

WENLOCKIAN BRYOZOA FROM DUDLEY, NIAGARA, AND GOTLAND AND THEIR PALAEOGEOGRAPHIC IMPLICATIONS

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ABSTRACT. A comparison is made between the Wenlockian bryozoan faunas of Dudley and those of the Niagaran region of New York State, and localities near Visby, in Gotland. Their occurrence fits a narrow Atlantic, the Niagaran and Dudley faunas occupying a different climatic zone from that of Gotland. The following new species are described from the British material: *Meekopora dudleyensis*, *Stenopora primaeva*, and *Batostomella maniformis*. The new genus *Asperopora* is proposed for Silurian and lowermost Devonian species of *Leioclema* with numerous, often cystose mesopores, and acanthopores which frequently inflect zoecial apertures.

IN 1911, Bassler described 155 species and 6 varieties of bryozoa from numerous Ordovician collections from the Baltic provinces, some made especially for the study. He was clearly interested in possible links with American species and compared the faunas from the two regions. He found 62 species and 1 variety (pp. 50–3) common to both. He commented (p. 32) that, leaving out bryozoa from the Lyckholm and Borkholm Limestones, which he believed to be of early Silurian age, the number of species common to Baltic and American regions was 52 out of 134. The above beds are now considered to be of late Ordovician age.

In 1965, I was able to examine Bassler's material in the U.S. National Museum, but would not be prepared to admit that any of the species was, in fact, common to the two areas. Furthermore, he wrongly recorded the American Silurian forms *Hallopora elegantula* (Hall) and *Lichenalia concentrica* Hall from Baltic Ordovician rocks. His named sections in the Smithsonian Institution bear little resemblance to the American types. With further study it is possible that some of the material which he believed to be common to both areas will turn out to be conspecific, though the Baltic bryozoan fauna has a very different aspect from the American equivalents.

In my own work on Silurian bryozoa, I had been struck by the differences between the British and American species. Further, material I had collected in Gotland in 1959 seemed quite different again. Until recently, it has been difficult to compare published figures of species described from different countries. Many have been illustrated by drawings and where photomicrographs have been used, sections have often been too thick to show the detailed structures. In consequence, I collected material from the Niagara region in 1965 for comparison with my own Wenlockian material, and Llandoveryan and Wenlockian bryozoa from Gotland in 1959. In both Sweden and America my time was short and my small collections were made largely from localized spoil heaps. My British Wenlockian material is from the classic locality of Dudley in Worcestershire, where I have had longer in the field and have collected my fossils *in situ*.

In order to make the closest comparisons, I have tried to compare faunas from strata of similar lithology. This has not been difficult, for the shaly limestones of Dudley, which lie between the two thick beds of reef limestone which have been extensively quarried, are lithologically very like the Lower Rochester Shales of the Niagara region.

I was also able to collect from some thinly bedded, argillaceous limestone of the Högkint group near Visby, a rock of similar lithology to the other two.

In British Silurian and Carboniferous deposits, bryozoa occur most commonly in fore-reef calcirudites rather than in more massive reef limestones. The latter frequently contain fenestellids and certain incrusting forms, but their bryozoan fauna as a whole is small in numbers and in variety. A similar distribution was noted by Cuffey (1967) in Permian rocks. Stach (1936), working on the Tertiary Cheilostomata of New Zealand, noted a number of zoarial shapes, some of which could stand strong wave action and littoral conditions. These included certain fenestrate colonies and those incrusting flexible algae. Articulated zoaria could also stand wave action though some lived in waters of greater depth. The cylindrical forms, however, needed more shelter. Lagaij and Gautier (1965), working on modern bryozoan assemblages of the Rhône delta, found them rarest in places of most rapid deposition, particularly in front of the main distributory mouths, and the rate of sedimentation appeared to be a major factor controlling distribution. Working with slight modifications of Stach's zoarial shapes, they showed that colonies incrusting a solid substratum and ramose forms occupied the deeper, quiet waters, but that those incrusting flexible algae or of fenestrate habit could stand stronger currents and wave action. Bifoliate forms tended to inhabit waters of around 40–50 m. depth floored by sandy coralline beds.

Thus, the distribution of Palaeozoic bryozoa would not appear to have differed much from that of Tertiary and Recent species and may have been influenced by the same factors. A further possible cause may have been the apparent mutual exclusiveness of ramose bryozoans and tabulate corals in some deposits. They may have competed for food.

Powell (1967), describing Recent bryozoans from north New Zealand, found the richest fauna at around 53 fathoms. This would present quiet conditions which apparently suit ramose forms. It would also be at the limit of, or just beyond the reach of light, and consequently beyond the range of corals.

COMPARATIVE FAUNA

In order to compare the Wenlockian faunas from the three localities, I have calculated the percentage distribution of the specimens collected. These figures could be improved by more detailed and representative collecting, but nevertheless give a clear picture of the relative frequency of the commoner species. Further, the percentages of American species which I collected agree with the notes 'common' etc. used by Bassler (1906). The percentages of British species collected are as follows:

	<i>Percentage</i>
<i>Fistulipora nummulina</i> Nicholson and Foord	24
<i>Eridotrypa cava</i> Owen	20
<i>Rhombopora mawi</i> Owen	14
<i>Hallopora elegantula</i> (Hall)	5
<i>Batostomella maniformis</i> sp. nov.	4
<i>Stenopora primaeva</i> sp. nov.	4
<i>Asperopora multipora</i> (Bassler)	4
<i>Asperopora aspera</i> (Hall)	3
<i>Trematopota</i> sp.	3
Fenestrate Cryptostomata	5
Other species	14

Bifoliate Cryptostomata, though present, made up less than 1 per cent of the material collected. They include *Ptilodictya lanceolata* (Goldfuss) and *Pachydictya crassa* (Hall).

In contrast, the American Lower Rochester Shale species from two localities were represented as follows:

	<i>Percentage</i>
<i>Chilotrypa ostiolata</i> (Hall)	57
<i>Trematopora tuberculosa</i> Hall	17
<i>Hallopora elegantula</i> (Hall)	16
Fenestrate Cryptostomata	5
Other species	5

The other species include specimens of *Asperopora aspera* (Hall), *Asperopora multipora* (Bassler), and a few bifoliate Cryptostomata.

The Gotland Wenlockian fauna is quite different. The percentages are as follows:

	<i>Percentage</i>
<i>Helopora lindstromi</i> Ulrich	26
<i>Phaenopora lindstromi</i> Ulrich	22
<i>Fistulipora mutabilis</i> Hennig	16
<i>Hallopora</i> spp.	15
<i>Eridotrypa</i> spp.	8
<i>Ptilodictya lanceolata</i> (Goldfuss)	6
<i>Crepidopora lunariata</i> Hennig	3
Other species	4

Though species of *Hallopora* and *Eridotrypa* are common, their preservation is such that I would not be prepared to identify them specifically. None of them, however, bears any resemblance to species of *Hallopora* and *Eridotrypa* common in Britain and America. The bifoliate Cryptostomata are beautifully preserved, and no doubt this preservation led Hennig to devote the first of his three Gotland bryozoan papers to them. The small *Helopora lindstromi* Ulrich, first described by Ulrich (1890, p. 343) from Gotland and later by Hennig (1906, pp. 19–23), is also common and very well preserved. The Trepostomata, on the other hand, are poorly preserved, commonly worn, and would appear to have drifted some distance from their location in life. Perhaps the bifoliate lived in a slightly different habitat from that occupied by ramose forms (as with living bryozoa), and the latter were introduced as detrital material. If so, the Gotland percentages are not strictly comparable with those of Dudley and Niagara, but it is unlikely that this factor would alone account for such marked differences.

The species common to more than one locality are as follows:

<i>Species</i>	<i>America</i>	<i>Britain</i>	<i>Gotland</i>
<i>Hallopora elegantula</i> (Hall)	Very abundant	Very abundant	Missing
<i>Asperopora aspera</i> (Hall)	Common	Abundant	Missing
<i>Asperopora multipora</i> (Bassler)	Common	Abundant	Missing
<i>Pachydictya crassa</i> Hall	Fairly common	Occurs	Missing
			(occurs in Russia)
<i>Ptilodictya lanceolata</i> (Goldfuss)	Missing	Occurs	Common

Other species, notably *Berenicea consimilis* (Lonsdale) have been recorded in all three localities (Lonsdale 1839, p. 675; Bassler 1906, pp. 16–17; Hennig 1906, p. 25). I have not been able to examine specimens from each of the three localities, but the figures

suggest that the forms do not necessarily belong to one species. For instance, that shown by Bassler (1906, pl. 5, fig. 5) has a very different appearance from the form illustrated by Hennig (1906, pl. 3, fig. 8), while that of Lonsdale (1839, pl. 15, fig. 7) is too small to illustrate the specific features.

It would seem that *Ptilodictya lanceolata* (Goldfuss) is the only bryozoan species recognized with certainty both in Britain and in Gotland. This species has been restudied by Phillips Ross (1960). The Gotland specimens examined were mostly Ludlovian, though one was upper Llandoveryan. Phillips Ross stated (p. 445): 'Specimens of *P. lanceolata* from the Wenlock limestone of Dudley, England, are more robust, longer and thicker than specimens from the Ludlovian calcareous clay of Mulde, Gotland.' These differences are relatively unimportant but serve to show that even this species is not identical in the two localities. Fragments which I collected from the Wenlockian beds of Gotland are not sufficiently complete to allow an accurate comparison with British examples.

This brief faunal comparison suggests that the British bryozoan fauna had a few links with the American but none with that of the Baltic area. Bryozoa today are worldwide in distribution and known to inhabit the seas from tropical to polar regions. Further, they are found in water of all depths, from littoral to oceanic. According to Hyman (1959, pp. 417-30) Arctic species are circumpolar, and extend southwards some way down the coasts. Boreal and Mediterranean faunas are a mixture of localized and widely spread species. Arctic and some boreal species occur on both sides of the Atlantic but most boreal forms are restricted to the east or the west. There is a temperature zoning, though some species extend from Alaska to Central America and the Galapagos Islands.

The Wenlockian British and American bryozoan faunas would appear to have behaved in a similar way to their modern counterparts. Some genera were common to both, but most species were localized, though a few appeared in both areas. A closer look at the actual species is revealing. The commonest American form is *Chilotrypa ostiolata* (Hall) and the commonest British one *Fistulipora nummulina* Nicholson and Foord. These two fistuliporids are remarkably similar in many respects, the main difference being in form. The hollow cylinders of *Chilotrypa ostiolata* appear to have incrustated a particular non-calcareous stem, probably algal. *Fistulipora nummulina* was also incrustating but is found covering a variety of objects. The genera *Batostomella* and *Trematopora* are represented in both areas though by different species. The place occupied in America by the very common *Trematopora tuberculosa* Hall appears to have been taken in Britain by *Eridotrypa cava* Owen. Though species of *Eridotrypa* occur in America, none has any resemblance to the British species.

A comparison of Atlantic and Baltic species yields markedly different results. The exception to this is the common incrustating form *Fistulipora mutabilis* Hennig, which compares with *Fistulipora nummulina* and probably occupied a similar niche. Otherwise the dominant cryptostome element gives the bryozoan fauna of Gotland a distinctive character.

PALAEOGEOGRAPHY

An examination of the British and American bryozoan faunas of Wenlockian age shows similarities and contrasts not unlike those obtaining today. This suggests that

the areas were separated by an early Atlantic ocean, though that ocean need not have been as wide as at present. Each side had its own local fauna but a few species, notably *Hallopora elegantula* (Hall), were common to both. Perhaps these species had a greater climatic tolerance and were able to range along the northern shores of the ancient Atlantic. *Hallopora elegantula* was not an incrusting species and is unlikely to have floated across the waters in its adult state.

The difference in the faunas suggests that there was a considerable water barrier between the two regions even at that time. Free-floating bryozoan larvae exist for a limited period before becoming attached. It is not known whether the larvae of the extinct orders were cyphonautes or were comparable to the cheilostome and cyclostome brooded larvae of today. In the latter case, their unattached life would have been a few hours only. As ovicells and brood chambers are only known from a few forms in the extinct orders, their larvae may have been cyphonautes with an unattached life of as much as two months in certain circumstances.

If the Silurian Atlantic was very narrow, such larvae may have drifted across it. In like manner, the more fragile incrusting species might have been carried on drifting algae. In these circumstances the same species of fistuliporid might well be looked for on both sides. This has not happened. Today driftwood is known to cross the Atlantic. Scheltema (1966) gave a table of drift bottle data which showed that the minimum time taken by bottles drifting from the North American coast to the coasts of Europe or Africa was 364 days. The shorter journey from North America to the Azores took no less than 125 days. Such journeys were well within the survival limits of small immature gastropods but too long for bryozoan larvae.

Had the width of the Silurian Atlantic been half the present distance from the American coast to the Azores, it might still have formed a barrier to most species. If much less, it would scarcely have been a barrier at all. These comments are necessarily tentative, since the free-floating life of Palaeozoic bryozoa may have been much shorter, and ocean currents and winds may not have carried across narrow waters in Silurian times. Nevertheless, the existence of a narrower ocean which acted as a partial barrier between the British and American Silurian basins is suggested by the bryozoan fauna.

An interesting study of the effect of a water barrier was made by Cheetham (1963), describing the late Eocene zoogeography of the American eastern Gulf Coast. He postulated a bank of considerable size, the Ocala Bank, separated from the continental shelf by a strait, the Suwannee Strait. This was 50–70 miles across, with a variable depth of about 500 ft., and the bottom waters were slightly colder than those on the surface. This proved a barrier to a few species, though most occurred on both sides. It would seem that the Silurian Atlantic must have been a much more formidable barrier than the Eocene Suwannee Strait.

Spjeldnaes (1961) considered Ordovician climatic zones. He found evidence for a number of faunal provinces in Western Europe, North Africa, and eastern America, which could be considered to mark climatic zones if the poles and equator occupied positions different from those of today. He showed that such zones would be consistent with a pole somewhere in or west of Africa, and that such a position accorded with palaeomagnetic observations. Most of Britain including the Welsh Borderland lay in the Anglo-Scandic Province throughout Ordovician times, and this province extended into the Oslo region but not into the Baltic. The Appalachian Province was intimately related

and was evidently in the same climatic zone. The climatic zones of Europe and America were found to fit better if the continental blocks were considered to be 40° closer together than now. Such a position would still allow for a narrow intervening Atlantic Ocean. If the same situation obtained in Silurian times, and the Niagara and Welsh Borderland regions were in the same climatic province but separated by a narrow Atlantic, the similarities and differences of the bryozoan fauna would be explained. The distinctive Baltic Silurian fauna might also be explained, if it lay in a different climatic zone.

Bulman (1964) considered the distribution of lower Palaeozoic plankton; he plotted the occurrences of an Ordovician and a Silurian graptolite, and found that they were consistent with a pole west of Africa. In the case of the Ordovician graptolite, the occurrences showed a better fit with the continents in their present positions and the Atlantic its present width. Though the occurrences of the Silurian graptolite would fit either the present positions of the continents or a narrower Atlantic, it would be hard to picture the Atlantic narrowed by Wenlockian times and wider again at the present.

Størmer (1967, pp. 209, 210) noted that the highly fossiliferous coral reefs of the Silurian of Gotland may have formed the coastal facies of a syncline, a basin of marine deposits on the eastern European Platform. Such a basin might have had little or no physical connection with the Caledonian geosyncline which included the Welsh Borderland and possibly eastern American Silurian deposits. Such circumstances would explain the similarities of the American and British bryozoan faunas and their differences from those of Gotland.

In his work on Silurian cystoids, Paul (1967) found that the two families represented in Britain, the Echinoencrinidae and the Callocystitidae, originated from the Baltic and from North America respectively. This would suggest separate provinces, but the British intermingling would have called for connections at some period.

Thus, though no completely satisfactory answer is at present available, there must be a reasonable and natural explanation for the links between the bryozoan faunas of Britain and New York State, and the marked differences between those faunas and that of the Baltic in Wenlockian and, I believe, in upper Ordovician times. It seems likely that the distribution of climatic zones and presence of a narrower Atlantic Ocean offer the best hypothesis.

SYSTEMATIC PALAEOLOGY

All material described is in the collection of the Manchester Museum, whose registration numbers are quoted.

The following species have been identified in my collection from Dudley:

- Amplexopora* sp.
- Asperopora aspera* (Hall)
- Asperopora densipora* (Owen)
- Asperopora multipora* (Bassler)
- Batostomella maniformis* sp. nov.
- Calamotrypa millichopensis* Owen
- Ceramopora* sp.
- Eridotrypa cava* Owen
- Eridotrypa* sp.
- Favositella interpuncta* (Quenstedt)
- Fistulipora crassa* (Lonsdale)

Fistulipora nummulina Nicholson and Foord
Fistulipora sp.
Hallopora elegantula (Hall)
Meekopora dudleyensis sp. nov.
Monotrypa macropora Foord
Monotrypa paterella nom. nov.
Monotrypella benthallensis Owen
Monotrypella pulchella (Edwards and Haime)
Nicholsonella parva Owen
Pachydictya crassa (Hall)
Ptilodictya lanceolata (Goldfuss)
Rhombopora mawi Owen
Stenopora primaeva sp. nov.
Trematopora sp.

A description of new species, of species common to Dudley and Niagara, and those requiring special comment is given below.

Order CYSTOPORATA Astrova 1964

Family FISTULIPORIDAE Ulrich 1882

Genus FISTULIPORA McCoy 1850

Fistulipora nummulina Nicholson and Foord

Plate 114, figs. 1, 2

1885 *Fistulipora nummulina* Nicholson and Foord, pp. 506-7, text-fig. 4, pl. 15, figs. 2-2b.

1885 *Fistulipora dobunica* Nicholson and Foord, p. 511, pl. 17, figs. 3-3b.

Material. LL3214, 3215.

Description. Zoaria highly variable, disc-shaped, incrusting, or thin expansions, occasionally rising into low domes or branches. When incrusting, cover shells, crinoid stems, and other bryozoans. Low monticules, consisting of cystopores, occur at intervals of c. 4 mm.

Zooecia, at first recumbent, turn up rapidly to reach surface at or near right angles. Wall thickens in exozone on one side to form deep-seated lunaria. Cystopores, closed at surface, separate zooecia, and occur in groups. In tangential section, zooecia have prominent lunaria which sometimes give clover-leaf effect to apertures. Slightly larger apertures surround monticules, lunaria directed towards each monticule. Apertures average 0.2 mm. across; 8 occur in 2 mm. Lunaria average 0.10-0.14 mm. across.

Remarks. I had considerable difficulty in deciding whether the many specimens which I collected were *F. nummulina* or *F. dobunica*. The former is described as 'discoid, lenticular, concavo- or plano-convex, also forming thin, irregular crust-like expansions', and the latter 'extremely thin, encrusting'. The former is dotted with monticules consisting of mesopores, and the latter with maculae. In both, the lunaria are well developed, the apertures in *F. nummulina* being larger, 4 in 1 mm., and those in *F. dobunica* smaller, 6 in 1 mm.

I have been unable to locate the types of either species. That of *F. nummulina* was presented to either Nicholson or Foord by W. Madeley of Dudley and these authors refer to the fact that other specimens occur in the Holcroft Collection, now in Birmingham University museum. The type of *F. dobunica* was also said to be in Madeley's Collection. Named specimens in the collections of the British Museum (Natural History) appear to be indistinguishable from *F. nummulina*. Furthermore, my own collections

show every gradation from one to the other and I regard *F. dobunica* as less mature zoaria of *F. nummulina*. As *F. nummulina* was described first, *F. dobunica* appears to be a junior synonym.

F. nummulina is the commonest species in the Dudley area, *Chilotrypa ostiolata* (Hall) is by far the commonest in New York State, and *F. mutabilis* Hennig is the third most common species in my Wenlockian Gotland collection. Careful examination shows these three to have close similarities even though they are unrelated. Each is incrusting, though *C. ostiolata* is always hollow. All have well-developed monticules, particularly in the larger zoaria, and these are raised above the surface and consist of closed cystopores. All have well-developed lunaria, though only those of *F. nummulina* are deep-seated. The three species would seem to have occupied the same ecological niche.

According to Borg (1965) maculae and monticules originated as points of growth. Whether this is correct in any or all instances, there is little doubt that raised monticules in larger zoaria would have been protective. Whether they consisted of cystopores, closed mesopores, or acanthopores, they would be a protection against abrasion, whether from a free-swimming host, a series of waving fronds, or the tumbling of shells by wave action.

Genus MEEKOPORA Ulrich 1889

Meekopora dudleyensis sp. nov.

Plate 114, figs. 3, 4

Material. LL3216, 3217 (paratypes).

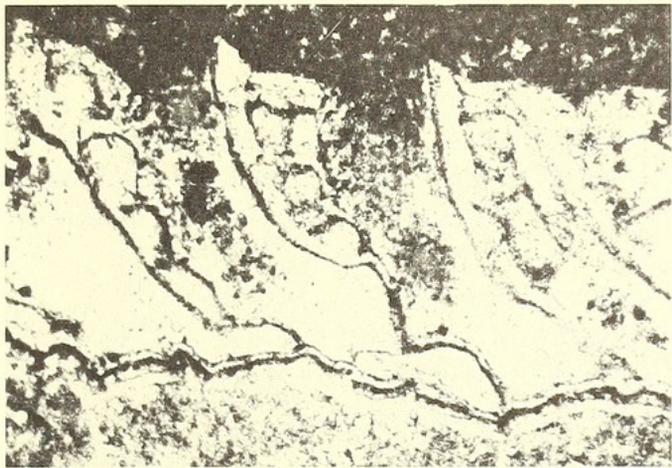
Diagnosis. *Meekopora* with well-developed lunaria and maculae consisting of small circular groups of cystopores.

Description. Zoaria bifoliate, variable in size, from strap-like forms 4–5 mm. across, to leaf-shaped examples up to 15 mm. wide and 1–1.5 mm. thick. Small circular maculae occur, consisting of cystopores, surrounded by apertures whose lunaria lie towards each macula. Zooecia arise from imperforate mesotheca which consists of two transparent layers separated by dark laminar layer; zooecia separated by cystopores whose surface layer is formed of dense, granular tissue. Apertures oval, averaging 0.12–0.16 mm. \times 0.16–0.20 mm., with well-developed lunaria 0.08–0.10 mm. across.

Remarks. The strongly marked lunaria, the small apertures, the small circular maculae, and the flat, strap-like or leaf-like zoaria serve to identify this species even when there is no cross-section visible to show the mesotheca. It differs from *Meekopora foliacea*

EXPLANATION OF PLATE 114

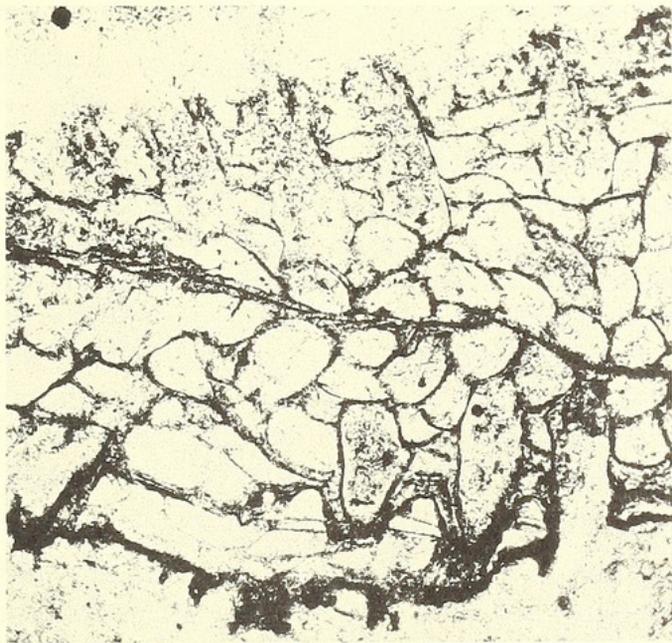
- Fig. 1. *Fistulipora nummulina* Nicholson and Foord from Dudley. Vertical section LL3214, \times 50.
 Fig. 2. *Fistulipora nummulina* Nicholson and Foord from Dudley. Tangential section showing clover-leaf-shaped apertures and lunaria. LL3215, \times 50.
 Fig. 3. *Meekopora dudleyensis* sp. nov. from Dudley. Vertical section showing mesotheca. Paratype, LL3216, \times 50.
 Fig. 4. *Meekopora dudleyensis* sp. nov. from Dudley. Tangential section showing small apertures with lunaria facing macula. Paratype, LL3217, \times 50.
 Fig. 5. *Batostomella maniformis* sp. nov. from Dudley. Vertical section showing thick exozone containing acanthopores. Holotype, LL3218A.
 Fig. 6. *Batostomella maniformis* sp. nov. from Dudley. Tangential section showing small apertures and acanthopores. Holotype, LL3218B, \times 50.



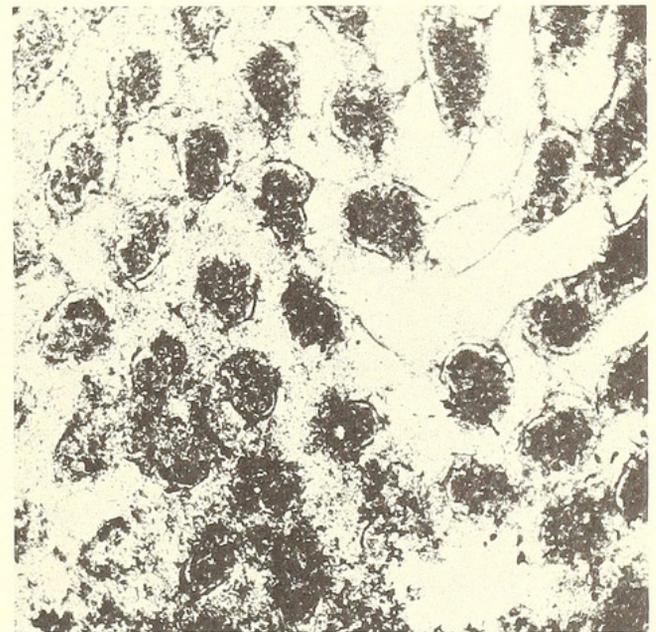
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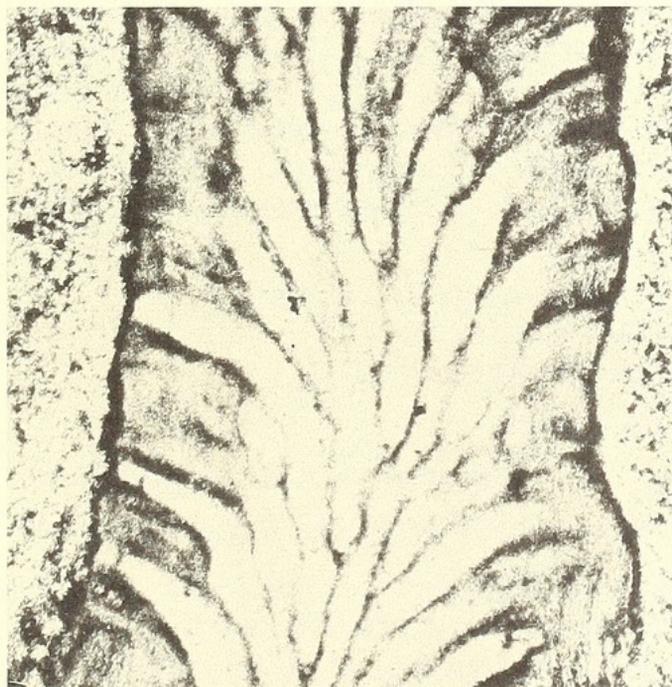
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3



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5



6

(Hall), which it most nearly resembles, in that the American species has larger apertures, and narrow, elongate dividing maculae. Like most fistuliporids, the species is variable but the characteristic shape of the maculae of *M. foliacea* seems to rule out the possibility of the two species being conspecific.

Order TREPOSTOMATA Ulrich 1882
 Family BATOSTOMELLIDAE Miller 1889
 Genus BATOSTOMELLA Ulrich 1882
Batostomella maniformis sp. nov.

Plate 114, figs. 5, 6

Material. LL3218 (holotype, specimen with five sections, LL3218A-E).

Diagnosis. *Batostomella* with a few large, deep-seated acanthopores in wide, laminate exozone.

Description. Zoaria ramose, with many branches apparently rising from a disc, each branch 1-1.5 mm. diameter, with small spines at surface marking position of acanthopores. Complete zoarium may be up to 30 mm. across with branches 25 mm. long. Zooecia arise axially, thin-walled, and turn sharply into exozone to reach surface at or near a right angle. Walls in exozone thick, laminate, with large, deep-seated, acanthopores with clear axes. No diaphragms. In tangential section, oval apertures widely separated, ringed. Acanthopores with clear axes occur intermediately, 3 or 4 surrounding each aperture. Mesopores absent. Apertures 0.1-0.12 mm. \times 0.05-0.07 mm., 10 in 2 mm. longitudinally, 15 in 2 mm. laterally or diagonally. Acanthopores 0.02 mm. in diameter.

Remarks. The holotype shows branches bifurcating at intervals of 5-8 mm. and the whole zoarium has a hand-like appearance. In section, it bears no resemblance to any described species. I have also collected fragments from the Lower Bringewood beds of Millichope, near Ludlow. The form is slightly smaller than the American *B. granulifera* (Hall), differing also in having relatively few acanthopores compared with the large numbers in that species, a thicker exozone, and no mesopores. In other respects, it is a closely allied species.

There is little difference between Silurian species of *Batostomella* and of *Rhombopora* and its allies. The latter have more clearly marked vestibules, often partly closed by hemisepta, but the genera must be closely related.

Family STENOPORIDAE Waagen and Wentzel 1886
 Genus STENOPORA Lonsdale 1844
Stenopora primaeva sp. nov.

Plate 115, figs. 1, 2

Material. LL3219A-C, 3220 A, B (paratypes).

Diagnosis. *Stenopora* with large, clear centred acanthopores.

Description. Zoaria ramose, with small spines marking positions of large acanthopores. Diameter 2.5-4 mm. Zooecia arise axially and curve gently to reach surface at *c.* 70°. Moderately thin walled in endozone, walls thicken rapidly in exozone, which varies in

width from *c.* 0.5 mm. in thinner branches to 1 mm. in stouter specimens. Exozone walls, commonly moniliform, have laminae which form wide, flat U distally. Within this region, large acanthopores with clear axes occur. Diaphragms present, few in number except in stoutest specimens. Examples frequently show an incipient development of exozone marking slight pause in growth; this feature often seen in stenoporids. Mesopores absent. Apertures oval, ringed, 0.15–0.3 mm. \times 0.08–0.15 mm., the longer axis approximately parallel with that of growth; 5 occur in 2 mm. longitudinally, 7–8 laterally. Large acanthopores numerous, diameter 0.03–0.05 mm., sometimes inflect zooecial wall, 5–8 ringing each aperture. Thickened walls with numerous acanthopores may form maculae.

Remarks. Though *Stenopora tasmaniensis* Lonsdale is Permian, and the genus has not been recorded in rocks older than the Carboniferous, this species is so similar in section to the type material of *S. tasmaniensis* that I consider it congeneric. *S. tasmaniensis* is considered to have no diaphragms. None was visible in the type section I examined, but the solid specimen made me wonder if occasional diaphragms might occur. Diaphragms are few in *S. primaeva*, occurring at the base of the exozone, especially in thicker specimens.

S. primaeva differs from *S. tasmaniensis* in having fewer, much larger acanthopores and generally a rather thinner exozone. A thick exozone may, however, merely reflect greater longevity owing to congenial conditions.

Genus ASPEROPORA gen. nov.

Ulrich (1882) proposed the genus *Leioclema* for the Carboniferous species *Callopora punctata* Hall, which he considered to be quite distinct from *Callopora elegantula* Hall. The original description (p. 141) was as follows:

Zoarium ramose, branches slender, smooth and sometimes hollow. Cell apertures small, rounded, and with two or three series of subangular interstitial cells surrounding them. Longitudinal sections show the tubes in the axial portion of the branch to be thin-walled, and crossed by remote diaphragms. In the peripheral region the interstitial tubes and spiniform tubuli are developed in great numbers. The walls of all the tubes are much thickened, and diaphragms in the interstitial tubes are straight and remote, while in the true tubes they appear to be wanting. In tangential sections the visceral cavity of the proper zooecia is often indented by the encroachment of the rather large spiniform tubuli, of

EXPLANATION OF PLATE 115

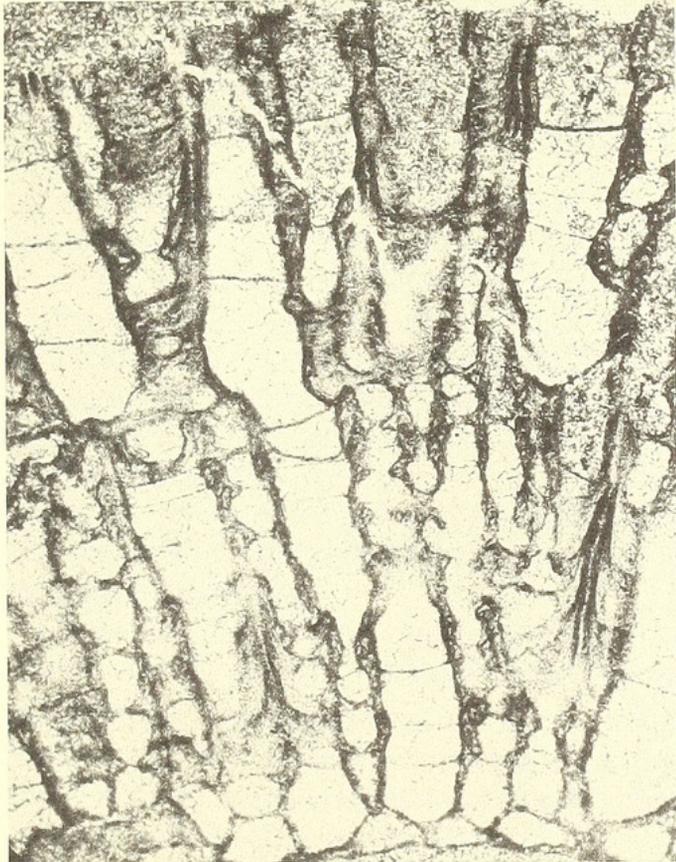
- Fig. 1. *Stenopora primaeva* sp. nov. from Dudley. Tangential section showing large, clear-centred acanthopores. Paratype, LL3219A, \times 50.
 Fig. 2. *Stenopora primaeva* sp. nov. from Dudley. Vertical section showing wide exozone and deep-seated acanthopores. Paratype, LL3220A, \times 50.
 Fig. 3. *Asperopora aspera* (Hall) from Dudley. Vertical section showing deep-seated, clear-centred acanthopores. LL3221, \times 50.
 Fig. 4. *Asperopora aspera* (Hall) from Dudley. Tangential section showing apertures surrounded by mesopores, and acanthopores inflecting the apertures. LL3222, \times 50.
 Fig. 5. *Asperopora aspera* (Hall) from Niagara. Vertical section showing deep-seated, clear-centred acanthopores. Diaphragms are fewer in this specimen. LL3223A, \times 50.
 Fig. 6. *Asperopora aspera* (Hall) from Niagara. Tangential section; the specimen is partly recrystallized but the large acanthopores are seen to inflect the apertures. LL3223B, \times 50.



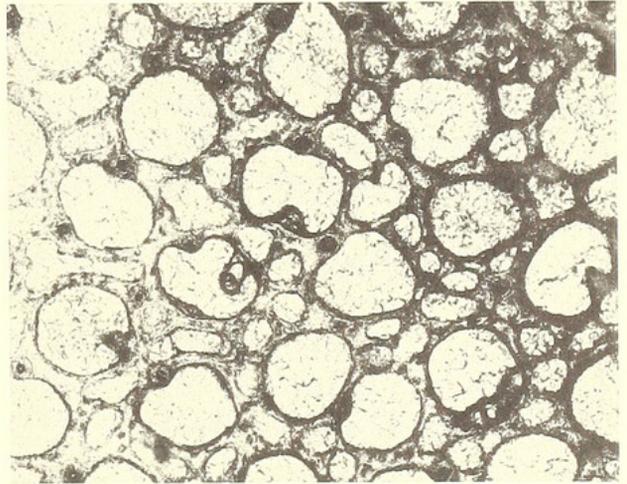
1



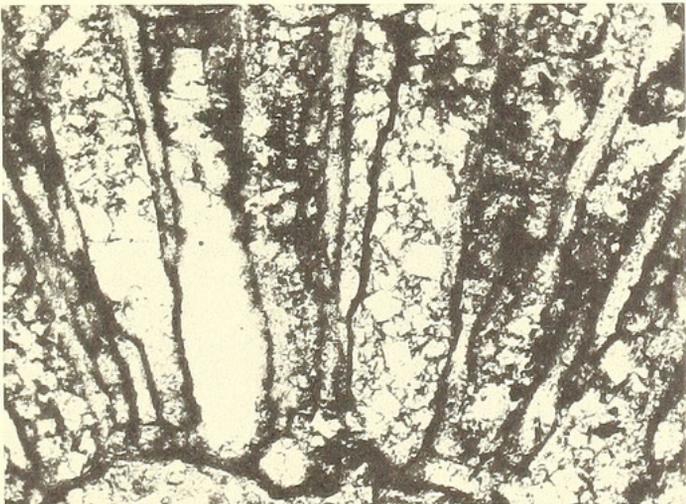
2



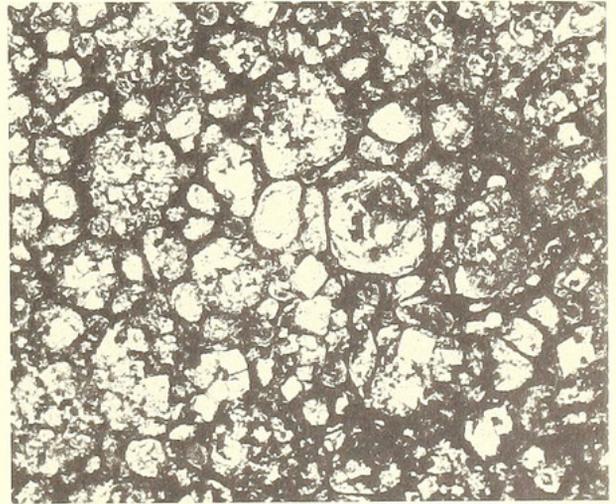
3



4



5



6

which there are, in the type species, from four to seven round the orifice of each tube. The interstitial tubes are small, and of irregular shape; two or three rows occupy each intertubular space.

He noted that the species was Carboniferous (p. 154). Ulrich (1890, p. 425) stated:

When this genus was proposed I was acquainted with the type species, *Callopora punctata* Hall, only. Now by extending the limits, fifteen species are united under the name.

He suggested that more than one generic group might be included in the genus as he then defined it. The 15 species occurred in rocks of Upper Ordovician to Pennsylvanian age.

Since then many other species have been added. In 1965, Boardman drew my attention to the fact that the Devonian species of *Leioclema* were markedly different from the Carboniferous species. I examined the type material in the U.S. National Museum and realized that, with *Dyscritella* Girty 1910, it appeared to be related to such genera as *Rhombopora* Meek 1872 and other rhabdomesids which are normally placed in the order Cryptostomata.

I then examined the sectioned types of many species of *Leioclema* described by Ulrich, Bassler, Girty, and others which are housed in the U.S. National Museum collections. Those from Silurian and Helderbergian deposits formed a moderately tight group which probably also includes those from upper Ordovician rocks. These forms did not survive the Helderbergian and differ markedly from Devonian and Carboniferous species.

Vinassa de Regni (1920) proposed a new type species for *Leioclema*, the Silurian *L. explanatum* Bassler, and suggested a new genus *Leioclemina*, based on *L. ramulosum* Bassler, for species with few or no diaphragms. The first suggestion is invalid since Ulrich's type species exists and is well known. The diagnosis of *Leioclemina* precludes this genus from embracing the many common typical Silurian species, and appears to be quite unnecessary.

I therefore propose the genus *Asperopora* based on *Callopora aspera* Hall, *Leioclema asperum* (Hall) Bassler, for the Silurian species.

Diagnosis. Zoaria incrusting, massive or ramose; zooecial walls relatively thick; mesopores numerous, sometimes cystose; acanthopores large, with clear axes, commonly deep-seated and inflecting the apertures, which may become petalloid; diaphragms few to many, particularly in mesopores.

The species I have examined which belong to this genus are:

<i>Leioclema asperum</i> (Hall)	Silurian: Niagaran and Wenlockian
<i>Leioclema concinctum</i> Bassler	„ „
<i>Leioclema densiporum</i> Owen	„ Wenlockian
<i>Leioclema explanatum</i> Bassler	„ Niagaran and Ludlovian
<i>Leioclema globulare</i> Bassler	„ „
<i>Leioclema halloporoides</i> Owen	„ Ludlovian
<i>Leioclema inornatum</i> Bassler	„ Waldron Shale
<i>Leioclema ludlovensis</i> Owen	„ Ludlovian
<i>Leioclema multiporum</i> Bassler	„ Niagaran and Wenlockian
<i>Leioclema pulchellum</i> Bassler	Devonian: Helderbergian
<i>Leioclema ramosum</i> Owen	Silurian: Wenlockian
<i>Leioclema ramulosum</i> Bassler	„ Niagaran
<i>Leioclema subramosum</i> Ulrich and Bassler	Devonian: Helderbergian
<i>Leioclema variaporum</i> Billings	Silurian

Asperopora aspera (Hall)

Plate 115, figs. 3-6

- 1852 *Callopora aspera* Hall, p. 147, pl. 40.
 1884 *Fistulipora ludensis* Nicholson, p. 120.
 1890 *Leioclema asperum* (Hall); Ulrich, p. 425.
 1900 *Lioclema asperum* (Hall); Nickles and Bassler, p. 302.
 1906 *Lioclema asperum* (Hall); Bassler, p. 32, pl. 11, figs. 1-3; pl. 24, figs. 14-16.
 1965 *Leioclema asperum* (Hall); Owen, p. 106, pl. 3, figs. 5, 6.

Material. LL3221, 3222, 3223, 3223 A, B.

Description. Zoaria incrusting to massive, often layered. Under certain circumstances very large specimens may occur. No. 564 of the Holcroft Collection, Birmingham, completely covers upper and side surfaces of *Heliolites* sp., extending for 30 mm. over one side of the base. Total size of specimen is 114 × 105 mm. diameter, 59 mm. high. Overlap on to lower surface on one side suggests coral was already dead and had been dislodged and tilted. Most other zooecia examined have been of much smaller size.

Slightly raised monticules containing zooecia of somewhat larger than normal size are visible on careful examination. Spines marking large acanthopores are also seen on unworn surfaces.

In longitudinal section, moderately thin-walled zooecia lie horizontally along epitheca in short endozone and turn at right angles into broad exozone, where walls are thicker, sometimes slightly beaded, and many mesopores separate zooecia. Large acanthopores occur throughout exozone and protrude as spines. Zooecial diaphragms few, but those in mesopores are about a tube width apart.

In tangential sections, circular or oval apertures are completely separated by mesopores and inflected by large, axially clear acanthopores, which are also associated with mesopores. Structure of wall not apparent. Dimensions of zooecia, etc., as in Owen (1965, p. 106).

Remarks. The species is relatively common in the Niagara region and in the Wenlock Limestone of Dudley and Wenlock Edge. In both, the spiny acanthopores are a marked feature of unworn specimens. The size of apertures is almost identical, as is the size and disposition of both mesopores and acanthopores. Walls appear to be somewhat thicker in the British specimens and diaphragms are more numerous but these features were probably linked with environmental conditions, and I have no doubt that the species is the same in both localities.

Needless to say such large zoaria have not escaped notice in Britain and have been described under the name of *Fistulipora ludensis* Nicholson. There is an undoubted similarity of appearance between the mesopores of this species and some fistuliporid cystopores, though the general structure is typically trepostomatous. Further, the numerous large acanthopores, noted and figured by Nicholson (1884, p. 120) are quite distinctive.

Asperopora multipora (Bassler)

Plate 116, figs. 1, 2

- 1906 *Lioclema multiporum* Bassler, p. 34, pl. 11, figs. 4-6; pl. 23, fig. 18; pl. 27, fig. 20.

Material. LL3224.



Owen, David E . 1969. "Wenlockian bryozoa from Dudley, Niagara, and Gotland and their palaeogeographic implications." *Palaeontology* 12, 621–636.

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