern can determine the shape of the whole colony. He also suggested that changes in branching frequency could indicate that dendroids had a 'latent gradient of morphogenetic ability', or that the branching pattern was part of the essential predetermined normal structure or blueprint of dendroid construction. The main obstacle to the systematic use of such zones in classification (Bulman 1950) is the need for well-preserved rhabdosomes. Such specimens are uncommon. As noted below, when some species grow beyond a certain size the growth pattern can appear to revert irregularly to the juvenile pattern; the whole structure of the rhabdosome can then become contorted. Some *Dictyonema* species are characterized by stipes that bifurcate irregularly and sporadically (Bouček 1957); others do not have zones of stipe bifurcation recognizable as regularly spaced branching zones.

Autothecae. The autothecae of this species were previously thought to be the bithecae (Bull 1987). Further study has revealed more detail, and an idealized reconstruction is given in Text-figure 3. From their base, the thecae expand rapidly to form a tube with a diameter occupying most of the stipe (0·2 mm). Towards the end of the theca the tube again swells rapidly to form the large (up to 0·3 mm diameter), bulbous, spherical termination, which narrows again to form a narrow aperture. This aperture is a simple opening in the middle of the ventral wall of the autotheca, *c.* 0·06 mm in diameter, considerably narrower than the main body of the theca. The thecal aperture is adjacent to the thecal wall of the succeeding theca. The autothecae are not isolated, but their terminal swellings are displaced alternately to either side of the main stipe so that the apertures are angled at 60–70° to either side of the ventral line of the stipe. The upper surface of the autotheca curves inwards, and in some cases back on itself, forming a distinct notch in the wall of the main stipe above the flat upper surface of the autotheca. This notch is occupied by the bitheca curving over the top of the autotheca (Text-fig. 2). It is the distal swellings of the autothecae, regularly spaced along the stipe at intervals of 0·6 mm (28–30 in 10 mm), that gives the rhabdosome the very distinctive knobbly appearance (Pl. 1; Text-fig. 2). There is as yet no clear explanation for the terminal swelling of the autothecae, although it is probably related in some way to zooecial behaviour.

Lateral views of the autothecae show that each theca has a slight geniculum, and the supra-genicular wall is strongly convex; each autotheca has a large ventral sub-apertural spine. This spine is angled towards the open end of the dendroid rhabdosome cone at about 70° to the stipe. The spines are about 0·07 mm wide for most of their length, tapering very slightly distally. Spines can

reach up to 0·1 mm long but the average length observed in 0·3 mm. These dimensions are almost identical to those of the dissepiments; in normal preservation, therefore, the thecal spines and dissepiments are indistinguishable and can only clearly be differentiated in profile view (Pl. 1, fig. 3; Text-figs 3–4, 7).

Ruedemann (1947, p. 27) discussed spinosity in dendroids and suggested that species armoured in this way were the weaker taxa. Since then, very few spinose specimens have been described. The bulbous, spinose nature of the autothecae of D. pentlandica may have evolved to protect the zooids, particularly from predation. This species had relatively slender stipes, possibly as an aid to directing the currents through the mesh with maximum efficiency and least drag; the spines may also have directed water currents within the cone.

Spines may have been developed by this species to form platforms enhancing zooidal feeding efficiency. By providing support for the zooids to extend themselves considerable distances from the aperture of the theca, this may have resulted in a greatly improved water sampling capacity for the colony. Living Cephalodiscus zooids (Rigby 1994) have been observed using spines for feeding in this way. The distinctive swellings of the ends of the autothecae may suggest that the autothecal zooids could have been larger than average. This is unlikely, however, as it has been shown that graptoloid (Sudbury 1991) and pterobranch (Rigby and Dilly 1994) zooids are generally small relative to their thecae.

The dorsal faces of the autothecae of this species are often subject to slightly more weathering than neighbouring parts of the stipe. It is relatively common in even fairly well preserved specimens for a number of thecae to be abraded, leaving the matrix infilling the thecal cavity exposed (Pl. 1; Pl. 2, fig. 2). These openings appear superficially to be the autothecal apertures, although none have the distinct edges expected for apertural margins. This pattern has been studied using the Scanning Electron Microscope; they are clearly artefacts caused by weathering. The true position of the thecal apertures is described above. The autothecae originally may have had thinner walls at the point of curvature; they certainly protrude a little from the plane of the rock because of the partial three-dimensional preservation, being therefore more prone to abrasion and weathering. Alternatively, this feature could be a result of compression and stretching at the time of deposition.

Dissepiments. A dissepiment is associated with every other autotheca. In the area of normal rhabdosome growth they are very thin (0·06 mm diameter; Text-fig. 5), and arranged in a regular pattern with 11–13 in 10 mm (0·8 mm apart) and perpendicular to the main stipe. The fenestellae

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EXPLANATION OF PLATE 1

Figs 1–3. Dictyonema pentlandica Bull, 1987; Gutterford Burn; Reservoir Formation, Oktavites spiralis graptolite Biozone, Upper Llandovery. Examples of holes in the rhabdosome. 1, RMS.GY.1985.29.5. An area of normal growth with regular spacing of stipes and dissepiments, suddenly interrupted as two stipes terminate, presumably when they constituted the outer growth margin, as a result of either growth pattern defect or predation. Neighbouring blocks of stipes have moved relative to one another due to weakening in one area, and surrounding stipes bifurcate after the termination of the two stipes to regain normal stipe spacing. Some of the autothecae have been slightly weathered where they protrude from the specimen, giving the false impression of being matrix-filled thecal apertures; × 7. 2, RSM.GY.1985.29.2. Extra growth of one stipe has caused it to bulge (middle arrow); and withered stipes (lower arrow). Stipe termination is followed by bifurcation of other stipes to fill the gap (top arrow); × 10. 3, RSM.GY.1985.29.2. Edge of flattened cone of the rhabdosome. The upper portion (top arrow) shows the stipes rotated into profile view, showing the apertural spines. The middle arrow indicates the result of a hole formed in a strong section of the rhabdosome; the surrounding stipes crumpled with the extra load that they were forced to bear and became secondarily thickened to strengthen the remaining stipes. The ends of the stipes left trailing backwards appear to have withered slightly. The lowest arrow indicates a sudden growth within the rhabdosome, which probably formed a bulge in the side of the cone, which is seen here compressed; × 10.

PLATE 1
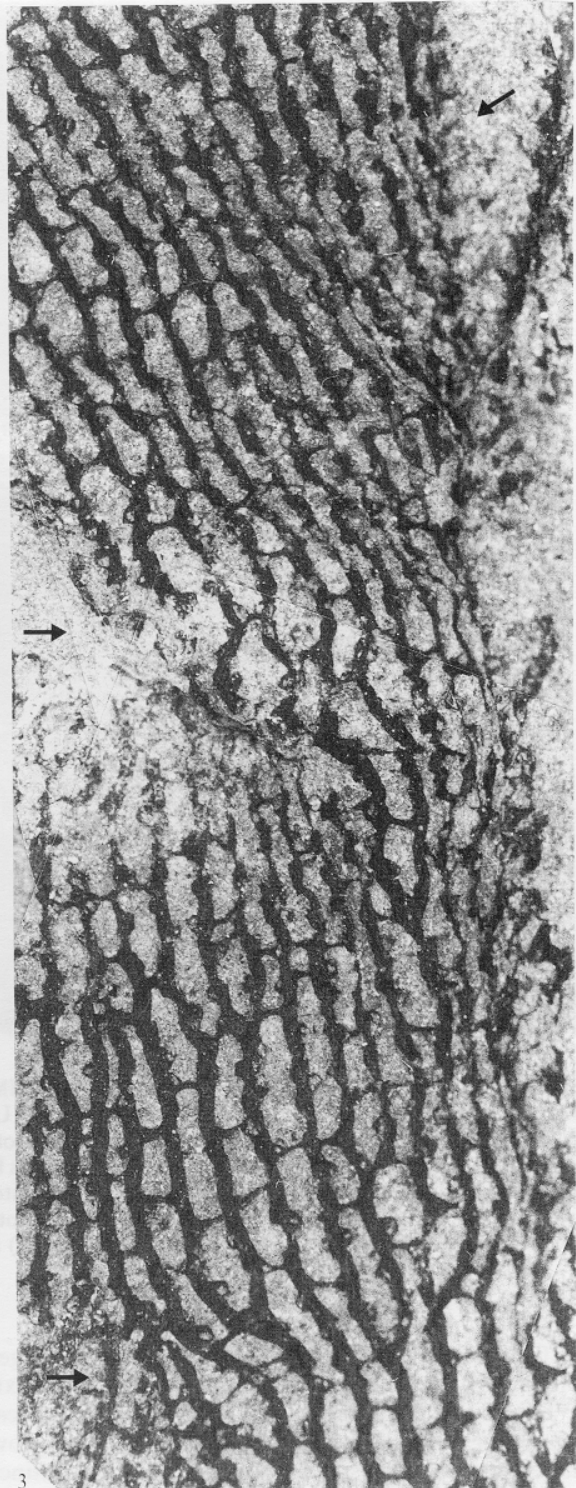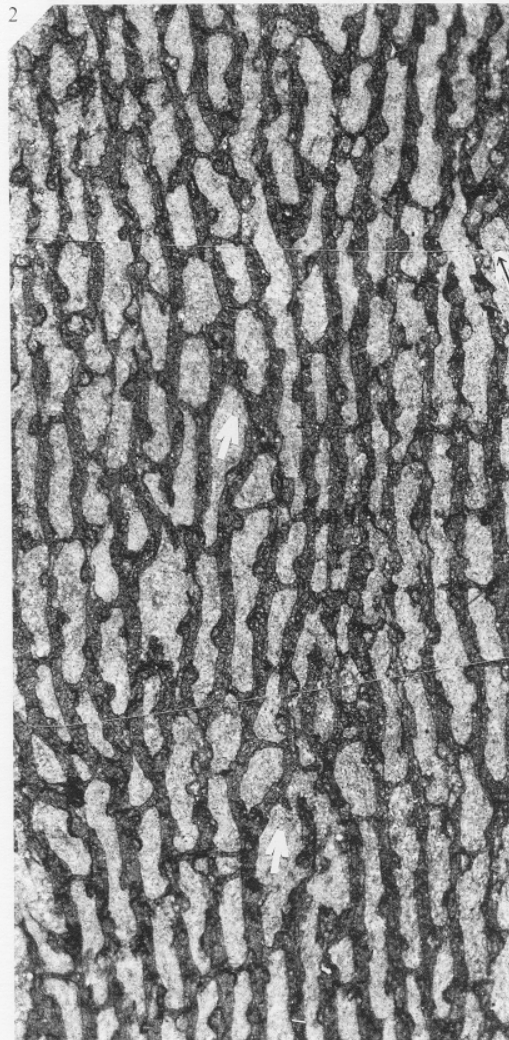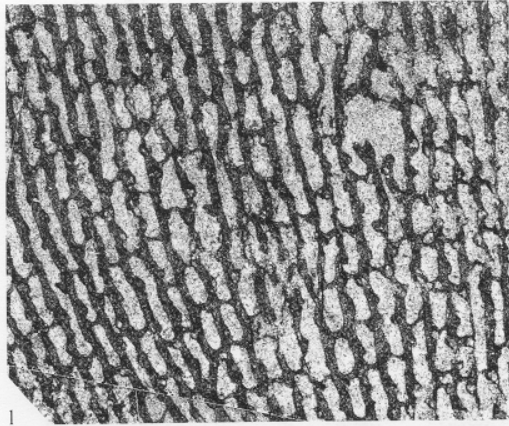
BULL, *Dictyonema pentlandica*
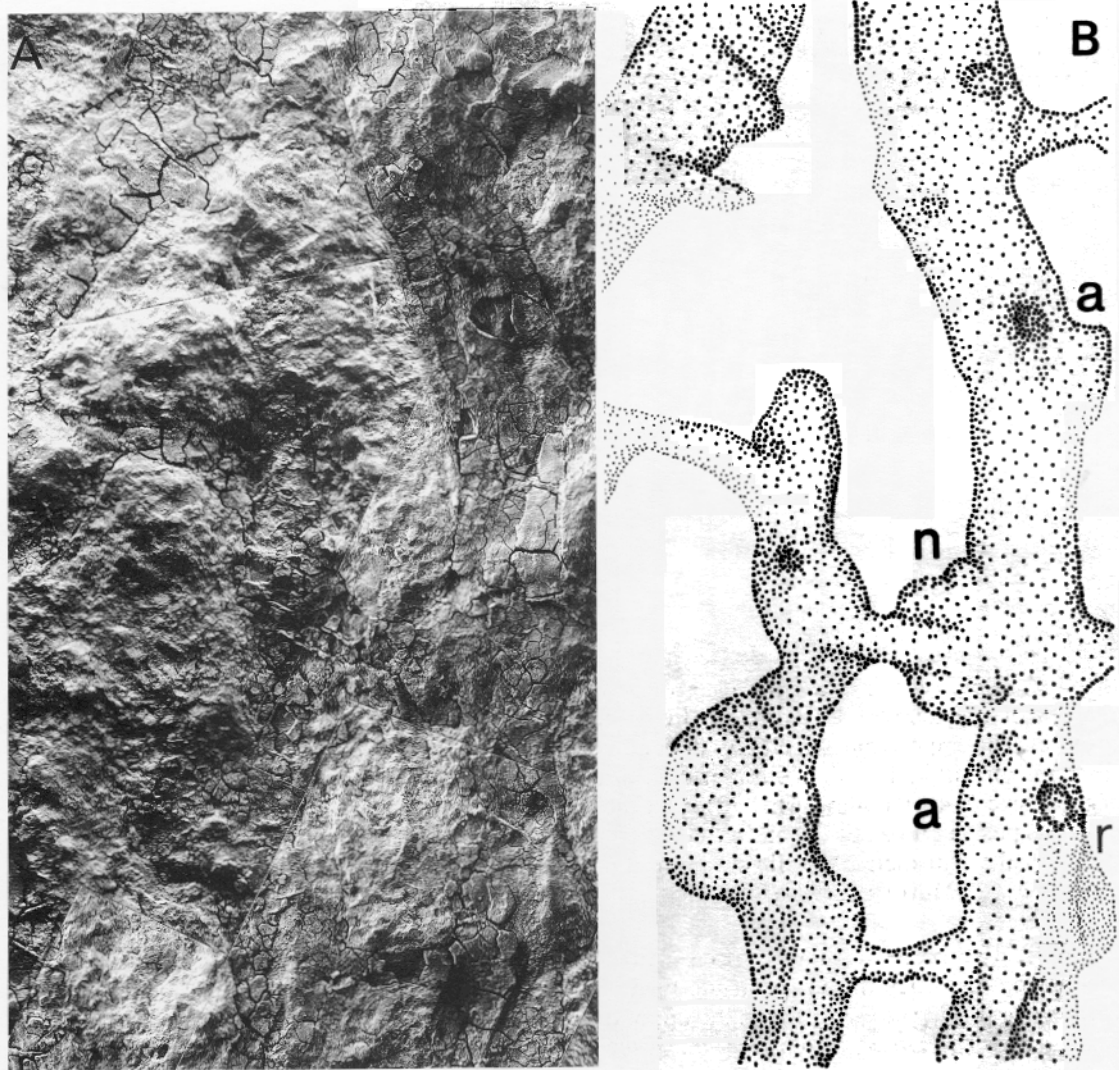
TEXT-FIG. 2. *Dictyonema pentlandica* Bull, 1987; NMS.G.1955.95.1; *O. spiralis* Biozone, Reservoir Formation; North Esk Inlier, Pentland Hills, Lothian, UK. A, montage of scanning electron micrographs; ×70. B, drawing to illustrate important features. The autothecae (a) form large bulges on alternate sides of the stipe. The upper surface curves inwards and in some cases back on itself forming a distinct notch (n) in the wall of the main stipe above the flat upper surface of the autotheca. This notch is observed in some cases to be occupied by a bitheca curving over the top of the autotheca. Bithecae occupy the ridge seen crossing the autotheca at (r), and structures seen at (a) are thought to be bithecal apertures.

so formed are of fairly constant size, one-fifth longer than wide. Continuous lines of dissepiments often form at the site of bifurcation (Bull 1987, text-fig. 8).

Dissepiments probably originated from the bithecae as described by Bulman (1927) and therefore consist of bithecal tissue, formed by continued growth of alternate bithecae. They arise from the stipe close to, opposite, or passing over, the distinctive bulge of the autothecae (Text-figs 2, 5A).
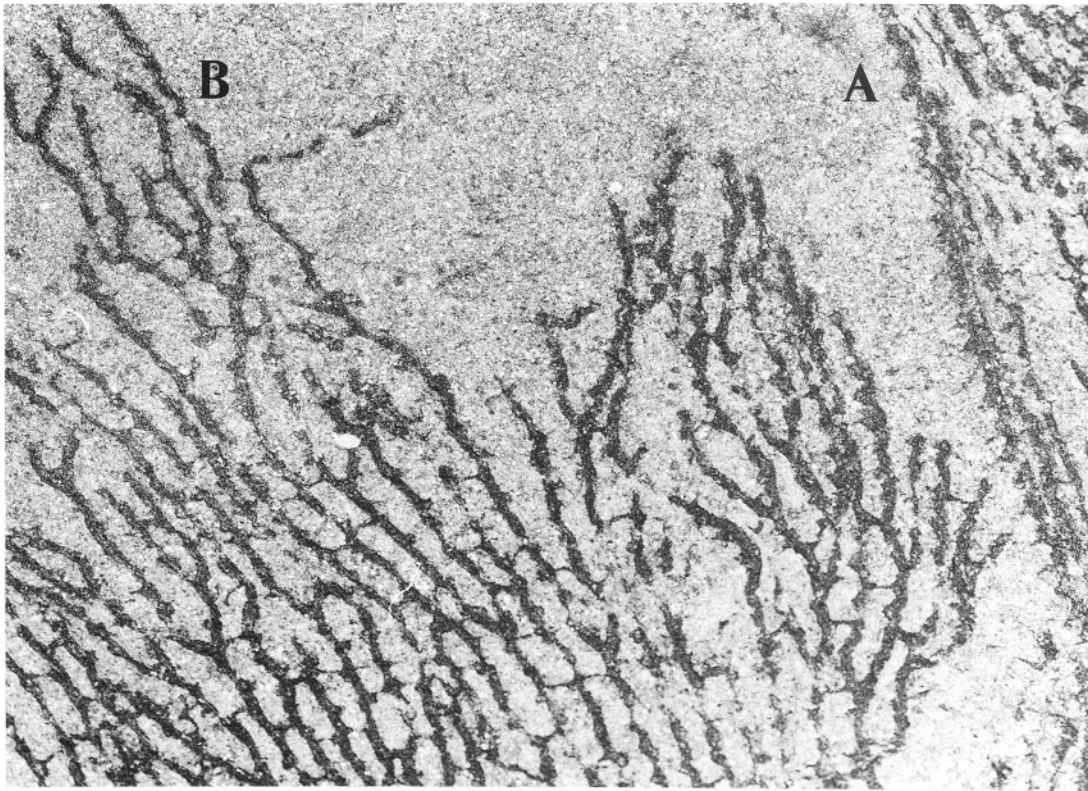
TEXT-FIG. 3. *Dictyonema pentlandica* Bull, 1987. Reconstruction of the idealized thecal structure, showing the relative positions of the autothecae and bithecae in profile view, and the apertural spines and bulbous nature of the genicular margin.

Strengthening, seen in scanning electron micrographs as concentric rings, appears to follow the margin of the fenestrule symmetrically rather than supporting a dissepiment in its direction of growth. The stipe from which the dissepiments originate is, therefore, not apparent; rather the dissepiments and stipes define the margin of the fenestrule, maintaining the rectangular shape at a regular size (0.4×0.6 mm). This latter feature may reflect the importance of controlling the water currents passing through the mesh to the zooids within, as the size of any aperture and the thickness of the walls will dictate the flow rate and turbulence of currents passing through that aperture (Stratton and Horowitz 1974).

Bithecae. The bithecae of this species are narrow, with a constant width of 0.03 mm, and are inconspicuous. They do not protrude from the stipe in normal circumstances, but are thought to form a slight ridge crossing above the upper margin of the terminal swelling of the autothecae. Each autotheca is associated with a bitheca, which loops across the side and curves around the bulbous part above the aperture of the adjacent autotheca before the swelling of the next autotheca commences. This can give the impression of an apparent geniculum when viewed in profile. The bithecae have simple, unornamented apertures, opening in the side of the stipe (Text-figs 2–3).

Discussion. The taxonomically significant features of this species have been described and discussed above and in the original systematic description (Bull 1987, 1995), in which comparisons with other species are made. The presence of a holdfast structure confirms the attribution to *Dictyonema*. Combinations of the following features allow its distinction from other described species: the presence of simple (unforked) autothecal apertural spines; the identification of the swelling of the stipe giving its distinctive knobbly appearance being caused by swelling of the autothecae and not by bithecae passing round the outside of the stipe; the very slender dimensions of the stipes and high stipe density; and the regular, close arrangement of the dissepiments. *D. pentlandica* is subject to growth of aberrant structures on both microscopic and macroscopic scales, including tubular outgrowths of the bithecae and large scale regrowth or mending of the rhabdosome, following changes in growth patterns or predatorial attacks, or as a result of other environmental factors. The details of these aberrant structures are described below.
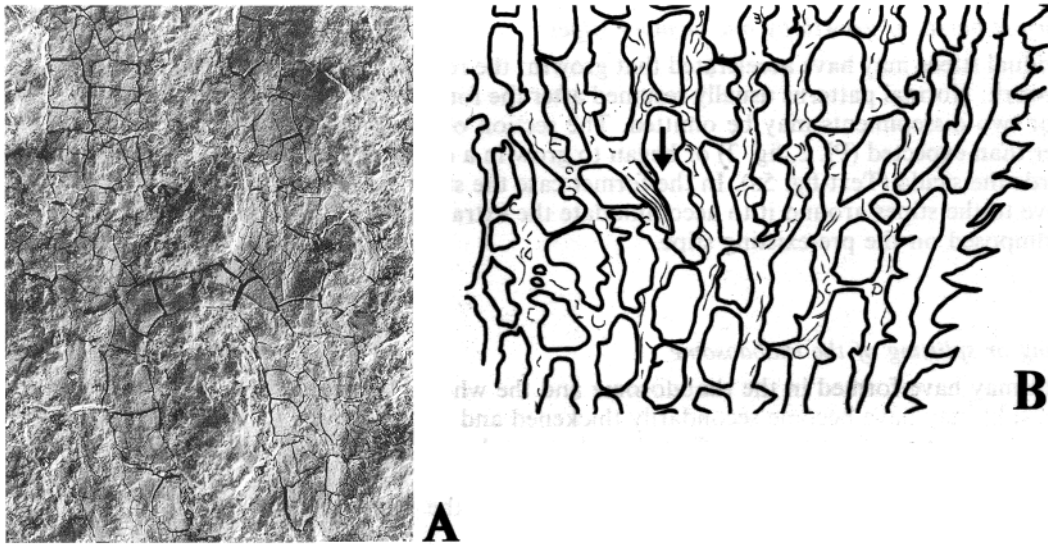
TEXT-FIG. 4. *Dictyonema pentlandica* Bull, 1987; RSM.GY.1985.29.5; from the same horizon and locality as the specimen in Text-figure 2. The slab shows two specimens (A and B), preserved with the openings of the cones facing one another. A, an area of rhabdosome with an inverted view of the stipes, with the thecae rotated giving a profile view and showing the apertural spines of the autothecae. B, an uneven regeneration zone at the growing margin of the rhabdosome; the specimen started to grow again in one region, but was not able to reinstate the normal pattern of growth, being unable to produce dissepiments; ×7.

DESCRIPTION OF TYPES OF ABERRANT AND ABNORMAL STRUCTURES

Abnormal structures are not usually discussed in taxonomic work as they distract attention from the features considered typical of (or normal for) the species. Yet almost every specimen of *D. pentlandica* has some feature which does not conform to the standard taxonomic description. Despite the abnormalities, however, much of the rhabdosome of each specimen is of the normal size and shape, with a normal stipe and dissepiment distribution pattern. Examples of the different types of aberrant structure observed are illustrated and explained in Plates 1–2 and Text-figures 4–7. They fall into five main categories.

Stipe truncation and compensatory growth by neighbouring stipes

1. One or more stipes may be truncated within a section of otherwise unaffected rhabdosome. The surrounding stipes filled the gap so formed either by bifurcation, or by curving across the gap (Pl. 1, figs 1–2; Text-fig. 4). The normal pattern of rhabdosome growth was continued afterwards.

TEXT-FIG. 5. *Dictyonema pentlandica* Bull, 1987; from the same horizon and locality as the specimen in Text-figure 3. A, NMS.G.1995.95.1; scanning electron micrograph of a dissepiment not preferentially attached to either stipe; strengthening appears to follow the margin of the fenestrule rather than showing a dissepiment growing from one stipe to another; × 50. B, RSM.GY.1985.29.2; showing growth (arrowed) of a single stipe towards the sicula. The right hand margin shows thecae twisted partially to show a profile view; × 20.

2. A hole was formed in the centre of an otherwise strong section of rhabdosome; the surrounding stipes may have crumpled with the extra load they were forced to bear and became secondarily thickened to support the remaining stipes (Pl. 1, fig. 3). The ends of the truncated stipes, which were left trailing backwards, may appear to have withered slightly.

Change in rhabdosome growth pattern

An increase or decrease in the rate of growth could have affected large areas of a rhabdosome at the same time. Not every stipe was necessarily involved. Some stipes may be terminated (Pl. 2, fig. 4; Text-figs 1, 7); some continue unaffected through the area of disruption, while neighbouring stipes seem to have been unable to regenerate, forcing those stipes that were able to grow to bifurcate immediately and regularly thereafter, presumably in order to reunite the mesh. In some areas of the rhabdosome, all of the stipes bifurcated at the same time, causing the rhabdosome to grow in another plane, giving the appearance of a frill forming at the margin (Pl. 2, fig. 3). In other areas the stipes started to regrow but did not attain the normal pattern (Text-fig. 4). This is the type of rejuvenation described by Bulman (1950; Text-fig. 1). The growth pattern that emerged following renewed activity can represent either a return to the juvenile pattern (Bulman 1950), a continuation of the adult pattern, or growth in an apparently random fashion.

One section of the main body of the rhabdosome may be enlarged, forming a bulge in the normal surface of the cone. An increase in the density of stipes commenced with a number of stipes bifurcating at the same time. The resultant bulge may have been resorbed into the main body of the rhabdosome by one or more stipes terminating. More usually, however, the normal bifurcation pattern of the main rhabdosome continued in the surrounding stipes and, eventually, regular stipe spacing was achieved. The extra sections of the stipes were compressed on top of one another on burial (Pl. 2, figs 1–4; Text-fig. 7).

Abnormal bursts of growth by one or more stipes

Individual stipes may have accelerated that growth; the result is a distortion of the regularity of the meshwork. Normal patterns usually resumed after the formation of the next dissepiment, although one or two dissepiments may be omitted. The section of stipe in question became either slightly longer than expected (Pl. 2, fig. 2) or began to grow in a completely different fashion, e.g. growing towards the sicula (Text-fig. 5B). In the former case the stipe was deflected because it had to curve relative to the stipes around it to accommodate the extra length. In the latter case the growth was superimposed on the pre-existing stipe.

Tearing or splitting of the rhabdosome

A split may have formed in the rhabdosome and the whole mesh pulled apart. The proximal end of the split may have become secondarily thickened and the remainder of the stipes on either side of the split continued growing unaffected, with normal stipe spacing (Text-fig. 7). The stipe on one side of the split has not been observed to have attempted to form dissepiments to join up with the stipe on the other side, or to have grown new stipes in the gap formed.

Abnormal thecal growth

Although the bithecae of *D. pentlandica* are usually narrow (0·03 mm) and inconspicuous, rarely they are enlarged and distorted, and have developed tubular outgrowths, which form no regular pattern. Such growth structures are usually difficult to distinguish from broken or incomplete dissepiments, and only in exceptionally well-preserved material can they be identified clearly. Bithecal outgrowths are normally either narrower than dissepiments (0·03 mm compared with 0·06 mm dissepiment diameter), or, where they grew around the dissepiment, this appears thickened for at least part of its length. Initially apparent as disruption of the regular dissepiment arrangement (Text-fig. 6), they are easily confused with autothecal apertural processes (spines). These are usually of constant diameter, are straight, and arise from the centre of the bulbous part of the autotheca on the ventral surface of the rhabdosome. Thus, if spines are seen in the normal, dorsal view of the rhabdosome, they will be displaced to one side of the centre of the autotheca and will not be in any other position; abnormal outgrowths occur at irregular intervals and positions, and usually are not straight.

EXPLANATION OF PLATE 2

Figs 1–4. *Dictyonema pentlandica* Bull, 1987; Gutterford Burn; Reservoir Formation, *Oktavites spiralis* graptolite Biozone, Upper Llandovery. Examples of bursts of growth of the rhabdosome. 1, RSM.GY.1985.29.1. Sudden surge in growth indicated in the centre of the rhabdosome. Increase in stipe density in one area only, forming a bulge in the side of the cone as a response to increased activity and growth of a few stipes, which have been superimposed on one another on deposition; × 10. 2, RSM.GY.1985.29.1. One stipe has grown longer than normal, relative to the stipes around it. The stipe that has experienced extra growth had to curve to accommodate the extra length on deposition. Normal growth resumed after the formation of the next dissepiment; × 10. 3, RSM.GY.1985.30.1. All of the stipes are involved in this case; some terminate, the rhabdosome expands and the new growth area forms a frill at its outermost margin (the dendroid is attached to the brachiopod *Leptaena*); × 3. 4, RSM.GY.1985.29.5. Some stipes terminate (arrowed); neighbouring stipes bifurcated and curved to fill the gap, resulting in stipes obliquely approaching one another. Some stipes then terminate on reaching normal stipe separation distance from the adjacent part of the cone. Pattern continues until normal stipe separation is achieved distally; × 3.

PLATE 2
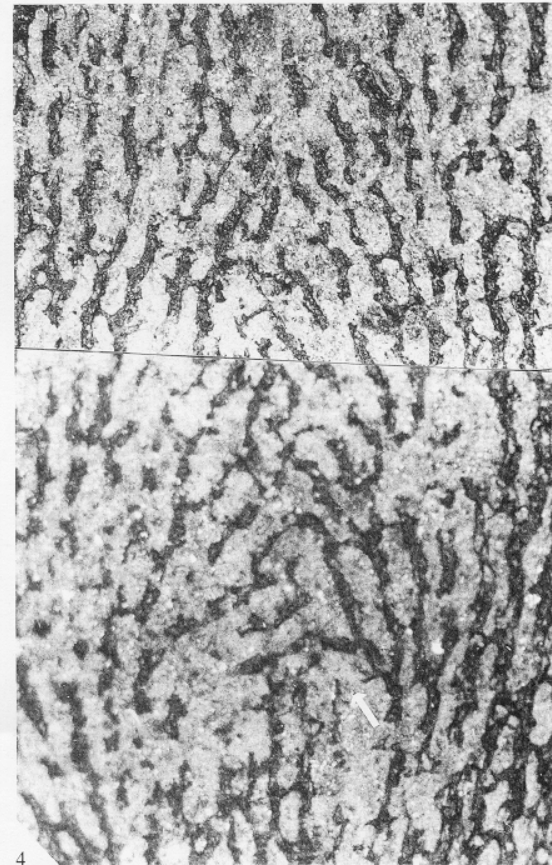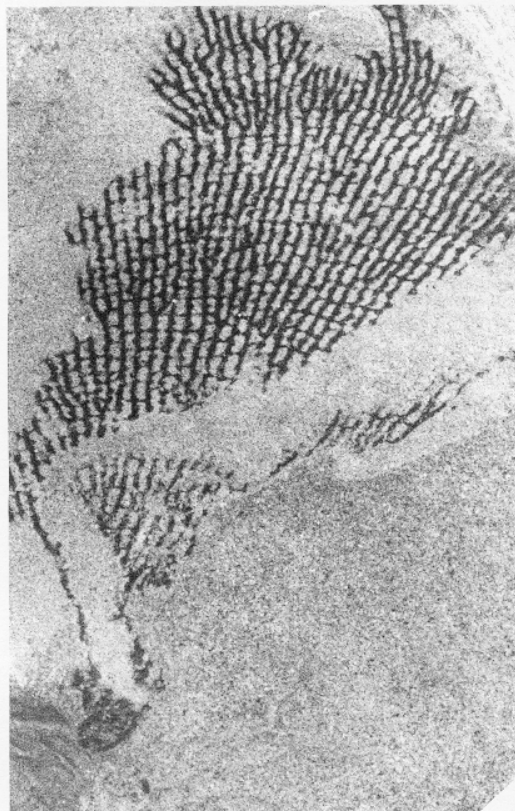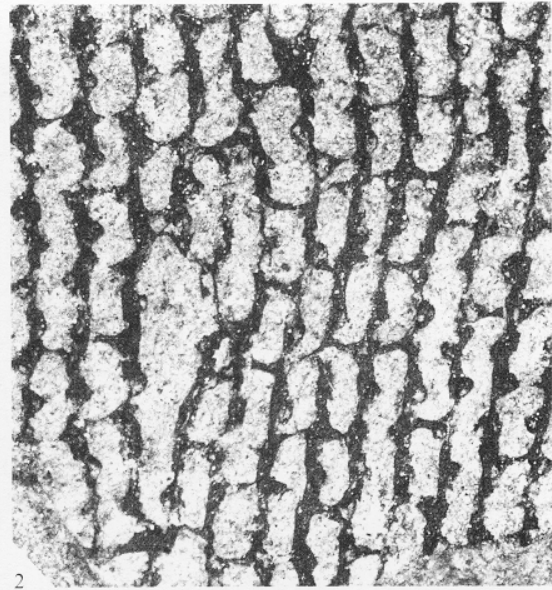
BULL, *Dictyonema pentlandica*
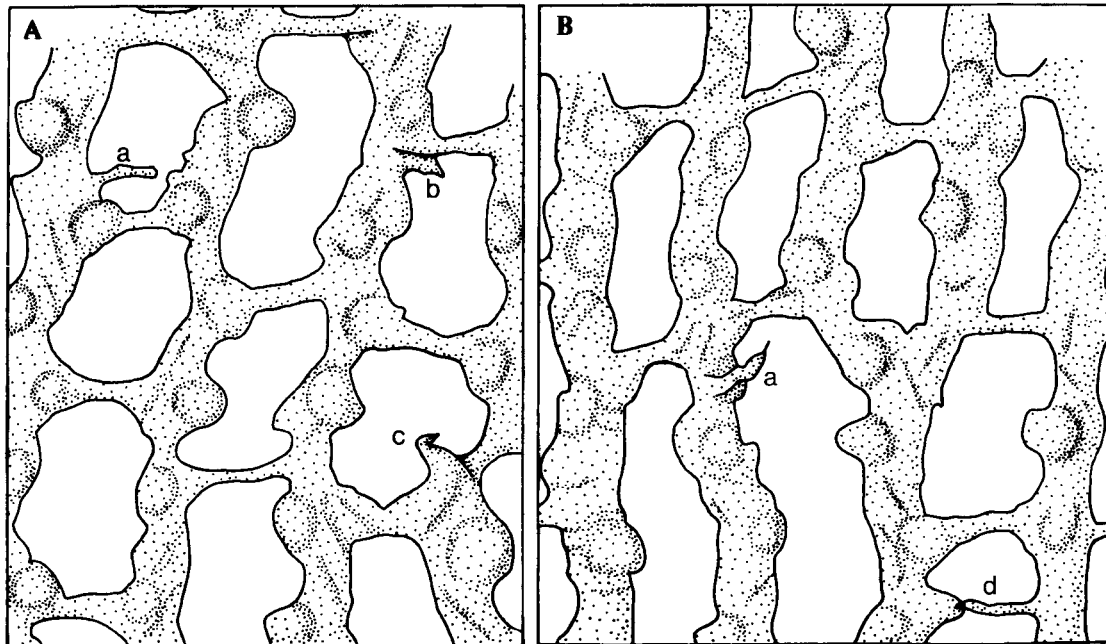
TEXT-FIG. 6. *Dictyonema pentlandica* Bull, 1987; RSM.GY.1985.30.1; from the same horizon and locality as the specimen in Text-figure 2. A and B, camera-lucida drawings of specimens oriented with proximal portions towards base of drawing. Types of aberrant growth of bithecae. a, tubular outgrowth; b, growth along a dissepiment; c, outward growth from the stipe, recurving back later; d, outgrowth crossing to adjacent stipe; c. × 12.

Bithecal outgrowths (Text-fig. 6) are short, narrow (0·02 mm diameter), tubular structures, most commonly extending the bithecae across the fenestrule instead of following the normal path and wrapping around the top of the autotheca. This is usually followed by the next autotheca at a reduced spacing, and the stipe may be thinner at that point. Alternatively the outgrowth may eventually curve back towards the original stipe, or approach another stipe, or may have grown around or along a dissepiment, giving the impression of thus being further strengthened. In other examples, the outgrowths are indistinguishable from broken parts of the stipe wall.

As yet, no distinctive abnormal structures of the autothecae have been observed, although apertural spines may be broken. Abnormal growth of the dissepiments and bithecae were noted by Bulman (1927, 1933); two types of abnormal growth were illustrated. Similarly Chapman *et al.* (1993) illustrated abnormal dendroid growth, in the form of sac-like outgrowths, which may be composed of autothecal tissue.

POSSIBLE CAUSES OF AND RESPONSES TO DENDROID ABNORMALITIES

The standard patterns of normal dendroid growth were probably controlled by a simple epigenetic phenomenon which dictated the species' 'blueprint', or normal structure common to each species.

It is possible to identify five processes which might have caused the identification of disruptions in normal growth patterns. These are: (1), mutation; (2), injury or trauma; (3), disease and/or parasites; (4), change in environmental conditions; and (5), preservation. Additionally, the timing of such changes cannot be identified, as a cessation of growth for a period will appear identical to a sudden change in growth, unless obvious 'wear and tear' of the margin during a halt in rhabdosome secretion can be seen.
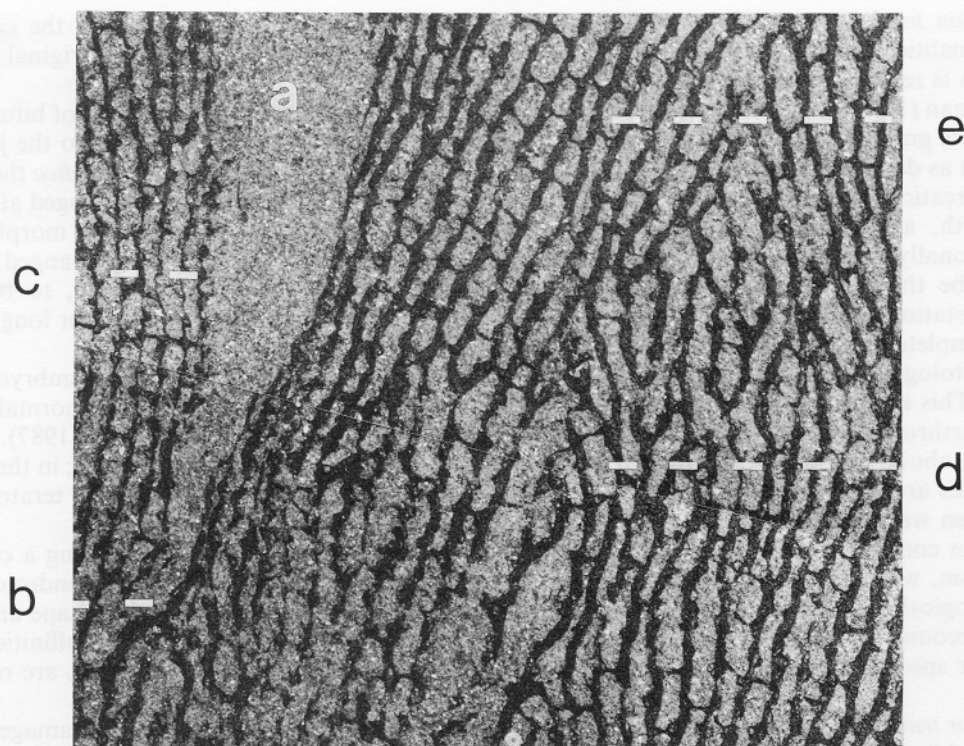
TEXT-FIG. 7. *Dictyonema pentlandica* Bull, 1987; RSM.GY.1985.29.5; from the same horizon and locality as the specimen in Text-figure 2. Major split formed in the rhabdosome (a). The stipes on either side of the split have not formed dissepiments to join the stipes on either side of the split. The base of the split is secondarily thickened (b). Some of the autothecae are seen in profile as the stipes to the left of the split have been rotated on deposition, and autothecal spines are visible (c). An area (d) to the right of the split shows some stipes terminating, while those that continue to grow, curve in both directions until aligned with an adjacent stipe at the appropriate spacing. Certain areas of the rhabdosome are involved in stipe termination, whilst other areas (e) continued more or less unaffected growth; × 8.

Although it is possible that each rhabdosome was subject to more trauma than that for which there is morphological evidence, it is unlikely that the colonies were able to effect repairs to their framework that have no preserved trace (effectively 'invisible repairs'). We may, however, now be seeing the results of repairs which were incomplete at the time of death. Alternatively it is possible that *D. pentlandica* was not able to effect 'invisible repairs', leaving clear scars to be fossilized, or that it had an increased susceptibility to damage if it lived in a high energy environment.

Every specimen of *D. pentlandica* has at least one departure from a normal growth pattern. This suggests that these colonies suffered more trauma than species from other areas, and that the effects of trauma are possibly more common elsewhere than has been previously recorded.

This species attained larger than average sizes, with some specimens reaching at least 0·6 m long. It is uncertain if the attainment of this size was the result of an extended growth period, or of more rapid growth. Estimates of graptolite growth rates have been attempted by comparison with living pterobranchs (Rigby and Dilly 1994), and study of the response of pterobranchs to trauma, predation, and change in conditions, might lead to more information about dendroid growth patterns. Estimates of the degree of regeneration that the animal was able to effect for itself may then become possible.

Mutation in the genetically controlled growth pattern. If mutations were generally the cause of abnormalities, the growth pattern would be irrevocably changed. In most cases the original growth pattern is resumed after a change.

Bulman (1970, fig. 13) noted that for some species the distance between the regions of bifurcation increases gradually distally. If a regrowth had been spurred by mutation, a return to the juvenile pattern as described by Bulman (1950), would be unlikely (Text-fig. 1). In *D. pentlandica* the zones of bifurcation are approximately evenly spaced (Pl. 2, fig. 3) and this remains unchanged after any regrowth, as does the size and shape of fenestellae, and general rhabdosome morphology. Occasionally, the growth pattern of a section of rhabdosome appears completely changed, which could be the result of an individual zooid mutation; it is more likely, however, to be local manifestation of disease. Growth in a distorted fashion does not seem to continue for long before the complete cessation of growth (Text-fig. 4).

Teratology is the study of genetically or externally controlled malfunctions at an embryological stage. This is considered quite an important and relatively common factor in the abnormalities of some arthropods, including trilobites (Owen 1985) and conulariids (Babcock *et al.* 1987). In the former, abnormalities usually involve substantial deviation from normal morphology; in the latter, examples are exceedingly rare, in the reference quoted above only one indisputable teratological specimen was identified in a sample of 5000.

When considering teratology of dendroids, there is the added difficulty of studying a colonial organism, with poorly known embryology and juvenile stages. It is unlikely that dendroids with teratological abnormalities would have survived into adult form in a recognizable shape and they may account for some of the species described from a single specimen but with affinities with another species. It is thought that teratological dendroid specimens, like conulariids, are rare.

Injury or trauma. Large splits occurring in the mesh are almost certainly the result of damage (Text-fig. 7). After tearing, the broken remnants of the dissepiments might have dangled loosely at the edge of the mesh. Such irregular margins have not been observed however, suggesting that they have probably been resorbed, possibly to avoid impairing the action of the remaining zooids. The normal pattern of growth for this species is to fill all of the available space, and the obvious growth direction to the side of the torn stipe is not exploited. No further growth seems to occur in the gaps formed by splits, and it does not seem possible to trigger regrowth in an already mature area. Such growth would rapidly result in the two sides of the mesh becoming superimposed or interfering with one another. In Bull (1987, p. 124) it was noted that 'Bifurcation is concentrated on certain stipes, while others are continuous, straight and unbroken.' This phenomenon also seems to have been a control on the ability of the rhabdosome to spread out and fill any gaps caused by injury to its structure. The areas at the bases of splits are secondarily thickened, acting as strengthening for a weakened area.

Different responses to injury might be expected depending on whether it was the outermost growing edge of the cone or the already formed central part of the mesh that was attacked. As small holes in the structure are fairly common, in most cases the reaction of the dendroid has resulted in a mesh stretched around the hole (Pl. 1, fig. 1). The dendroid seems to have been capable, almost always, of repairing its mesh at whatever point it had been attacked, although details of early stages of astogeny of this species are unknown. The zooids are thought to have been able to plaster cortical bandages on the surface of the mesh (Crowther and Richards 1977), and this method could have been used to mend damage to the rhabdosome, particularly in cases where the stipes are now seen to be slightly thickened at the site of damage (Pl. 1, fig. 3; Text-fig. 7).

The sites of individual predatorial attacks may be determined by looking at patterns of regrowth. Thus, where the associated, succeeding and surrounding stipes were activated to either bifurcate, or curve and stretch across to heal the gap (Pl. 1, figs 1–2; Text-fig. 2) it is probable that the attacks took place at the outermost growing edge. It is only here that new growth in an outward direction would be expected to have occurred and new phases of bifurcation and thecal production stimulated. In order to rejoin with pre-existing stipes on the other side of an area of damage, it is

unlikely that the stipes would have been able to grow back towards the sicula for any distance (Text-fig. 5B), as this would have involved either producing thecal apertures that faced the 'wrong way' (into the current passing through the cone), or secreting the distal end of the theca first.

A traumatized area, particularly in the main body of the rhabdosome, where a hole had been made through the side of the pre-existing mesh, could have been mended by the application of cortical bandages to the damaged area by the zooids from neighbouring thecae (Pl. 1, fig. 3; Text-fig. 7). Any obvious holes remaining in the fossilized rhabdosome are usually fairly large (Pl. 1, fig. 1), involving two or more stipes, where the injury incurred was too much for the dendroid to mend without disrupting the normal growth pattern. The impetus was only for onward growth, and dendroids appear to have had little capacity for reinstatement of growth in an area already abandoned (Pl. 1, fig. 3; Text-fig. 7). This does seem to have occurred rarely, however, although it was not always completely successful (Pl. 1, fig. 2).

Parasites and disease. Conway Morris (1981, p. 497), suggested that tubular outgrowths on graptolites consist of thickened cortical tissue plastered on by the zooids in an attempt to contain intruding parasites. It is thought possible that the tubular outgrowths of the bithecae described above, could be the result of parasitic invasion (Text-fig. 8.). The sac-like outgrowths, possibly of autothecal tissue, described by Chapman *et al.* (1993, p. 307) are suggested to have been possibly also caused by parasites.

It is difficult to attribute observed features to disease, but it is possible that it may have caused the apparent abrupt loss of the ability to grow in a normal pattern (Text-fig. 4). That this can occur to just a few stipes of one colony, suggests that only zooids in that area of the colony were affected. Where only part of a single stipe seems to have withered away (Pl. 1, fig. 2) it is possible that only part became infected.

Change in environmental conditions. If prevailing conditions changed, it is highly likely that growth patterns would have been affected. There is no certainty as to which conditions dendroids were sensitive, but various can be suggested (see Berry and Boucot 1972). Although graptolites were possibly generally widely dispersed throughout the oceans, some planktonic forms were affected by depth of water, as could benthonic *Dictyonema* species also have been. Changes in both salinity and water temperature are not known to have affected graptoloids, but it is possible that we are observing their effects here. It is possible that a change in temperature, or shortage in food, would cause a dendroid temporarily to cease growth, and to regrow on reinstatement of the original conditions. In a high energy environment, inevitable damage would be followed by a temporary halt in growth; this would not be seen in calm conditions. Short-term changes, such as caused by storms, could contribute to irregular growth patterns, as could the presence of some impediment to growth, such as another dendroid growing close by. Temporarily turbid water conditions, such as caused by the fall of volcanic ash, would leave the water column unsuitable for filter feeding by the zooids for some time; many graptolite bearing beds are associated with bentonite horizons (Batchelor and Weir 1988). If changes in environmental conditions are considered to be causes of cessation of growth, they would have to be major and universal to affect so many of the dendroid colonies.

Regular bifurcation is one of the few ways in which an expanding cone consisting of longitudinal rods of constant diameter and constant spacing can grow. Zones of bifurcation may be triggered by seasonal fluctuations in external conditions, such as a new spurt of growth in the spring after a relatively dormant winter period. Rough calculations of the life span of fossilized colonies can be based on estimates of the growth rates of pterobranchs (Rigby and Dilly 1994), and result in estimates of age in years approximately consistent with the number of zones of bifurcation present. But such growth rate calculations applied to dendroids rely on making many assumptions; more research on pterobranchs and dendroids is necessary before these calculations can be confirmed.

Preservation. Growth abnormalities can usually be distinguished from preservational breakage. Post-mortem damage and displacement of the rhabdosome on deposition were mentioned by

Bulman (1950) as a possible cause of the distorted structures observed at the margins of dendroid rhabdosomes. This is commonly observed, and where damage has occurred during the depositional process, it usually forms a recognizable pattern. Whole sections of stipe are displaced, so that all of the affected stipes take up the same angle of curvature, or the mesh is visibly stretched, and the stipes are either superimposed on other stipes, or the distance between stipes is reduced or increased (Pl. 2, fig. 2). This is shown well in a specimen of *Palaeodictyota* from the Pentland Hills (Bull 1987, pl. 20, fig. 2). Stipes are unlikely to have remained in positions producing a great deal of torsion in life; the elasticity of the rhabdosome would have returned the stipes to their stable position.

COMPARISONS WITH OTHER GROUPS

Other authors have discussed the biological implications of abnormalities in other fossil groups. Such abnormalities are considered as possible indicators of pathways to evolutionary change (Gould 1980).

It has been established (Owen 1985) that trilobite abnormalities provide important data on the biology of an extinct group and should therefore not be considered as mere morphological curiosities. The abundance of abnormalities has been used in the study of trilobite palaeoecology, and has provided indicators of selection pressures, and direct evidence of aspects of trophic structure. Unlike dendroids however, trilobite growth involved regular ecdysis. High mortality rates were associated with the moulting process, as trilobites had a very vulnerable period prior to the mineralization of the new exoskeleton; thus, many injuries were inflicted in this period, and include damage caused not only by predation, but also by the moulting process itself. But, most trilobites were capable of enrollment, which might have been to protect themselves, and additionally were able to escape by moving away. These factors make application of conclusions drawn from trilobite abnormality patterns difficult to compare directly with dendroid rhabdosomes.

Following injury to trilobites, it is thought that their survival was promoted by some degree of healing, expressed by exoskeleton thickening and callus formation (Owen 1983, 1985). Other groups of invertebrates developed their own response to injury. Particularly well known is the ability of crinoids to regenerate, following the loss of brachia or even part of the calyx. Also, bivalve molluscs and brachiopods are known which have disruption to their normal shell ridge patterns. However, none of these groups have colonial representatives, and whilst the biological implications of their abnormal features are important, they are not immediately comparable with colonial animals such as dendroids.

From Conway Morris (1981) it is clear that the fossilized remains of animals with relatively robust and solid skeletons or exoskeletons are more likely to preserve the remains of parasites and their related borings, galls, or tumours. The effects of parasitism at ultrastructural level on graptolites were discussed, but a great deal more evidence is required before parasitic relationships can be identified and fitted into evolutionary models.

The effects of disease upon fossil animals has been studied, particularly with respect to human remains. Palaeopathology remains of interest to those studying the evolution of current diseases; Moodie (1923) noted that 'disease is apparently one of the manifestations of life'. He also noted that not many diseases will leave traces in 'bones', that diseases affect individuals and not whole races, and that diseases become extinct as do animal species. He also suggested that early faunas were disease-free, and that parasitism did not appear until the Devonian. However, Conway Morris (1981) gave evidence of parasites from the Cambrian, but commented that the low level of disease and parasite interaction recorded in these early metazoan faunas seems to be a feature of the relatively simple ecosystems of the Precambrian and early Palaeozoic. .

It is difficult in fossil material to differentiate between the effects of changes in environmental conditions and the effects of disease. If every fossil specimen above or below a certain horizon is affected, then a change in external conditions should be suspected. Moodie (1923) suggested that an increase of salinity would result in shell thickening, and diminution could be caused by crowding, or by a change in chemistry, such as a decrease in the oxygen content of the water. This does not

account for long-lived individuals having to cope with rapid fluctuations in conditions. In this study, although more than 50 specimens have been considered, from a number of horizons, no overall trend has been recognized. Each specimen has a different range of 'aberrant' features. Therefore, it is difficult to imagine that any one disease or change in environmental conditions was responsible for all of these aberrant features.

Urbanek (1973) described regrowth of monograptids after fracture. He noted that the resultant pattern depended upon whether the sicula remained. If the sicula was present in the regrown fragment, then the growth pattern returned to the juvenile form; if the sicula was not present the regrowth was in the adult form. This is consistent with the pattern observed for dendroids; with the sicula present return is to the juvenile pattern (Text-fig. 1). Urbanek (1990) discussed the viability of the 'regenerative morphoses'; although he was describing planktonic forms, his comments are relevant to the regeneration of dendroids, as he suggested that although the regenerated forms were viable, in the normal environment they were inferior compared with their parent colonies. Their survival would be constrained by imperfect hydrodynamic stability, feeding depression as a result of the presence of fewer zooids, and as a direct result of the injury.

The study and comparison of dendroids with their nearest living relatives, the pterobranchs, is as yet in its infancy. Living pterobranchs, although secreting their skeleton from the same material and in a homologous manner to graptolites and dendroids (Rigby 1994), have not yet been described as having a strongly ordered growth pattern. The zooids of Cephalodiscus can recolonize old tubes, and mend them to some extent. They can either work on (or feed from) many different tubes at one time or all work from one tube at the same time. They seem to co-operate to expand the colony into the available space, growing tubes with seemingly no preferred polarity (Rigby and Dilly 1994). The zooids of Rhabdopleura generate the material of their own aperture, and if damaged can repair what is within their reach, either from inside or outside of the tube (Dilly 1986). Successive generations of zooids secrete each tube to a precise pattern, and each tube is completed to (and possibly maintained to) a precisely predetermined overall size and shape (Rigby 1994).

Therefore, by comparison, it is reasonable to suggest that dendroid zooids were to some extent able to mend their rhabdosome, and this could have been done without formation of calluses for small areas of damage. Some areas of damage may have been out of the range of the zooids. It seems that, unlike pterobranchs, however, dendroids were not able easily to reverse the polarity of their growth, and do not seem to have been readily able to regenerate stipe growth in a proximal direction. This may have some bearing on our understanding of whether zooids were concentrated at the outer margin of the cone or whether most of the rhabdosome's thecae were occupied at any one time. More information on this will require more research on the relationship between dendroids and pterobranchs.

One group of colonial animals with known modern and fossil representatives is the bryozoans. The effects of damage on and the regrowth capabilities of this group, may give clues to the response of colonial animals in general to damage, and potentially lead to the development of models of the environmental pressures acting on colonial animals. A few of the observations made about bryozoans are relevant to dendroid abnormalities even though, during growth, bryozoan colonies have a more complex and more commonly changing colony morphology than dendroids.

If living bryozoans are intentionally broken they are able to continue growing, and partially to repair the damage (Lutaud 1983). The resultant structures depend upon the original degree of damage, but the overall tendency is to cover up any weaknesses and resume normal growth as soon as possible; it is more usual to leave a much enlarged fenestrule than to effect a perfect repair. Maintenance of physiological continuity by providing intramural links between living zooids, despite the mortality of intervening zooids, seems to be a most important factor to the bryozoans (Taylor 1988). The same factors probably controlled dendroid regrowth in similar conditions. Like modern pterobranchs, bryozoan zooids can extend the colony with either polarity. Similarly, bryozoan reparative buds clearly can occupy the same sites as the damaged zooids and completely overgrow the original structure (Taylor 1988); dendroid growth patterns seem to have been less flexible, with large holes in the rhabdosome being sealed less efficiently.

Clearly, as more information from all fossil groups becomes available, fossil abnormalities and their causes and implications have the potential to yield more valuable evolutionary, palaeo-biological, palaeoecological, and palaeoenvironmental information. Study of abnormalities has implications for workers in other fossil groups, particularly if members of these groups were to be discovered in the same sedimentary horizons. Where similar abnormalities occur in other fossil groups, conclusions drawn for one fossil group should be considered for their implications to others.

CONCLUSIONS

Dictyonema pentlandica, figured here, and the other dendroids described from the Pentland Hills (Bull 1987), are generally slender forms. They had well developed holdfasts and were able to withstand the effects of some currents, and probably required the presence of constant current action to bring regular food supplies. The 11 species of dendroid and six graptoloids (Bull and Loydell 1995) preserved, probably co-existed in the same environment, which appears to have suited the dendroids particularly well (Bull 1991). These dendroid specimens have not been transported far, or damaged badly on deposition, which is why so many of the growth features of the species can be described.

The mode of preservation and amount of detail remaining can give information about the environment of deposition. The conditions at the time of deposition of the late Llandovery sediments in the North Esk Inlier must have been subject to frequent changes; it was possibly a relatively shallow environment with strong sediment-laden currents and frequent storms. Spinosity, large overall size with slender stipes and the ability to withstand injury may be adaptations that allowed *D. pentlandica* to survive with an attached mode of life in a harsh environment.

The bulbous, spinose nature of the autothecae of *D. pentlandica* may have been a form of protection for the zooids. Slender stipes possibly facilitated efficient current deflection through the mesh. Spines may have enhanced zooid feeding strategies, protected zooids from predation, or further directed water currents through the cone.

Each dendroid rhabdosome housed zooids for some time, which secreted the meshwork in a very regular pattern according to a genetic code. Each was subject both to mutations, and to ever-changing and probably often quite harsh external conditions. Consequently, fossilized rhabdosomes are rarely perfect. For convenience and for clarity of identification, particularly for descriptions of new species, only the most characteristic areas are usually mentioned in systematic descriptions. Descriptions of abnormalities can be used in analysis of palaeoenvironment, palaeobiology and palaeoecology.

Dendroids could rejuvenate after a cessation of growth, probably caused by change in external conditions. They could also regenerate after trauma, such as injury caused by predation, natural abrasion or disease.

Dendroids could repair damage to the rhabdosome, the nature of the repair being dependent on where the injury had taken place. Following injury at the periphery of the rhabdosome the characteristic pattern of growth for each species was returned to as soon as possible, although some stipes may have been too greatly affected to return to the 'standard' pattern. Dendroids appear to have been able, to a limited extent, to patch up holes made in the side of the rhabdosome. They do not seem to have been able to repair growth in a mature area opened up by damage, such as a major split in the mesh in the side of the rhabdosome.

Aberrant growth structures were also observed on a microscopic scale; tubular outgrowths, probably from the bithecae, could be the result of parasitic invasion.

Further comparison of dendroids with modern pterobranchs and other colonial animals, studying the latter's mode of generation and secretion of normal rhabdosome and their response to environmental change, trauma, mechanical damage, predation, disease and other changes, may lead to a more complete understanding of the generation of the normal and abnormal features observed in dendroids. Each of the variations from the norm that is observed can tell us something of the life history of each individual specimen and by implication the environment in which the animal lived.

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