

A NEW UPPER ORDOVICIAN BRYOZOAN FAUNA FROM THE SLADE AND REDHILL BEDS, SOUTH WALES

by CAROLINE J. BUTTLER

ABSTRACT. A diverse bryozoan fauna has been discovered in South Wales in the Slade and Redhill Beds (upper Rawtheyan, Ashgill), exposed in a new road-cutting near Whitland. This is the first account of a moderately diverse Ordovician bryozoan fauna from Britain. The fauna is represented by 15 species belonging to four orders, the majority being Trepostomata. One new genus is described, *Pinnatoporella* (Fenestrata), and three new species *Heterotrypa sladei*, *Dekayia pengawsensis*, and *Anaphragma gwyndyense* (all Trepostomata). New information has led to the redescription of the cystoporate family Rhinoporidae and its reassignment to the suborder Ceramoporina. Ordovician bryozoans are poorly known in Britain, partly because well-preserved diverse faunas such as this are very rare. The fauna is compared biogeographically with previously described Bryozoa. At generic level it is cosmopolitan; however, approximately half the species are endemic to Wales. The remaining species have greatest affinity with Baltoscandia; species level affinities with North America are poorer.

BRYOZOANS are one of the major components of Ordovician faunas. They have been described extensively from North America and the Soviet Union but have been largely neglected in Britain. This neglect may be attributed partly to poor preservation and the time required to prepare specimens, but it is also due to the lack of any great tradition of research on British Palaeozoic bryozoans. No entire bryozoan fauna has previously been described from a British upper Ordovician locality. Worldwide biogeographical comparisons of Ordovician bryozoans therefore omit Britain.

PREVIOUS RESEARCH ON BRITISH ORDOVICIAN BRYOZOANS

Bryozoans are frequently decalcified in British Ordovician rocks, making them easy to distinguish in the field but hard to identify taxonomically even to family level. In faunal community studies bryozoans are often only identified by their gross morphology, for example 'stick bryozoans' or 'prasoporid', the latter term covering any dome-shaped trepostome. Calcified specimens tend to go unnoticed in the field, except in a few localities such as the Slade and Redhill Beds at Pengawse Hill in South Wales, described herein, where a large proportion of the rock consists of bryozoans.

In major British museums (e.g. Natural History Museum, London; Sedgwick Museum, Cambridge) there are numerous decalcified bryozoans, typically fenestrates, collected from North Wales. Locality information is often minimal, for example 'Bala Beds'. Many of these specimens were collected early this century and the material is often of little palaeontological value.

Ordovician bryozoans from Britain were first examined in the mid-nineteenth century when they were identified as corals (e.g. M'Coy 1850; Milne-Edwards and Haime 1854). Many of these early descriptions are scanty, with poor illustrations, often showing no internal morphology. Nicholson and Etheridge (1877) and Nicholson (1879) began to include detailed diagrams of sections of specimens showing internal features.

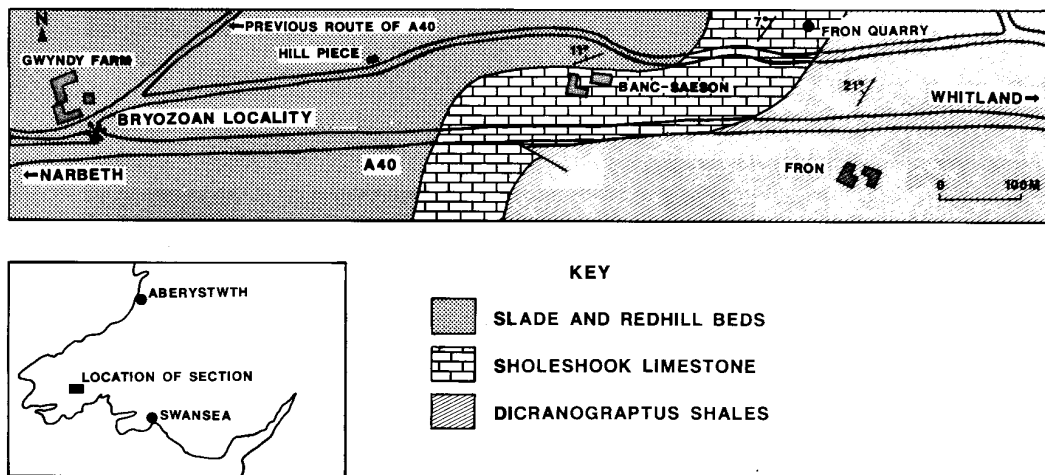
No major monographic study of British Ordovician bryozoans has been completed and only a few papers dealing with small aspects of the fauna have been published. Spjeldnaes (1957) re-

described some type specimens of British species and later examined some silicified specimens from the Llandeilo of South Wales (Spjeldnaes 1963).

Ross, in three papers (1962, 1963, 1965), examined some of the Caradoc (Cautleyan) bryozoans of Shropshire. This is the most extensive study of an Ordovician bryozoan fauna from Britain to date. Eight species were described from three localities. The fauna includes seven trepostomes and one cryptostome.

There are a few papers describing just one Ordovician species or genus (e.g. Etheridge 1879; Shrubsole 1885). The latest of these is by Taylor and Cope (1987), who describe a specimen of the trepostome genus *Orbipora* from the Lower Arenig of South Wales, noteworthy because it is the oldest bryozoan described in the literature.

Virtually no palaeoecological work has been done on British Ordovician bryozoans. One exception is a study by McNamara (1978) on the symbiosis between gastropods and trepostomes in the Coniston Limestone Group of Cumbria. Detailed systematic descriptions are essential before more interpretive studies can be undertaken on the British fauna.



TEXT-FIG. 1. Map showing the bryozoan locality in the Slade and Redhill Beds near Whitland, Dyfed.

MATERIAL

All study material was collected recently from the Slade and Redhill Beds (upper Rawtheyan, Ashgill), west of Whitland, Dyfed (National Grid Reference SN 164170). The outcrop is a long road section (800 m), revealed during the construction of a new route for the A40 trunk road at Pengawse Hill, exposing horizons from the Dicranograptus Shales (Caradoc) in the east, through the Sholeshook Limestone (lower Ashgill), to the Slade and Redhill Beds in the west (Text-fig. 1). The majority of bryozoans were confined to a 0.3 m thick band composed almost entirely of trepostome bryozoans in a matrix of argillaceous limestone. Crinoid fragments, trilobites (e.g. *Stenopareia* sp. and *Tretaspis* sp.), bivalves, cephalopods and brachiopods (e.g. *Leptaena* sp.) were also found.

The majority of specimens examined from Pengawse Hill were calcified, although many of the bryozoans at or near the surface of the outcrop were partially or totally decalcified. Silicification is seen to occur in some of the calcified colonies. This process can destroy the microstructure, but in the majority of affected colonies the silicification is not too advanced. In tangential sections of some colonies a clear ring of silica can be seen around the zoecial apertures, replacing the bryozoan calcite which forms the zoecial linings (Pl. 3, fig. 7).

The bryozoan fauna at Pengawse Hill is very diverse by British standards. A total of fifteen species has been identified, three of which are new. Four orders are represented: Trepostomata, Cystoporata, Fenestrata and Cyclostomata. Trepostomes dominate with ten species. Fourteen bryozoan species are described in detail in the present work; the cyclostome *Kukersella borealis* (Bassler) is described fully elsewhere (Buttler 1989) and only a brief description is given here.

SYSTEMATIC PALAEOONTOLOGY

The terminology used in all descriptions is that of Boardman *et al.* (1983). All genera are placed in families based on the following sources: trepostomes – Astrova (1978); cystoporates – Utgaard (*in* Boardman *et al.* 1983); and phylloporinids – Lavrentjeva (1985). Classification of Palaeozoic trepostome and fenestrate bryozoans at family level is generally unsatisfactory and is currently being revised for the *Treatise on invertebrate paleontology*.

Not all taxa can be identified to species level due to poor preservation or lack of material. In these cases, the species are left in open nomenclature and are referred to as 'cf.' or 'sp.', as recommended by Bengtson (1988).

Biometric details for each trepostome species are tabulated (Table 1). Each measurement was made up to seven times per specimen. The range and mean are calculated for each parameter. All the raw data and further statistical details can be found in an unpublished Ph.D. thesis (Buttler 1988). All specimens described are thin sections/acetate peels unless otherwise stated.

Repository abbreviations: BMNH, Natural History Museum, London; SM, Sedgwick Museum, Cambridge; BGS, British Geological Survey, Keyworth; NMW, National Museum of Wales, Cardiff.

Phylum BRYOZOA Ehrenberg, 1831
 Class STENOLAEMATA Borg, 1926
 Order TREPOSTOMATA Ulrich, 1882
 Suborder HALLOPOROIDEA Astrova, 1965
 Family HETEROTRYPIDAE Ulrich, 1890
 Genus HETEROTRYPA Nicholson, 1879

Heterotrypa sladei sp. nov.

Plate 1, figs 1–5; Text-fig. 2A

Holotype. BMNH PD8167, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Paratypes. BMNH PD8168–70, from the same horizon and locality as holotype.

Etymology. The species is named after the type horizon.

Diagnosis. Colony ramose. Zoecia parallel branch axis in endozone, curving gradually outwards in exozone. Endozonal walls thin and slightly wavy. Autozoecia rounded-polygonal in transverse section; rounded, occasionally very slightly petaloid in shallow tangential sections. Polygonal mesozoecia present, originating throughout colony. Diaphragms present along entire length of autozoecia, common in exozone; very abundant in mesozoecia, constricting walls and producing a slightly beaded appearance. Acanthostyles small and common throughout colony.

Description. Zoaria erect with cylindrical branches, on average 7.5 mm in diameter. Autozoecia are parallel to branch axis in the inner endozone and gradually curve outwards to meet the zoarial surface at 90°. The autozoecia within the endozone have thin, slightly wavy walls. The exozone has an average diameter of 1.26 mm, and is recognized by a slight thickening of the zoecial walls. Autozoecia all originate in the endozone where they are rounded-polygonal in transverse section. They become rounded and occasionally slightly petaloid in the exozone, as seen in tangential sections of branches. Autozoecial diameters average 0.23 mm by 0.27 mm in the exozone. Thin, orally deflected basal diaphragms are found along the entire length of the

colony, spaced 0.32 mm apart in the endozone and becoming more abundant in the exozone where they are spaced 0.13 mm apart. In the outer endozone and exozone occasional cystiphragms are found.

Mesozooecia are present and originate throughout the colony. In the endozone they are polygonal in transverse section and become polygonal-rounded in the exozone, as seen in shallow tangential sections. The maximum diameter of the mesozooecia averages 0.11 mm in the exozone. They contain abundant orally deflected diaphragms, spaced on average 0.18 mm apart in the endozone and 0.1 mm apart in the exozone. Mesozooecial walls are sometimes constricted at the position of the diaphragms, producing a slightly beaded appearance.

Acanthostyles are common and are small with an average diameter of 0.04 mm and density of 9 mm⁻². They originate throughout the colony, some are confined to the autozooecial walls but others indent the zooecial apertures, producing a slight petaloid effect. The acanthostyles are composed of a hyaline core surrounded by steeply dipping laminae.

Autozooecial walls are thin and average 0.4 mm in thickness in the exozone. Wall microstructure is composed of steeply inclined, U-shaped laminae. The zooecial wall boundaries are granular and indistinct.

In one specimen (PD8169) there is a layer of thick exozonal type wall within the middle endozone. This type of feature has been regarded as evidence of an abandoned growing tip (Boardman 1960).

Remarks. This is the first species of *Heterotrypa* described from Great Britain. *Heterotrypa sladei* sp. nov. is characterized by very abundant diaphragms throughout the zoarium, beaded mesozooecia, thin endozonal walls and small acanthostyles common throughout the colony. It is unusual for the genus in having abundant diaphragms within the endozone. Boardman and Utgaard (1966, p. 1105) in their revision of *Heterotrypa* state that diaphragms within the endozone are rare to moderately abundant.

H. sladei is similar to *H. frondosa* (d'Orbigny, 1850) illustrated by Boardman and Utgaard (1966, pl. 140), although diaphragms are more abundant in the endozone of the new species. *H. magnopora* Boulange, 1963 was described from the Montagne Noire (upper Ordovician) and has a similar exozone to *H. sladei* but differs in having sparse acanthostyles in the endozone.

Genus DEKAYIA Milne-Edwards and Haime, 1851

Dekayia pengawsensis sp. nov.

Plate 1, figs 6–8; Plate 2, fig. 1; Text-fig. 2b.

Holotype. BMNH PD8176, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

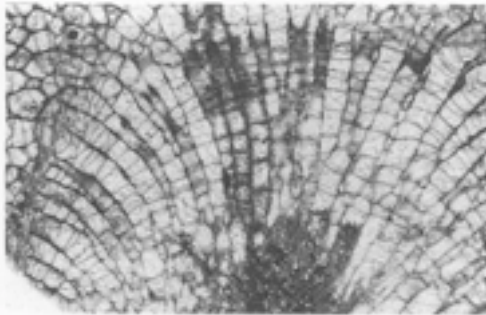
Paratypes. BMNH PD8178–9, from the same horizon and locality as holotype.

Etymology. The species is named after the type locality.

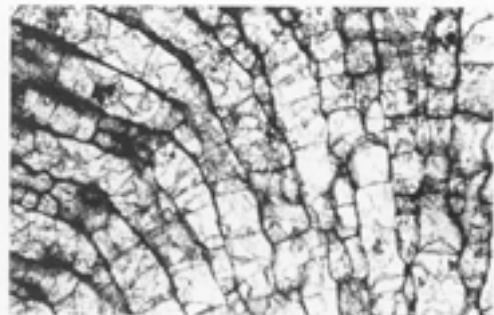
EXPLANATION OF PLATE I

Figs 1–5. *Heterotrypa sladei* sp. nov. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8167 (paratype), longitudinal section, × 15. 2, BMNH PD8167 (holotype), longitudinal section, × 28. 3, BMNH PD8170 (paratype), longitudinal section, showing layer of thicker exozonal material within the endozone, × 48. 4, BMNH PD8169 (paratype), tangential section, × 48. 5, BMNH PD8169 (paratype), tangential section, showing an acanthostyle inflecting an autozooecium, × 120.

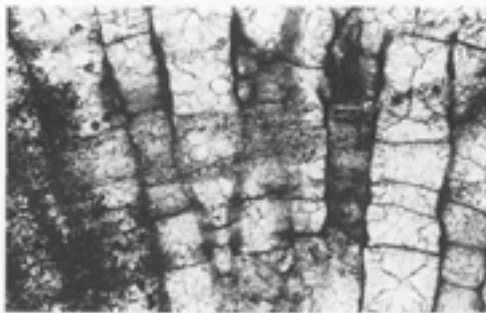
Figs 6–8. *Dekayia pengawsensis* sp. nov. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 6, BMNH PD8179 (paratype), longitudinal section, × 15. 7, BMNH PD8179 (paratype), longitudinal section, showing large acanthostyles in endozone, × 28. 8, BMNH PD8176 (holotype), tangential section, × 48.



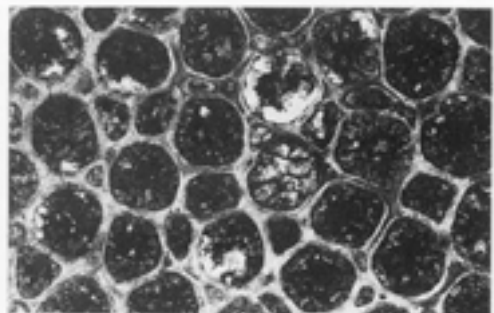
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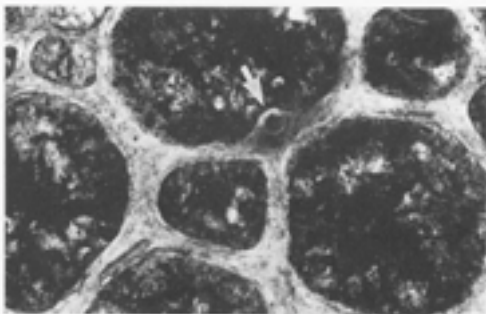
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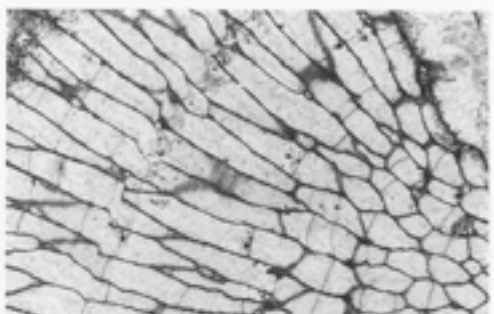
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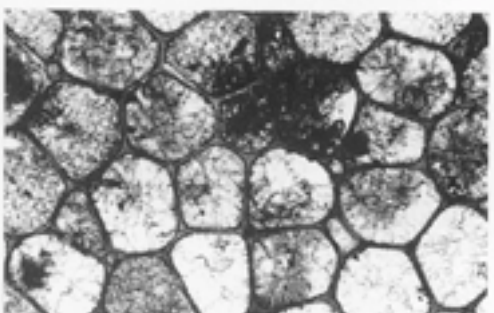
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Diagnosis. Colony hemispherical. Zooecia originate from the basal lamina. Zooecial walls wavy, slightly thickened in exozone. Autozooecia polygonal to polygonal-rounded in transverse section throughout colony. Polygonal mesozooecia uncommon. Diaphragms present in all zooecia. Acanthostyles abundant throughout colony.

Description. Zoaria are hemispherical with an average diameter of 11 mm. Autozooecia all originate at the centre of the colony and curve outwards towards the zoarial surface. Autozooecial walls are slightly wavy throughout the colony. Endozone:exozone boundary indistinct. Autozooecia are large, with an average diameter of 0.29 mm by 0.32 mm, and are polygonal to polygonal-rounded in transverse section throughout the colony. Thin diaphragms are present, though not abundant, in all zooecia, and are spaced between 0.13 mm and 0.86 mm apart, with an average of 0.48 mm. They increase in frequency slightly at the periphery of the colony. These basal diaphragms are all deflected orally at their junctions with the zooecial walls and their laminae are continuous with the autozooecial linings.

Mesozooecia are present but not common. They are polygonal in transverse section and have an average maximum diameter of 0.12 mm. Mesozooecia contain orally deflected basal diaphragms, spaced on average 0.11 mm apart in the exozone.

Acanthostyles are abundant and originate throughout the colony. They are composed of a large hyaline core surrounded by steeply dipping laminae.

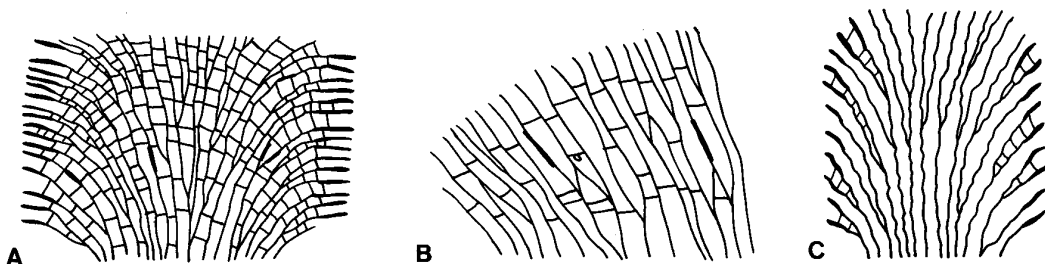
Autozooecial wall thickness averages 0.02 mm in the exozone. Wall microstructure is composed of inclined U-shaped laminae. Zooecial boundaries are distinguished by a darker granular zone in the centre of the walls.

In one specimen (PD8176) hollow 'cyst' structures are found within the autozooecia. These are spherical, average 0.03 mm in diameter, and occur singularly or in pairs. The 'cysts' are attached to the sides of the zooecial walls and their laminae are continuous with the zooecial linings.

Two of the specimens (PD8176, 8178) use colonies of *Leioclema orbicularis* as substrata for encrustation. In all of the colonies, periods of growth cessation can be inferred by the presence of a row of thick basal diaphragms followed by a change in the orientation of the zooecia.

Remarks. *Dekayia pengawsensis* sp. nov. is primarily characterized by the hemispherical form, the thin wavy zooecial walls and the rare mesozooecia. Diaphragms are present and acanthostyles are abundant throughout the colony. Prior to this study the genus *Dekayia* had not been recorded in Britain.

D. pengawsensis is similar internally to the ramose *D. aspera* Milne-Edwards and Haime, 1851, which was well illustrated by Boardman and Utgaard (1966, pl. 138). The Welsh specimens, however, have smaller acanthostyles and more abundant diaphragms. *D. semipilans* (Ulrich, 1890), figured by Brown and Daly (1986, pl. 4, figs 9–12), has a similar wall structure and acanthostyles to *D. pengawsensis* but again lacks diaphragms. *D. cf. crenulata* Prantl, 1940 has been found from the same locality. This differs from *D. pengawsensis* by the ramose colony form, the beaded mesozooecia and the greater abundance of acanthostyles.



TEXT-FIG. 2. Longitudinal sketch sections of new species of bryozoans described from the Slade and Redhill Beds. A, *Heterotrypa sladei*. B, *Dekayia pengawsensis*. C, *Anaphragma gwyndyense*.

Dekayia cf. crenulata Prantl, 1940

Plate 2, figs 2-4

Material. BMNH PD8171-3, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, W of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria erect with cylindrical branches, on average 7 mm in diameter. The surfaces of all specimens are slightly abraded. Autozoecia are generally parallel to the branch axis in the endozone and they gradually curve outwards and meet the zoarial surface at 90°. The autozoecia within the endozone have quite thin crenulated walls. The exozone is relatively narrow with an average diameter of 0.06 mm. It is recognized by a slight thickening of the zooecial walls and a change in the zooecial orientation, which occur simultaneously. Autozoecia all originate in the endozone where they are polygonal-rounded in transverse section. They become rounded in the exozone as seen in tangential sections of branches. Autozoecial diameters average 0.22 mm by 0.27 mm. Diaphragms are absent in the endozone but are occasionally present within the autozoecia in the exozone where they are spaced on average 0.25 mm apart. These diaphragms are all deflected orally at their junctions with the zooecial walls and their laminae are continuous within the autozoecial linings.

Mesozoecia are present but uncommon, and originate in the outer parts of the endozone and inner parts of the exozone. They are rounded-polygonal in shape, as seen in shallow tangential sections, and have a maximum diameter of 0.12 mm. The mesozoecia contain orally deflected basal diaphragms, spaced on average 0.15 mm apart in the endozone and 0.13 mm in the exozone. Mesozoecial walls often have a beaded appearance in longitudinal section. In the exozone this is caused by the zooecial walls constricting slightly at the position of the diaphragms. In the endozone the mesozoecial walls appear to pinch together, producing a similar beaded appearance.

Acanthostyles are very abundant, with an average diameter of 0.05 mm and density of 7 mm⁻² the exozone. They are large and long, originate randomly throughout the colony, and may indent autozoecial walls. Acanthostyles all have a wide hyaline core, surrounded by steeply dipping conical laminae.

Autozoecial wall thickness averages 0.03 mm in the exozone. Wall microstructure is composed of inclined, U-shaped laminae, with indistinct zooecial boundaries. Some zoecia are infilled with laminar calcite close to the colony surface. In longitudinal section this infilling consists of very broad U-shaped laminae.

Remarks. The specimens described herein are distinguished by the thin crenulated walls in the endozone, the rare mesozoecia and the large abundant acanthostyles throughout the colony.

Prantl (1940) described the Ashgillian species *Dekayia crenulata* from east of Grange du Pin, Herault, Montagne Noire, France. This species has slender branches, an absence of mesozoecia, crenulated autozoecial walls in the axial region of the zoarium and numerous acanthostyles throughout the colony. The walls and acanthostyles are similar in specimens from Wales and the Montagne Noire. The autozoecial apertures of *D. crenulata* described by Prantl are generally smaller than those of the specimens from Wales (0.17-0.21 mm Montagne Noire; 0.19-0.32 mm Wales); however, the ranges overlap. The size of the colonies also varies: *D. crenulata* has a branch diameter of 3.6-4.6 mm, the Welsh specimens are larger at 7-8 mm. Mesozoecia are stated as absent in *D. crenulata* by Prantl. In the Welsh specimen PD 8173 they are present but they are very rare in specimen PD 8172. This may reflect within species variability. For the present, until further material can be examined, the specimens are assigned to *D. cf. crenulata*.

Genus LEIOCLEMA Ulrich, 1882

Leioclema orbicularis Modzalevskaya, 1953

Plate 2, figs 5-8; Plate 3, figs 1 and 2

1921 *Leioclema spineum ramosum* Bekker, p. 41, pl. 6, figs 14-18.1953 *Leioclema spineum* Ulrich var. *orbicularis* Modzalevskaya, p. 147, pl. 9, figs 4-6; text-fig. 23.

Material. BMNH PD8159-8164, 8166a, b; Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Other occurrences. ?Kuckers Stage (middle Ordovician), NE Estonia, USSR. Middle Ordovician, Leningrad Oblast'. USSR (Modzalevskaya 1953).

Description. Zoaria erect with cylindrical branches, on average 6.4 mm in diameter. Autozoecia are roughly parallel to the branch axis within the endozone and gradually curve outwards to meet the zoarial surface at 70°–90°. Autozoecial walls are thin within the endozone and slightly wavy. The exozone has an average diameter of 1.66 mm, and is recognized by a thickening of the zoecial walls. Autozoecia originate within the endozone, where they are polygonal-rounded in transverse section. They become rounded-petaloid in the exozone, as seen in tangential sections of branches. Autozoecial diameters in the exozone average 0.25 mm by 0.34 mm. Diaphragms are rare and often absent. If present, there are usually only one or two per autozoecium and they are located in the exozone.

Mesozoecia are common, originate within the endozone and have an average maximum diameter of 0.16 mm. In shallow tangential sections they are polygonal-rounded in shape. Mesozoecia contain abundant orally deflected basal diaphragms, spaced on average 0.15 mm apart in the endozone and 0.08 mm in the exozone, with successive diaphragms generally increasing in thickness distally along the mesozoecium.

Acanthostyles are large and abundant, with an average diameter of 0.1 mm and density of 8 mm⁻². They can occur throughout the exozone and they frequently indent the autozoecial apertures to produce a petaloid shape. A hyaline calcite core is surrounded by steeply dipping conical laminae.

Autozoecial wall thickness averages 0.12 mm in the exozone. Microstructure is difficult to distinguish because the walls are considerably disrupted by the presence of the large acanthostyles; however, walls can be seen to be composed of steeply inclined, U-shaped laminae. Diaphragms in the distal exozone are continuous with the zoecial wall laminae. Some of the zoecia, especially mesozoecia, become infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Remarks. This species is characterized by an erect colony form, and thin autozoecial walls in the endozone which become thickened in the exozone. Autozoecial apertures are rounded-petaloid in shallow tangential section. Diaphragms are rare in autozoecia but common in mesozoecia. Acanthostyles are large and abundant in the exozone.

Leioclema spineum Ulrich var. *orbicularis* Modzalevskaya, 1953 was first described from the middle Ordovician of Leningrad Oblast' and Estonia. The *L. spineum* Ulrich as described by Bassler (1911) was characterized by a ramose colony form, numerous diaphragms in the abundant mesozoecia and occasional ones in the autozoecia, and exceedingly large acanthostyles. *L. spineum orbicularis* differs from *L. spineum* in having more abundant smaller acanthostyles and fewer mesozoecia. This internal structure is similar to *Leioclemella clava* Bassler, 1911. The genus *Leioclemella* is, however, characterized by having a club-shaped zoarium seemingly jointed at the base. Articulation is unknown in trepostomes and this feature may instead be a paraboloid base of the sort described by McKinney (1977). The differences between *L. spineum orbicularis* and *L. spineum* are herein considered to be significant enough to raise the subspecies *L. spineum orbicularis* to species rank.

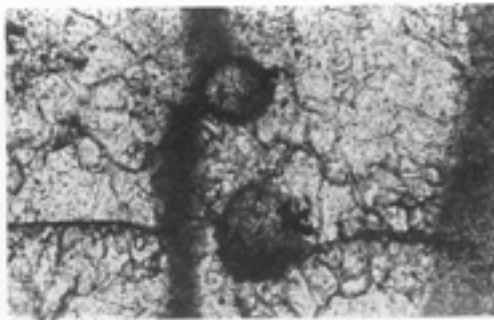
The specimens described here are very similar to *L. orbicularis* from the USSR. Although the acanthostyles of the Welsh material are larger than those shown in Modzalevskaya (1953, text-fig. 23), her tangential sections are deeper than those of the Welsh material.

EXPLANATION OF PLATE 2

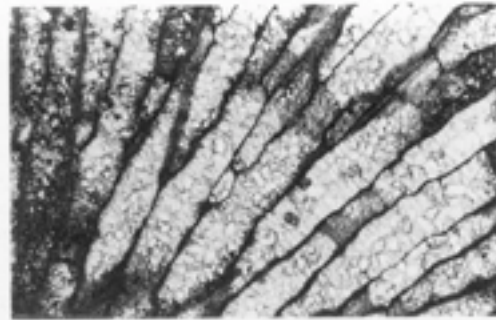
Fig. 1. *Dekayia pengawsensis* sp. nov. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, BMNH PD8176 (holotype), longitudinal section, showing 'cyst' structures, × 120.

Figs 2–4. *Dekayia* cf. *crenulata* Prantl, 1940. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 2, BMNH PD8172, longitudinal section, × 28. 3, BMNH PD8173, longitudinal section, × 28. 4, BMNH PD8172, tangential section, showing acanthostyles, × 38.

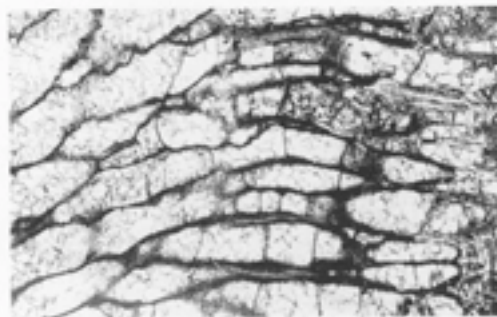
Figs 5–8. *Leioclema orbicularis* Modzalevskaya, 1953. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 5, BMNH PD8161, longitudinal section, × 15. 6, BMNH PD8161, longitudinal section, showing the endozone, × 28. 7, BMNH PD8161, longitudinal section, showing large acanthostyles in the exozone, × 55. 8, BMNH PD8161, transverse section, × 28.



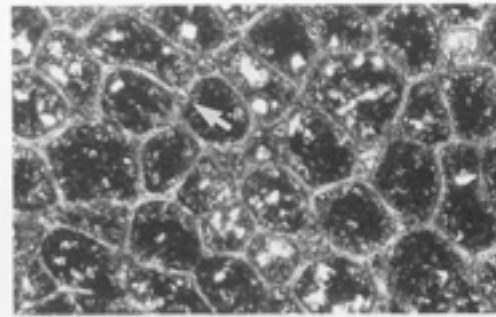
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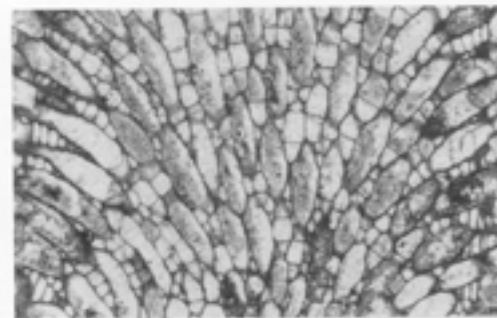
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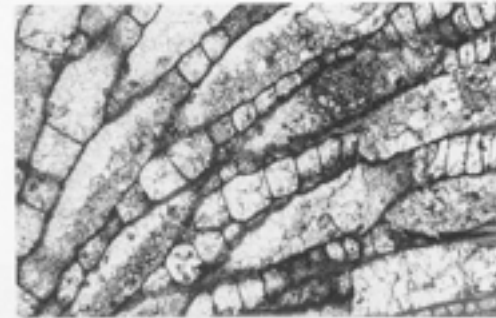
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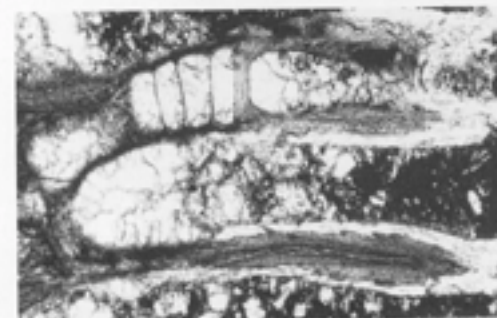
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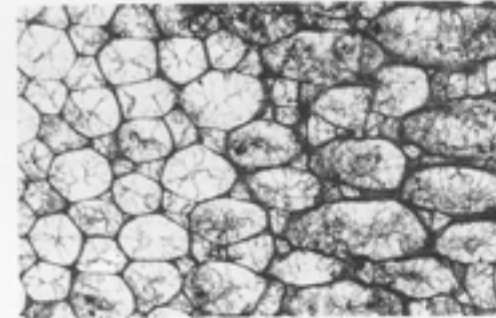
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Bekker (1921) described the variety *L. spineum ramosum* from the Kuckers Stage (middle Ordovician) of NE Estonia, which he regarded as an intermediate form between *L. spineum* and *Leioclemella clava*. Bekker explained 'The acanthostyles of my specimen agree much more with those of *Leioclemella*, but the habit of growth (*Leioclemella clava* - clubshaped) separates them'. This would suggest that *L. spineum ramosum* is an erect ramose form, but Bekker's plate (1921, pl. 6, fig. 18) shows the cone-shaped origin of the colony suggesting a possible paraboloid base like that of *Leioclemella*. The illustrations are, however, poor and the type material (housed in the Geological Museum at the University of Tartu, Estonia) would have to be examined for a positive identification, pending which this species is tentatively placed within *L. orbicularis*.

Family HALLOPORIDAE Bassler, 1911

Genus HALLOPORA Bassler, 1911

Hallopora peculiaris Pushkin (in Ropot and Pushkin, 1987)

Plate 3, figs 3-8

1987 *Hallopora wesenbergiana peculiaris* Pushkin in Ropot and Pushkin; p. 153, pl. 8, fig. 5; pl. 9, fig. 1.

Material. BMNH PD8237-82, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170)

Other occurrence. Piriguskii Stage (lower Ashgill), Shikipi, Latvia, USSR (Pushkin in Ropot and Pushkin 1987).

Description. Zoaria erect with cylindrical branches on average 8.3 mm in diameter. Autozoecia curve gradually away from the branch axis in the endozone and meet the zoarial surface at approximately 80-90°. In the endozone the zooecial walls are very thin. The exozone, recognized by a thickening of the zooecial walls, has an average width of 1.65 mm. Autozoecia are circular in transverse section throughout the colony and average 0.37 mm in diameter in the exozone. There is an average of 5 autozoecia mm⁻² in the exozone. Diaphragms are rare within the autozoecia and when present, usually occur closely spaced in the distal exozone. These basal diaphragms are deflected orally at their junctions with the zooecial walls and their laminae are generally continuous with the zooecial linings. The average spacing between the diaphragms is 0.16 mm in the endozone and 0.15 mm in the exozone.

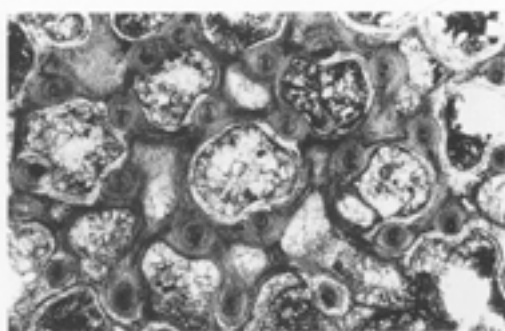
Mesozoecia are common throughout the whole zoarium, often originating in the inner parts of the endozone. Mesozoecial walls are thin in the endozone and thicken in the exozone. They are polygonal to polygonal-rounded in shallow tangential sections, with an average maximum diameter of 0.16 mm in the exozone. Basal diaphragms are present throughout their length, spaced on average 0.13 mm apart in the endozone and 0.07 mm in the exozone. Diaphragms tend to increase in thickness distally along the mesozoecia. In some colonies mesozoecial walls are constricted at the position of the diaphragms, producing a slightly beaded appearance.

Autozoecial wall thickness averages 0.08 mm in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae. The precise contact between the zooecia is indistinct. The thickened exozonal

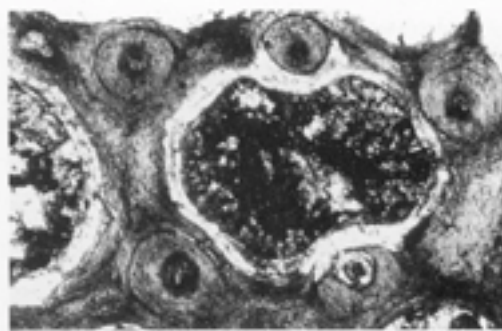
EXPLANATION OF PLATE 3

Figs 1 and 2. *Leioclema orbicularis* Modzalevskaya, 1953. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8161, tangential section, ×35. 2, BMNH PD8161, tangential section, showing large acanthostyles, ×80.

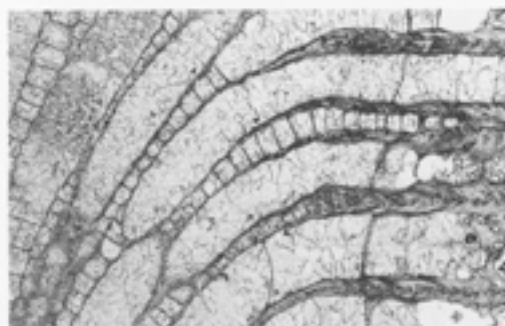
Figs 3-8. *Hallopora peculiaris* Pushkin (in Ropot and Pushkin, 1987). Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 3, BMNH PD8278, longitudinal section, ×28. 4, BMNH PD8282, longitudinal section, ×28. 5, BMNH PD8278, transverse section, ×28. 6, BMNH PD8278, longitudinal section, showing the V-shaped microstructure, ×75. 7, BMNH PD8278, tangential section, showing rings of clear silica replacing the autozoecial linings, ×40. 8, BMNH PD8257, tangential section, showing maculae composed predominantly of mesozoecia, ×28.



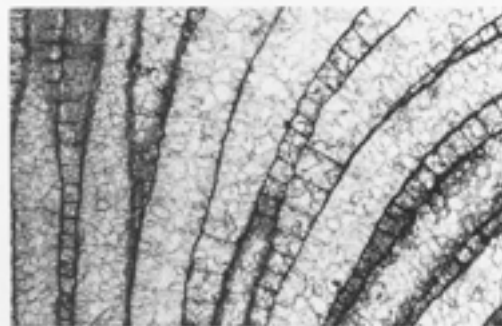
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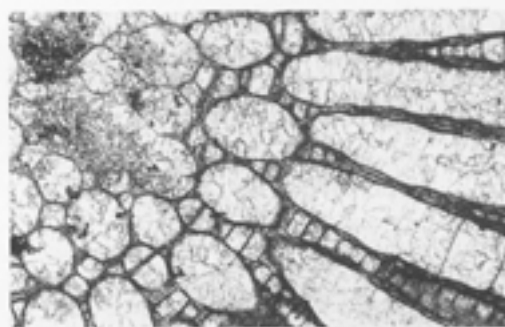
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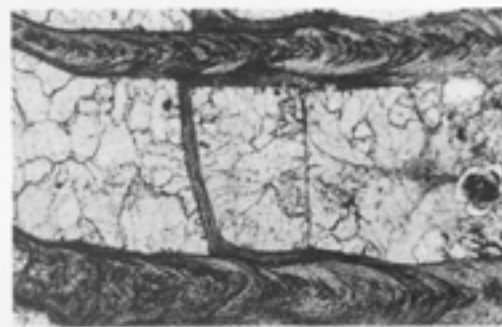
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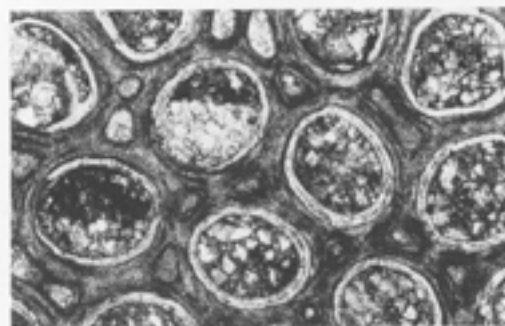
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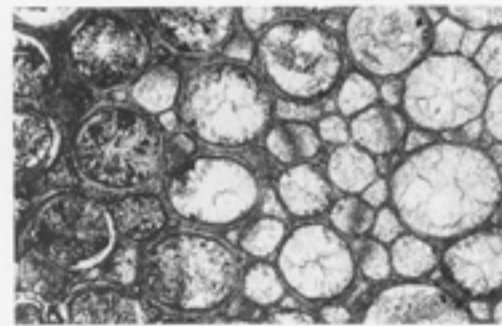
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diaphragms in the mesozoecia are also laminar and are continuous with the wall laminae. Some zoecia, especially mesozoecia, are infilled with laminar calcite close to the zoarial surface. In longitudinal sections this infilling consists of broad U-shaped laminae.

Maculae composed of a concentration of mesozoecia have been recognized in thin sections (Pl. 3, fig. 8).

Overgrowths are present in several colonies (e.g. PD8237). These are composed of endozonal and exozonal elements, and often contain abundant diaphragms.

Remarks. *Hallopora peculiaris* is primarily characterized by the extensive beaded mesozoecia which originate in the inner endozone. The autozoecia are circular throughout the colony, and diaphragms are rare in the endozone, becoming more abundant in the outermost regions.

Pushkin (*in* Ropot and Pushkin, 1987) created a new sub-species *H. wesenbergiana peculiaris*, which differed from the Estonian *H. wesenbergiana* (Dybowski) by the absence of diaphragms within the endozonal autozoecia. The mesozoecia in *H. wesenbergiana* are less prominent than in *H. wesenbergiana peculiaris* and are not beaded. The differences are considered significant to raise *H. wesenbergiana peculiaris* to species rank.

One other species of *Hallopora* is here described from Pengawse Hill, *H. cf. elegantula*, a very slender form, with large and abundant mesozoecia.

Hallopora peculiaris is similar to *H. solbergiensis* described from the upper Ordovician *Dalmanitina* beds of Borensult, Ostergötland, Sweden by Brood (1978). The Swedish species, however, differs from the Welsh by its smaller size (colony branches 3–5 mm wide), the more abundant diaphragms within the autozoecia, and the relatively greater size of the mesozoecia.

Hallopora cf. elegantula (Hall, 1852)

Plate 4, figs 1 and 2

Material. BMNH PD8180–82, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria erect with slender cylindrical branches, on average 3.2 mm in diameter. Autozoecia curve outwards from the branch axis to meet the colony surface at 90°. The autozoecia within the endozone have thin walls. The exozone is narrow with an average width of 0.86 mm and is recognizable by a slight thickening of the zooecial walls.

Autozoecia are circular in section throughout the colony and average 0.26 mm by 0.31 mm in diameter in the exozone. Diaphragms are found along the whole length of the autozoecia, but are rare in the exozone. They are spaced on average 0.17 mm apart in the endozone.

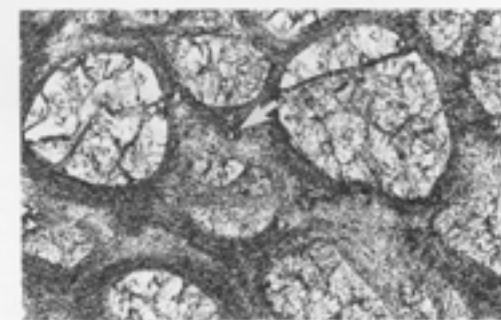
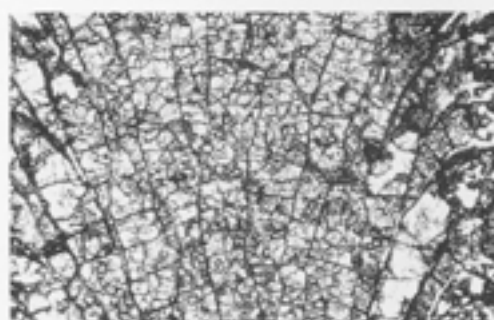
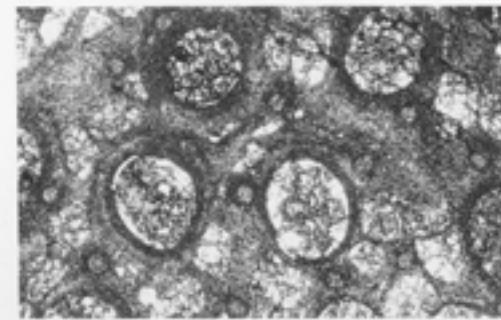
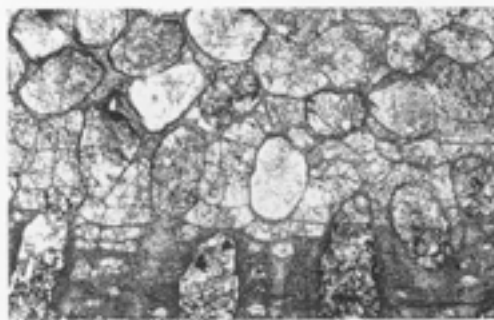
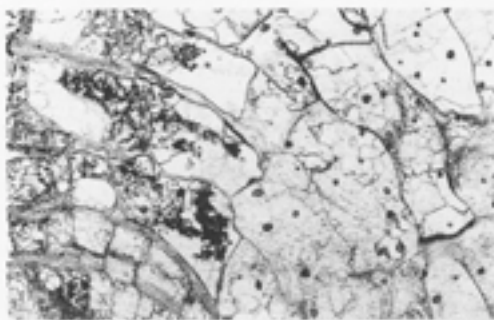
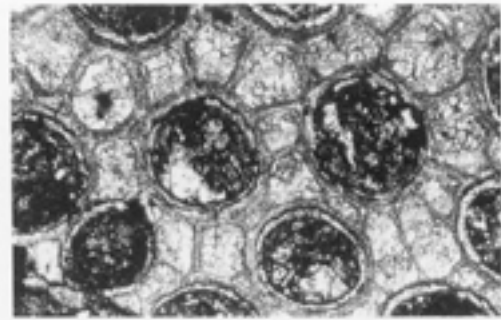
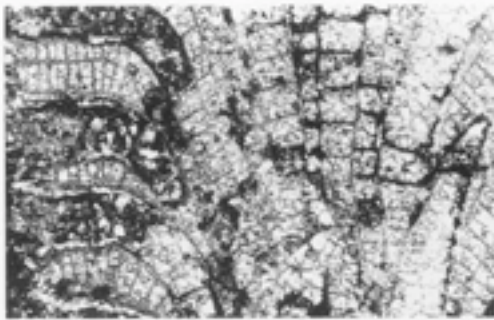
Mesozoecia are common, originate within the endozone and have an average maximum diameter of 0.15 mm. In shallow tangential section the polygonal mesozoecia are seen to fill in the spaces between the circular autozoecia. Mesozoecia contain orally deflected diaphragms throughout their length which are spaced on average 0.1 mm apart in the endozone and 0.05 mm in the exozone, increasing in abundance distally along each mesozoecium.

EXPLANATION OF PLATE 4

Figs 1 and 2. *Hallopora cf. elegantula* (Hall, 1852). Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8181, longitudinal section, $\times 38$. 2, BMNH PD8181, transverse section, $\times 48$.

Figs 3–6. *Batostoma* sp. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 3, BMNH PD8332, longitudinal section, $\times 32$. 4, BMNH PD8332, longitudinal section, showing large acanthostyles which lack sheathing laminae, $\times 60$. 5, BMNH PD8236*d*, transverse section, showing the irregularly shaped autozoecia within the endozone, $\times 28$. 6, BMNH PD8236*d*, tangential section, $\times 48$.

Figs 7–8. *Eridotrypa* sp. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 7, BMNH PD8319*a*, longitudinal section, $\times 38$. 8, BMNH PD8319*a*, tangential section, showing small acanthostyle-like structures, $\times 105$.



BUTTLER, *Hallopora*, ?*Batostoma*, *Eridotrypa*

Autozooeical wall thickness averages 0.1 mm in the exozone. Wall microstructure is composed of inclined, U-shaped laminae. Zooeical boundaries are indistinct.

Remarks. This species is only known from randomly oriented peels of poorly preserved specimens. It is characterized by the narrow colony branches and thin-walled autozooeicia curving out gradually from the branch axis. Autozooeicia are circular in cross section throughout the colony. Polygonal mesozooeicia are common and surround the autozooeicia. Diaphragms are present in the autozooeicia and very abundant in the mesozooeicia.

Internally, the specimens are very similar to *Hallopora elegantula* Hall, an Ordovician and Silurian species with an extensive distribution. They have similar polygonal mesozooeicia surrounding the autozooeicia, and similar diaphragms. *H. elegantula* is, however, characterized by ornamented, perforated terminal diaphragms found usually at the outer ends of the autozooeicia but also within the exozone (Conti and Serpagli 1987). As these have not been observed in the Welsh specimens, this material is therefore identified as *H. cf. elegantula*.

Family TREMATOPORIDAE Miller, 1889
Genus BATOSTOMA Ulrich, 1882

? *Batostoma* sp.

Plate 4, figs 3–6

Material. BMNH PD8332, 8236d, 8319b, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria erect with cylindrical branches, on average 5.3 mm in diameter.

Autozooeicia appear to curve out from the branch axis to meet the zoarial surface at 70°. The autozooeicia within the endozone have very thin wavy walls.

The exozone has an average width of 1.37 mm. It is recognized both by a slight thickening of the zooeical walls and a change in zooeical orientation.

Autozooeicia all originate in the endozone where they are irregular-polygonal in transverse section, becoming circular in the exozone as seen in tangential sections of branches. Autozooeical diameters average 0.26 mm by 0.31 mm within the exozone. Diaphragms are present in autozooeicia in the exozone and may also occur in the endozone but are hard to distinguish here owing to the poor preservation. These basal diaphragms are all deflected orally at their junctions with zooeical walls and their laminae are continuous with the autozooeical linings.

Mesozooeicia are present and originate in the endozone. They are polygonal in shallow tangential section and have an average maximum diameter of 0.12 mm. They contain orally deflected basal diaphragms in the exozone, spaced on average 0.2 mm apart and often slightly increasing in thickness distally along the mesozooeicum.

Acanthostyles are very large and abundant, with an average diameter of 0.06 mm and a density of 10 mm⁻². They originate deep in the exozone, occasionally indent autozooeical apertures, and are composed of a very wide hyaline calcite core without a surrounding sheath of lamellae.

Autozooeical wall thickness averages 0.14 mm in the exozone. Wall microstructure consists of steeply inclined U-shaped laminae and is hard to distinguish because of the presence of the large acanthostyles. Some zooeicia, especially mesozooeicia, are filled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Remarks. Only three poorly-preserved specimens (two in randomly oriented peels) have been found. This species is very unusual and is characterized by the irregularly polygonal autozooeical apertures, which become circular in shallow tangential sections. Autozooeical walls are very thin and irregular within the endozone and become greatly thickened in the outer exozone. Diaphragms are present in the exozonal autozooeicia and are irregularly spaced. Acanthostyles are abundant, large and composed entirely of a hyaline core with no surrounding laminae.

Generic assignment of this species is difficult because of the poor preservation of the specimens. The erect colony, the occurrence of diaphragms in the autozooeicia, and the presence of

acanthostyles fit the generic concept of *Batostoma*. However, the detailed structure of the acanthostyles and endozonal walls is apparently unique and provides a basis for the suggestion that this material may represent a new genus. The large, simple acanthostyles are similar to those observed in early Ordovician forms such as *Nekhorosheviella* Modzalevskaya. As three poorly preserved specimens do not provide sufficient information to erect a new genus, the assignment is given tentatively as ?*Batostoma* sp.

Genus ERIDOTRYPA Ulrich, 1893

Eridotrypa sp.

Plate 4, figs 7 and 8

Material. BMNH PD8319a, 8236e, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria erect with very narrow cylindrical branches, on average 1.5 mm in diameter. This species has only been recognized in randomly oriented peels. Autozooezia are parallel to the branch axis within the endozone and then curve slightly in the exozone to meet the zoarial surface at 45°. The autozooezia within the endozone have thin, straight walls. The exozone is narrow with an average diameter of 0.53 mm. It is recognized by a slight thickening of the zooecial walls. Autozooezia all originate in the endozone (though no specimens have been observed in transverse section), and are oval in the exozone, as seen in tangential sections of the branches. Autozooezial diameters average 0.11 mm by 0.15 mm within the exozone. Diaphragms are present throughout the autozooezia and are widely-spaced, on average 0.21 mm apart in the endozone and 0.12 mm in the exozone. These basal diaphragms are all deflected orally at their junctions with zooecial walls.

Small polygonal mesozooecia may be present in the exozone, but are hard to distinguish. Acanthostyle-like structures have been observed in the exozone; their structure cannot be distinguished.

Autozooezial wall thickness averages 0.04 mm in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae, but is, however, indistinct.

Remarks. The specimens of *Eridotrypa* from Pengawse Hill are from randomly orientated peels. They are characterized by a narrow ramose colony form; autozooezial walls are thin and diaphragms are found throughout the colony. Autozooezial apertures are oval in shallow tangential sections; mesozooecia are present.

Suborder AMPLEXOPOROIDEA Astrova, 1965

Family AMPLEXOPOROIDAE Miller, 1889

Genus ANAPHRAGMA Ulrich and Bassler, 1904

Anaphragma dnestrense Astrova, 1965

Plate 5, figs 1-4

1965 *Anaphragma dnestrense* Astrova, p. 235, pl. 56, figs 1a and b.

1966 *Anaphragma portranense* Ross, p. 111, pl. 1, figs 1, 2, 4, 6; pl. 6, figs 4, 6.

Material. BMNH PD8204-34, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Other occurrences. Molodovskii Stage (upper Ordovician), Podolia, USSR (Astrova 1965). Portrane Limestone (Cautleyan, Ashgill), Portrane, Co. Dublin, Ireland (Ross 1966).

Description. Zoaria erect with cylindrical branches, on average 6.4 mm in diameter. The surfaces of all specimens are abraded. Autozooezia generally parallel the branch axis in the endozone. They then gradually curve outwards to meet the zoarial surface at approximately 80°. Within the endozone the autozooezial walls

are thin and crenulated. The exozone, recognized by a slight thickening of the zooecial walls and a change in the orientation of the zooecia, has an average diameter of 1.34 mm. Autozooecia are polygonal in the endozone in transverse section and become rounded in the exozone as seen in tangential sections of branches. Autozooecia average 0.33 mm by 0.43 mm diameter in the exozone. Diaphragms are absent in all of the autozooecia.

Exilazooecia are common and originate in the outer parts of the endozone. They are rounded-polygonal in shape in shallow tangential sections, with a maximum diameter which averages 0.16 mm.

Acanthostyles are abundant, usually small and inconspicuous. Their diameter ranges from 0.01 mm to 0.06 mm. In some acanthostyles a calcite hyaline core has been observed, surrounded by conical calcite laminae.

Autozooecial wall thickness averages 0.08 mm in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae. Zooecial boundaries are distinguished by a darker granular zone. Some autozooecia and exilazooecia are infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Overgrowths, composed of exozonal elements, have been recognized in a few specimens.

Remarks. *Anaphragma dnestrense* was described from the Molodovskii Stage of Podolia in the Arctic Soviet Union by Astrova (1965) and has hitherto not been recognized elsewhere. *A. portranense* was described by Ross (1966) from the Portrane Limestone in Ireland. It was diagnosed as 'Anaphragma with slender branches having large zooecial openings, numerous small acanthopores which penetrate the junctions of the zooecial walls and mesopore walls, and numerous mesopores'. *A. dnestrense* is similar in most aspects to *A. portranense*. The colony size of the Welsh material (4–9 mm zoarial diameter) is generally larger than that of *A. portranense* (3 mm); however, the Soviet material has a very wide range of colony size (3–14 mm) spanning the two groups. All other measurements given for the holotype of *A. portranense* (Ross 1966, p. 112) extend into the range measured from the Welsh specimens of *A. dnestrense*. Therefore, *A. portranense* is placed in synonymy with *A. dnestrense*.

A. dnestrense is similar to *A. mirabile* Ulrich and Bassler, 1904 which was redescribed by Boardman (1960). *A. mirabile* has been recognized from the upper Ordovician of North America (Richmondian Group, Illinois and Wisconsin) and Estonia (Lyckholm Limestone, Island of Dago). However, the walls of *A. mirabile* are less crenulated in the endozone, there are fewer exilazooecia, and the exozone is larger in relation to the endozone than in *A. dnestrense*. In the outer exozone of *A. mirabile* the acanthostyles become very large (Boardman 1960, pl. 4, fig. 2), whereas in *A. dnestrense* they remain small.

One other species of *Anaphragma* has been recognized in this study from the same locality (Pengawse Hill, near Whitland). *A. gwyndyense* sp. nov. has thick walls in the endozone, tabulated polymorphs (i.e. mesozooecia) and rare acanthostyles which distinguish it from *A. dnestrense*.

Anaphragma gwyndyense sp. nov.

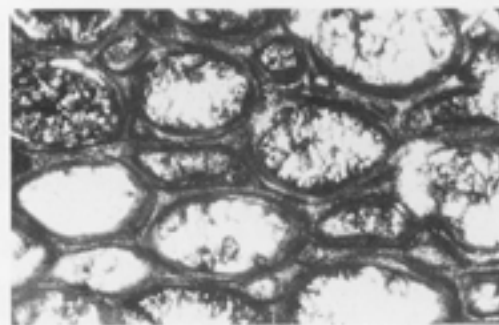
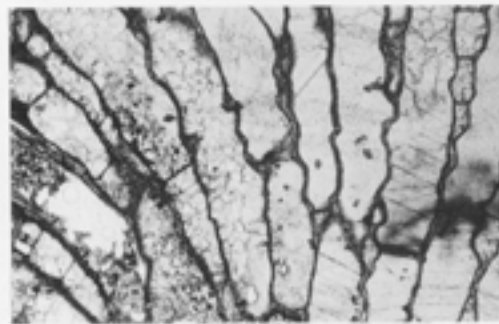
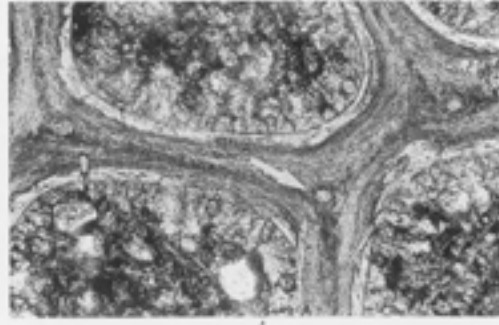
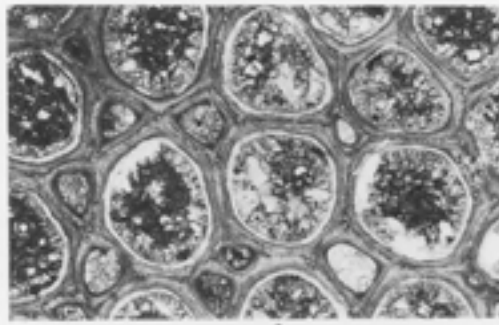
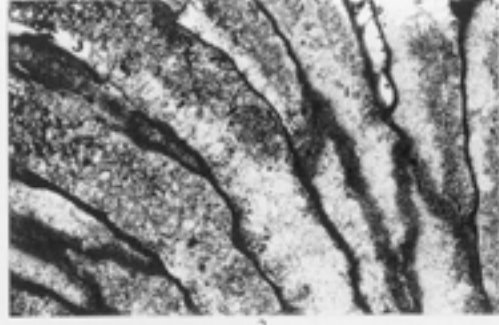
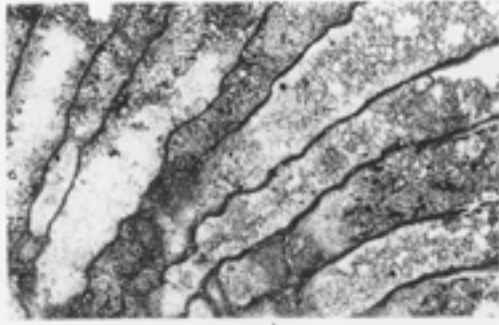
Plate 5, figs 5–8; Text-Fig. 2c

Holotype. BMNH PD8195, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

EXPLANATION OF PLATE 5

Figs 1–4. *Anaphragma dnestrense* Astrova, 1965. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8232, longitudinal section, $\times 28$. 2, BMNH PD8229, longitudinal section, $\times 28$. 3, BMNH PD8235, tangential section, $\times 38$. 4, BMNH PD8235, tangential section, showing small acanthostyles within the walls, $\times 110$.

Figs 5–8. *Anaphragma gwyndyense* sp. nov. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 5, BMNH PD8195 (holotype), longitudinal section, showing the thick crenulated walls within the endozone, $\times 28$. 6, BMNH PD8196 (paratype), longitudinal section, $\times 48$. 7, BMNH PD8195 (holotype), tangential section, $\times 48$. 8, BMNH PD8192 (paratype), tangential section, showing small acanthostyles in the zooecial walls, $\times 110$.



Paratypes. BMNH PD8183–8194, 8196–8200, 8303–8305; same locality and horizon as holotype.

Etymology. The species is named after Gwyndy Farm, which is adjacent to the type locality.

Diagnosis. Colony ramose. Zooecia, with thick crenulated walls in endozone, parallel branch axis, then curve gradually out to meet zoarial surface. Autozooecia polygonal in transverse section; oval-circular in shallow tangential sections. Mesozooecia oval, originating in outer endozone. Diaphragms rare in autozooecia, present in mesozooecia. Acanthostyles extremely rare; small and inconspicuous in exozone.

Description. Zoaria erect with cylindrical branches, on average 5.2 mm in diameter. The surfaces of all specimens are slightly abraded. Autozooecia generally parallel the branch axis in the endozone and then curve outwards gradually to meet the zoarial surface. The autozooecia within the endozone have thick, highly crenulated walls. The exozone is usually narrow with an average diameter of 1.4 mm. It is recognized by a thickening of the zooecial walls. Autozooecia originate in the endozone where they are polygonal in transverse section, becoming oval-circular in the exozone, as seen in tangential sections of branches. Autozooecial diameters average 0.33 mm by 0.25 mm within the exozone. Diaphragms are usually absent in the autozooecia and, if present, only one or two are found. These basal diaphragms are deflected orally at their junctions with zooecial walls. The diaphragm laminae are all continuous with the autozooecial linings.

Mesozooecia are common and originate in the endozone, their maximum diameter averaging 0.14 mm. They are oval in shape in shallow tangential sections. Orally deflected basal diaphragms are common in the exozone and are spaced on average 0.11 mm apart.

Acanthostyles are rare; when present (e.g. PD8192), they are usually small and very inconspicuous and occur in the outer exozone; their structure is indistinct (Pl. 5, fig. 8).

Autozooecial wall thickness averages 0.08 mm in the exozone. Wall microstructure is composed of steeply inclined, U-shaped laminae and the wall boundaries are dark and granular. The thickness of the endozonal walls enables the microstructure to be clearly seen within them. Some zooecia, especially mesozooecia, are infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Conspecific overgrowths have been recognized in a few specimens (e.g. PD8186). They appear continuous with the underlying branch suggesting that they are intrazoarial overgrowths. The overgrowths are composed of exozonal components.

Remarks. *Anaphragma gwyndyense* is distinguished by the thick, highly crenulated nature of the endozonal walls, the numerous diaphragms in the mesozooecia and the small rare acanthostyles. This species is assigned to *Anaphragma* because it fits the redefined genus concept proposed by Boardman (1960). Species of *Anaphragma* possess common laminate acanthostyles whose size can be extremely variable. However, in virtually all specimens of *A. gwyndyense* acanthostyles have not been recognized. This may partly be because the majority of the tangential sections are relatively deep and acanthostyles are only found in the very outer exozone. Alternatively, they may be truly absent.

A. shucknellense was described by Owen (1962) from the Aymestry Limestone (Ludlow Series, upper Silurian), Ludlow District. This species has a few thin diaphragms within the autozooecia; mesozooecia and acanthostyles are absent. This is the only species of *Anaphragma* previously described from the Welsh Basin.

A. gwyndyense is similar to *A. mirabile* Ulrich and Bassler, 1904, known from the upper Ordovician of North America and Estonia, but is primarily distinguished by the presence of mesozooecia, the thick crenulated endozonal walls, and the rare acanthostyles. Three other species of *Anaphragma* have been recognized from the USSR: *A. mirabile* var. *cognata* Bassler, 1911; *A. vetustum* Modzalevskaya, 1953; and *A. minutum* Astrova, 1965. *A. gwyndyense* is readily distinguished from these species by the numerous diaphragms within the mesozooecia. *A. gwyndyense* is very similar to *Hallopora anaphragmoides* Pushkin, 1987 (in Ropot and Pushkin, 1987), described from White Russia. Acanthostyles are apparently absent in the Russian species, whereas they have been recognized, albeit rarely, in *A. gwyndyense*.

Order FENESTRATA Elias and Condra, 1957

Suborder PHYLLOPORINA Lavrentjeva, 1979

Family CHASMATOPORIDAE Schulga-Nesterenko, 1955

Genus PINNATOPORELLA gen. nov.

non 1884 *Pinnatopora* Vine; p. 191.

1884 *Pinnatopora* Shrubsole (*in* Shrubsole and Vine); p. 330.

1885 *Pinnatopora* Shrubsole; p. 100.

Type species. *Ramipora hochstetteri* var. *carinata* Etheridge, 1879: Bala Beds (upper Ordovician Caradoc), Corwen, Gwynedd, Wales.

Diagnosis. Colonies erect and pinnate, branches at same height on opposite sides of the parent branch. Tertiary branches may anastomose. Autozoecia in two longitudinal rows on the frontal side of the colony. Central ridge and striae on colony reverse.

Remarks. *Pinnatoporella* is similar to the Carboniferous genus *Penniretepora* d'Orbigny, 1849 (redescribed by Olaloye 1974). Both genera have two longitudinal rows of ovoid zoecial apertures on the front of the colony, and a central ridge with striae on the reverse. The difference between them is that the branches of *Pinnatoporella* often anastomose but this never occurs in *Penniretepora* (Olaloye 1974). The Silurian genus *Arcanopora* Shrubsole and Vine, 1882a differs from *Pinnatoporella* by the large open apertures (zoecia lack frontal walls) and the presence of three or more rows of autozoecia.

The generic status of *Glaucanome* Goldfuss, 1829 (non Gray, 1828), *Penniretepora* d'Orbigny, 1849, *Pinnatopora* Vine, 1884 and *Pinnatopora* Shrubsole (*in* Shrubsole and Vine, 1884) has frequently been discussed (e.g. Ross 1966, p. 121; Olaloye 1974, p. 474; Spjeldnaes 1983, p. 17). A summary of the nomenclatural history is given below with some new evidence regarding the validity of the genus '*Pinnatopora*' and its relationship to *Pinnatoporella*.

Goldfuss (1829) created the genus *Glaucanome* and mentioned four species, all Tertiary cheilostomes from the Eiffel. In 1831 he described a fifth species, *G. distincta* from the Silurian of Dudley. Lonsdale (1839) redefined the genus based on additional material from the Wenlock Limestone of Dudley, and not on Goldfuss' original specimens. Lonsdale made *G. distincta* the type species, but this was invalid because the species was not available as the type. The Silurian *G. distincta* has more than two rows of zoecia on each branch, and the zoecia have large open apertures.

The new *Glaucanome* is, however, preoccupied by *Glaucanome* Gray, 1828 (a bivalve). In an abstract by Shrubsole and Vine (1882a, b) a new genus *Arcanopora* was proposed with *G. distincta* named as the type species. Vine later (1884) gave the species *Flustra* (?) *parallela* Phillips as the type of *Arcanopora* but this is invalid as the type species has already been validly designated. Bassler (1952) proposed *Glaucanomella* as a new name for *Glaucanome* Goldfuss, citing *G. distincta* as the type species. As *Glaucanomella* Bassler, 1952 and *Arcanopora* Shrubsole and Vine, 1882a share the same type species, *Glaucanomella* is a junior objective synonym of *Arcanopora*.

In 1849 d'Orbigny proposed the genus *Penniretepora*, with the type species *Retepora pluma* Phillips. This is a Carboniferous species with two rows of 'box-like' zoecia having ovoid apertures. In 1850 d'Orbigny redescribed *Penniretepora*, making *G. distincta* (*sensu* Lonsdale) the type species and renaming it *P. lonsdalei*. This action is invalid and *R. pluma* remains the type species of *Penniretepora*.

Two papers were published in 1884, one by Shrubsole and Vine, the other by Vine, both proposing *Pinnatopora* as a new genus. In Vine's paper of 1884, no type species was given but nine Carboniferous species were mentioned, including *Pinnatopora elegans* Young and Young which was illustrated. *Pinnatopora* has since been placed in synonymy with *Penniretepora* by Bassler (1935). In the 1884 paper by Shrubsole and Vine, no type species was designated but as only *Pinnatopora sedgwicki* was described, this would be regarded as the type species by monotypy; *P. sedgwicki* is an Ordovician species with two rows of autozoecia and ovoid apertures. This species has been

TABLE 1. Summary of the biometric details of all trepostome species from the Slade and Redhill Beds, near Whitland.

Species	ZOW	EXW	MXZD	MNZD	MXMD
<i>Heterotrypa sladei</i>	7.5 ^a (4) ^b 5.5–10.0 ^c	1.26 (4) 1.14–1.43	0.27 (4) 0.21–0.32	0.23 (4) 0.17–0.3	0.11 (4) 0.06–0.17
<i>Dekayia pengawsensis</i>	11.0 (3) 8.0–13.0	—	0.32 (3) 0.27–0.38	0.29 (3) 0.23–0.36	0.12 (3) 0.04–0.19
<i>Dekayia cf. crenulata</i>	7.0 (3) 6.0–8.0	1.1 (2) 1.05–1.14	0.27 (2) 0.23–0.32	0.22 (2) 0.19–0.29	0.12 (2) 0.08–0.15
<i>Leioclema orbicularis</i>	6.38 (8) 5.0–9.0	1.66 (8) 1.33–2.09	0.34 (8) 0.25–0.44	0.25 (8) 0.13–0.36	0.16 (8) 0.1–0.25
<i>Hallopora peculiaris</i>	8.3 (46) 5.0–13.0	1.65 (43) 1.33–2.28	0.37 (41) 0.13–0.57	0.32 (41) 0.19–0.48	0.16 (40) 0.06–0.29
<i>Hallopora cf. elegantula</i>	3.17 (3) 2.5–4.0	0.86 (1) 0.86–0.86	0.31 (3) 0.25–0.38	0.26 (3) 0.19–0.34	0.15 (3) 0.1–0.19
<i>Eridotrypa sp.</i>	1.5 (2) 1.5–1.5	0.53 (2) 0.38–0.67	0.15 (2) 0.13–0.19	0.19 (2) 0.1–0.13	0.1 (1) 0.1–0.1
<i>Anaphragma dnestrense</i>	6.43 (35) 4.0–9.0	1.34 (18) 0.95–1.71	0.43 (34) 0.29–0.61	0.33 (34) 0.23–0.42	—
<i>Anaphragma gwyndyense</i>	5.2 (20) 4.0–7.0	1.35 (15) 0.95–1.9	0.33 (13) 0.19–0.49	0.25 (13) 0.17–0.4	0.14 (13) 0.06–0.29

Species	MXED	ZWT	ZMM	DEX	DEN
<i>Heterotrypa sladei</i>	—	0.04 (4) 0.02–0.06	9.36 (4) 7.0–11.0	0.13 (4) 0.06–0.21	0.32 (4) 0.13–0.64
<i>Dekayia pengawsensis</i>	—	0.02 (3) 0.02–0.04	9.14 (3) 7.0–11.0	—	0.48 (3) 0.13–0.86
<i>Dekayia cf. crenulata</i>	—	0.03 (2) 0.02–0.04	8.57 (3) 7.0–10.0	0.25 (2) 0.1–0.42	—
<i>Leioclema orbicularis</i>	—	0.12 (8) 0.04–0.19	4.38 (8) 3.5–6.0	0.4 (1) 0.4–0.4	0.23 (3) 0.13–0.38
<i>Hallopora peculiaris</i>	—	0.08 (41) 0.02–0.17	5.24 (40) 3.0–8.0	0.15 (14) 0.02–0.29	0.16 (2) 0.11–0.23
<i>Hallopora cf. elegantula</i>	—	0.11 (3) 0.06–0.21	4.9 (3) 4.0–6.0	—	0.17 (3) 0.1–0.23
<i>Eridotrypa sp.</i>	—	0.04 (2) 0.02–0.06	—	0.12 (2) 0.08–0.21	0.21 (2) 0.08–0.34
<i>Anaphragma dnestrense</i>	0.16 (34) 0.04–0.38	0.08 (32) 0.02–0.19	4.6 (34) 3.0–7.0	—	—
<i>Anaphragma gwyndyense</i>	—	0.08 (15) 0.04–0.21	6.22 (14) 4.0–8.0	0.24 (10) 0.11–0.32	0.22 (2) 0.1–0.32

Species	DMEX	DMEN	AD	AZ	AMM
<i>Heterotrypa sladei</i>	0.1 (4) 0.06–0.15	0.18 (2) 0.08–0.27	0.04 (4) 0.03–0.06	1.84 (3) 1.0–3.0	8.8 (3) 5.0–12.0
<i>Dekayia pengawsensis</i>	0.11 (3) 0.06–0.23	—	0.03 (3) 0.02–0.05	—	5.0 (1) 5.0–5.0
<i>Dekayia cf. crenulata</i>	0.13 (6) 0.1–0.19	0.15 (3) 0.1–0.17	0.05 (3) 0.03–0.07	1.4 (3) 1.0–2.0	7.2 (2) 6.0–8.0
<i>Leioclema orbicularis</i>	0.08 (8) 0.04–0.19	0.15 (6) 0.08–0.25	0.1 (8) 0.08–0.14	3.8 (8) 2.0–5.0	8.0 (8) 6.0–12.0

Table 1. (cont.)

Species	DMEX	DMEN	AD	AZ	AMM
<i>Hallopora peculiaris</i>	0.07 (45) 0.2-0.15	0.13 (43) 0.06-0.23	—	—	—
<i>Hallopora</i> cf. <i>elegantula</i>	0.05 (3) 0.02-0.08	0.1 (3) 0.6-0.17	—	—	—
<i>Eridotrypa</i> sp.	0.056 (2) 0.04-0.08	—	—	—	—
<i>Anaphragma dnestrense</i>	—	0.03 (29) 0.01-0.06	10.2 (4) 4.0-18.0	12.0 (4) 4.0-17.0	—
<i>Anaphragma gwyndyense</i>	0.11 (18) 0.04-0.27	—	0.03 (1) 0.3-0.3	—	—

All measurements are in mm except for ZMM, AD and AMM. Abbreviations: a, mean; b, number of specimens; c, range; ZOW, zoarial diameter; EXW, exozonal width; MXZD, maximum autozooeical diameter; MNZD, minimum autozooeical diameter; MXMD, maximum mesozooeical diameter; MXED, maximum exilazooeical diameter; ZWT, autozooeical wall thickness; ZMM, autozooeicia mm⁻²; DEX, distance between exozonal autozooeical diaphragms; DEN, distance between endozonal autozooeical diaphragms; DMEX, distance between exozonal mesozooeical diaphragms; DMEN, distance between endozonal mesozooeical diaphragms; AD, acanthostyle diameter; AZ, number of acanthostyles per autozooeicia; AMM, acanthostyles mm⁻².

described previously as *Glauconome sedgwicki* Shrubsole (*in* Shrubsole and Vine, 1882). Spjeldnaes (1983) tried to determine which of the two 1884 papers appeared first. He discovered that Shrubsole and Vine's was published in the *Quarterly Journal of the Geological Society of London* on 1 May, 1884 and although he could not find the exact date of issue of Vine's paper in the *Annual Report of the British Association for the Advancement of Science*, he considered it to be late in 1884. He therefore suggested that 'Shrubsole and Vine 1884 was legally issued before Vine 1884 and that *P. carinata* [which Spjeldnaes regarded as a senior synonym of *P. sedgwicki*] therefore is the type species of *Pinnatopora*'.

New evidence has since been found pertaining to the publication date of Vine (1884). The *Register of Serial Publications* at the BMNH records the dates of acquisitions to their General Library. The BAAS Annual Report volume containing Vine's paper was acquired by the BMNH on 30 April 1884, one day before Shrubsole and Vine (1884) was published. Therefore Vine (1884) has priority over Shrubsole and Vine (1884) and the type species of the genus *Pinnatopora* must come from the nine Carboniferous species mentioned by Vine (1884). Among these are *Glauconome elegans* Young and Young which Bassler (1935) named as the genotype. Species of the so-called Ordovician *Pinnatopora*, as exemplified by *P. carinata*, are inappropriately assigned to *Pinnatopora*. They differ from Carboniferous species by the very common anastomosing nature of their branches. The new name *Pinnatoporella* is herein proposed to encompass these species including *Pinnatopora* sensu Shrubsole (*in* Shrubsole and Vine, 1884). One further description of *Pinnatopora* 'gen. nov.' Shrubsole was published in 1885, in the *Proceedings of the Chester Society of Natural Sciences*. This included a description of the species *P. sedgwicki* which would be regarded as the type by monotypy. However, Vine (1884) has priority over this publication.

Distribution. The genus is currently known only from Wales.

Range. Upper Ordovician.

TABLE 2. Summary of the nomenclature and distinguishing characteristics of the pinnate fenestrate genera *Pinnatoporella*, *Arcanopora* and *Penniretepora*

Genus and author	Valid type species	Age of type species	Synonymous genera	Distinguishing characteristics
<i>Pinnatoporella</i> gen. nov.	<i>Ramipora hochstetteri</i> var. <i>carinata</i> Etheridge, 1879	Upper Ordovician	<i>Pinnatopora sensu</i> Shrubsole and Vine, 1884 <i>Pinnatopora sensu</i> Shrubsole, 1885	Anastomosing branches 2 rows of autozoecia Ovoid zoecial apertures
<i>Arcanopora</i> Shrubsole and Vine, 1882	<i>Glauconome distincta</i> Goldfuss, 1829	Middle Silurian	<i>Glauconome</i> Goldfuss, 1829 <i>Glauconomella</i> Bassler, 1935	Non-anastomosing branches 3 or more rows of autozoecia Large open zoecial apertures
<i>Penniretepora</i> d'Orbigny, 1849	<i>Retepora pluma</i> Phillips, 1836	Lower Carboniferous	<i>Pinnatopora</i> Vine, 1884	Non-anastomosing branches 2 rows of autozoecia Ovoid zoecial apertures

Pinnatoporella carinata (Etheridge, 1879)

Plate 6, figs 1 and 2

- 1839 *Glauconome distincta* (pars) Lonsdale, p. 49.
 1879 *Ramipora hochstetteri* var. *carinata* Etheridge, p. 241, pl. 6.
 1882a *Glauconome sedgwicki* Shrubsole (*in* Shrubsole and Vine), p. 245.
 1882b *Glauconome sedgwicki* Shrubsole (*in* Shrubsole and Vine), p. 381.
 1884 *Pinnatopora sedgwicki* Shrubsole (*in* Shrubsole and Vine), p. 330.
 1885 *Pinnatopora sedgwicki* Shrubsole, p. 100.
 1908 *Ramipora hochstetteri* Toulou var. *carinata* Etheridge; Groom and Lake, p. 572.

Lectotype. Designated herein, NMW 27.110 G37 (Etheridge 1879, pl. 6, fig. 1a, b); Bala Beds (Caradoc), Garth Gell, Corwen, Gwynedd, Wales.

Paralectotypes. Designated herein, BMNH D48661 (Etheridge 1879, pl. 4, fig. 3), Bala Beds (Caradoc), Corwen, Gwynedd, Wales; and BGS 85495-6 (Etheridge 1879, pl. 4, fig. 2), S. of Cefn Coch, near Llangollen, Gwynedd, Wales.

Additional material. BMNH PD8405 (hand specimen), Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, W. of Whitland, Dyfed, Wales (SN 164170).

Other occurrences. Dolhir Beds (Ashgill), Plas Einion, and Pant, Glyn Ceiriog, Gwynedd, Wales; upper Bala Beds (Caradoc), Corwen, Gwynedd, Wales.

Diagnosis. As for genus.

Description. Zoaria are erect and pinnate, known only from decalcified specimens. The colony from South Wales is 26 mm in height and 32 mm in width. Primary branches are 1 mm in diameter, and secondary

branches 0.4 mm in diameter. Secondary branches occur in pairs on opposite sides of the main branch, and are common; tertiary branches also occur. In the lectotype, illustrated by Etheridge (1879, pl. 6, fig. 1b), V-shaped fenestrules are observed; they appear to develop by the fusion of adjacent tertiary branches.

The reverse surface of the colony has a central ridge with striae on either side. On the frontal side there are two longitudinal rows of autozoecia. Autozoecial apertures are ovoid in shape, and approximately 0.15 mm in diameter.

Remarks. This species is characterized by the pinnate colony form and two longitudinal rows of ovoid autozoecia. The reverse sides of colonies have a central ridge and are striated.

The species was first described by Etheridge (1879) as a variety of the species *Ramipora hochstetteri* from the Permo-Carboniferous of Spitzbergen. *Ramipora hochstetteri* is, however, a cystoporate (Utgaard in Boardman *et al.* 1983; Nakrem 1988). Shrubsole (in Shrubsole and Vine 1882) described a new species *Glauconome sedgwicki* and two years later (in Shrubsole and Vine 1884) re-assigned it to a new genus, *Pinnatopora*. The synonymy list for this species includes the variety described by Etheridge. *Pinnatopora* Shrubsole in Shrubsole and Vine, 1884 is preoccupied by *Pinnatopora* Vine, 1884 (discussed above p. 95) and the name *Pinnatoporella* is here erected. The variety name proposed by Etheridge (1879) is raised to specific level and *sedgwicki* becomes a junior synonym. *P. carinata* is the only known species of *Pinnatoporella*.

Order CYSTOPORATA Astrova, 1964
Suborder FISTULIPORINA Astrova, 1964
Family FISTULIPORIDAE Ulrich, 1882
Genus FISTULIPORA M'Coy, 1849

Fistulipora sp.

Plate 6, figs 3 and 4

Material. BMNH PD8236c, 8385f, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria are only recognized in randomly oriented peels and appear as long bands, on average 1 mm in height.

Autozoecia are perpendicular to the base. Vesicles are oval in longitudinal section, with irregular bases where they interlock. The average distance between zooecia is 0.53 mm. Zooecial walls are thin throughout the colony and usually straight, although adjacent vesicular tissue can indent them, giving an undulating appearance. Vesicular tissue is abundant between autozoecia throughout the colony. There is periodically a marked thickening of the vesicle roofs from 0.09 mm to 0.15 mm.

Lunaria are present and seen in longitudinal section as hyaline rods on the sides of the autozoecia.

The microstructure is hard to distinguish but laminar walls can be identified.

Remarks. No species of *Fistulipora* have previously been described from the Ordovician of the Welsh Basin. Owen (1962, 1969) described several Silurian members of the genus from Shropshire. *F. strawi* Owen, 1962 has similar thin walls and abundant vesicular material to the Ordovician specimens but lacks basal diaphragms and has less distinct lunaria. The species *F. nummulina* Nicholson and Foord, 1885, described by Owen (1969) from Dudley, has similar distinct lunaria to the Pengawse Hill material but less abundant vesicles and no basal diaphragms. The Pengawse Hill species is left in open nomenclature until more complete specimens can be examined.

Suborder CERAMOPORINA Bassler, 1913

Family CERAMOPORIDAE Ulrich, 1882

Genus CERAMOPORELLA Ulrich, 1882

Ceramoporella distincta Ulrich, 1890

Plate 6, figs 5–8

- 1890 *Ceramoporella distincta* Ulrich, p. 464, pl. 39, figs 6, 6a.
 1908 *Ceramoporella distincta* Ulrich; Cummings, p. 799, pl. 10, fig. 7; pl. 11, figs 2, 2a.
 1909 *Ceramoporella distincta* Ulrich; Grabau and Shimer, p. 122.
 1953 *Ceramoporella distincta* Ulrich; Bassler, p. G81, text-figs 44, 2a, b.
 1968 *Ceramoporella distincta* Ulrich; Utgaard, p. 1405, pl. 181, fig. 4; pl. 182, figs 1–3.
 1973 *Ceramoporella distincta* Ulrich; Utgaard, figs 16, 23.
 1984 *Ceramoporella distincta* Ulrich; Karklins, p. 189, pl. 38, figs 1, 4.

Material. PD8386–8388, 8395, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Other occurrences. Eden and Waynesfield Formation, Cincinnati; Brannon and Millersburg Members, Shermanian Stage, Lexington Limestone, Kentucky.

Description. Zoaria encrusting, consisting of up to five superimposed layers of zooecia. The basal layer, observed in thin section, has an average thickness of 0.8 mm, and the basal laminae of the zooecial layers have a laminated microstructure. It is difficult to distinguish endozone from exozone. In the endozone the autozooecia are slightly recumbent and the zooecial walls are thin and straight. In the exozone the walls remain straight and the zooecial apertures in shallow tangential section are circular-polygonal and on average 0.26 mm in diameter. Lunaria are abundant throughout the colony.

Diaphragms are occasionally present in the autozooecia, sometimes pierced by pores, and apparently aborally deflected and continuous with the zooecial linings. These diaphragms frequently occur at the same level in adjacent zooecia. Basal diaphragms are rare.

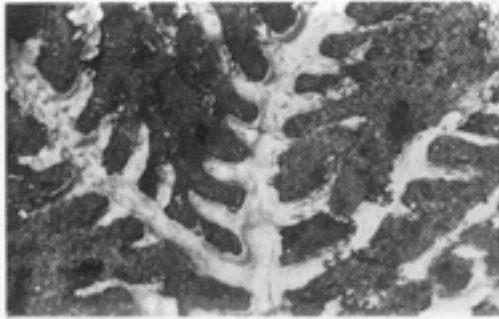
Small exilazooecia are present in the outer endozone and exozone. These contain no diaphragms and are rounded in shallow tangential section, on average 0.09 mm in diameter.

Communication pores have not been observed. Possible acanthostyle-like structures have been observed but not identified conclusively. The microstructure is hard to distinguish but appears to be laminar.

Remarks. The species is characterized by the multilayered zoaria, thin autozooecial walls, sparse diaphragms and the presence of distinct lunaria. It is very similar to *Ceramoporella distincta* Ulrich, 1890, recently re-described by Karklins (1984, p. 189), from the McMiken Member, Eden Formation (upper Ordovician), Cincinnati, Ohio, USA. The main difference is that the specimens from Wales have fewer exilazooecia than those from North America.

EXPLANATION OF PLATE 6

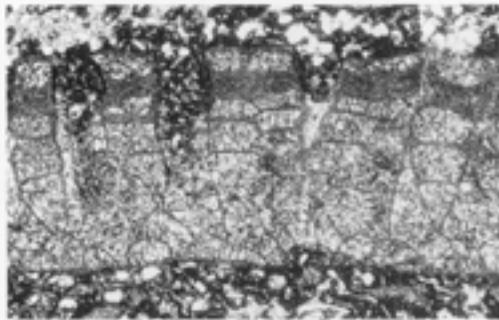
- Figs 1–2. *Pinnatoporella carinata* (Etheridge, 1879). Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8405, mould of a pinnate colony, $\times 5$. 2, BMNH PD8405, mould of a pinnate colony showing rounded autozooecial apertures, $\times 9$.
 Figs 3–4. *Fistulipora* sp. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 3, BMNH PD8385f, longitudinal section, $\times 48$. 4, BMNH PD8385f, longitudinal section, showing the vesicular tissue between the autozooecia and lunaria at the side of the autozooecia, $\times 68$.
 Figs 5–8. *Ceramoporella* aff. *distincta* Ulrich, 1890. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 5, BMNH PD8386, longitudinal section, $\times 28$. 6, BMNH PD8386, longitudinal section showing specimen encrusting a halloporid colony, $\times 18$. 7, BMNH PD8386, longitudinal section, showing subterminal diaphragms at the same level in adjacent autozooecia, $\times 38$. 8, BMNH PD8387, tangential section, showing lunaria, $\times 110$.



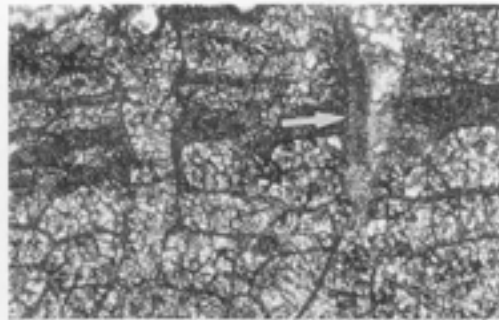
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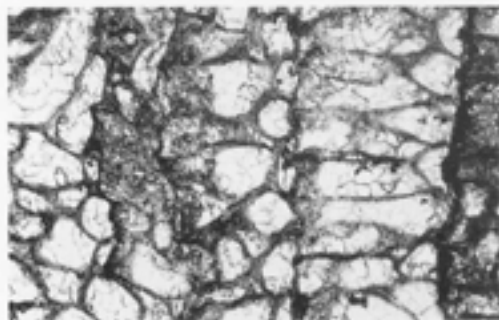
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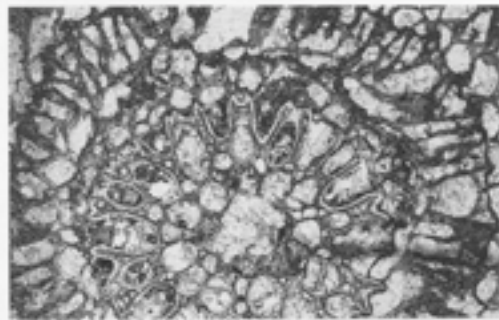
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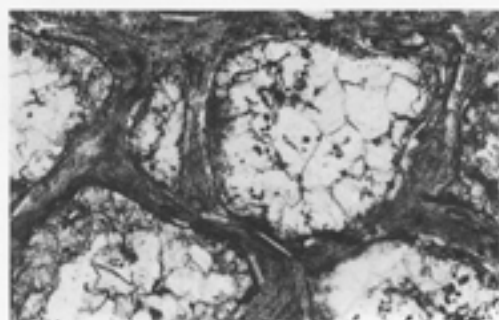
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Family RHINOPORIDAE Miller, 1889

Emended diagnosis. Zoaria thin, encrusting or bifoliate. Autozooeccial apertures elongate. Hyaline lunaria present. Walls laminated or granular-prismatic. Autozooeccia recumbent close to the basal lamina, bending to become perpendicular to base in later ontogeny. Small polygonal exilazooeccia present between autozooeccia. Communication pores often present, up to three per zoecium. Anastomosing tunnel structures present, with roofs elevated above zoarial surface, some tunnels containing barriers.

Remarks. The family Rhinoporidae is characterized by the unusual tunnel structures found in the two constituent genera *Rhinopora* and *Lichenalia*. It was previously placed within the suborder Fistuliporina because of the occasional presence of blister-like vesicular tissue. This tissue has been described as irregular, and unlike that commonly found in fistuliporines. Vesicular tissue has been observed in *Lichenalia* (Utgaard *in* Boardman *et al.* 1983, fig. 192, 2*b*) but does not appear to be a consistent feature in all colonies. The tunnel structures are easy to mistake for vesicles in section when they have been overgrown by the colony. Well-preserved specimens of *Rhinopora* and *Lichenalia* have been examined during this study and abundant communication pores observed. These are common in the suborder Ceramoporina but have not been identified conclusively in Fistuliporina. Therefore, the family is herein reassigned to Ceramoporina.

Genus LICHENALIA Hall *in* Silliman, Silliman and Dana, 1851

Type species. *Lichenalia concentrica* Hall, 1852; Rochester Shale (middle Silurian), Lockport, New York State, USA; by monotypy.

Emended diagnosis. Zoaria encrusting with laminated basal layer; autozooeccia with long recumbent portion, walls thin and laminated. Diaphragms uncommon. Small polygonal exilazooeccia present between autozooeccia. Lunaria hyaline, elevated at colony surface. Bifurcating and anastomosing tunnel structures are common, some with internal partitions. Communication pores may be present in exozone.

Remarks. The diagnosis has been revised from Utgaard (*in* Boardman *et al.* 1983, p. 407) to include the presence of communication pores.

Distribution. The genus was previously known from North America and the USSR.

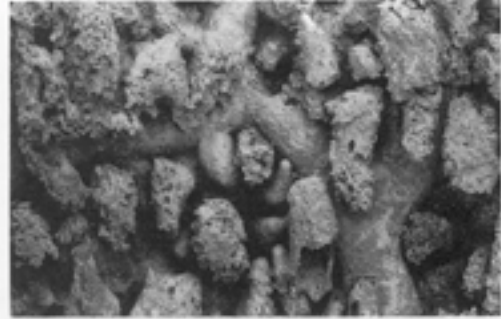
Range. Upper Ordovician–middle Silurian.

EXPLANATION OF PLATE 7

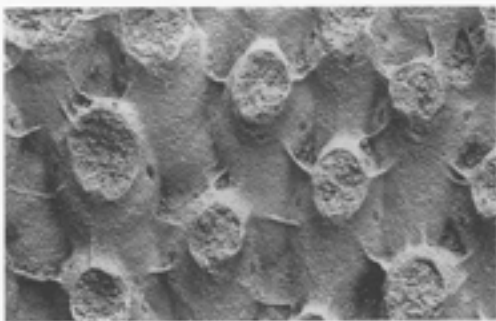
- Figs 1–2. *Lichenalia cf. concentrica* Hall, 1852. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD9873, decalcified colony showing unusual tunnel structures meandering between the autozooeccia, $\times 15$. 2, BMNH PD9873, tunnel structures, $\times 34$.
 Figs 3–6. *Lichenalia cf. concentrica* Hall, 1852. Wenlock Shales (Homerian, Wenlock, Silurian), Dudley, West Midlands. 3, BMNH PD9885, surface of colony showing abundant communication pores and small polygonal mesozoeeccia, $\times 31$. 4, BMNH PD9885, bifurcating tunnel structure, $\times 15$. 5, BMNH PD9885, tunnel overgrown by a subsequent layer of the colony, $\times 40$. 6, BMNH PD1886, tangential section showing bifurcating tunnel structures, $\times 28$.
 Figs 7–8. *Kukersella borealis* (Bassler, 1911). Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 7, BMNH PD8154*a, b*, longitudinal and transverse sections, $\times 18$. 8, BMNH PD8236*a*, transverse section with abundant pseudopores in frontal wall, $\times 43$.



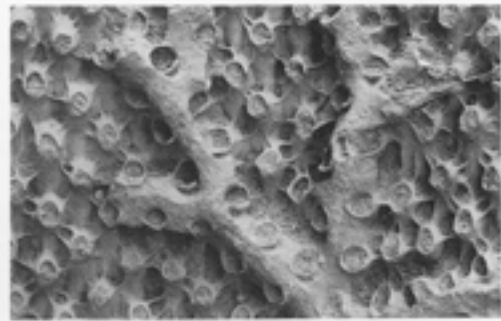
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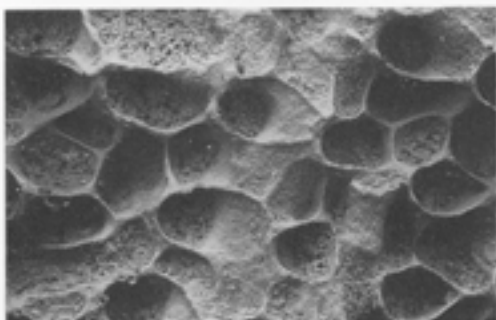
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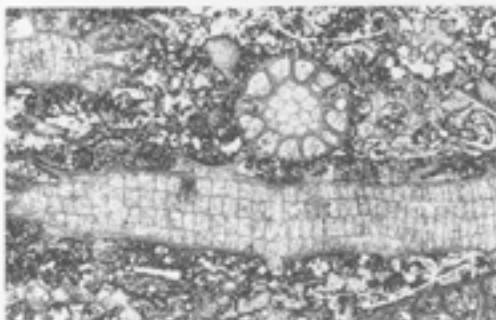
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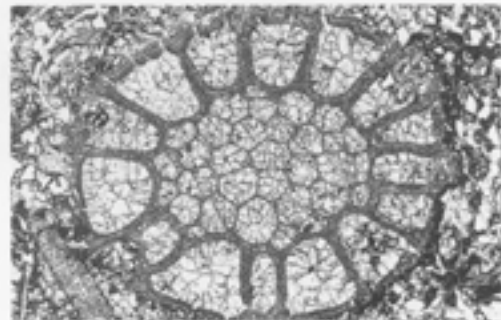
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Lichenalia cf. concentrica Hall, 1852

Plate 7, figs 1-6

Material. BMNH PD9885-6 (hand specimens); Wenlock Shale, Dudley, West Midlands. BMNH PD9871, 9873, 9874, 9876, 9878 (hand specimens); Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, W. of Whitland, Dyfed, Wales (SN 164170).

Description. All colonies are unilaminar and encrusting. The Silurian specimens encrust brachiopods, whereas the Ordovician material forms unilaminar hollow cylindrical colonies which may have encrusted a soft-bodied organism such as a hydroid.

Autozoecia have a recumbent portion in contact with the basal lamina and then bend to become perpendicular to the base. Autozoecial apertures are rounded with an average diameter of 0.22 mm by 0.16 mm. Small polygonal exilazoecia occur between the autozoecia (average maximum diameter is 0.08 mm). Hyaline lunaria are observed in the autozoecia in shallow tangential section. Rare basal diaphragms have been recognized.

Bifurcating and anastomosing tunnel structures are common, positioned a distance from the edge of the colony (2 mm in PD9885). The tunnels are on average 0.21 mm wide and extend for 1.11 mm in length between bifurcations. At the site of bifurcation a crescent-shaped exilazoecium occurs. The tunnels are divided internally by thin-walled barriers.

Communication pores are present in the exozone, commonly two, but up to three, pores per autozoecium. They are situated on either side of the autozoecial aperture, occasionally with one in between.

Microstructure is hard to distinguish but appears to be laminar.

Remarks. The species *Lichenalia concentrica* Hall has been recognized in North America from the Rochester Shale (middle Silurian), New York State and Ontario (Hall 1852; Bassler 1906; Hewitt and Cuffey 1985), and in the USSR from the Borkholm Limestone, Borkholm, Estonia (Bassler 1911). *Lichenalia cf. concentrica*, described in the present study, is very similar to previous descriptions of *L. concentrica*, e.g. by Bassler (1906) and Hewitt and Cuffey (1985). The major difference is the presence of communication pores, which have not been recognized previously. This difference may be significant or merely due to the exceptional preservation of the material described herein from Dudley. The majority of examples of *Lichenalia* described previously do not show the frontal surface of the colony as it adheres to the rock matrix, and communication pores may therefore have been present but not observed. The type material from the Rochester Shale (middle Silurian), Lockport, New York State, USA, needs to be re-examined in conjunction with this new British material to establish if they are indeed conspecific.

Order CYCLOSTOMATA Busk, 1852
Family CROWNOPORIDAE Ross, 1967
Genus KUKERSELLA Toots, 1952

Kukersella borealis (Bassler, 1911)

Plate 7, figs 7 and 8

Description. Colony erect with narrow subcylindrical branches (average diameter 1.08 mm), arising from an encrusting base. Endozonal zoecia are very thin-walled and are oriented parallel to the branch growth direction to form an axial bundle which reaches the colony surface only at the distal growth tips. Abundant, closely-spaced (0.09 mm) diaphragms occur throughout the length of the endozonal zoecia and are deflected orally at their junction with vertical interzoecial walls.

Exozonal zoecia surround the axial bundle of endozonal zoecia. They are thick-walled, average 0.48 mm in length and their walls contain sparse communication pores at levels close to the colony surface. Occasional diaphragms are developed at levels close to the colony surface. They are deflected orally where they meet the interzoecial walls. Frontal walls of exozonal zoecia have distal subcircular apertures with an average diameter of 0.15 mm and slight peristomes. Frontal walls are densely pseudoporous, the pseudopores being variable in size but consistently large, on average 0.02 mm in diameter. They are crater-like in external morphology, with funnel-shaped openings.

The encrusting bases are composed entirely of zoecia resembling those of the exozone in erect branches.

Remarks. A more complete description of this species and a synonymy may be found in Buttler (1989).

BIOGEOGRAPHICAL COMPARISONS

A total of twelve genera have been recognized from the Slade and Redhill Beds at Pengawse Hill. One, *Pinnatoporella*, has been described only from Wales, whilst the rest are cosmopolitan. A wide generic distribution may have been caused by a long-lived, planktotrophic larval phase which encouraged dispersal. This was suggested for the Ordovician genus *Orbipora* by Taylor and Cope (1987). Living cyclostomes have non-planktotrophic larvae but Taylor and Cope consider that some early stenolaemates may have inherited a planktotrophic larval stage from their inferred ctenostome ancestors.

Of the fifteen species identified from this locality seven have not been previously recognized elsewhere. Three of these are new species and the rest are left in open nomenclature. It is difficult to know whether this is true endemism or the result of sampling and/or preservation. Three species have very wide geographical ranges: *Kukersella borealis*, *Hallopora elegantula* and *Lichenalia concentrica*. They have all been described previously from both North America and Baltoscandia.

The Welsh taxa show the greatest affinity with Baltoscandia, sharing six of the fifteen species. The faunal similarities between Baltoscandia and the Anglo-Welsh Region have been examined in detail for other groups (e.g. Cocks and Fortey 1982; Vannier *et al.* 1989), although poor knowledge of British bryozoans has previously prohibited comparison. The bryozoans support the hypothesis that Tornquist's Sea, which separated the two regions during the early Ordovician, was no longer a physical structure effecting faunal separation in the late Ordovician. The exact time of its closing is hard to ascertain but the similarity in faunas from the Caradoc onwards suggests that by the late Ordovician Tornquist's Sea was nearly if not actually closed.

North America, or Laurentia, was separated during the lower Ordovician from Baltoscandia and the majority of the British Isles by Iapetus. Faunal and structural studies have examined the exact timing of the closure. Pickering *et al.* (1988), using a variety of palaeontological, stratigraphical, structural, geophysical and igneous evidence, considered that by the end of the Ordovician Iapetus was partially closed with only marine seaways persisting to the mid-Silurian. During the late Ordovician Iapetus did not form an impenetrable barrier to the bryozoans. Four species (17% of the fauna) from Pengawse Hill are also known from the early Palaeozoic of North America.

Only one species (*Dekayia cf. crenulata*) from Wales is similar to the bryozoan fauna described from the Montagne Noire region of France. This region would have formed part of Gondwana, which was separated from Laurentia, the British Isles and Baltoscandia during the late Ordovician by the Rheic Ocean, explaining why the similarity of the two faunas is minimal.

Any biogeographical findings concerning bryozoans can only be preliminary because of the poor knowledge of British (and European) Ordovician bryozoans, especially when compared with other groups. This emphasizes the great need for further research and the importance of systematic studies of British Ordovician bryozoans.

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