

LUDLOVIAN BRYOZOA FROM THE LUDLOW DISTRICT

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ABSTRACT. The rich Ludlovian bryozoan fauna is discussed and twenty-five species are described, thirteen of them new—*Dekayella whitcliffensis*, *Leptotrypella leintwardinensis*, *Batostomella hemiseptensis*, *B. hexamesopora*, *Bythopora parallela*, *Eridotrypa umbonensis*, *Leioclema ludlovensis*, *L. halloporoides*, *Anaphragma shucknellensis*, *Calamotrypa millichopenensis*, *Monotrypa patera*, *Nematopora hexagona*, and *Rhombopora mesopora*. The hollow *Calamotrypa* is described as a new Trematoporid genus. *Monotrypa crenulata* Nicholson is discussed and a lectotype chosen. The restricted range of a few species makes them of value to the stratigrapher.

LUDLOVIAN rocks are richer in bryozoa than faunal lists would seem to indicate. This is largely due to the fact that most of the species are small and often fragmentary. Older collections sometimes contain specimens from the Aymestry Limestone but these mostly belong to the few large species *Ptilodictya lanceolata* (Goldfuss), '*Favosites*' *fibrosus* (Goldfuss), and fenestellids. The wealth of smaller bryozoa, particularly at certain levels of the Ludlovian, is only really seen when the rocks are sectioned. Calcareous deposits are rich in species, often beautifully preserved. Much of the succession, even in the 'Shelf' facies around Ludlow, consists of shales with thin, calcareous bands; these, however, quickly decalcify in the weathered section leaving moulds which are useless for identification. In such cases it is essential to locate unweathered rock where the fossils are properly preserved.

Bryozoa, like many other fossils, are best preserved in certain rock types. The thin, muddy limestones of the Lower Bringewood Beds are often crowded with forms, while the typical upper 'Aymestry' limestone, with its shell banks, is much less rich. The Upper Whitcliffe Beds are locally extremely rich in specimens though not in species. The interesting thesis developed by L. W. Stach (1937), and referred to by R. S. Boardman (1960a), that bryozoa can be divided into stable and unstable forms, the former unable to modify their growth with different environments and the latter capable of doing so, may well find examples in Ludlovian forms. *Fistulipora umbrosa* Owen is present in ramose and in encrusting forms though originally described as a nodular bryozoan (1960). *Orbignyella fibrosa* (Lonsdale) is mostly encrusting, but large, ramose forms have been described from the Woolhope area (Owen 1960). On the other hand, *Monotrypa patera* Owen is always encrusting and *Bythopora parallela* Owen always ramose. How far the forms of unstable zoaria can point to the presence or absence of wave action has yet to be decided. It is interesting that the only occurrence yet noted of the encrusting form of *Fistulipora umbrosa* Owen is when that species is in association with the shell banks of the Upper Bringewood Beds of Weo Edge, where the results of wave action are to be expected.

Like many other workers, I have found difficulty with the present classification of trepostomes into Amalgamata and Integrata. A detailed examination of the wall structure suggests that this is an unnatural classification and recent work by R. S. Boardman (1960a) suggests more valuable criteria within the formation of the wall. He points out

in a later paper (1960*b*) that *Anaphragma mirabile* Ulrich and Bassler shows both amalgamate and integrate structures in different parts of the exozone of the same wall and similar features are observable in *Anaphragma shucknellensis* Owen described here. Unfortunately the minute structure of the walls is not preserved equally well in all Ludlovian specimens. I have therefore clung to the accepted classification (R. S. Bassler 1953) and have noted such details of wall structure as can be made visible. At times it is difficult to decide whether to place a form with the trepostomes or the cryptostomes. R. C. Moore (1929) noted this with respect to species of *Rhombopora* and certain Batostomellids, and G. E. Condra and M. K. Elias (1944) stated that *Rhombotrypella* (a Stenoporid), *Rhombotrypa* (an Amplexopodid), and *Rhomboporella* (a Rhabdomesid) may, in fact, belong to the same family. I found this difficulty in placing *Batostomella hemiseptensis* Owen which, though possessing the cryptostome hemisepta, has no properly developed vestibule. I decided that its amalgamate walls and thin cortex were much more typically trepostome, and placed it with the Batostomellidae.

STRATIGRAPHICAL VALUE

The bryozoan fauna appears to be quite different from that in the underlying Wenlock Series. The similarity in the lithology of the Aymestry Limestone and the Wenlock Limestone would lead one to look for the same species in the two deposits, but this does not appear to be the case. Further, though some species are fairly long range, others appear to be sufficiently restricted to make their occurrence of stratigraphical importance. *Orbignyella fibrosa* (Lonsdale) is an instance, and its appearance in the Lower Leintwardine Beds seems to be clear cut. I have now found it encrusting a gastropod in the Lower Whitcliffe Beds near Ludlow but it appears to be missing in the rich fauna of the Bringewood Beds. *Nematopora hexagona* Owen is a very common species in the Lower Bringewood Beds and occurs in the underlying Elton Beds. I have not found it in the Upper Bringewood strata or higher in the Ludlovian. The presence or absence of particular species, however, does not appear to be nearly as important as the percentage of each species present. Good collections from the Lower Bringewood Beds, Upper Bringewood Beds, and the Lower Leintwardine Series show marked differences in the relative numbers of each species. It has yet to be ascertained if this is of purely local significance or may be used stratigraphically.

DESCRIPTION OF SPECIES

Order CYCLOSTOMATA Busk 1852

Family CERAMOPORIDAE Ulrich 1882

Genus FAVOSITELLA Etheridge and Foord 1884

Description. Zoarium irregular, concavo-convex, frequently encrusting, the base covered with a concentrically striated epitheca. Zooecia rounded to subpolygonal, mesopores numerous, often grouped into clusters raised slightly above the general level of the zoarial surface [monticules]. Diaphragms few in normal zooecia, more numerous in mesopores. No acanthopores. Walls granular with large, irregularly distributed mural pores. (This description is as given by Etheridge and Foord except that the terminology is brought up to date.) They stressed in their observations the mural pores which, they

believed, unite the genus to the Favositid corals. Such pores are common in Ceramoporids.

Favositella interpuncta (Quenstedt)

Plate 28, figs. 1, 2

Remarks. This species was described by Quenstedt from the Wenlock Limestones of Dudley. The zoarium is large, about 50 mm. in diameter and 30 mm. high, hemispherical, with a deeply concave underside resting on a striated epitheca, so that the actual thickness is very much less than the total height. Internally, the zooecia run obliquely out from the centre, bending to reach the zoarial surface at right angles. The walls are thick and ceramoporid; the zooecia are tabulate. The more closely tabulate mesopores are numerous. Apertures are rounded polygons, 4 or 5 in 2 mm. Lunaria are present but not conspicuous. (I am indebted for these details to Dr. K. P. Oakley, who has studied the only specimen—probably the holotype—in Quenstedt's collection in the museum of the Institute of Geology and Palaeontology at Tübingen.) Within the zooecial tubes are frequently to be found 'Pearls' or 'Brown Bodies'. Their origin was discussed by Oakley (1934).

The specimens of *Favositella interpuncta* (Quenstedt) from the Ludlovian rocks are all encrusting. They occur in masses up to 20 mm. in diameter, but seldom more than 1 mm. deep. Otherwise they agree closely with other Wenlock Limestone forms. The apertures are oval, 0.5–0.7 mm. by about 0.3 mm. and 3–4 are found in 2 mm. The mesopores average 0.2 mm. by 0.1 mm. and the diaphragms in them are about a tube width apart. Lunaria are visible but not distinctive. Pores in the walls are clearly defined. The species occurs sporadically throughout the Elton and Bringewood Beds and is one of the relatively few Wenlock Limestone forms to be found in the Ludlovian.

Genus *FISTULIPORA* M'Coy 1850 emend. Nich. and Foord 1885

Description. Zoarium massive, encrusting or ramose. Zooecia simple tubes often with granular walls which do not change throughout their length. Diaphragms few and simple. Apertures oval with more or less well-marked lunaria. Mesopores numerous, occasionally occurring as simple tubes with curved diaphragms but more often as vesicular masses where the individuals cannot be separated from each other. Mesopore apertures polygonal, sometimes large. Species are common from Ordovician to Carboniferous rocks.

Fistulipora crassa (Lonsdale)

Remarks. Nicholson (1884) redescribed this species as ramose, the branches rounded or somewhat compressed, varying in diameter from 2.5–12.5 mm. Surface smooth and devoid of monticules or maculae. The zooecia are oval, not markedly indented, 0.25–0.3 mm. in diameter with a few straight diaphragms. The interspaces are occupied by polygonal mesopores, about 0.2 mm. in diameter, which appear in longitudinal section to be vesicular due to the incompleteness of their walls and the dominance of their curved diaphragms. Nicholson's specimens came from the Wenlock Limestones and Shales of Dudley and other neighbouring localities.

In the Lower Bringewood Beds of Ludlow I have found occasional specimens of this

species. The zoarium is long and ramose, about 3 mm. in diameter. Zooecia, which develop in the axis and curve gently towards the zoarial surface, are separated in the exozone by a vesicular mass of mesopores which are themselves covered in places by thickened calcareous tissue. The oval apertures show slight lunaria and are about 0.3 by 0.2 mm. in size. These specimens seem to be quite typical of the Wenlockian species.

Fistulipora strawi Owen

Plate 28, figs. 3, 4

Remarks. This species is probably the most widespread bryozoan in all but the highest Ludlovian rocks. It was first described from fragments in the Ludlovian of Builth (Owen 1960) but has now been collected in complete specimens. One such specimen LL2584 which encrusts a stromatoporoid and is itself covered by the same form, has a zoarial breadth of 30 mm. and a height of 10 mm. In nodules in the Upper Wootton Beds of Backbury Hill near Woolhope specimens occur of 35 mm. diameter and 25 mm. height. My attention was first drawn to these nodules and their enclosed fossils by Dr. E. V. Tucker.

The zooecial tubes are often very long and extend straight or in a gentle curve to the zoarial surface. The intervening tissue is tabulate or vesicular but the tubes are more closely spaced than in most described Silurian species of *Fistulipora*, such as *F. crassa* (Lonsdale) (see above), *F. cornavica* Nich. and Foord, and *F. dubonica* Nich. and Foord. The apertures are oval and there is the faintest suggestion of lunaria. There are no acanthopores. At times the mode of growth of *F. strawi* Owen and *F. umbrosa* Owen is strikingly similar but the thickness of the walls is so much greater in the latter species that the two could never be confused.

F. nummulina Nich. and Foord is a very similar species. Described as discoid, lenticular, concavo- or plano-convex also encrusting and sometimes rising into a conical mass, it is clearly similar in zoarial shape to *F. strawi* Owen. Two special features noted are monticules and 'folds' in the walls of the zooecial aperture (lunaria). I have examined sections from the syntypes in the British Museum (Natural History) from the Wenlock Limestone of Dudley, and have noted the very marked lunaria clearly thickened in tangential sections near the surface, and the fact that there are relatively less tubes separated by more vesicular tissue than in *F. strawi*. *F. incrassata* (Nicholson) (1874), from the Hamilton group, is also very similar to *F. strawi* in section and shows no marked lunaria. It differs in having much more vesicular tissue between the zooecia. In Nicholson's original description the hemispherical, layered masses are described as being sometimes as large as a man's head. It would appear that these three species are related and perhaps represent three stages in an evolutionary series.

EXPLANATION OF PLATE 28

- Figs. 1, 2. *Favositella interpuncta* (Quenstedt). 1, Vertical section showing zooecia and tabulate mesopores. 2, Tangential section. LL 2582; $\times 50$.
 Figs. 3, 4. *Fistulipora strawi* Owen. 3, Vertical section. 4, Tangential section showing zooecia separated by mesopores. LL 2584 and LL 2604; $\times 50$.
 Figs. 5, 6. *Fistulipora umbrosa* Owen. 5, Vertical section of cylindrical form. 6, Tangential section showing shadowy walls. LL 2585 and LL 2586; $\times 50$.

Occurrence. *Fistulipora strawi* Owen has been collected from the Elton Beds and from other levels up to the Lower Leintwardine Beds but has not been found higher.

Fistulipora umbrosa Owen

Plate 28, figs. 5, 6

Remarks. This species was first described from the Ludlovian of Builth (Owen 1960). In those beds the zoarial shape was nodular and it was often possible to distinguish layers. Thus the nodules had been built up with encrusting layers of zooecia. In the Upper Bringewood Beds, particularly of Weo Edge, the species is well represented. The zoarial form is most commonly cylindrical, rising from a broad base and with short, stout branches. A typical form measures 15 mm. across the base, 7 mm. across the main cylinder, and is 22 mm. high. In addition to this form, the species occurs in these beds as a thin encrusting expansion up to 20 mm. across and less than 2 mm. thick. Both forms occur in the same deposit but not side by side.

The zooecia are exactly as described in specimens from Builth, and in the cylindrical forms they occur as long tubes originating parallel to the zoarial surface and curving gently to reach it at right angles, with diaphragms at 'tube-width' intervals. The encrusting forms are layered and the zooecia are short and straight with few diaphragms. The mesopores have numerous diaphragms and acanthopores are absent. The walls are of uniform thickness in the endozone and the exozone and show no differentiation. They are porous and shadowy. The apertural diameters average 0.3 by 0.25 mm. and there are seven in 2 mm. The mesopores are variable and about half the diameter of the normal zooecia and the thick walls measure 0.03–0.07 mm. The species is quite distinctive wherever it occurs and is found typically in Upper Bringewood Beds.

Order TREPOSTOMATA Ulrich 1882

Sub-Order AMALGAMATA Ulrich and Bassler 1904

Family MONTICULIPORIDAE Nicholson 1881

Genus ORBIGNYELLA Ulrich and Bassler 1904

Orbignyella fibrosa (Lonsdale)

Remarks. The typical encrusting form and the less common ramose form of this species have recently been described fully by the author (Owen 1961). Further specimens have now appeared in the Lower Whitcliffe Beds of Ludlow, but there seems little doubt that its effective range is confined to Upper Ludlow rocks (Leintwardine and Whitcliffe Beds). Earlier records, including that of d'Orbigny (1850), suggest this view and it is likely that this species, recorded in the Lake District as well as the Welsh Borderland, may become useful stratigraphically.

Family HETEROTRYPIDAE Ulrich 1890

Genus DEKAYELLA Ulrich 1882

Remarks. Described by Ulrich as ramose with cylindrical or compressed branches, it has angular or rounded zooecia, the shape depending on the number and disposition of the

mesopores. The mesopores may be few or more or less numerous distributed between zooecia, sometimes in clusters. Acanthopores of two sizes, the larger ones commencing in the axial region, the smaller ones in the periphery only. The relationship of this genus with *Heterotrypa* and *Dekayia* is so close that the species of the three genera make a connected series. *Dekayella* is distinguished from the other two genera in having more mesopores and two sizes of acanthopores. Ordovician and Silurian.

Dekayella ramosa Owen

Remarks. Typical cylindrical, branching specimens occur with tabulate mesopores, and acanthopores, of variable size up to 0.05 mm. in diameter, occur at the junctions of three zooecia. The wall structure in the exozone shows laminae curving distally in a U-shape. The mesopore diaphragms are thick, though they seldom occur on the same level in adjoining mesopores. Zooecial diaphragms are few and much thinner. Occurs sporadically in Bringewood and Lower Leintwardine Beds.

Dekayella whitcliffensis sp. nov.

Plate 29, figs. 1, 2

Holotypes. Manchester Museum LL 2587.

Diagnosis. Zoarium ramose, 1.5–2 mm. in diameter. Zooecia thin-walled in the endozone, running nearly parallel to the axis and turning at right angles into the exozone where the walls thicken markedly. Wall structure in the exozone amalgamates with laminae curving distally into a U-shape. Apertures oval, averaging 0.15 by 0.2 mm., seven in 2 mm. Mesopores numerous, frequently surrounding normal zooecia in the exozone, often very small, diameter 0.02–0.08 mm. Acanthopores numerous in the exozone, variable in size, some as large as 0.05 mm. in diameter. Diaphragms absent in mesopores and normal zooecia. Upper Whitcliffe Beds.

Remarks. This species shows a very strong similarity to *Dekayella megacanthopora* Owen (1960). It differs in having more numerous mesopores, fewer and smaller acanthopores, and a total absence of diaphragms. The mode of growth and microscopic structure of the zooecial walls in the exozone suggest that the two are closely allied.

Genus LEPTOTRYPELLA Vinassa de Regny 1920 emend. Boardman 1960

Description. Zoarium ramose, sub-ramose, encrusting or a combination of ramose and encrusting habits. Conspecific overgrowth common. Monticules present normally in-

EXPLANATION OF PLATE 29

- Figs. 1, 2. *Dekayella whitcliffensis* sp. nov. 1, Vertical section showing mesopores in the exozone. 2, Tangential section. Holotypes LL 2587; $\times 50$.
 Figs. 3, 4. *Leptotrypella leintwardinensis* sp. nov. 3, Tangential section showing thick walls and acanthopores. 4, Vertical section showing diaphragms extending distally up the zooecial wall. Holotype, British Museum (Natural History) PD 209; $\times 50$.
 Figs. 5, 6. *Batostomella hemiseptensis* sp. nov. 5, Vertical section showing hemisepta and calcareous tissues in the exozone. 6, Tangential section. Holotype LL 2589; $\times 50$.
 Figs. 7, 8. *Batostomella hexamesopora* sp. nov. 7, Vertical section. 8, Tangential section showing zooecia ringed by six mesopores. Syntypes LL 2590 and LL 2591; $\times 50$.

cluding megazooecia, mesopores, and enlarged acanthopores. In most species a zonal lining can be distinguished and the laminae are parallel to the zooecial wall for a considerable distance (Leptotrypella wall of Boardman 1960a). Diaphragms complete, cystiphragms and mural spines present in some species. Mesopores variable, sometimes lacking. Acanthopores typically numerous, may be only rare in some species.

Leptotrypella leintwardinensis sp. nov.

Plate 29, figs. 3, 4

Holotype. British Museum (Natural History) PD 209.

Diagnosis. Zoarium ramose, 4–5 mm. in diameter, several centimetres long, monticules apparently lacking. Zooecia curve out gently from the axis to the zoarial surface, moderately thin-walled in the endozone, very thick-walled in the exozone. Walls show beautifully Leptotrypella structure (Boardman 1960a), the laminae of the moderately thin diaphragms entering the zooecial walls and continuing distally up to 0.5 mm. or even more, sometimes passing under the laminae of the next diaphragm. They then merge with the wall laminae and curve distally into a U-shape. Although the walls are amalgamate there is a slightly darker central zone. Zooecial diameters 0.2–0.3 mm. with diaphragms few in the endozone and spaced at about twice tube width in the exozone. Apertures oval, averaging 0.2 by 0.3 mm., 5–6 in 2 mm. Acanthopores large and numerous in the exozone, but not distorting the zooecial wall, average diameter 0.05 mm. Wall thickness in the exozone up to 0.2 mm. No mesopores, cystiphragms, or mural spines.

Remarks. This beautiful bryozoan differs markedly from all others in Ludlovian rocks. It is described from a single, well-preserved specimen from the *Monograptus leintwardinensis* Zone of the Ludlovian from Church Hill, Leintwardine. The lack of mesopores, monticules, cystiphragms, and mural spines may all be primitive features. There is little doubt that this is a species of Boardman's sub-genus *Leptotrypella* which contains the main conservative lineages of the genus.

Family BATOSTOMELLIDAE Miller 1889

Genus BATOSTOMELLA Ulrich 1882

Description. Branches slender without monticules. Zooecia with thick walls in the exozone, amalgamate, with remote, delicate diaphragms. Apertures small, circular to oval. Mesopores and acanthopores present. Ordovician to Carboniferous.

Batostomella hemiseptensis sp. nov.

Plate 29, figs. 5, 6

Holotype. Manchester Museum LL 2589.

Diagnosis. Zoarium ramose, branching frequently, slender, 1.5 mm. in diameter. Zooecia long, thin-walled, amalgamate, diameter 0.1–0.2 mm., running obliquely but nearly parallel to the zoarial surface and turning outwards to reach the surface at 45°. In the short exozone the walls are thickened and there is considerable addition of

calcareous tissue. Diaphragms few, hemisepta present. Apertures circular with marked rims, 0.15 mm. in diameter, 9–10 in 2 mm. Mesopores only in short exozone, sometimes tabulate, sometimes closed by thickened tissue. The walls appear to be Leioclemid though the detailed structure is not easy to determine. No acanthopores. Lower Bringlewood Beds.

Remarks. This species is at present represented by a single specimen in section, but the section is good and shows all details very clearly. It is typically Batostomellid except in the presence of hemisepta and of the narrow coating of calcareous tissue in the exozone, both of which features are reminiscent of Rhabdomesid Cryptostomes. The general appearance, however, and the wall structure, in particular, are Amalgamate Trepostome and it appears to be most nearly related to other species of *Batostomella*. The hemisepta, which are both inferior and superior, are short and appear at slight angles in the walls. They are firmly a part of the wall whose laminae run down into them.

Batostomella hexamesopora sp. nov.

Plate 29, figs. 7, 8

Syntypes. Manchester Museum LL 2590 and LL 2591.

Diagnosis. Zoarium cylindrical, branching dichotomously, 1.5–2 mm. in diameter. Zooecia long, thin-walled tubes which run nearly parallel to the zoarial surface and then curve gently out to it. Diaphragms absent. Walls slightly thickened in the exozone. Mesopores in the exozone, tabulate, and constricted slightly at each diaphragm. Acanthopores small. In deep tangential sections, the oval zooecia are shown to be ringed with six polygonal or triangular mesopores, but at the zoarial surface the walls are thicker, and the mesopores are larger, more oval, and less different in appearance from the normal zooecia. Apertures 0.16 by 0.1 mm., eight in 2 mm. Ranges from Elton to Lower Leintwardine Beds.

Remarks. In the weathered specimen and in the transverse section this is a distinctive species with its oval zooecia surrounded by mesopores. The acanthopores are small and insignificant. In this last feature and in the large open mesopores, this species differs from *Batostomella granulifera* (Hall), from the Rochester Shale of New York State (Bassler 1906), with its many acanthopores and closed mesopores.

Genus BYTHOPORA Miller and Dyer 1878

Description. Slender, branching zoaria with completely amalgamate walls. The zooecial tubes are long, with few or no diaphragms and no mesopores. Acanthopores neither numerous nor distinctive and often absent altogether. It thus differs from *Batostomella* mainly in the absence of mesopores. Though the range is from Ordovician to Devonian, most of the species described are from Ordovician rocks.

Bythopora parallela sp. nov.

Plate 30, figs. 1, 2

Syntypes. Manchester Museum LL 2592 and LL 2593.

Diagnosis. Zoarium slender, cylindrical, branching dichotomously, 1–2 mm. in diameter. Zooecia long, slender, thin-walled, running nearly parallel for much of their length, and curving slightly to reach the zoarial surface. The walls are very slightly wavy. Near the zoarial surface, the walls thicken markedly, reaching a thickness as great as the diameter of the zooecial tubes. The wall laminae lie almost parallel and seem to open out as the wall thickens. The oval apertures are surrounded by a thickness of tissue. They are 0.08 by 0.2 mm. and 6–8 in 2 mm. There are neither mesopores nor acanthopores and diaphragms are occasional or absent. Bringewood Beds.

Remarks. This species is very easy to distinguish from all others in the deposits. *Bythopora spinulosa* (Hall) is the only other described Silurian species of this genus (Bassler 1906) and is recorded from the Rochester Shale of Longport, N.Y. This is apparently very similar but differs in having small spines on the surface.

Genus ERIDOTRYPA Ulrich 1893

Description. A slender, ramose Batostomellid with, in the exozone, thick walls round which is deposited extra calcareous tissue. Diaphragms are most common in the proximal part of the short exozone. Mesopores occur, but acanthopores are neither large nor common. Most species are described from Ordovician rocks though a few are recorded from Silurian and Devonian strata.

Eridotrypa umbonensis sp. nov.

Plate 30, figs. 3, 4

Holotype. Manchester Museum LL 2594.

Diagnosis. Zoarium broad-based and encrusting, rising centrally to a tall boss. Diameter of the base up to 5 mm., height about 6 mm. Zooecia at the edges of the basal extension short with thick walls and in the endozone rapidly expanding into thick calcareous tissue which may close the aperture completely. In the boss-like portion, the walls in the endozone are much thinner though the exozone is frequently closed by the growth of calcareous tissue. Amalgamate walls are Leioclemid in the way the diaphragm-wall unit can be traced across adjoining mesopores (Boardman 1960a). Diaphragms are well spaced. A few mesopores occur, some closed. Small acanthopores are numerous in the exozone. Apertures round to oval, 0.15–0.2 mm. in diameter, 8–9 in 2 mm. Lower Bringewood Beds.

Remarks. Many of the sections pass through the expanded base and miss the boss-like central portion. This species is extremely like *Eridotrypa ramea* Hennig (1908), described from the Silurian rocks of Gotland, but differs mainly in the fact that that species is closely tabulate, whilst *Eridotrypa umbonensis* has few diaphragms.

Family STENOPORIDAE Wangen and Wentzel 1886

Genus LEOCLEMA Ulrich 1882

Description. Zoarium explanate, encrusting, massive or ramose. Zooecia subcircular or irregularly petalloid, separated by abundant mesopores. Acanthopores may be small and

inconspicuous or sometimes very large. Diaphragms few in zoecial tubes, many in mesopores. Boardman (1960a) has taken this genus as an example of a particular type of wall structure which he has named after it. In it the mesopore wall laminae, as seen in longitudinal section, are separated into well-defined diaphragm-wall units which may be traced across two or three adjacent mesopores. The individual laminae trend approximately parallel to the longitudinal directions of the zooecia and mesopores for a short distance before curving into the zoecial boundaries. Ordovician to Permian.

Leioclema explanatum Bassler

Plate 30, figs. 5, 6

Remarks. This species was identified in Ludlovian rocks of Builtth (Owen 1960) from poor fragments. It is much better preserved in nodules from the Upper Wootton Beds of Backbury Hill near Woolhope and there is little doubt that it is very similar to the American examples from the Rochester Shales described by Bassler (1906). It does not appear to have Boardman's typical Leioclemid wall structure, the diaphragms being thin except in the extreme distal exozone.

The zoaria are laminate, often encrusting. The zooecia are simple tubes, moderately thick-walled, with few diaphragms. Apertures 0.15–0.25 mm. in diameter, 6–7 in 2 mm. Numerous closely tabulate mesopores separate the zooecia. Acanthopores 2–4 in each zoecium, large enough to distort the distal zoecial walls, diameter 0.03 mm. Elton and Lower Bringewood Beds.

Leioclema halloporoides sp. nov.

Plate 30, figs. 9, 10

Syntypes. Manchester Museum LL 2596 and LL 2597.

Diagnosis. Zoarium ramose, about 2 mm. in diameter. Zooecia develop centrally and curve gently outwards to reach the zoarial surface at right angles. In the endozone the wall is thin but it thickens in the exozone, and the laminae appear to curve forward in a U-shape. Diaphragms are frequently oblique and curved. Mesopores occur with thicker diaphragms, the laminae running into them and occasionally extending from one to the next adjoining. The walls seem to be Leioclemid but the preservation is not sufficiently perfect to confirm this. Small acanthopores occur, usually at the junctions of three walls, but they do not distort the zoecial wall. Lower Bringewood Beds.

EXPLANATION OF PLATE 30

- Figs. 1, 2. *Bythopora parallela* sp. nov. 1, Vertical section. 2, Tangential section. Syntypes LL 2592 and LL 2593; $\times 50$.
 Figs. 3, 4. *Eridotrypa umbonensis* sp. nov. 3, Vertical section showing closed mesopores. 4, Tangential section. Holotype LL 2594; $\times 50$.
 Figs. 5, 6. *Leioclema explanatum* Bassler. 5, Tangential section showing acanthopores. 6, Vertical section. LL 2616 and LL 2595; $\times 50$.
 Figs. 7, 8. *Leioclema ludlovensis* sp. nov. 7, Tangential section. 8, Vertical section of encrusting portion. Holotype LL 2598; $\times 50$.
 Figs. 9, 10. *Leioclema halloporoides* sp. nov. 9, Tangential section. 10, Vertical section. Syntypes LL 2597 and LL 2596; $\times 50$.

Remarks. This species looks very like *Leioclema explanatum* Bassler in section but differs in its ramose habit and the fact that the acanthopores are smaller and do not distort the wall. The structural difference between the zooecial diaphragms and those in the mesopores is typically Leioclemid. The vertical sections are reminiscent of the Silurian species of *Hallopora*, but the wall structure and presence of acanthopores emphasize the difference. At present I have seen this species in the Shucknell Hill Beds only.

Leioclema ludlovensis sp. nov.

Plate 30, figs. 7, 8

Holotype. Manchester Museum LL 2598.

Diagnosis. Zoarium encrusting, sometimes rising into tall cylinders. Zooecia short, thick-walled tubes, except in the cylindrical portions where they are thin-walled in the endozone. Wall structure typically Leioclemid (Boardman 1960a) with the laminae from the mesopore diaphragms curving into the boundary walls to form a U-shape. Diaphragms in the zooecia few, thin and nearly straight. Mesopores numerous with many thick diaphragms. Apertures oval, averaging 0.15 by 0.1 mm., 9–10 in 2 mm. Mesopore apertures variable, some very small, some closed. Acanthopores numerous and large. Occurs in levels from Bringewood to Upper Whitcliffe Beds.

Remarks. This common species is little changed throughout its range. In some localities it occurs most commonly as thin, encrusting masses and at others the cylindrical form rising from the encrusting base is most frequently found, though, at all levels, both occur side by side. In its encrusting habit it is not unlike *Leioclema elasmaticum* Boardman but differs in having more acanthopores and in its frequent cylindrical form.

Sub-Order INTEGRATA Ulrich and Bassler 1904

Family TREMATOPORIDAE Miller 1889

Genus ANAPHRAGMA Ulrich and Bassler 1904

This genus was described to include Trematoporids with markedly integrate walls, which compared closely with the genus *Batostoma*, differing mainly in having undulating walls in the endozone, and fewer diaphragms.

Anaphragma shucknellensis sp. nov.

Plate 31, figs. 1, 2

Holotype. Manchester Museum LL 2599.

Diagnosis. Zoarium ramose, stout, sometimes nodular or massive, branches 3–4 mm. across and a whole colony up to 40 mm. in diameter. Zooecia thin-walled in the endozone, the walls undulating and thickening and becoming markedly integrate in the early exozone with a strongly marked central black line, but again amalgamate near the surface as the walls thicken further. Diaphragms few and thin, the laminae of the diaphragms merging with the outer part of the zooecial wall and not extending into it. Apertures oval, 0.2–0.25 mm. in diameter, 6 in 2 mm. Mesopores and acanthopores absent. Walls in the exozone up to 0.3 mm. thick. Lower Bringewood Beds.

Remarks. This large, irregular bryozoan is very common in the Lower Bringewood Beds of Shucknell Hill near Woolhope, and its sturdy walls are distinctive in the weathered specimen. It compares very closely in wall structure with *Anaphragma mirabile* Ulrich and Bassler as described by Boardman (1960*b*), but differs in its less regular form, absence of mesopores and acanthopores and presence of diaphragms.

Genus *BATOSTOMA* Ulrich 1882, emend. Boardman 1960

Remarks. Boardman's emended definition (1960*b*) draws particular attention to the walls between zooecial boundaries, as seen in longitudinal section, in which the laminae 'lie nearly parallel to zooecial boundaries then curve distally just before intersecting the boundaries to form a V-shaped pattern that has extremely long, convexly curved limbs. In tangential sections, the walls of adjacent zooecia are generally integrate in appearance'.

In addition, the genus can be described as ramose or encrusting, often both, the ramose portion arising from an expanded base. Zooecia thin-walled in the endozone, but thick-walled and integrate in the exozone. Diaphragms numerous. Mesopores, often large, with numerous diaphragms; some of these may curve convexly outwards. Acanthopores variable, often numerous. A common Ordovician genus represented by many species, but not previously described from Upper Silurian rocks.

Batostoma sp.

Plate 31, fig. 3

Description. Zoarium small and bosslike arising from an expanded encrusting base, 3–4 mm. in diameter and 3–4 mm. high. Zooecia thin-walled in the endozone, but the walls thicken as they curve out to the zoarial surface, 0.15–0.25 mm. in diameter, 11–12 in 2 mm. The zooecial wall laminae form a V-shape pointing distally and show a dark line in the centre. Diaphragms lie close together in the exozone 2–3 to a 'tube width'. Small acanthopores numerous, mesopores absent. Upper Bringewood and Lower Leintwardine Beds.

Remarks. This is a typical small species of *Batostoma*, and fragments are common in the levels in which it occurs. I am not sufficiently satisfied with the preservation of the specimens which I have examined to describe them specifically.

Genus *CALAMOTRYPA* gen. nov.

Type species. *Calamotrypa millichopensis* sp. nov.

EXPLANATION OF PLATE 31

Figs. 1, 2. *Anaphragma shucknellensis* sp. nov. 1, Vertical section showing the dark line of laminae in the early part of the exozone. 2, Tangential section showing thick walls and dark line in the deeper section. Holotype LL 2599; $\times 50$.

Fig. 3. *Batostoma* sp. Vertical section showing tabulate zooecia in the exozone. LL 2600; $\times 50$.

Figs. 4–6. *Calamotrypa millichopensis* gen. et sp. nov. 4, Transverse section showing hollow centre and integrate walls. 5, Tangential section. 6, Vertical section showing hollow centre. Syntypes LL 2602, LL 2603, and LL 2601; $\times 50$.

Figs. 7–9. *Monotrypa crenulata* Nicholson. 7, Tangential section showing large and small zooecia. 8, Vertical section showing crenulate walls. 9, Vertical section showing more frequent diaphragms near surface. 7, 8, Lectotype British Museum PD 2998 A and B. 9, LL 2581; $\times 50$.

Diagnosis. Zoarium cylindrical, hollow. Zooecia short, rising obliquely from the central hollow and turning out to reach the zoarial surface at right angles. Zooecial wall markedly integrate, the laminae in longitudinal section form a V-shape, pointing distally, the wall centre darkened. Occasional thick diaphragms. Mesopores few and large. Acanthopores small.

Remarks. Hollow bryozoa are common in the Cyclostomata (Fistuliporidae) and in the Cryptostomata (Rhabdomesidae and others). They have been described among Amalgamate Trepostomata (Stenoporidae) but not previously among Integrate Trepostomata. The integrate character of the walls and the clearly marked V-shape of the laminae within the walls, when seen in longitudinal or transverse sections, ally this genus to such genera as *Batostoma* and *Monotrypa* and I therefore place it with them in the family Trematoporidae.

Calamotrypa millichopensis sp. nov.

Plate 31, figs. 4, 5, 6

Syntypes. Manchester Museum LL 2601, LL 2602, and LL 2603.

Diagnosis. Zoarium as described for the genus 1–1.5 mm. in diameter, 3–5 mm. long. Central hollow cylindrical in shape but variable in size, 0.2–0.4 mm. in diameter, surrounded by epitheca 0.01–0.02 mm. thick. Zooecia thick-walled throughout, 0.3–0.4 mm. long with occasional thick diaphragms. Mesopores few and large, with apertures indistinguishable from those of auto-zooecia, and with a few thick diaphragms. Apertures circular, 0.1–0.2 mm. in diameter, well separated by calcareous tissue, twelve in 2 mm. Acanthopores few and small, and visible only near to the zoarial surface. Bringewood Beds.

Remarks. This is a common species in the Bringewood Beds and is quite distinctive wherever sections pass through the central hollow cavity. Even when sections miss the cavity, the small size of the apertures and the integrate nature of the walls are characteristic.

Genus MONOTRYPA Nicholson 1879

Description. Zoarium massive, discoidal, ramose, laminar or encrusting. The zooecia may be of uniform size or groups of larger zooecia may occur in monticules. Diaphragms complete, may be few or many. The zooecial walls are markedly integrate. Mesopores absent; Nicholson noted that acanthopores were absent except in the species *Monotrypa discoidea* (James), which has now been removed from the genus. Bassler (1906) drew attention to two main groups of species, those with straight or curved walls and many diaphragms and those with crenulate walls and few or no diaphragms. Species are common throughout Ordovician, Silurian, and Devonian rocks.

Remarks. Three species of *Monotrypa* have been collected from Ludlovian rocks of the Welsh Borderland, *M. crenulata* Nicholson, *M. flabellata* Owen, and a new species, *M. patera*, described below. As *M. crenulata* was described by Nicholson without the designation of a holotype, I redescribe it here, choosing as lectotype a fine specimen in the British Museum (Natural History) from the collections of Mr. Madeley. As

Nicholson knew these collections and their owner, it is probable that he knew the actual specimen and may have named it.

Monotrypa crenulata Nicholson 1884

Plate 31, figs. 7, 8, 9

Lectotype. B.M. (N.H.), PD 2998.

Diagnosis. Zoarium massive, hemispherical, with flat base covered by concentrically striated epitheca. Height 31 mm., maximum diameter 52 mm. Groups of larger zooecia visible on the surface, their centres 5–6 mm. apart, but not raised up to form monticules. Zooecia long, thin-walled tubes, originating from the basal epitheca and running nearly straight to the zoarial surface. The zooecial walls are thin throughout their length and crinkled; the crinkles, where most strongly developed, occur 6–10 in 1 mm., the distance between the crest and trough of a wave up to 0.05 mm. The thin walls are not obviously integrate, but in thin section, lines of separation often occur in the centre of the wall. Diaphragms thin, straight or curved. In some zooecia they are relatively frequent, as close as 0.4 mm. Apertures polygonal, normally pentagonal or hexagonal, the diameters in groups of larger zooecia 0.5–0.6 mm., four in 2 mm., and those in groups of smaller zooecia 0.25–0.35 mm., seven in 2 mm. Mesopores and acanthopores absent. Wenlock Limestone, Dudley.

Remarks. Nicholson figured a typical specimen similar to the lectotype. His description is as follows:

The corallum of this species is hemispherical or subglobular, ordinary examples having a height of an inch, or an inch and a half and a diameter of about the same at the base. The base is flat or concave and is covered by a striated epitheca; and the corallites radiate from the base to open over the whole convex upper surface of the colony. The corallites are prismatic, mostly pentagonal, thin-walled and not firmly united with one another, their walls being regularly and uniformly crenulated in such a manner that contiguous tubes are accurately dovetailed together. The corallites vary in size from $\frac{1}{8}$ inch to $\frac{1}{35}$ inch there being occasionally definitely defined groups of larger tubes. No spiniform tubuli are developed. The surface is apparently smooth and devoid of monticules. As seen in long sections, the tubes are found to be crossed at considerable intervals ($\frac{1}{25}$ – $\frac{1}{10}$ inch) by a few horizontal tabulae which are not uniformly placed at corresponding levels in contiguous corallites.

I think it tolerably certain that this form corresponds with part of the *Favosites fibrosa* of Mr. Lonsdale (Sil. Syst. pl. xv, *bis.*, figs. 6–6d), and I should willingly have retained the specific name *fibrosa* if this had seemed at all advisable.

He further stated that *Calamopora fibrosa* Goldfuss, from which Lonsdale took this name, is a very different coral in all respects.

A further typical Wenlock Limestone form, which I have sectioned (Manchester Museum collections LL 2581), is similar in all respects to the lectotype, except that the diaphragms become numerous near the zoarial surface, as many as five occurring in the space of 1.5 mm.

Nicholson stated that *Monotrypa crenulata* occurs in the Wenlock Limestones and Lower Ludlow rocks of Sedgeley. I have seen many typical tall hemispherical forms from the Wenlock Limestone (often labelled *Favosites fibrosus* Lonsdale) in older collections, but the only undoubted Ludlovian forms which I have examined are much flatter and similar in shape to the head of a mushroom. There are good examples, now in the

National Museum of Wales, from the Ludlovian of the Cardiff St. Helen's road borehole (North 1916). A typical specimen has a diameter of 32 mm., a height of 10 mm. and, having a slightly concave base, a thickness of 7–8 mm. The walls are thin throughout, the zooecia are of two sizes, the larger 0.4–0.5 mm. in diameter and the crenulations in the walls six in 2 mm. Very few diaphragms were noted. *Favosites fibrilla* Smith was described from Upper Valentian rocks and is certainly *Monotrypa crenulata* Nicholson (Owen 1960).

Monotrypa flabellata Owen

Plate 32, figs. 1, 2

Remarks. This species was described in 1960, the wall structure differing markedly from that of *Monotrypa crenulata* Nicholson. The wall is thicker throughout and the laminae, viewed in longitudinal section, form a V-shape pointing distally so that the centre of the wall is dark. Tangential sections near the surface also show a dark line between the polygonal zooecia. Other differences are as follows. The zooecia are all the same size, approximately 0.3–0.4 mm. in diameter, no larger groups being observable. The crenulations are less regular and less even and can be described more as wrinkles than as waves. Fewer diaphragms occur though they are occasionally massed close together near the zoarial surface. Such a massing in both species may have been due to special living conditions surrounding the colonies.

Specimens of *Monotrypa flabellata* Owen have also been collected from the Upper Wootton Beds of Backbury Hill, Woolhope. These have been found encrusting brachiopod shells. The zoarial width is between 13–20 mm., and the thickness 4–5 mm. The walls are relatively thick, the diaphragms few and the crenulations occur as wrinkles.

Monotrypa patera sp. nov.

Plate 32, figs. 3, 4

Syntypes. Manchester Museum LL 2604 and LL 2605.

Diagnosis. Zoarium flat, disk-shaped, buttonlike, occasionally encrusting, 10–20 mm. in diameter and 1–2 mm. thick, without monticules but with groups of larger zooecia visible on the surface. Zooecia arise obliquely from a thick, striated epitheca and turn immediately to rise vertically to the zoarial surface. Walls relatively thick throughout, crenulate with uneven wrinkles, and showing a marked V-shape in the alignment of the laminae when viewed in longitudinal section. Diaphragms absent. Apertures polygonal, larger ones occasionally up to 0.5 mm. in diameter and five in 2 mm., and normal ones 0.3–0.35 mm. in diameter and 7–8 in 2 mm. Mesopores absent, though occasionally normal zooecia rise fairly high in the zoarium and appear to be smaller in tangential section. Bringewood Beds.

Remarks. This small species is common in Bringewood Beds and is easily recognizable with the hand lens, particularly when seen in section. It differs in zoarial shape from the two species described above. In its thicker, integrate walls and crinkles it resembles *M. flabellata*, and in its small groups of rather larger zooecia it compares with *M. crenulata*. There is little doubt that the three species are closely related.

Order CRYPTOSTOMATA Shrubsole and Vine 1883

Family ARTHROSTYLIDAE Ulrich 1886

Genus NEMATOPORA Ulrich 1888

Dichotomously branching zoaria, articulated at the base only, with apertures opening on all sides. Zooecial chambers short. Common in Ordovician and Silurian rocks.

Nematopora hexagona sp. nov.

Plate 32, figs. 5, 6, 7

Syntypes. Manchester Museum LL 2594 and LL 2605.

Diagnosis. Zoarium thin, branching, six-sided with apertures on all sides, slightly flattened. Zooecia short, rectangular, grouped round a central, thread-like axis, the apertures opening into a shallow vestibule in thick, calcareous tissue. Apertures oval, 0.2 by 0.12 mm., five in 2 mm. No diaphragms or hemisepta. No mesopores or acanthopores. Elton and Lower Bringewood Beds.

Remarks. These small forms are very common and highly distinctive in section. Numerous small transverse sections demonstrate the six-sided nature. When a vertical section cuts the central axis it is often seen to be transparent, though the zooecial walls are opaque and fibrous. This characteristic is also noted in Fenestellids.

Family RHABDOMESIDAE Vine 1883

Genus RHOMBOPORA Meek 1872

Description. Zoarium small, ramose, rather solid and stick-like. Zooecia radiate from an axis to reach the zoarial surface obliquely. Apertures within vestibules, irregularly arranged in longitudinal or oblique-spiral rows. No mesopores. Acanthopores numerous, often represented on the surface by minute spicules. Silurian to Carboniferous.

Rhombopora mesopora sp. nov.

Plate 32, figs. 9, 10

Holotype. Manchester Museum LL 2607.

Diagnosis. Zoaria of branching cylinders 0.7–1 mm. in diameter, occasionally encrusting.

EXPLANATION OF PLATE 32

Figs. 1, 2. *Monotrypa flabellata* Owen. 1, Vertical section showing thicker walls. 2, Tangential section. LL 1526 A; $\times 50$.

Figs. 3, 4. *Monotrypa patera* sp. nov. 3, Vertical section showing central dark line in walls. 4, Tangential section. Syntypes LL 2604 and LL 2605; $\times 50$.

Figs. 5–7. *Nematopora hexagona* sp. nov. 5, Vertical section. 6, Tangential section showing zooecial apertures. 7, Transverse section showing hexagonal zoarium. Syntypes LL 2594 and LL 2605; $\times 50$.

Fig. 8. *Rhombopora minima* Owen. Part tangential section showing apertures and acanthopores. LL 2608; $\times 50$.

Figs. 9, 10. *Rhombopora mesopora* sp. nov. 9, Vertical section showing simple zooecia and thickened walls. 10, Tangential section showing mesopores. Holotype LL 2607; $\times 50$.

Zooecia thin-walled in the endozone, running obliquely to the zoarial surface and becoming very thick-walled, up to 0.1 mm. in thickness. No diaphragms. Apertures oval, 0.15 by 0.08 mm., nine in 2 mm. Occasional small mesopores develop in the exozone. Small acanthopores numerous but not clearly defined in the opaque wall tissue. Upper Leintwardine Beds.

Remarks. This species is a small, stick-like form and its thick walls are clearly visible to the naked eye. It differs from *Rhombopora minima* Owen in having simpler zooecia without hemisepta, and small mesopores. Although Meek, in his original description of the genus, noted the absence of mesopores, this species fits so well in all other particulars that there is little point in erecting a new and allied genus for its reception. It is very much the commonest species in the Upper Leintwardine Beds.

Rhombopora minima Owen

Plate 32, fig. 8

Remarks. This little bryozoan, described from Builth (Owen 1960), though seldom common, is found at all levels from the base of the Elton Beds to the Lower Leintwardine Series. It is most distinctive with its small, stout-walled zoarium and its calcareous exozone where lie the vestibules of the zooecia. There is little variation between specimens throughout the range.

Very few specimens were seen in the beds at Builth and, as really good tangential sections were hard to find, none was illustrated. It occurs much more commonly around Ludlow, notably throughout the Bringewood Beds, and good tangential sections have been prepared showing the distal end of the vestibule, and the numerous, strongly developed acanthopores. Longitudinally, five apertures occur in 2 mm., and the mouth of the vestibule, which is oval, measures 0.15 by 0.08 mm. The acanthopores are circular in section and up to 0.03 mm. across.

Family PTILODICTYDAE Zittel 1880

Genus PTILODICTYA Lonsdale 1839

Ptilodictya gracile Owen

Remarks. Complete specimens of this species were not seen in the Ludlovian rocks of Builth from which it was described (Owen 1960). In the Lower Bringewood Beds at Millichope Lodge Gates near Ludlow and in the Upper Bringewood Beds of Weo Edge it is very common indeed, and numerous complete specimens have been collected. They are up to 20 mm. long and 3–4 mm. across. In zoarial shape they resemble *P. lanceolata* (Goldfuss) but they are smaller in every way. One might consider that they were immature forms of this species were it not for the fact that the full-sized *P. lanceolata* also occurs and there are no intermediate forms, and also that their zooecial measurements and apertures are markedly smaller than those of the young sections of the Gotland Ludlovian *P. lanceolata* (Ross 1960), the apertures averaging in the median range of zooecia 0.19 by 0.09 mm. (young *P. lanceolata* 0.22–0.28 by 0.12–0.15 mm.) and in the lateral range 0.20 by 0.08 mm. (0.26–0.36 by 0.13–0.17 mm.). Incidentally, Mrs. Ross notes that the Wenlock Limestone forms of *P. lanceolata* are more robust than those of the Gotland Ludlovian. Lower Elton to Upper Bringewood Beds.

In the Upper Bringewood Beds of Weo Edge, where the species is particularly common, 'pearls' are also very numerous. They have previously been associated with *Favositella interpuncta* (Quenstedt) (Oakley 1934) which also occurs in these beds but is very much less common. The 'pearls' are sometimes so numerous that they form an appreciable part of the rock. They were certainly noticed in section inside zooecia but never sealed in. It is to be wondered if they have any connexion with this species.

Ptilodictya lanceolata (Goldfuss)

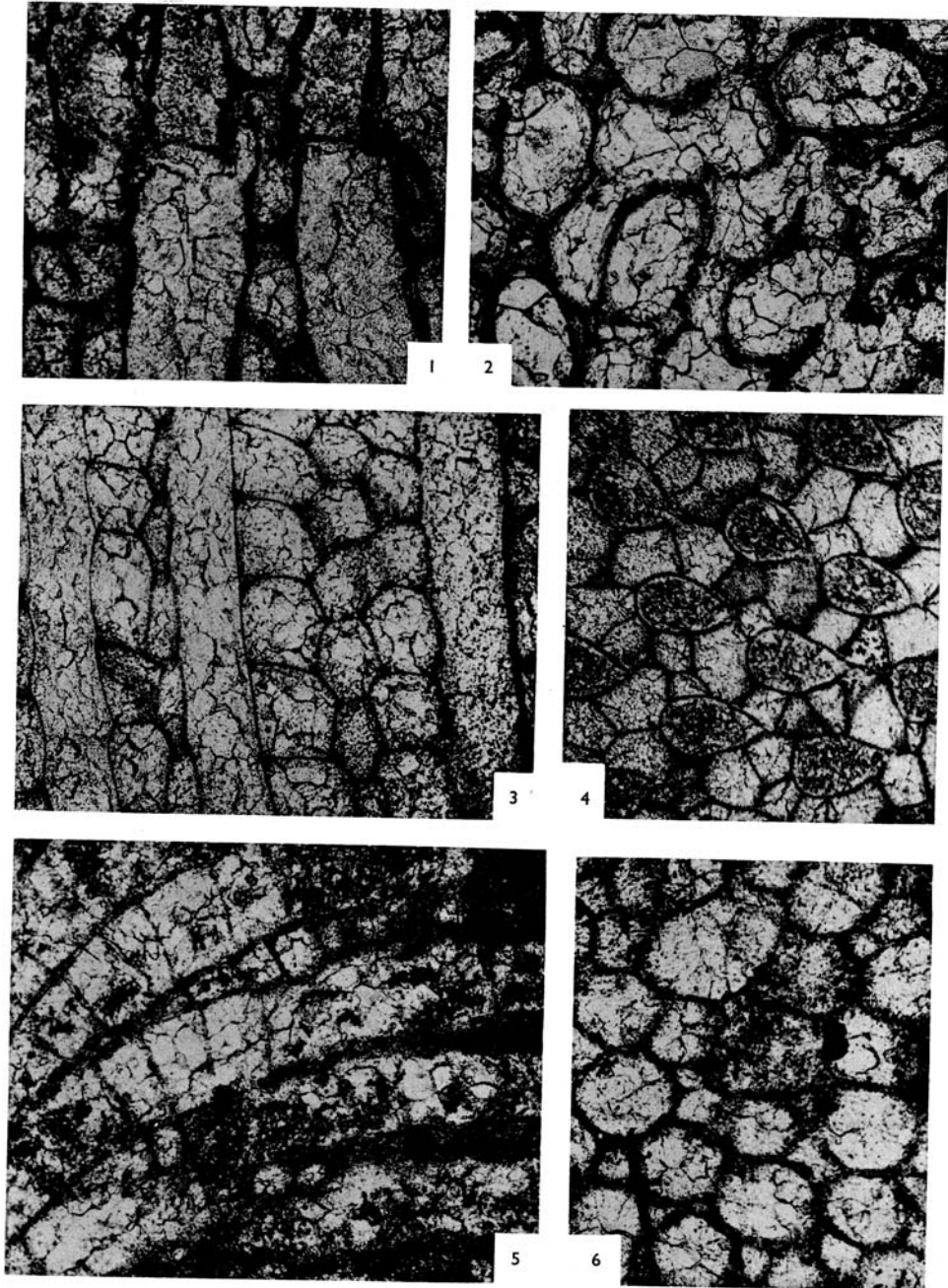
Remarks. I have not collected this species myself from the Ludlovian rocks of the Welsh Borderland, but have examined specimens in the older collections which are reputed to have come from the Aymestry Limestone. Up to 100 mm. or even more in length and 10–15 mm. in breadth, they appear to be indistinguishable from typical Wenlock Limestone examples.

Acknowledgements. I should like to record my thanks to members of the Ludlow Research Group who have helped me to find the most prolific localities and have discussed other faunal problems with me.

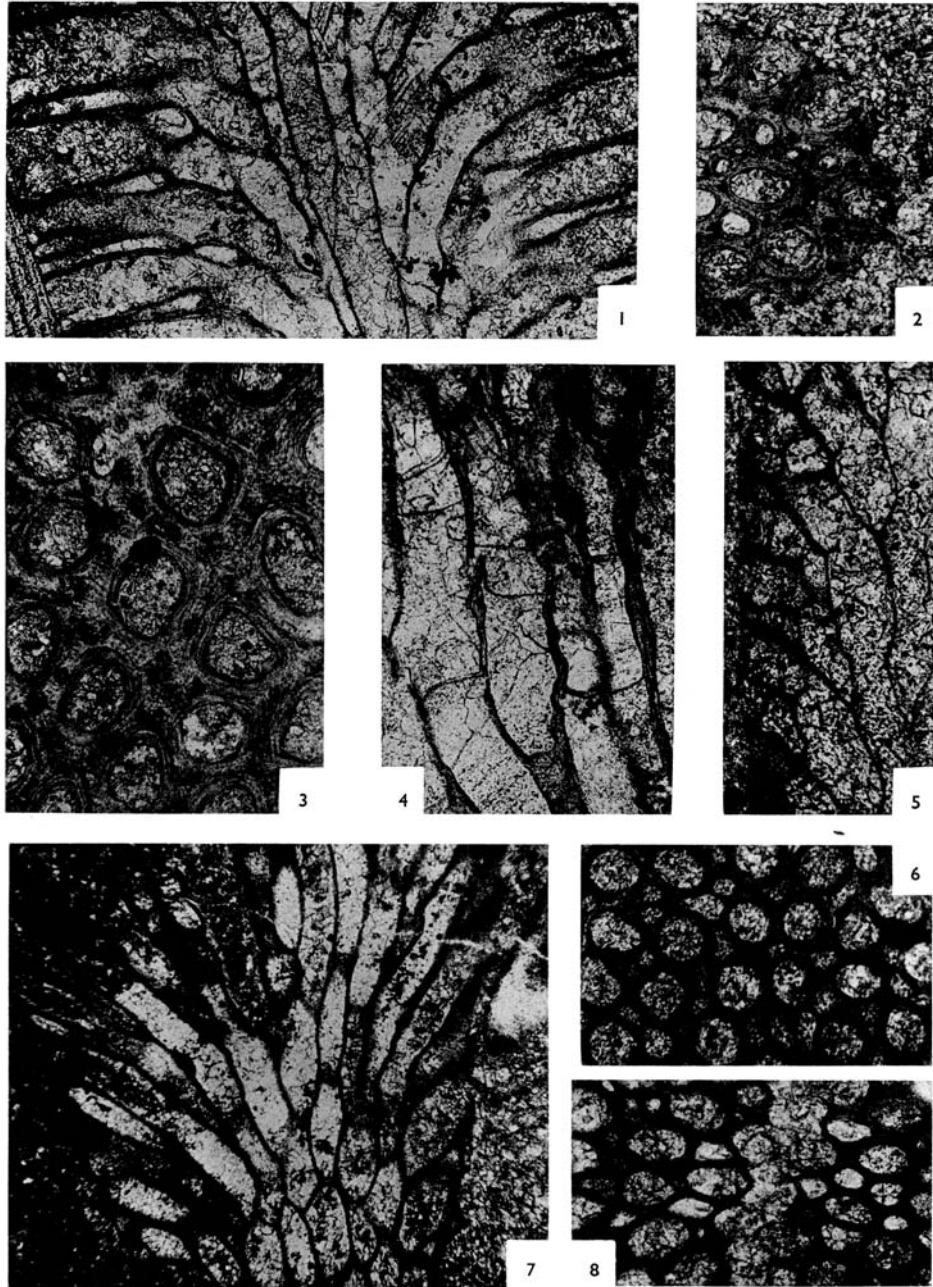
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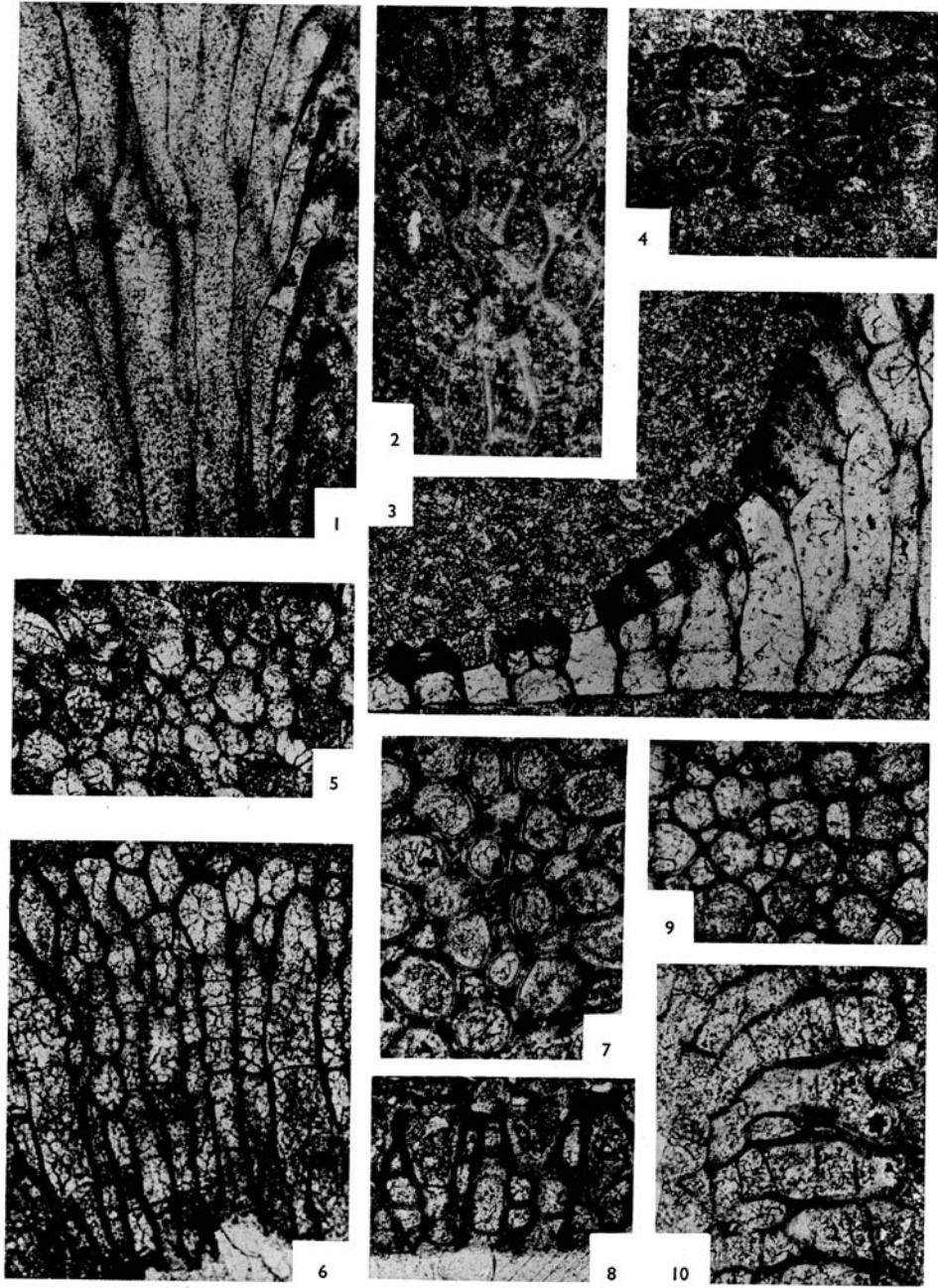
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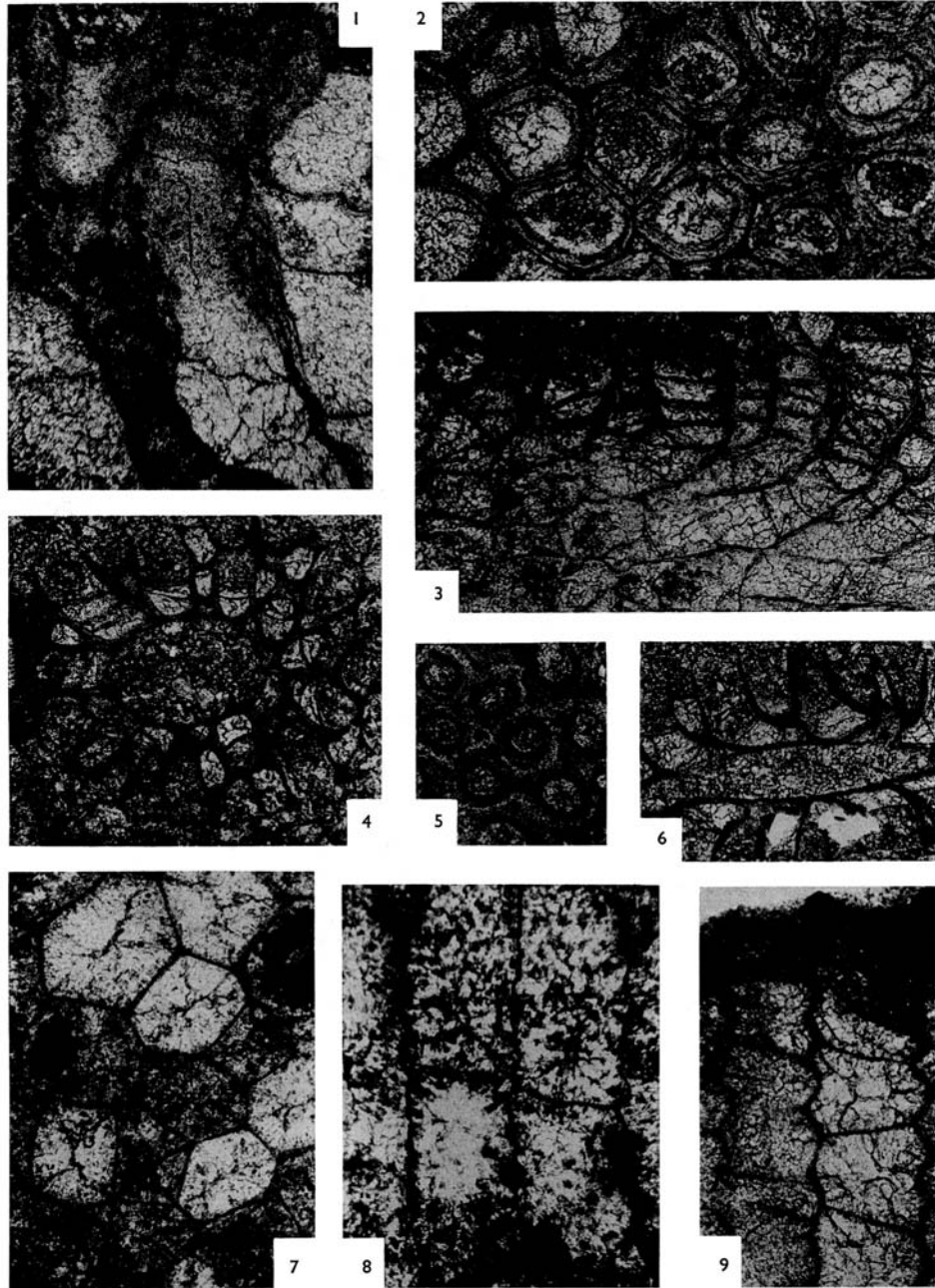
OWEN, Ludlovian bryozoa



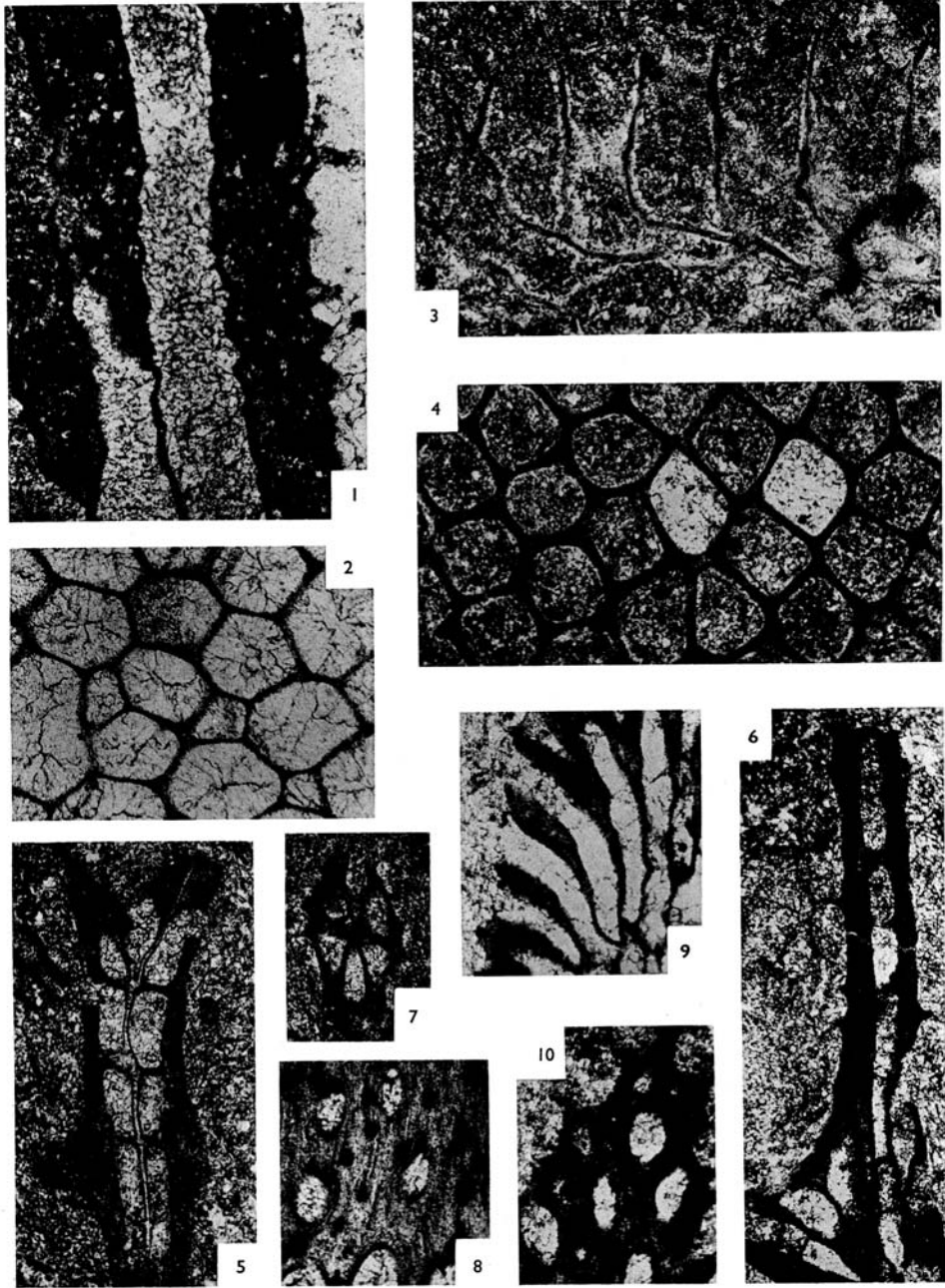
OWEN, Ludlovian bryozoa



OWEN, Ludlovian bryozoa



OWEN, Ludlovian bryozoa



OWEN, Ludlovian bryozoa