

Upper Ordovician Bryozoans from Ojl Myr, Gotland, Sweden

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A revision is given of the bryozoan fauna described by Wiman (1901), from a series of glacial erratic boulders found in Ojl Myr, Gotland, Sweden. The fauna is of Late Ordovician age, and correlates well with the Porkuni Stage in Estonia, probably most closely with its younger part. Twenty-five species are described, eight of them new: *Ceramopora hennigi*, *Ceramopora corniforme*, *Bactropora solida*, *Eridotrypa peculiare*, *Arcanopora (?) wimani*, *Ptilodichtya irregularis*, *Cyclophaenopora minor* and *Cyclophaenopora annulata*. A new species, *Cyclophaenopora robusta*, has been made on well preserved material, from the Middle Ordovician of Sweden. A new genus, *Cyclophaenopora*, and a new family, Nematotrypidae, have been erected. A discussion of the classification of Ordovician bryozoans is given and a provisional scheme suggested, based on the observations on both the Ojl Myr material, and well preserved material from the Ordovician and Silurian of other areas. The cryptostomes are divided according to the three main units used by Astrova & Morozova (1956), but because this classification is largely artificial, each unit is subdivided into a central group, assumed to be genetically related, and other forms (the unit *incertae sedis*), which are placed in the unit according to external morphology and convention. The general chapters include discussions on the budding pattern as a possible aid in classification, and a description of various types of zoecial specialisations and zoarial appendages, some of which may be related to reproduction. The available evidence points to a relationship of the cryptostomes with the other stenolaematous groups. The anatomy of the peculiar jointed base of the Ptilodichtyidae has been studied, and a functional anatomical explanation is given. A review of the occurrence of phosphatic bodies in Ordovician and Silurian bryozoans is given, based in part on the Ojl Myr material, and studies of other material. The physiological importance of the various phosphatic bodies is also discussed. A discussion is given on the use of zoarial form in early Palaeozoic bryozoans for palaeoecological analysis. In spite of the poor preservation of histological detail, the shapes of the colonies are often well preserved, and can be studied free of sediment and post-depositional deformation. The Ojl Myr fauna is used as an example of an analysis of this type; it is concluded that it lived in quiet water, on a soft bottom, perhaps within the photic zone.

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Contents

Abstract	1	<i>Bactropora solida</i> sp. nov.	6
Introduction	2	Family Monticuliporidae	8
Material	2	<i>Homotrypella</i> sp. a.	8
Previous Work	3	<i>Homotrypella</i> sp. b.	8
Methods of Study	3	<i>Orbignyella (?) expansa baltica</i> (Bassler)	10
Acknowledgements	4	Family Halloporidae	10
Description of Fossils	4	<i>Hallopora elegantula</i> (Hall)	10
Class Stenolaemata	4	Family Batostomellidae	11
Order Cyclostomata	4	<i>Lioclema (?) sp.</i>	11
Fam. indet. gen. et sp. indet.	4	<i>Eridotrypa peculiare</i> sp. nov.	11
Order Cystoporata	4	Indeterminable trepostomateous bryozoans ...	12
Family Ceramoporidae	4	Suborder Cryptostomata	12
<i>Ceramopora hennigi</i> sp. nov.	4	Fenestelloidea <i>incertae sedis</i>	13
<i>Ceramopora corniforme</i> sp. nov.	5	<i>Enallopora oeilensis</i> (Wiman)	13
<i>Ceramopora</i> sp.	6	Family Phylloporinidae	15
Order Trepostomata	6	<i>Chasmatopora</i> sp.	16
Family Bactroporidae	6	Fenestelloidea <i>sensu stricto</i>	16

<i>Thamniscus (?) orosus</i> Wiman	16
Nomenclature of some feather-branched bryozoans referred to <i>Glauchonome</i>	17
<i>Arcanopora plumula</i> (Wiman)	22
<i>Arcanopora (?) wimani</i> sp. nov.	23
Superfamily Ptilodichtyoidea	25
Ptilodichtyoidea <i>incertae sedis</i>	25
<i>Stictopora (?)</i> sp.	25
<i>Pachydichtya bifurcata</i> (Hall)	27
<i>Pachydichtya borkholmensis</i> (Wiman)	28
Ptilodichtyoidea <i>sensu stricto</i>	28
<i>Ptilodichtya</i> sp.	30
<i>Ptilodichtya irregularis</i> sp. nov.	30
<i>Ptilodichtya</i> cf. <i>nitidula</i> Billings	30

<i>Graptodichtya perelegans</i> (Ulrich)	31
Superfamily Rhabdomesonacea	34
Nematotrypidae fam. nov.	34
<i>Cyclophaenopora robusta</i> sp. nov.	36
<i>Cyclophaenopora minor</i> sp. nov.	36
<i>Cyclophaenopora annulata</i> sp. nov.	37
General remarks	37
Budding and classification	40
Specialised zoecia and zoarial appendices	48
The articulated base of the ptilodichtyonidae	54
Phosphatic bodies in bryozoans	58
Palaeoecology of the Ojl Myr fauna	62
References	

1. Introduction

This paper is a revision of the description of Upper Ordovician, silicified bryozoans from Ojl Myr (formerly Öjle Myr) given by Wiman (1901). The project was suggested to the author by Professor I. Hessland, Stockholm (then Uppsala) early in 1948, and the initial work was done at the Swedish Museum of Natural History (Palaeozoology Section) during 1948–1950. The first edition of the manuscript was finished in 1950, but was, for a number of reasons, not printed. Work on the project, and revised editions of the manuscript were made during the years 1950–65 in Oslo, and from 1965 on in Aarhus. Copies of the various versions of manuscript have been circulated among colleagues, and this has in many cases resulted in changes and improvements, (cf. Acknowledgements). The descriptive part has not been much changed, but the general parts have evolved considerably during the long time of preparation. The earlier version contained rather voluminous taxonomic and nomenclatorial discussions, which have been dropped, as these would be better, and more appropriate in the forthcoming revision of the bryozoan volume(s) of the Treatise on Invertebrate Paleontology. Only a chapter on the nomenclature of the species referred to "*Glauchonome*" Goldfuss has been retained.

Some of the ideas presented are now considerably less radical than they would have appeared in 1950. The idea that the cryptostomes – in spite of their resemblance to the cheilostomes in budding pattern – are more related to the trepostomes and cyclostomes (in Borg's group *Stenolaemata*), is now generally accepted (cf. Ryland, 1970). The method of using functional morphology and the colonial shape of bryozoans for a palaeoecological analysis is also much less novel than in 1950.

It is the author's hope that the results may be of some interest, at least as a demonstration of the

possibilities of palaeoecological and systematic studies on silicified bryozoan faunas.

2. Material

The Ojl Myr material was collected from some 85 limestone boulders found in a ditch at Ojl Myr in Gotland. The boulders are glacial erratics, and probably form a "train" of boulders resulting from the disintegration of a large ice-transported block of Upper Ordovician limestone.

The fossils are usually silicified; they were freed from the matrix by means of hydrochloric acid (cf. Wiman 1901). All the specimens are labelled with the boulder number, but since no definite horizon can be discerned among the boulders, reference is not made to these numbers in the descriptions, except for identification purposes.

The material of Ojl Myr described in this paper, is kept in the Paleontologiska Institutionen, Uppsala, as also the material from Porkuni, Estonia introduced for comparison. The material from the Silurian of Gotland (of *Phaenopora lindstroemi* and other species) is kept at Naturhistoriska Riksmuseet, Stockholm (Palaeozoologiska Sektionen). The Middle Ordovician bryozoans partly belong to that organization (i.a. the holotype of *Cyclophaenopora robusta* gen. et sp. nov.) and partly to Paleontologisk Museum, Oslo. Some foreign (extra-Scandinavian) Silurian specimens belonging to the two last mentioned institutions are also mentioned in this paper.

Specimens belonging to Paleontologiska Institutionen, Uppsala, have four digit numbers starting with 1001 prefixed Bz, those belonging to Naturhistoriska Riksmuseet have numbers with the prefix By, and the ones belonging to Paleontologisk Museum, Oslo are prefixed PMO.

3. Previous Work

In his paper on the Ojl Myr fauna, Wiman (1901) described six species of bryozoans. His figures are good as to the external appearance of the specimens, but his descriptions are partly incomplete. Wiman did not discuss the generic position of the species.

The six species originally described, are approximately one fourth of number of species now known. They comprise, however, about 85 % of the total number of specimens which have been collected.

Bassler (1911) redescribed some of the Ojl Myr bryozoans based on the figures and descriptions of Wiman. He corrected the names of some species, and made notes on their occurrence in other areas. However, studies in connection with this paper have shown that some of Wiman's figures and descriptions are incomplete, which reduces the value of Bassler's observations.

There are numerous later references to the Ojl Myr material, but no original work has been done on it since Wiman's day. Männil (1958, 1959, 1960, 1961 and 1966) referred to the age and stratigraphic distribution of the Ojl Myr material in his studies of the Estonian Ordovician bryozoans, and Kiepur (1962) has described similar material from erratic boulders in Poland. Eisenach (1968) refers briefly to the material, and it has also been mentioned by Brood (1978). Ross (1966) described a related (in age and preservation) fauna from Ireland, without mention of the Ojl Myr material. Schallreuter (1975 and others) have described ostracodes from "Öjle Myr Boulders". It should be noted that this term includes generally all Ordovician flints (cherts) found in Quaternary beds on Gotland. Although there can be little doubt that the material is of the same general age and provenance as the material described here, the term used by Schallreuter is considerably wider than that used in this paper. The Ordovician flints on Gotland are widespread (cf. Laufeld, 1971), and most of them probably come from the submarine exposures of Upper Ordovician (Porkuni age) beds to the immediate north of the island. There are also possibilities that some of the material came from the submarine exposures of Middle and Upper Ordovician carbonates in the Bay of Bothnia (Veltheim, 1962).

4. Methods of study

Silicified bryozoans, such as the Ojl Myr specimens, are generally not very suitable for detailed studies. Usually only the external features can be examined, whereas the internal structures are generally completely destroyed.

The author's experience with the Ojl Myr material and other silicified bryozoans is, that in most cases, only the surface layers of the fossils are silicified. In these specimens it is of no use to attempt to study the internal structures, since the fossils are merely hollow, empty coatings. In other cases, especially among the larger forms, the silicification is not complete in the outer layers, and therefore it is impossible to study the surface. In other instances, the specimen are replaced by globular siliceous masses which have destroyed all structures, external as internal. These specimens probably represent the last stage in the process of silicification.

It took the author considerable time to find specimens from which acceptable thin sections could be made, but after having studied various types of silicification, some intermediate specimens were eventually found, where more of the bryozoan calcareous tissue was silicified without being transformed into globular masses. In a few cases, the cavities of the specimens were filled with a clear siliceous matter that had not destroyed the internal structures, which were surprisingly well preserved in these few specimens.

The initial method for preparation of thin sections was rather complicated, as the cavities of the specimens had to be filled with a solid medium in order to protect the very delicate and fragile internal walls during grinding. At first, this was done by dropping the specimens into a solution of canada balsam (or a similar substance) in much xylene. Then the air was evacuated from the specimens, and they and the liquid were placed in a thermostat at a temperature just below the boiling point of the xylene. In 2 or 3 days the canada balsam was completely hardened, and the specimens were orientated and ground in blocks of canada balsam.

However, it soon became evident that this complicated procedure was unnecessary in most cases. With small specimens it was sufficient to place them on a glass slide, cover them with liquid canada balsam and heat slowly, until the canada balsam had the required hardness for making thin sections. The specimens were then sufficiently penetrated by the balsam to support the structures during the grinding, even if there usually were some gas bubbles. The specimens were orientated under a binocular microscope before the balsam hardened, and were ground down with the fine carborundum powder on a glass plate until the desired surface was obtained. Then the balsam was reheated, the specimens turned over with the ground surface down against the glass slide, and ground down until the section was clearly translucent (at appr. 40–50 μ). Attempts were made to use various plastics as embedding media, but most of them appear to have elastic properties which

make the fragile silicified walls break under stress. Cracks often appeared, especially with machine grinding, and in the end, a synthetic "canada balsam" was used as the routine embedding medium.

The non-silicified specimens introduced for comparison were studied in the ordinary manner, with thin sections and dry peels.

5. Acknowledgements

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The directors of several museums should be thanked, not only for their willingness to supply material, both types and comparatives, but especially for their great patience in extending loans over a very long period of time. This includes especially Professor G. Säve-Söderbergh (†), Professor P. Thorslund (†) and Professor R.A. Reymont (Uppsala), Professor E. Stensiö (†), Professor E. Jarvik, Professor T. Ørvig and Professor V. Jaanusson (Stockholm), Professor A. Heintz (†) and Professor G. Henningsmoen (Oslo).

Due to the kindness of Mr. A.G. Brighton of the Sedgwick Museum, Cambridge, England, the author has been able to compare the Ojl Myr bryozoans to similar British forms.

The final editions of the manuscript were typed by G. Grønlund. The drawings were made by A-M. Graversen, and the language was revised by M. Szegenda.

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6. Description of Fossils

The classification used in this paper generally follows Ryland (1970). The discussion on the classifica-

tion is found in the chapter "Budding and classification" under General Remarks.

CLASS STENOLAEMATA BORG

Order Cyclostomata Busk 1852

Familia indet.

Gen. et sp. indet.

Plate 1, fig. 6.

Material. One specimen from Ojl Myr. (No. PM Bz 1022).

Description. The encrusting zoarium is of an irregular shape, possibly reflecting the form of the object upon which the bryozoan grew. It is 10 mm in largest dimension. The base is epitheated. The zooecia are long, tubular and without lunaria. There are no real mesopores. The arrangement of the zooecia is irregular, the zoecial tubes are partly free in the same way as in *Hederella*, but differ from that genus in having an epitheated base. The zoecial tubes are elevated at the apertures, which are circular, with a small slit. The diameter of the apertures perpendicular to the slits is somewhat variable, between 0.15 mm and 0.18 mm. The area between the zoecial tubes is covered with a cryptocystlike membrane with a great number of irregularly distributed small pores.

Remarks. This specimen is unlike any Palaeozoic bryozoan seen by the author. It has a striking resemblance to certain recent incrusting cyclostomate bryozoans, both as to the development of a calcified (now silicified) cryptocyst, and as to the shape and the way in which the zoecial tubes are placed. The specimen resembles species of *Diplosolen*, though of course the existence of any relationship between them cannot be proved. This may indicate that cyclostomate bryozoans, which at least externally resemble recent ones, were developed as early as in the Ordovician. This species has not been formally named, because of the small amount of material available, and its apparently isolated position. It may be that some of the remarkable features, such as the supposed calcified cryptocyst is a silicification artefact, but this has to be solved on the basis of better material.

Order Cystoporata

Family CERAMOPORIDAE Ulrich 1882

Ceramopora hennigi sp. nov.

Plate 1, fig. 8.

Material. 11 specimens from Ojl Myr.

Type data: The holotype is nr. bz 1001, from boulder 74, Ojl Myr, figured on plate 1, fig. 8.

Diagnosis. *Ceramopora* species without spongiöse base, and with comparatively large, elongate apertures. The mesopores are arranged in semi-radial rows from a large central maculum, and frequent perforations in the walls between the mesopores, and the zooecia and the mesopores, but not in the walls between the zooecia.

Description. Incrusting zoarium with concentrically wrinkled epitec. Largest diameter observed, about 8 mm. Only one center of growth is found in each zoarium, but this may be due to the small size of the colonies.

The zooecia are elliptical to pyriform in cross section. Their width is variable, from 0.37 to 0.45 mm. The observed length of the zooecial apertures varies because of the angle towards the surface. The centrally placed zooecia have more elongate apertures than the marginal ones, which are more circular. The lunaria, which rarely are well preserved, are high and pointed and do not protrude into the lumen of the zooecia. The mesopores are specially numerous in the central, oldest part of the zoarium, where they are arranged in semi-radial rows. The mesopores are comparatively large, and irregular in cross section. The walls show the typical *Ceramopora* perforations, which can easily be seen as the specimen are free from matrix, and the internal features can be studied through the apertures. The perforations in the wall are arranged in regular rows, and are only found in the wall between a zooecium and a mesopore, or between mesopores, never in the walls between two zooecia. The perforations in *C. hennigi* are circular to rounded quadrangular. In some cases, the perforations are so numerous that the perforated walls are reduced to a more or less regular system of ribs. No diaphragms has been observed in the zooecia.

Remarks: Because of the lack of diaphragms, the shape of the lunaria and the perforated walls, this species probably belongs in *Ceramopora*, as defined by Utgaard (1969). According to this author, the spongiöse base, which is absent in *C. hennigi*, cannot longer be regarded as a generic criterion, in fact not even a specific one. *C. hennigi* appears to be closely related to *C. niagarensis*, the type species (from the Silurian of U.S.A.), and *C. niagarensis germana* Bassler (*in* Twenhofel, 1928) (from the lower Silurian of Anticosti Island, Canada), but differs from these forms in the size of the zooecial apertures, the arrangement of the mesopores, and especially in the perforations of the walls.

Ceramopora corniforme sp. nov.

Plate 1, figs. 4–5.

Material. One complete specimen from the Porkuni Stage, Porkuni, Estonia.

Type data. The holotype, specimen Bz 1002, figured on pl. 1, fig. 4 och 5, is from the Porkuni Stage, Estonia.

Diagnosis. *Ceramopora* species with zoaria like an irregular spiral. It has small, flat expansions with a few zooecia with high, pointed lunaria.

Description. Zoarium with epithecated base. Instead of being incrusting, this species grows upwards in a spiral, expanding at different levels to form "platforms", each of them like a small zoarium, which are about 4 mm in diameter. The zooecia are arranged semiradially from a macula-like centre on the "platforms". The zooecia are irregular in shape, and from 0.44 to 0.63 in diameter. The lunaria are very high and prominent. There are only a few mesopores. In the central part of each cluster of zooecia, the walls are strongly perforated, but at the lateral margin, they are more coherent. No thin sections have been made, but judging from what can be seen inside the zooecia, there are no diaphragms, at least not in the upper parts. The walls are perforated, but not to the same extent as in *C. hennigi* and *C. sp.* The upper part of the holotype is broken away, so that the figures only show the lower two thirds of the original specimen.

Remarks. This peculiar type of growth has not yet been described among ceramoporids. It might be an adaption to life on a soft bottom, since the vertical direction of growth of this type of zoarium both will prevent sinking into the sediment as well as burial by rapid sedimentation. The severe modification of the ordinary zoarial type, the arrangement of the zooecia in small, macula-like spots placed above one another, is certainly a result of the manner of growth. Similar zoarial shapes have been observed by the author in trepostome bryozoans and in living lichenoporoids and cheilostomes, all of which appear to have lived on a soft bottom. Other spiral, upright zoarial types, such as those found in *Archimedes* and *Retiflustra* tend to increase the active area of the colony, rather than to compensate for the sedimentation rate.

Under these circumstances, there may be doubt as to whether it is justified to make a new species of a single specimen. In this case, however, the changes are so important, that even if the specimen is only a simple adaptional form, genetically close to or identical with an ordinary, incrusting species, it will be convenient to have a specific name for it, since it will be almost impossible to trace the "parent species".

Ceramopora sp.

Plate 1, fig. 7.

Material. One fragmentary specimen from Ojl Myr (Boulder 73).

Description. The specimen available is a fragment with largest dimension about 6 mm. It appear to be part of a considerably larger zoarium. The zooecia are difficult to measure precisely, but are from 0.25 to 0.36 mm in greatest diameter. The characteristic feature of this specimen, is the two-winged lunarium. Both sides of the lunarium are more strongly developed than the central part. This structure does not resemble the lunarium of *Crepipora*, since there are no spinose terminations directed inwards. The terminations in this specimen are blunt and directed upwards, resembling the lunaria of *Anolotichia* and *Papillalunaria* (cf. Utgaard, 1969, pl. 51, Figs. 1b–c). These genera, however, do not have perforated walls.

The structure of the interzooecial walls is unusual. All the walls, both between the mesopores and between the zooecia, are very much reduced, so that the whole zoarium consists of a delicate framework of fine ribs. Only the lowest parts of the walls are not so much reduced. The mesopores are small and evenly distributed. The basal membrane is not preserved in this specimen.

Remarks. This specimen does not fit into any described species of *Ceramopora* or other cystoporate for that matter, but the material is too limited for a more definite assignment. It was originally taken for a very badly calcified specimen of *Ceramopora hennigi*, but this is hardly possible because of the significantly different size of the zooecial apertures, the different perforations of the walls and the special lunaria.

Order Trepostomata

Family BACTROPORIDAE Simpson 1897

The author has redefined the old family Bactroporidae Simpson, as it is convenient to have a group for the trepostomateous bryozoans with pointed base. The new definition and the discussion of the family, will be found under: "General remarks".

Genus BACTROPORA Hall and Simpson 1887

Bactropora solida sp. nov.

Plate 2, fig. 4; Text-fig. 1A–B.

Material. Five specimens, two of which have a pointed base.

Type data. The holotype, specimen nr. Bz 1008, figured on pl. 2, fig. 4 and textfig. 1. A–B, is from Ojl Myr, Boulder 7.

Diagnosis. Comparatively small *Bactropora* species with very strong acanthopores, indentating the irregularly arranged zooecia. There is no visible surface ornamentation except in the basal part.

Description. Thin, ramose unbranching zoaria with pointed base. The branches are 1.1–1.2 mm. in diameter, except near the pointed base, where they are thinner. The basal parts are heavily calcified, and show some faint longitudinal lines. Apart from this, there is no external sculpture on the specimens. The zooecia are placed in indistinct longitudinal rows. The zooecial apertures are elliptical and slightly indentated by fairly large acanthopores. The long diameter of the zooecia is 0.20 to 0.25 mm. The acanthopores have a diffuse outer boundary, and a central tube or stem with a diameter of about 0.025–0.03 mm. The number of acanthopores is approximately four times that of the zooecia. No mesopores, hemiphragms and diaphragms have been observed. The pointed base has a cone-ring in the oldest specimen. The budding pattern is that found in typical ramose trepostomes and differs fundamentally from the sectorial pattern found in most rhabdomesids.

Remarks. This species is the oldest of the genus, and links *Bactropora* to *Lioclemella*. It could in fact have been a gerontic *Lioclemella*, where the mesopores have been completely obliterated by deposition of calcareous tissue, but then the younger parts would have shown traces of mesopores. This is, however, not the case. This species is therefore believed to be a real *Bactropora*. It is not recorded from other localities than Ojl Myr.

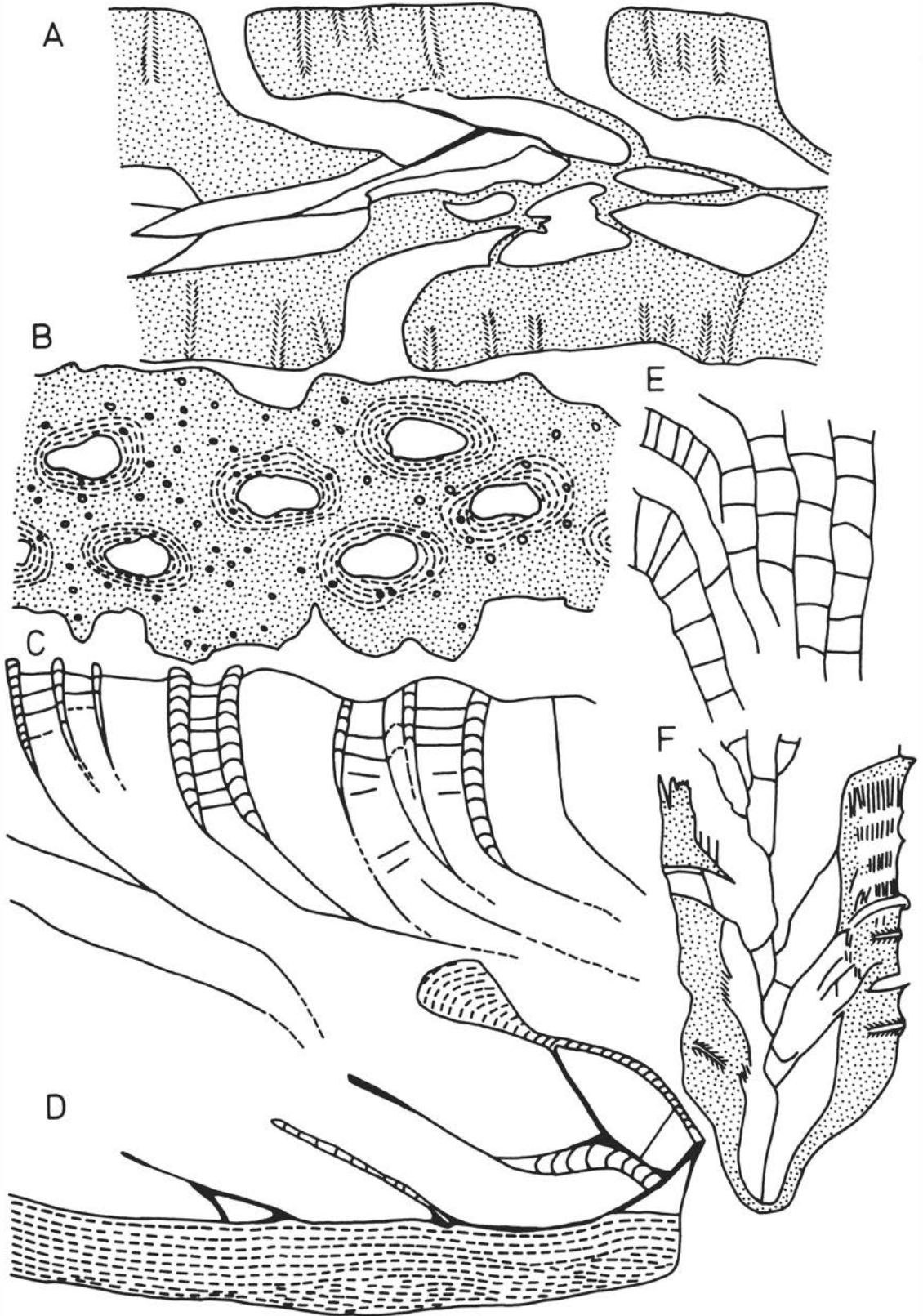
Three species have previously been described as belonging to this genus. Two of them are Devonian, of which one is the type species *B. granistriata* (Hall). The third, *B. simplex* Ulrich (1890, p. 633,

Fig. 1. *Bactropora* and *Lioclema*. All figures 22x.

A–B. *Bactropora solida* sp.n. A. Vertical section. B. Tangential section showing the thick peristomes of the zooecia, and the distribution of the acanthopores. From the holotype, specimen Bz 1008, cf. plate 2, fig. 4., from Ojl Myr, boulder nr. 7.

C–D. *Lioclema* (?) sp. C. Vertical section of the basal part of the zoarium, showing tabulated mesopores. The structures in the central part of the stem is obscured diagenetically. D. Vertical section of one of the monofoliate branches. The peripheral part of the celluliferous side of the branch is badly silicified, and the interzooecial walls are therefore lost in all but one zooecium (which can be seen to the right). From the specimens figured on plate 2, figs. 2, 3 and 5, no. Bz 1007, from boulder 29, Ojl Myr.

E–F. *Lioclema spineum ramosum* Bekker. E. Vertical section of the upper part of the zoarium. F. Vertical section of the basal part of the same zoarium. Note the calcifications of the mesopores and the structure of the base, different from that in *Phaenopora lindstroemi* (textfig. 11D–E and 13). From the Middle Ordovician Kukruse Formation in Estonia (Redrawn from Bekker 1921, pl. 6, figs. 16, 18).



pl. LXX, fig. 14, pl. LXXI, fig. 6) is from the Carboniferous, and is the only one of the three where the internal structures are known. It differs from *B. solida* in the zoarium being slightly annulated and having stellate acanthopores which do not indentate the zoecia. The structures of the acanthopores, may, however, easily be due to re-crystallization. Similar features are found in many badly preserved specimens of acanthopore-bearing species. As for the two other species, these seem to have the same internal structures, judging from Ulrich's figure (1890, pl. LXXI, fig. 6A).

Family MONTICULIPORIDAE Nicholson 1881.

Genus HOMOTRYPELLA Ulrich 1886.

Two species, which probably belong to this genus, are found in the Ojl Myr fauna. They are referred to *Homotrypella* and not to *Homotrypa*, mainly because of their numerous tabulated mesopores. Most species of *Homotrypella* are found in the Middle Ordovician (6 out of 8 acc. to Nickles and Bassler (1900)). With the diagnosis used here, however, also the Upper Ordovician *Homotrypa anticostiensis*, Bassler 1928, should be included in *Homotrypella*.

Homotrypella sp. a.

Plate 3, figs. 3–4; Text-fig. 2c.

Material. Six specimens from Ojl Myr, and five specimens from Porkuni.

Diagnosis. Small *Homotrypella* with short mature zone. Cystiphragms developed in the oldest part of the zoecia, and only one or two in each zoecium. Younger parts of zoaria like *Bythopora*.

Description. Zoarium consisting of thin ramose stems, 1.5–2.5 mm in diameter, with incrusting or discoidal base. The zoecial apertures are rounded polygonal, 0.16–0.23 mm in diameter, with some mesopores in between. The cystiphragms can be seen from the surface in some of the zoecia. The internal structures are comparatively well preserved. In the younger, upper part of the zoaria, the zoecia resemble *Bythopora*, as they have a very short mature zone and no cystiphragms. Only faint indica-

tions of acanthopores are seen in the tangential section, probably because of the short mature region. However, the surface of the well preserved specimens is spinose, indicating the presence of acanthopores.

Remarks. At first the species was believed to belong to *Bythopora*, but thin sections of the lower, old parts, of the zoaria showed that there were cystiphragms in almost every zoecium, but only one or two in each. This is probably due to the short mature zone, which is believed to be characteristic of this species. Usually a short mature zone in this type of bryozoan, indicates that they are quite young specimens, but in this case all the old specimens have the same feature, and it is improbable that all the specimens were killed at a young age, leaving no adults in this special locality. The base is incrusting, and in the specimens preserved, the basal zoecial apertures are obliterated by secondary calcareous deposits even in young colonies (pl. 3, fig. 4). This species is readily distinguished from all other members of the genus by its short mature zone, and by the small size of the zoecia.

It resembles *H. (?) ovalis* Ulrich 1893 (pl. XVIII, fig. 23, p. 231) but the mature zone is longer in that species.

The *Bythopora*-like younger parts of this species induces a note on the genus *Bythopora*. It is probable that at least some of the species referred to this genus are quite young specimens of other trepostomateous bryozoans. *Homotrypella* sp. a. would no doubt have been referred to *Bythopora* if the internal structure of the basal parts of the zoaria had not been known. The author does not suggest that all species of *Bythopora* are young individuals of other genera, but one must take this possibility into account when describing a species of this genus.

Homotrypella sp. a. is known from the Ojl Myr fauna and from Porkuni.

Homotrypella sp. b.

Plate 3, fig. 5; Text-fig. 2D–E.

Material. Twenty-one specimens from Ojl Myr, and some from Porkuni.

Diagnosis. *Homotrypella* with a few cystiphragms,

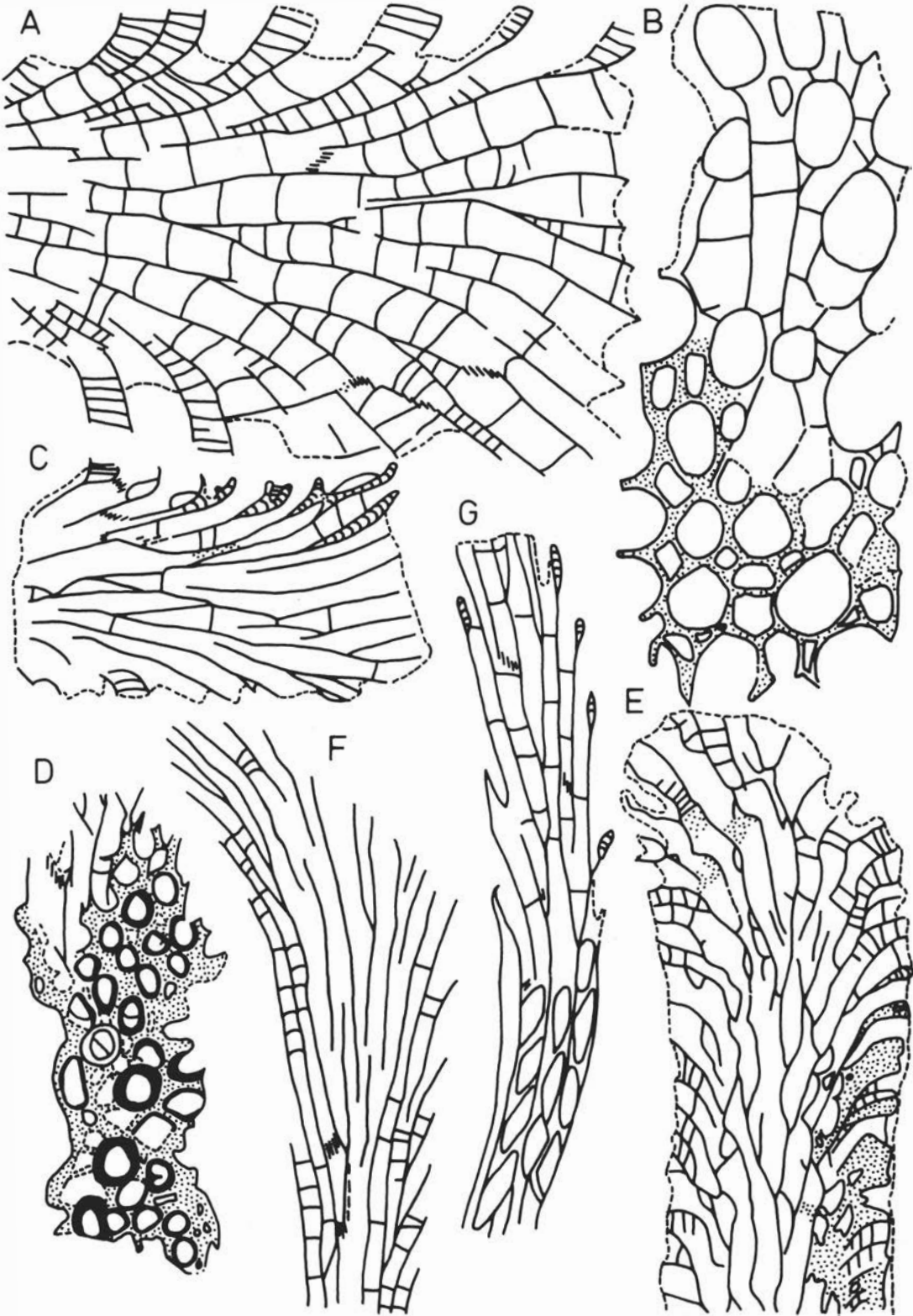
Fig. 2. *Hallopora*, *Homotrypella* and *Eridotrypa*. All figures 22 x.

A–B. *Hallopora elegantula* (Hall). A. Vertical section showing tabulation of zoecia and mesopores. B. Tangential section of the same specimen (Bz 1050). From boulder 27, Ojl Myr.

C. *Homotrypella* sp. a. Vertical section of a zoarium, showing only one cystiphragm in each zoecium. Specimen Bz 1051, from the Upper Ordovician Porkuni horizon at Porkuni, Estonia.

D–E. *Homotrypella* sp. b. D. Tangential section. E. Vertical section, showing cystiphragms in the deeper parts of the zoecia only. Specimen Bz 1052, from the Upper Ordovician Porkuni horizon, at Porkuni, Estonia.

F–G. *Eridotrypa peculiare* sp. n. F. Vertical section of an old specimen, the surface of which is corroded, so that the thickening of the mature part of the zoecia is absent. Specimen Bz 1053, from boulder 53, Ojl Myr. G. Combined vertical (upper part) and tangential (lower part) section of a young specimen, Bz 1054, from boulder 53, Ojl Myr.



mainly in the lowest portion of the mature part of the zooecia.

Description. Frequently branching ramose stems, about 1.5 mm in diameter. The base is missing in all specimens. Zooecia of irregular size, 0.11–0.22 mm in diameter, usually surrounded by closely tabulated mesopores. The zooecia themselves have few diaphragms, and the cystiphragms, one or two in each zooecium, are placed in the deepest part of the mature zone, just where the zooecia turn perpendicularly towards the surface.

Remarks. This species differs from *H. sp. a.* in the zooecia having a comparatively longer mature part, and in the deep position of the cystiphragms. It differs from most older species in always having a small number of cystiphragms.

It is found in Ojl Myr and Porkuni only.

Orbignyella (?) *expansa baltica* Bassler 1911
Plate 3, fig. 10.

Orbignyella expansa baltica new variety – Bassler 1911 p. 183–189; Textfig. 96.

Material. One complete specimen from Ojl Myr, (Boulder 6).

Description. Incrusting zoarium, about 7 mm broad and 1.5 mm thick. Epitheated base. The zooecia are angular, about 0.36 mm in longest dimension, in the central part, and considerably smaller towards the margin. Small acanthopores occur in the corners between the zooecia. Tabulae very few and curved. The interzooecial walls are comparatively thick, more like those of *O. germana* (Bassler, 1911, p. 182).

Remarks. This specimen differs from that described by Bassler only in having slightly thicker walls and an epitheated base. Both features are probably due to this specimen being older.

It is often difficult to find the cystiphragms in species belonging to Monticuliporidae. In many instances curved diaphragms are mistaken for cystiphragms, and the author believes that this has been the case with some species of *Orbignyella*. The real cystiphragms are fused to the zoecial wall only, or to the zoecial wall and another cystiphragm. A curved diaphragm, terminating on the next lower diaphragm, and not all around on the zoecial wall, cannot be termed a cystiphragm. It is a common feature in many species with closely tabulated zooecia. Bassler's (1911, textfig. 95), figures of *Orbignyella germana* is a very good example of this. In the *O. expansa baltica* the tabula are further apart, and therefore it has fewer "cystiphragms". The granulose wall structure in the latter species is probably due to bad preservation.

Consequently the Baltic species of *Orbignyella* (*germana* and *expansa baltica*) probably does not belong to the Prasopoidae, but possibly to the Batostomellidae.

However, no change has been made in the taxonomy, partly because of the limited and badly preserved material, and partly because it is not yet clear if only the Baltic species, or if the whole genus should be removed from the family.

Family HALLOPORIDAE (Ulrich 1890)
Bassler 1911

Genus HALLOPORA Bassler 1911

Hallopora elegantula (Hall)

Plate 3, figs. 1, 2, 6; Textfig. 2A–B.

References to this common, and often cited species can be found in Nickles & Bassler (1900, p. 188), Bassler (1911, p. 334) and McKinney (1975, p. 66). There is some doubt as to the nomenclature of the generic name (*Calopora* or *Hallopora*) cf. Singh (1970) and Ross (1970). In the author's opinion, this question will have to be solved by the ICZN.

Material. 101 specimens from Ojl Myr, and 4 from Porkuni.

Description. Zoaria consisting of irregularly branching, ramose stems, or crusts and hemispherical bodies. The two latter types probably represent young specimens. The stems are up to 3–4 mm in diameter. The zooecia are 0.29–0.4 mm in diameter, and the mesopores are from 0.29 mm to less than 0.10 mm in longest dimension. The internal structure corresponds well to that described by Bassler (1906), except for the mesopores not being so numerous in the specimens from Ojl Myr and Porkuni, as in the American ones. In most of the specimens, the surface is destroyed, but the central parts of the stems are often surprisingly well preserved.

Remarks. This species differs from those described by Brood (1978), *H. solbergensis*, *H. dalmani* and *H. multipora*, from the Upper Ordovician of mainland Sweden in having larger zoecial apertures, and larger and more numerous mesopores.

The species concept is not very well defined in the halloporids, and a modern revision may show that the present species differs from the typical, Silurian one.

H. elegantula and some other species of the genus have ornamented and centrally perforated opercula. They were figured by Ulrich (1882, pl. XI, fig. 6 and 6a, reproduced by Bassler (1906, pl. XVII, fig. 11–12), Bassler (1911, textfig. 210a and d), Bassler (1953, textfig. G74, la and lc) and Bassler

(1906, pl. XVII, fig. 16), reproduced by Bassler (1911, textfig. 210f) and Bassler (1953, textfig. G74, 1e).

Bassler (1953, p. G112) and earlier believed that the operculae developed into diaphragms during the growth of the zooecia. As seen from Ulrich's figures (1882, pl. XL, fig. 6a), the distance between the diaphragms is normally smaller than the distance from the last regular diaphragm to the operculum, which also often has a shape and curvature differing from the diaphragms. There are no opercula in the Ojl Myr material, but the author has studied this phenomenon in some well preserved Ordovician species of *Hallopora*. Here the opercula have a different histology from the diaphragms, and the contact to the zoecial wall is also quite different. The operculae appear to have been formed from the outside, presumable from a gymnocyst, and may be related to a complete or partial regeneration of the zooids. This structure is interesting, as shown by the recent study of Serpagli & Conti (1982), and it deserves further study, as it may throw some light on the gymnocyst structure and function in these bryozoans.

This long-ranging and cosmopolitan species is very common in the Ojl Myr fauna. The species is recorded from the Lower and Middle Silurian of North America, from the Wenlock Shales in England, from the Silurian of Gotland and from the Rakvere, Saaremoisa and Porkuni stages in Estonia (Bassler, 1911, p. 335 and Männil, 1959, p. 34.)

Family BATOSTOMELLIDAE Ulrich 1890

Genus LIOCLEMA Ulrich 1882

Lioclema (??) sp.

Plate 2, figs. 2, 3, 5; Textfig. 1C–D.

Material. One specimen from Ojl Myr, (Boulder 29).

Description. The lower part of this peculiar specimen consists of a coarse, ramose stem 2.6–3.0 mm in diameter, which suddenly is divided almost at right angles into five monofoliate branches, about 1.8–2.05 mm in longest diameter, oval in cross section, and with oval apertures, 0.31–0.44 mm long, and 0.22–0.31 mm wide, with the non-poriferous sides inwards. A flat cup-shaped hollow is formed at the point of the branching. The non-poriferous walls have no sculptures or pores. The poriferous surface is the same all over the zoarium, consisting of zooecia, surrounded by large acanthopores with a central pore or canal ab. 0.02 mm wide, clearly visible at the surface. The microscopic structure of the two types of branches turned out to be quite different. The main stem has long tubular

zooecia without diaphragms, wide acanthopores, and tabulated mesopores. The monofoliate branches have a *Rhombopora*-like appearance where the mesopores are obscured, and their place filled with massive tissue. The non-poriferous walls are built up of tissue histologically different from that of the rest of the zoarium, but the bad state of preservation of the specimens prevents a closer study.

Remarks. The importance of this specimen for the taxonomy is discussed under "Superfamily Rhadomesoidea", p. xxx. Since only the incomplete specimen with no base is available of this species, it is of course impossible to give a correct specific or even generic determination of it. If the base was pointed, it would have been referred to *Lioclema*, but it is doubtful whether this would have been correct, as the specimen represents a type of growth which is not covered by the current systematics. With the material available, it is very difficult to decide if the zoarial form is genotypically determined, or if it is accidental or pathological.

Genus ERIDOTRYPA Ulrich 1890

Eridotrypa peculiare sp. nov.

Plate 3, figs. 8–9; Textfig. 2F–G.

Type data: The holotype is the specimen figured on pl. 3, fig. 8–9. nr. Bz 1007 from boulder 29, Ojl Myr, Gotland.

Diagnosis. *Eridotrypa* species with thin, straight stems, branching regularly at nearly right angles. There is always a non-poriferous band on the surface of the zoarium.

Description. Zoarium which consists of very thin (0.9 mm in diameter), slender, ramose stems, branching at nearly right angles at regular interval quite far apart (about 3.0–3.8 mm in holotype). Usually the branches, which have the same diameter as the main stem, grow at right angles to one another. Very seldom two successive branches grow in the same direction. The zoarium is therefore extended in all three dimensions, and not in, or almost in one plane, like many other ramose bryozoans.

The base is incrusting, partly on irregular and partly on tubular objects, like most small species in the Ojl Myr fauna. The zoecial apertures – which are about 0.22–0.30 mm long and 0.15–0.16 mm wide – are not evenly scattered over the surface of the stems. There is always a non-poriferous band which is inconsistent both as to width and direction. The zoecial apertures are oblique, surrounded by a few acanthopores. In vertical sections, the zooecia are straight, not bent towards the surface of the

stems. The mature parts of the zooecia are very short with a few diaphragms.

Remarks. This species is easily distinguished from all other Eridotrypas by having a non-poriferous band. The fine, slender stems, and the typical way of branching, separates it from all other species in the Ojl Myr fauna. The colonial shape of this species is rather unusual. Ramose colonies normally are either dense, bushy three-dimensional, to give maximum resistance to water movement (Cheetham, Hayek & Thomsen 1980, 1981), or they are loosely branching, often in one plane, with the branches directed upwards (towards the light), indicating that they lived in deep, quiet water (Riedl 1966, Abel 1959). Most living forms with the colonial shape of this species are articulated cellariforms. *E. peculiare* is only recorded from Ojl Myr.

Indeterminable trepostomateous bryozoans

A number of indeterminable trepostomateous bryozoans are found in the Ojl Myr fauna, some of them forming irregular bodies, some hemisphaerical or nearly so. The silicification has not only destroyed the surface and the internal structures, but also the shape of the zoaria. Any attempt at determining these specimens would therefore be of no avail.

There are also two specimens of another indeterminable trepostomateous bryozoan in the material from Ojl Myr. They consist of monofoliate thin bifurcating branches (Pl. 3, fig. 7), and they resemble badly silicified specimens of *Thamniscus orosus*. However, they differ from that species in having gradually tapering zooecia. They have no tabula, mesopores or acanthopores, and the apertures are long and badly preserved. The specimens might also belong to an unknown cyclostomateous species, but the material is too badly preserved to permit closer determination.

Suborder Cryptostomata

Astrova & Morozova (1956) have suggested a subdivision of the Cryptostomata based mainly on colonial shape, and Ross (1960 a–c, 1962, 1964a and others) and Karklins (1968, 1969, 1970 and 1983) have proposed subdivisions of parts of the suborder based on microscopic wall structure.

Astrova & Morozova's superfamilies based on colonial shape (Fenestelloidea is based on the reticulate zoaria, Ptilodichtyoidea on bifoliate zoaria, and Rhabdomesoidea on ramose zoaria) are

probably all polyphyletic, but represent a convenient first approximation in the classification of the group, as all the three superfamilies appear to contain a central core of closely related forms.

The Fenestelloidea are centred around the nominal group, which is structurally distinct and probably closely related, have a characteristic microstructure of the skeleton as shown by the work of Taverner-Smith (1969a, 1975).

In the Ordovician and Early Silurian, there is a high structural diversity among forms which resembled the typical ones, but lack some of the characteristic structural traits. There are also some non-reticulate forms (like *Thamniscus*), which seemed to relate to the fenestellids structurally, without having the typical zoarial shape.

The ptilodichtyids – which the author would like to restrict to the bifoliate forms which have primary walls between the longitudinal rows of zooecia at least in the basal part of the wall – fall in several (at least three) subgroups, based on wall structure. These groups may have different origins, from separate groups of unspecialized monoserial steno-laematous bryozoans, perhaps through rhabdomesids, or the differentiation of wall structure may have taken place at the rhabdomesid stage.

There are also bifoliate forms which have consistently single interzoecial walls. They may have originated from two-dimensional incrusting forms. This type of colony is very common in all groups of bryozoans, and has in itself, little taxonomic value.

The Rhabdomesoidea have, in the author's opinion, a central group with radial, sectorial budding with one or more rows of zooecia in each sector. This type of budding may indicate an origin from monoserial forms, or it may have developed from ramose trepostomes. In several, apparently independent lines, a reduction of the number of sectors may have led to development of bifoliate colonies.

Besides the central group, the superfamily contains both highly specialized forms with a central axis consisting of a bundle of longitudinal tubes, and zoaria with a hollow axis. The latter type is a general one, which is found in nearly all groups of bryozoans, as an ecological form of normally incrusting zoaria. Unfortunately the nominal genus, *Rhabdomeson* belongs here.

Some of the structural and phylogenetic problems mentioned here are treated in more detail under General Remarks.

Since the silicified material from Ojl Myr does only give very little information on wall structure, a pragmatic classification is adopted here, based on that of Astrova & Morozova (1956), with the modification that the superfamilies are divided into the central part, the superfamily *sensu stricto*, which

is supposed to be – if not strictly monophyletic – at least closely related, and a "fringe", consisting of the groups which from colonial shape and original designation have been referred to it, but where structural evidence indicates that the resemblance is due either to simple homeomorphy, or an indication that they may be primitive, shortlived sister-groups of the superfamily *sensu stricto*. These marginal groups are referred to the superfamily as *incertae sedis*.

Fenestelloidea incertae sedis

Genus ENALLOPORA d'Orbigny 1849

The type species of this genus, *Gorgonia perantiqua* Hall 1847 is, like most of the types of d'Orbigny's Palaeozoic genera, not known in detail. This makes the diagnosis of the genus, transferred from the supposed synonym *Protocrisina* Ulrich 1889, somewhat uncertain. However, after having studied Hall's types of *Gorgonia perantiqua*, Bassler (1911, p. 72) presumed that this species is identical with, or at least congeneric with *Protocrisina exigua*, the type species of *Protocrisina*. His studies seem, however, to be based on the external features only, and the identity has therefore not been definitely proved. The species described below, is probably congeneric with *Protocrisina exigua*. A study of the internal structures of *Enallopora perantiqua*, will show if *Protocrisina* is a separate genus or not. Until then, all species in question can be included in *Enallopora*. These nomenclatorial and systematic problems have also been mentioned by Kieppura (1962, p. 393–4) and Ross (1966, pp. 119–120).

This genus (as *Protocrisina*) was regarded as a cyclostome by Bassler (1911) and earlier authors, and the species from Ojl Myr was also referred to *Crisinella*, a badly known genus of supposed cyclostome affinity by Wiman (1901). Toots (1952) showed that the genus was a cryptostome one, and this was also accepted by Bassler (1953), who referred it to the fenestellids. In view of the present knowledge of the structure of this group, it is highly doubtful if *Enallopora* can be regarded as a typical member. The variable zoarial shape, and especially the heterozoecia differs very much from the fenestellids, and it may be more related to some of the phylloporinids (see below).

Enallopora oeilensis (Wiman 1901)

Pl. 1, figs. 1–3; Textfig. 3A–D.

1901 *Crisinella oeilensis* sp. n. Wiman. p. 181, pl. 6, figs. 12–16.

1911 *Protocrisina exigua* (Ulrich), Bassler, p. 73, textfig. 17 (reproduced from Wiman 1901).

? 1962 *Enallopora exigua* (Ulrich). Kieppura, p. 394–5, pl. VI, figs. 1–2.

? 1966 *Enallopora* sp. Ross, p. 119–20, pl. 6, figs. 6–7.

Material. 28 specimens, all from Ojl Myr. The base is preserved in 7 specimens. The holotype, nr. Bz 1018, from boulder 17, the specimen figured by Wiman (1901, pl. 6, figs. 14–16), and in this paper, is badly damaged.

Description

Zoarium. The zoarium consists of thin, erect, frequently bifurcating branches growing from an incrusting base. Two types of branching are found in this species. In most specimens the branching is symmetrical, in one plane. In the other type, one of the branches is always much longer than the other at each bifurcation, and only this longer branch forks off into new branches. In this type, the zoarium forms a narrow steep spiral with small branches inwards. Five specimens of this type have been found (to 23 of the ordinary type). The five specimens are from three different boulders, and there are no specimens of the ordinary type in these boulders. The branching of the holotype is symmetrical.

Since, however, the zoarial growth may differ considerably within a bryozoan species, and the two types are quite indistinguishable in all other respects, I can see no reason for making a new species or subspecies of the spiral variant.

The distance between the bifurcations varies considerably, especially in the specimens with symmetrical branching. In the holotype the distance between the bifurcations is 3 to 6 mm, but generally it is much smaller, 1 mm or even less. Near the base, the distance is usually smaller than higher up in the zoarium.

The highest zoarium measured is 17 mm (the holotype), and still the base is not preserved in this specimen. All other specimens are considerably smaller.

The width of the branches is 0.75 mm (average) including the lateral apertures, and 0.43 (average) without them.

Zooecia. Two types of zooecia occur. The ordinary ones are arranged in four irregular rows with the zooecia placed alternatively. Two rows are frontal and two lateral. The lateral zooecia have comparatively wide apertures (0.21–0.23 mm in diameter). The frontal zooecia have less protruding and therefore smaller apertures (0.13–0.14 mm in diameter).

The other type of zooecia is smaller, and is found below the lateral zooecia, one for each of them.

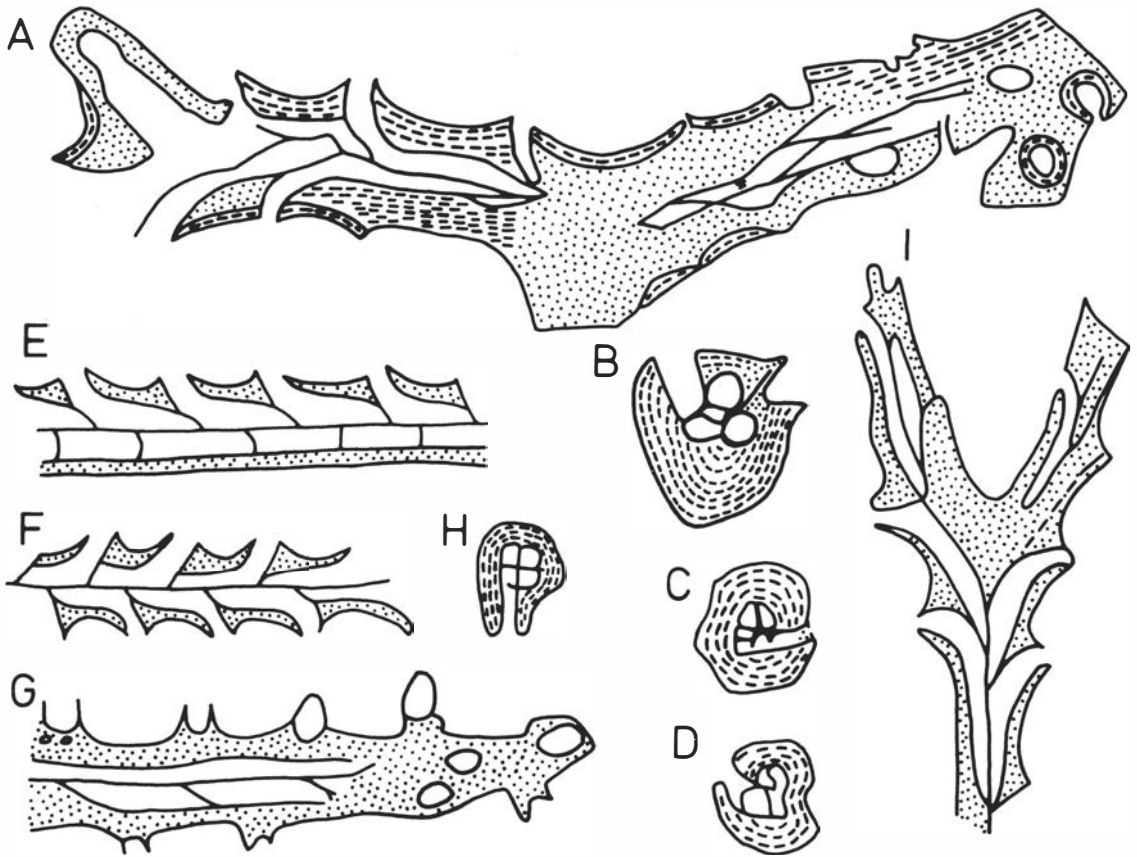


Fig. 3. *Enallopora*. All figures are magnified 22 times.

A–D. *Enallopora oeilensis* (Wiman) A. Oblique longitudinal section of a branch, showing both vertical and tangential views of this species. Specimen Bz 1055, from boulder 45, Ojl Myr. B. Cross section of a branch. Specimen Bz 1056, from boulder 58, Ojl Myr. C–D. Cross section of branches. Specimen Bz 1057 and 1058, from boulder 17, Ojl Myr. The three last figures (B–D) are the types of Wiman (1901, pl. 6, figs. 12–13). E–I. *Enallopora exigua* (Ulrich). (Redrawn from Ulrich 1890, pl. LIII, figs. 11, 11a, b, c, e). E. Vertical section F. "the same kind of sections as fig. I, taken from Trenton Falls, N.Y. specimens in which the zooecia are a little shorter than usual". G. "Portion of the same section when it passes just beneath the mouths of the dorsal row of cells". H. "Transverse section, showing the four rows of zooecia and the thickened outer walls". I. "A deep tangential section showing the tubes that open on the side of the branches throughout their length" (citations from Ulrich 1890, explanation to plate LIII).

They are not protruding and have rather narrow apertures (0.035–0.043 mm in diameter). Some small zooecia, which are found at the bottom of the bifurcations, have slightly wider apertures (0.055–0.065 mm in diameter).

Usually about seven large zooecia are found in 2 mm measuring longitudinally (approximately two zooecia in each row). Judging from the thin sections of this species (Textfig. 3 A–D), the zooecia rise from a central axis, and are arranged in longitudinal rows. The angular shape of the calcified frontal walls of the zooecia are of the cryptostomateous type of

structure. The small zooecia seem to bud directly from the lateral zooecia, like the mesopores of *Phaenopora*. They may correspond to the heterozooecia of the recent cyclostomateous bryozoans (Borg, 1926) or to the mesopores of the other cryptostomateous bryozoans.

No pores have been found on the reverse side of the zoarium. This may in some cases be due to the bad state of the preservation of the material, since this was the reason for no small zooecia being found in many of the specimens. However, pores have not been observed on the reverse side of even in

excellently preserved specimens. The pores on the reverse side in other species of *Enallopora*, *E. exigua* and *E. ulrichi*, are approximately the same size as the small zooecia of *E. oeilensis*, or larger. This indicates that the pores were not developed on the reverse side of *E. oeilensis*.

The base is always incrusting. In most specimens it is incomplete, but in well preserved ones, it is tubular. The bryozoans evidently grew upon cylindrical bodies, the diameter of which was about one mm.

In some specimens (three) there are also secondary attachments. They are like the base, but are placed higher up in the zoaria. The diameter of the tubes (cylindrical bodies) seem to be slightly smaller in the secondary attachments than in the base. No apertures are found in the incrusting parts of the attachments (see Pl. 1, fig. 3).

There is a fine irregular perforation, about 0.25 mm in diameter inside the base, just below the zoarium. This perforation may indicate that the presumably thin basal wall of the ancestrula has been broken.

Remarks. *E. oeilensis* differs from most other species of *Enallopora* in the regular position of the heterozooecia, and in that there are no pores on the reverse side. Similar features are found only in the Middle Ordovician *E. disposita* (Bekker, 1921, p. 40–41, pl. 8, figs. 16–18). The dimensions of *E. oeilensis* are similar to those of *E. exigua*, although the latter species seems to have a more regular way of branching, and usually a longer interval between the bifurcations. However, it is more important that there are no pores on the reverse side of the branches of *E. oeilensis*. This feature is regarded as being potentially important, and future studies of all species which are now referred to *Enallopora*, will show if the species with no pores on the reverse side of the branches, can be separated as a distinct group. The real nature, and place in the budding pattern of these pores must be investigated on non-silicified material.

E. wimani (Reed, 1910) from the Upper Ordovician Dufton Shale in England, resembles *E. oeilensis* in zoarial shape and dimensions. It differs in having an ornamented reverse side. In the original description (Reed, 1910, pp. 294–5, pl. 23, figs. 1–3) no mention was made of pores on the reverse side, but the author's studies of the type specimens (Sedgwick Museum, Cambridge, nrs. 29838a–b) show few, scattered, but distinct pores on the reverse side.

The holotype and the other available material of this species are preserved as casts, and this makes it difficult to place it precisely in relation to *E. oeilensis* and other species of the same genus.

The material described by Kiepora (1962, pp.

394–5, pl. 6, figs. 1–2) from erratic boulders in Poland have pores on the reverse side, particularly on the younger part of the branches. She suggested that the absence of pores in the Ojl Myr material was due to the age of the specimens.

Because of these doubts, and the difficulties caused by the imperfect preservation of the material, the Polish specimens – which probably came from the same part of the Baltic as the Ojl Myr material – are tentatively placed in *E. oeilensis*.

The specimens described by Ross (1966) as *Enallopora* sp. A. from the Upper Ordovician Portrane Limestone in Ireland, is rather close to *E. oeilensis* and is also tentatively placed in synonymy with this species.

Family PHYLLOPORINIDAE Ulrich 1890

This family was placed in the Trepostomata by Bassler (1953), but most other authors, including Shulga-Nesterenko (in Orlov, 1960) and Lavrentieva 1979 have referred it to the Cryptostomata. In fact, it is a veritable wastebasket for forms of widely different affinities. Some species referred to *Sarদেশনিনা*, *Subretepora* and *Phylloporina* are undoubtedly trepostomes, and others, showing two regular rows of box-shaped auto-zooecia with a median keel, differ from the fenestellids *sensu strictu* in having real anastomoses between the branches instead of dissepiments. Finally, there are numerous species which are difficult to place in the right suborder, partly because the structures are intermediate or insignificant, and – more often – that the relevant structures are unknown.

A further problem is that most of the type species of the involved genera are unknown as to microstructure, and the nomenclature is therefore very vague and uncertain. It is a time-consuming and unrewarding, though necessary task to revise this group. The genus *Pseudohornera* differs from the rest in having bifurcated branches, but is otherwise typical in that the type species, *Retepora diffusa* Hall 1852 is not well known, and that the species included is a rather heterogeneous lot. Some of them have fenestellid affinities, and one of them considered below, is removed to *Thamniscus*. Others, like *P. bifida* (Eichwald), described by Brood (1970) resemble fenestellids in a general way in their microstructure, but differ in having long, tapering zooecia with circular cross section.

The genus *Chasmatoporella* Nekhoroshev is removed to the family Arcanoporidae because of its dimorphic autozooecia (see below, under that family).

The author's experience with this group, based

mostly on Scandinavian and North American Ordovician material, indicate that the uniting characters of the family, the anastomosing branches, with zooecia on one side only (reteporiform zoaria) are subject to homeomorphy, and have arisen independently and at different times in numerous unrelated groups.

The material of this type of bryozoans from Ojl Myr is very small, and does not contribute to the solution of the problem. Among the comparative material studied, are some silicified specimens of *Chasmatopora tenella* Eichwald (the type of the genus) from the type locality, Porkuni, in Estonia. This material shows widely spaced, long (up to 3 mm) slender erect spines. They appear to be acanthopores, judging from their position in the budding pattern. Such large acanthopores are very rare in cryptostome bryozoans, but are met with in some of the definitively trepostome phylloporinids. This may indicate that *C. tenella* is a trepostome, but the preservation of the available material precludes a definite statement.

Chasmatopora sp.

Plate 5, fig. 7.

Material. 3 fragmentary specimens from Ojl Myr.

Description. All the specimens have a different manner of growth. In two of them the internal structures are completely destroyed, so that even the zooecial apertures cannot be seen. The first specimen is irregularly cone-shaped. This type of growth reminds of one of that in the fenestellids, but in that group, the growth is more regular.

The third specimen (plate 5, fig. 7) is better preserved than the two preceding ones. The fenestrules are exceptional in being heart-shaped. This is due to the suppression every second anastomosis, just after it has taken place. The zooecial apertures (circular, and 0.17 to 0.22 mm in diam.) and the way in which they are arranged, are the same as in *Chasmatopora tenella*, but the cardiform fenestrules might separate it from that species. Since only one fragment has been found, it is of course, impossible to say if the peculiar shape of the fenestrules is only an accidental feature, or if it is of any taxonomic significance. Single or a few fenestra of this type is not uncommon, in certain phylloporinids from the Ordovician of Scandinavia, but this specimen is the only one seen, where all the fenestrules are of this type.

The variability in the branching pattern differs among the phylloporinid species. Some appear to have a very rigid pattern, with always the same size and shape of the fenestrules, whereas others show

drastic variation, especially in length of the fenestrules and curvature of the colony. In most cases this variation appears to be in response to changes in the turbulence and current regime.

The three specimens from Ojl Myr could be regarded as extremes within one highly variable species, but in that case the absence of normal colonies, which even in the variable species make up the vast majority, is remarkable. *Chasmatopora tenella* from the contemporaneous beds in Estonia, has a moderate variability, and all the three specimens from Ojl Myr are outside the observed range of variability of this species.

Fenestelloidea sensu stricto

Family FENESTELLIDAE King 1849

Thamniscus (?) *orosus* Wiman 1901.

Pl. 5, figs. 1–5.

1901 *Thamniscus* (?) *orosus* Wiman, p. 181, pl. 6, figs. 8–11

1911 *Pseudohornera orosa* (Wiman), Bassler, p. 174, textfig. 91, (reproduced from Wiman 1901).

Material. 35 specimens. In 9 cases the base is preserved, and 6 have zoarial appendages.

Type data. The lectotype, nr. Bz 327, is the specimen figured by Wiman (1901), pl. 6, figs. 10–11, and in this paper, pl. 5, figs. 1–2. It came from boulder nr. 29.

Description. Thin, subcircular branches, 0.53–0.85 mm in diameter, branching frequently (distance between bifurcations is variable, from 1.4 to 4.1 mm), usually in one plane. The base is incrusting cylindrical bodies with a diameter of 1.3 to 1.7 mm in all specimens where it is preserved.

A few zooecial apertures are scattered over the comparatively large basal expansion. The zooids in these scattered zooecia probably were the individuals responsible for the supply of food and oxygen to the more distant parts of the base. The transport of nutrients and of building material from the normal zoarium itself would otherwise have been rather difficult, considering that there are no communication pores between the zooecia, and all transport must have taken place in the presumably rather thin external epithelium.

The manner of budding of these scattered zooids poses an interesting problem. The budding must have taken place by means of stolons from individuals which have later been totally obscured, or by budding from a common bud, which was stretched out far from the next zooecium in the colony. In any case the presence of these isolated zooecia gives

hints about the budding potential, and the communication and circulation system in these bryozoans. Unfortunately, the preservation of the microstructure of the base is not good, so this phenomenon cannot be studied in detail on the basis of the Ojl Myr material. The ordinary zooecia are placed in 2–3 irregular rows on one side of the zoarium, with no keels or ridges between them.

They are comparatively large and circular, or slightly elliptical. The longest diameter is between 0.21 and 0.33 mm. In well preserved specimens (pl. 5, fig. 3), one or two small acanthopores may be seen just at the margin of the apertures. Similar features are known from many younger fenestellids. The non-celluliferous side has a keel, which usually is strongly developed.

Due to the bad state of preservation, the internal structures of this species are not known in detail. The zooecia are box-shaped with oblique walls, a comparatively short vestibule and no hemiphragms or mesopores. The basal walls of the zooecia (the non-celluliferous side) are rather thin.

Remarks. This species was referred to *Pseudohornera* by Bassler (1911, p. 174). Like some other species of the same genus (i.a. *P. bifida* (Eichwald)), the type species of *P.*, *P. diffusa* has a very thick wall at the back (cf. Brood, 1970) like that of the Trepostomata or Cyclostomata. The zooecia are long, cylindrical and gradually tapering. None of the other species of *Pseudohornera* has a ridge on the non-celluliferous side. Whether this last feature is of any taxonomic value has not been proved, and the deposition of calcareous tissue might be a sign of individual age or degeneration. In *T. orosus*, however, all specimens have thin walls at the back, even in the basal parts of the zoaria.

The conically tapering zooecia might indicate that the typical group of *Pseudohornera* really belongs to the Cyclostomata and should be removed to that suborder. Species like *T. orosus* which undoubtedly are cryptostomateous, really should be placed in the Cryptostomata. Wiman referred the species to *Thamniscus* King, but the irregular way in which the zooecia are placed, and the fact that there is no median keel between the rows of zooecia, contradicts this. However, the internal structure quite resembles that of younger species of *Thamniscus*.

The differences between the typical *Thamniscus* and *T. orosus* might be due to the fact that the latter species is the oldest one known from the genus.

T. orosus is recorded only from the Ojl Myr fauna.

In the Middle and Upper Ordovician of Scandinavia and the Baltic Region, there are numerous, mostly undescribed, fine-branched, vinculariform bryozoans. They are sometimes quite common in

fragmental limestones. Many of them appear to have the same general features as the species described here, and it may be that both this species and related ones are rather widely distributed. The fact that they are mostly fragmentary, and often seen in thin sections only, has prevented a full description, both of their anatomy, systematics and distribution.

The specialized zooecia found in this species, both those at the basal expansion, and higher up in the zoaria, are described separately under "Specialized zooecia and appendages".

Nomenclature of some feather-branched bryozoans referred to Glauchonome

On erecting the genus *Glauchonome*, Goldfuss (1827–1831), mentioned four species. Three of them are from the Tertiary, and they are now regarded to be indeterminable, or members of *Vincularia*. The fourth, *G. disticha* was made the type species of the genus by Lonsdale (1839). The description and figures of this species was, however, given in an appendix to Goldfuss's paper issued some years after the original generic description (1829), and according to the rules of zoological nomenclature, it is not available as type species. As shown i.a. by Ross (1966, pp. 121–2) *Glauchonome* Goldfuss (1829) is also a synonym of *Glauchonome* Gray (1828, bivalvia). The generic name *Glauchonome* must therefore be abandoned for the Silurian species.

Bassler (1953) introduced the name *Glauchonomella* as a new name for *Glauchonome* Lonsdale, non Goldfuss (type species *disticha*, Goldfuss), but the following review shows that another name probably has priority. There has been some doubt as to whether Lonsdale's species was identical to that of Goldfuss (for reference to this discussion, see Ross 1966, p. 122).

In 1849, d'Orbigny made the genus *Penniretepora*, type species *Retepora pluma* Phillips 1836. In 1850 d'Orbigny again described *Penniretepora*, but now he made *Glauchonome disticha* the type species and called it *Penniretepora lonsdalei*. He supposed that Goldfuss's species was invalid. This procedure is obviously not in accordance with the rules of zoological nomenclature, and *Penniretepora pluma* (Phillips 1836) is still the type species of that genus.

In the years 1882–84 three important papers on these bryozoans appeared (Shrubsole & Vine, 1882, 1884; Vine, 1884). Unfortunately the authors changed their opinions about the type species of their new genera, and this has – together with the unequal publication delay – caused much confusion.

Shrubsole & Vine (1882) founded the genus

Arcanopora, type species *Glauchonome disticha* Goldfuss, and included it in the new family Arcanoporidae. The paper is an abstract, and Bassler (1935, p. 49) has neglected it. It is, however, undoubtedly valid, even if it at present is regarded as inadvisable to designate type species in such papers (cf. Opinion 172, 1946).

Shrubsole & Vine (1884) showed that the Carboniferous featherbranched bryozoans differed from "*Glauchonome*", as defined by Lonsdale, but did not mention *Arcanopora*. Instead they made a new genus, *Pinnatopora* for the species which differed from that genus. The type of *Pinnatopora* was not designated, but the only species mentioned, described and figured, *P. sedgwicki* from the Ordovician, became type species by monotypy. This specific name is, however, an objective synonym of *Ramipora hochstetteri* var. *carinata* Etheridge 1879. This raises a problem of which specific name is the correct one. *Carinata* was not used in a binominal sense, but as a variety (and *Ramipora hochstetteri* Thoula, of which it was supposed to be a variety, is from the permocarboniferous of Spitsbergen, and definitely not closely related to the species in question). *Sedgwicki* is a younger name, and Shrubsole & Vine appear to have been unaware of Etheridge's description of the same material. Since the material on which the two names are based comes from the same locality and horizon, possibly even the same specimen, this is a matter of minor importance. The name *carinata* is used here.

Vine (1884) mentioned *Flustra* (?) *paralella* Phillips 1836 as the type species of *Arcanopora*, and defined the family Arcanoporidae such as the present family Sulcoreteporidae. This was not in accordance with the rules of zoological nomenclature as the designation made by Shrubsole & Vine 1882 is valid.

In the same paper (Vine, 1884) *Glauchonome elegans* Young & Young 1874a was mentioned as the type species of *Pinnatopora*, which was treated as a new genus. In this case the designation of the type species will depend on which paper was issued first in 1884. According to the information kindly supplied by the librarian of the Geological Society of London, the part of their Quarterly Journal in which Shrubsole & Vine 1884 was printed, was issued May 1st. 1884. According to the information kindly supplied by the secretary of the British Association for the Advancement of Science, their Annual Report for 1883, in which Vine 1884 was printed, was issued in 1884, but the exact date is unknown, but "it must have been well into 1884, possibly as late as July of that year".

The available evidence does therefore indicate that Shrubsole & Vine 1884 was legally issued before

Vine 1884, and that *P. carinata* therefore is the type species of *Pinnatopora*.

The two disputed genera will, if they are defined according to Vine (1884) be suppressed as synonyms, *Arcanopora* of *Sulcoreteporia* d'Orbigny 1849 (objective) and *Pinnatopora* of *Pennireteporia* d'Orbigny 1849 (subjective). As defined by Shrubsole & Vine 1884, *Pinnatopora* is a valid genus, indicated also by Nekhoroshev (1929, 1930), who showed that *P. carinata* differs from the Carboniferous *Pennireteporia* species in several features.

Crockford (1942) described the new genus *Pesnastylus*, which is very much like *Arcanopora*. The only differences are the zoarial growth and the more numerous tabulae found in the lateral zooecia of *Arcanopora*. (The results of the author's studies of the microstructure of *Arcanopora* are described below). However, the peculiar manner of branching, which is characteristic for *Pesnastylus*, is also found in some specimens from the Wenlock of Norway, which have been regarded as belonging to *Arcanopora disticha*. In many cases *Pinnatopora carinata* also has the same type of branching (Etheridge 1879, pl. 4, figs. 1a–b). Studies in connection with this paper have shown that the number of tabula in the lateral zooecia of *Arcanopora disticha* is subject of wide variations.

This might indicate that *Pesnastylus* may be a synonym of *Arcanopora*, but since no material of that genus is available, I cannot make any conclusions on this point.

Arcanopora (= "*Glauchonomella*", "*Glauchonome*") was referred to the family Arthrostylidae by Bassler (1911, p. 160, 1935, pp. 20, 135, 1953, p. G128), but it differs from all genera of that family in having an unjointed, pinnate zoarium and two types of zooecia, and also in having an incrusting base. The absence of articulation might be secondary, but judging from other groups with jointed zoaria (i.e. Ptilodictyonidae) this feature must be regarded as being important enough to exclude *Arcanopora* (and *Pesnastylus*) from the Arthrostylidae, especially as this family is now currently included in the rhabdomesids, which have an entirely different pattern of budding. Kopajevich (1975) included some of the forms under discussion in the Phylloporinidae, and this is certainly a more logical arrangement.

Chasmatoporella Nekhoroshev (1936) has the same dimorphism of the zooecia (lateral and frontal ones), and is therefore probably related to *Arcanopora* in spite of the difference in colonial form. Because of the reticulate zoaria, *Chasmatoporella* has normally been placed in the Phylloporinidae.

These three genera with dimorphic zooecia differ considerably from all other cryptostomateous ones, and they are therefore referred to the family

Arcanoporidae Shrubsole & Vine 1882, which is defined as follows: "Cryptostomateous bryozoans with feather-branched or reticulate zoaria, with four rows of zoecia, the lateral rows consisting of long zoecia, and the central ones of about the same number of shorter ones". The family is, for the time being, placed under Fenestelloidea incertae sedis.

The genera of the family are:

Arcanopora Shrubsole & Vine 1882, (non Vine 1884). Type species: *Glauchonome disticha* Goldfuss 1829. Distribution: Upper Ordovician and Silurian of Europe.

Pesnastylus Crockford 1942. Type species: *P. humei* Crockford 1942. Distribution: Silurian of Australia and Europe.

Chasmatoporella Nekhoroshev 1936. Type species: *C. metzi* Nekhoroshev 1936. Distribution: Ordovician of Southern Europe and North Africa.

Pinnatopora (as defined here) is a good fenestellid (*sensu strictu*), which – together with other pinnate forms can be placed in the family Acanthocladidae, although some of the typical, Permian members of this family are rather aberrant, and may not be fenestellids in the strict sense.

Penniretepora is more difficult to place, since the original types are casts, and the interior structure unknown. Similar, pinnate, forms are common in the Middle and Upper Ordovician of Great Britain and Scandinavia. The few bits of information concerning their internal structure indicate that they are related to the fenestellids, but are more variable. They resemble in this respect some of the phylloporinids which may be suspected to be ancestors of the true fenestellids. At present, it may be the best to place this genus in the phylloporinids, as fenestellids *incertae sedis*.

Both *Pinnatopora* and *Penniretepora* must at present be regarded as homoemorphs of *Arcanopora*, without proven relationship beyond the fact that they are all cryptostome bryozoans. Just as a curiosity, it may be mentioned that the suborder Cryptostomata Vine (1884, pp. 329, 332) originally was made to comprise *Arcanopora* (admittedly in *sensu* Vine 1884 = *Penniretepora* d'Orb. 1849, and not in the sense used here) and similar forms.

Genus ARCANOPORA Shrubsole & Vine 1882, non Vine 1884

- 1831 *Glauchonome* Goldfuss (parte).
 1839 *Glauchonome* Goldfuss – Lonsdale, p. 677.
 1850 *Penniretepora* d'Orbigny, p. 45 (non *Penniretepora* D'ORB 1849).
 1882 *Arcanopora* Shrubsole & Vine (non Vine 1884).
 1953 *Glauchonomella* Bassler.
 1966 *Penniretepora* d'Orbigny – Ross, pp. 121–2.

According to the present rules of zoological nomenclature, it is not compulsory to revive a name, like *Arcanopora*, which has not been used for a long time (the only references the author have been able to find, is to Bassler (1935), and Blake (1975, p. 212), both of which treats it as a junior synonym). The use of the oldest name, *Arcanopora*, is recommendable in this case, in order to assure stability in nomenclature. If *Glauchonomella* Bassler 1953 was preferred, it may fall as a subjective synonym of *Pesnastylus* Crockford 1942, or even *Penniretepora* Shrubsole & Vine 1884, when the type material of these genera have been restudied. Even if these genera should be synonyms of *Arcanopora*, they have no priority over it, and the stability of nomenclature will be best preserved by the use of *Arcanopora*.

Arcanopora plumula Wiman 1901

Plate 6, figs. 1–4, Plate 5, fig. 6; Textfig. 4 A, B, G.

- 1901 *Glauchonome plumula* sp. n. – Wiman, p. 181, pl. 6, figs. 17–24.
 1911 *Glauchonome plumula* Wiman – Bassler, p. 160–161, textfig. 80.
 1962 *Glauchonomella plumula* (Wiman), Kiepur, p. 397–398 plate VIII, fig. 2.
 1966 *Penniretepora* sp. A. – Ross, pp. 123–124, pl. 6, fig. 3., pl. 8, fig. 5.
 1975 *Glauchonome plumula* Wiman – Kopajevich, p. 89.

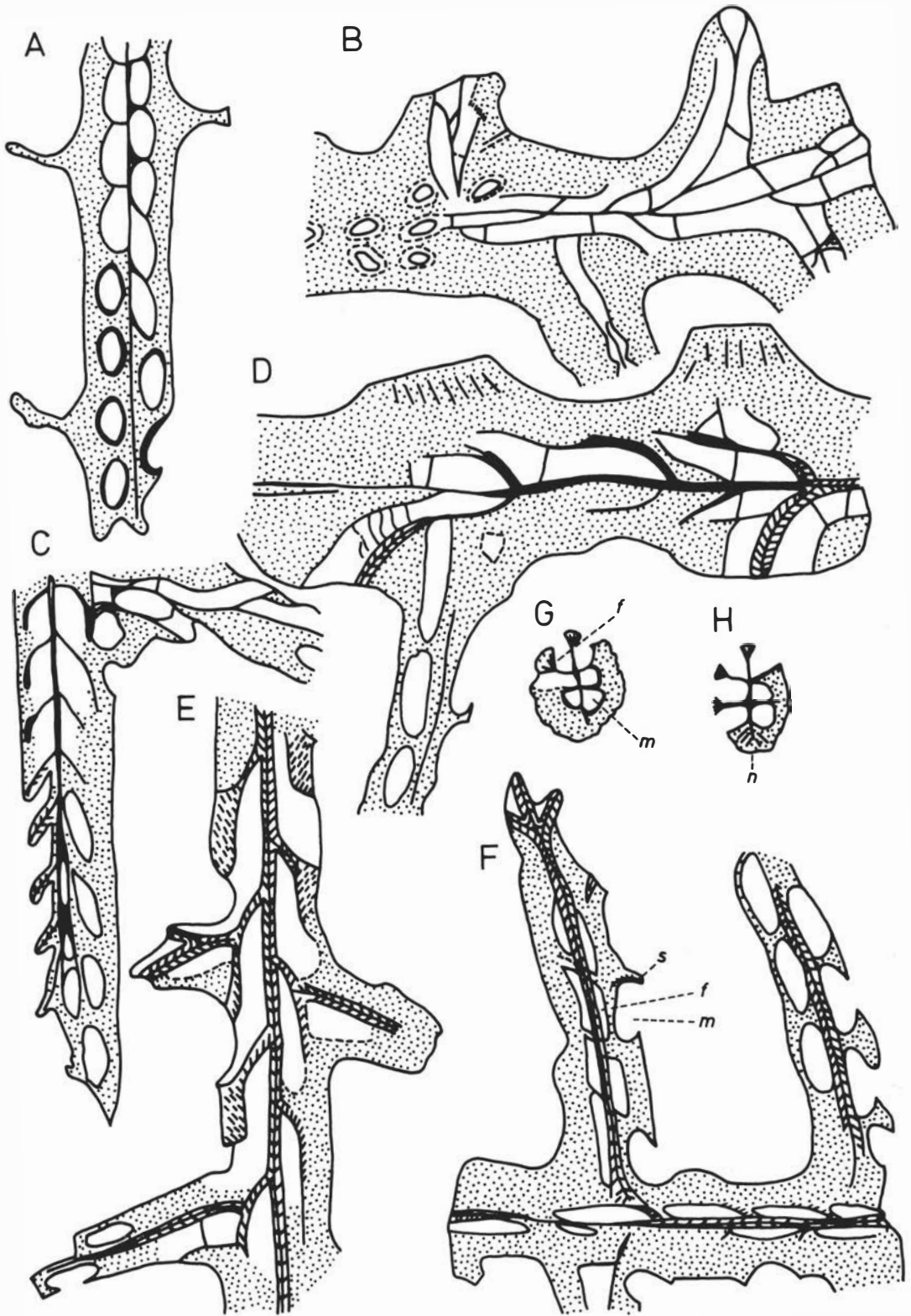
Type data. The holotype, is specimen nr. Bz 336, from boulder nr. 85, the specimen figured by Wiman (1901, pl. 6, fig. 18), in this paper pl. 6, fig. 1.

Material. 139 specimens from Ojl Myr. In 33 cases the base is preserved, and 19 have appendices (see below). 3 specimens from Porkuni, Estonia.

Description. Base incrusting, generally on cylindrical bodies. Secondary attachments (pl. 6, fig. 10) found in some specimens. The zoarium is pinnate. Secondary branching is comparatively rare. In some cases, the branches are in pairs, two branches projecting from opposite sides of the same point of the main stem. Usually the branches are placed alternatively along the main stem. For some reason the distribution of these two types of growth varies in the different boulders in which this species has been found.

This might indicate that there are two varieties of this species with different ways of branching, but intermediate types are also found with both types of growth on the same zoarium.

The zoaria (which all are fragmentary) are up to 30 mm long. The central branches are from 0.61 mm (proximal part of colonies) to 1.1 mm (basal part of old colonies) wide. The secondary branches are



0.5–0.6 mm wide. The frontal zoecial apertures are about 0.22 mm long, and 0.15 mm wide. The lateral zoecial apertures are about 0.29 mm long, and 0.19 mm wide.

Some of the zoaria are very robust, and have five instead of four rows of zooecia on the celluliferous side. It is very probable that the fifth row, which is a frontal one, fades away just above the base, is not a primary feature. It is probably formed in the last stage of growth of the zoarium, since it only occurs in the basal part of large zoaria with abundant secondary branching. The ordinary zoaria only have four rows of zooecia down to the base. Only three zoaria of the coarse type have been found, among them the holotype of *Arcanopora plumula*. The two types are regarded as belonging to the same species, at least provisionally, because of the identity of the structures of the zooecia, and because the younger (upper) parts of the robust zoaria are indistinguishable from the ordinary type.

The feature is rather remarkable, not only because it shows the great variability of the zoarial growth of this species, but also because it probably has some phylogenetical significance. It might either be the remains of an old structure, or a newly introduced one, which at the moment is suppressed in the later growth of the zoarium.

At the present it is impossible to decide which of these two alternatives is nearest to the truth. A reduction of the number of zoecial rows would lead to *Penniretepora*-like (as suggested by Nekhoroshev). An increase in number would lead to types like *Ichthyorachis* McCoy.

The zoecial apertures are slightly elevated, in the frontal zooecia equally round the margin, in the lateral ones more pronounced in the frontal part of the aperture. The frontal elevation of the apertures is very pronounced in the specimens from Porkuni, which have been referred to this species. The elevation is so large that it might externally be compared to a lunarium. The specimens from

Porkuni also deviate from the typical ones in having finer branches and more elongate apertures. Because of the insufficient material (3 specimens) it is impossible to decide whether the Porkuni specimens are only young specimens of the ordinary type, or if they are generically different. The possibility that these apertural features are due to, or exaggerated by silicification artefacts, could also be taken into consideration. They are therefore referred to as *Arcanopora* cf. *plumula*.

The basal parts of the zoaria are similar to those of *Enallopora ojlensis*, and are mentioned below, in connection with both the specialized zooecia, and the ecology, under General Remarks.

There is also a number of irregular tubes on some of the zoaria. They can be interpreted as gonozooecia (resembling those of the hornerids), or as tubes of symbiotic or parasitic animals. This problem has been discussed under General Remarks.

Internal structures. The internal structures of this species are not well preserved, but there seems to be considerable structural differences between the frontal and the lateral zooecia.

In order to study this problem, a number of thin sections were made of *Arcanopora disticha* from the Wenlock shales, Dudley, England (cf. textfig. 4). The lateral zooecia proved to be comparatively long and gradually tapering. There were tabula in most lateral zooecia, sometimes as many as 10 in each zooecium. The number varied considerably, even within the same zoarium. In some of the zooecia there were no tabula at all. The zooecia with numerous diaphragms were found near, or in the base of the secondary (pinnate) branches. The tabula were thin and complete. In the cases where many occurred in one zooecium, some of them might be curved. The frontal zooecia proved to be of a strictly cryptostomateous type, being rectangular, with a short, wide vestibulum, and no diaphragm. The zooecia are usually exactly like those of *Septo-*

Fig. 4. *Arcanopora*. All figures are magnified 22x, except B.

A–B. G. *Arcanopora plumula* (Wiman). A. Tangential section of badly preserved specimen. Boulder 39, Upper Ordovician, Ojl Myr (Bz 1069). The longitudinal section is similar to that of *A. wimani* (fig. G). B. Longitudinal section of one of the large specimens referred to this species. Note the long, tubular zooecia (the lateral ones), with numerous diaphragms, and the thick deposit of secondary tissue. 20x. Boulder 6, Upper Ordovician, Ojl Myr (Bz 1070). G. Cross-section of a branch, showing two frontal (F) and four lateral (m) zooecia. Boulder 53, Upper Ordovician, Ojl Myr (Bz 1071, also figured by Wiman 1901, pl. 6, fig. 21.). C. H. *Arcanopora* (?) *wimani* sp.n. C. Oblique longitudinal section, showing the apertures (lower right) and zooecia of various types. Note the long, tabulated zooecium (upper right). Boulder 73, Upper Ordovician, Ojl Myr. (Bz 1072). H. Cross-section of a branch, showing non-celluliferous band (N) and zooecia. The section is oblique, and the specimen looks higher than it really is. Boulder 39, Upper Ordovician, Ojl Myr (Bz 1073, also figured by Wiman 1901, pl. 6, fig. 31). D–F. *Arcanopora disticha* (Goldfuss). D–E are vertical sections of two specimens, to show the variability in this species. D. has numerous tabulated, long and tubular lateral zooecia. E. has fewer tabulae, and shorter, more box-shaped zooecia, even if both types of zooecia (frontal and lateral) can still be discerned. F. is a tangential section, showing the apertures of the frontal zooecia (right side) and both lateral and frontal zooecia deeper down (left side). Note the peculiar thickenings or spines (S) on one of the frontal zooecia. The sections shown in figs. E and F are from specimen By 16691, and D is from specimen By 16690. Both specimens are from the Wenlock Shale, at Wenlock, Dudley, England.

pora robusta and similar species figured by Ulrich (1890, pl. LVI, fig. 9c). The important difference between the lateral and the frontal zooecia, is that the lateral ones are twice as long as the others. Since each separate branch has the same number of zooecia of both types, the lateral zooecia overlap, while the frontal ones do not. Transverse sections of specimens of *Arcanopora*, show that generally 6 zooecia are cut, 2 frontal ones and 4 lateral ones. The latter are in different stages of development and of different size. It looks as if the lateral zooecia budded from the upper, inner side of the preceding ones.

In the pinnate branches, the first lateral zooecia emanate from the main stem. These zooecia, the apertures of which are covered with the base of the pinnate branches, are therefore very long, and often closely tabulated. However, the frontal rows of zooecia are not affected by the presence of pinnate branches.

It is not certain whether the first frontal zooecia of the pinnate branches budded from the frontal zooecia of the main stem, or from the lateral zooecia at the base of the branches.

A restudy of *A. plumula* from Ojl Myr showed that both the rectangular frontal zooecia, and the tabulated lateral ones are found in this species, too. (In fact, closely tabulated lateral zooecia have only been observed in the coarse type, with five rows of zooecia. In the ordinary type, the preservation is generally so bad that the tabula cannot clearly be seen. There are only a very few cases where one can be quite sure of their presence).

Remarks. *A. plumula* resembles *Arcanopora disticha*, the type of *Arcanopora* from which it only differs by the more irregular way of branching and by being slightly coarser, not only as to the size of the zoaria, but also as to the diameter of the apertures. *Arcanopora plumula* is also recorded from the Porkuni, and the upper part of the Saaremoisa stage of Estonia (Bassler, 1911, p. 161), but as mentioned above, the identity of the specimens from these localities have not been proved. However, some specimens which definitely are *Arcanopora plumula* have been found in the Ashgillian (Slade Beds and Sholeshook Limestone) of the Haverfordwest district, S. Wales. (Specimens 30 877 a–b and 31 318 in Sedgwick Museum, Cambridge). The latter specimen is a good example of the coarse type of *A. plumula*.

Specimens referable to *A. plumula* have been found in the Upper Ordovician of the Oslo Region (of 5b-age), and material which is closely related has been described by Ross (1966) as *Penniretepora* sp. A., from the Upper Ordovician Portrane Limestone in Ireland. In this time interval there were numerous

pinnate bryozoans in the Baltic-Scandinavian-British region, both *Arcanopora*, *Pinnatopora* and *Ptilopora* Eichwald (which is a pinnate ptilodichthyid, rather different from the fenestellids mentioned here).

It is strange to find two types of autozooecia in one species, so different as the two which were seen in *A. plumula*. It indicates that the genus had two structurally different types of autozoids, a feature which, as far as I can see, is unknown among recent bryozoans. It is, however, found in *Chasmatoporella* Nekhoroshev (1936, Prantl 1940). One of the two types of zooecia must be highly specialized. Since the frontal zooecia are like the zooecia of most cryptostomateous bryozoans, it is probable that the lateral ones are specially adapted. The overlapping, tabula-bearing part of the latter, might be homologous with the vestibulum of the other zooecia. Tabulae are only found in this distal part. Similar trepostomateouslike zooecia, with extremely long, tabulated vestibula, are found in some primitive ptilodichthyids, and also in certain gerontic specimens of more highly developed species. Therefore the question of whether the long, tabulated lateral zooecia of *Arcanopora* is a primitive feature, or a highly specialized one, is as yet unanswered.

Arcanopora (?) *wimani* sp. nov.

Plate 6, figs. 5–9; Textfig. 4 C,H.

1901 species no. 1 – Wiman. pp. 181–182. pl. 6, figs. 29–33.

1911 *Glauchonome strigosa* Billings-Bassler. pp. 160–161, textfig. 81 (reproduced from Wiman 1901).

Type data. The holotype, specimen nr Bz 1032, is a zoarium from boulder nr. 77. It was figured by Wiman (1901) pl. 6, fig. 29, and in this paper, pl. 6, fig. 8.

Material. 99 specimens, 13 with the base preserved, and one with zoarial appendices.

Diagnosis. Possibly an *Arcanopora* species with polygonal branches with zooecia of different sizes, and a distinct non-celliferous band. Infrequent secondary branching, and base formed by radicles.

Description. Somewhat irregularly branching zoarium which often branches at the base, forming a number of semiparallel major branches. The largest zoarium is 19 mm high, and still incomplete. The major stems send off scattered secondary branches nearly at right angles. The number of secondary branches is much smaller than in other species of *Arcanopora*. This way of branching gives the whole zoarium a bush-like appearance. The base is formed by a large number of hollow, root-like tubes,

probably transformed zooecia (rhizooecia). In most cases the roots form a complicated and irregular system. Transformed zooecia of the same type are also found in the higher parts of the zoarium, but seldom more than one cluster on each stem. In a few cases, incrusting attachments can be found high up on the zoarium (pl. 6, fig. 8). This indicates that the root-like base possibly is a newly acquired feature, due to adjustment to life on the mud of the bottom. The taxonomic value of this type of base is therefore small, and at least in this case, it is even doubtful if it can be regarded as being a specific characteristic.

The zooecial apertures are scattered over most of the surface of the polygonal-cylindrical stems. There is, however, always a band which is non-celluliferous. The width of this band varies even within the same branch from 1/10 to 1/3 of the circumference of the stem. The diameter of the apertures varies, too. The branches are about 0.6 mm in diameter (0.5–0.95 mm), and the apertures are from 0.15 mm to 0.20 mm wide, and from 0.33 mm to 0.39 mm long. The lateral zooecia which are nearest to the non-celluliferous band, are always larger than the central ones. This clearly shows that originally the zoarium was not ramose radial symmetrical, as it may appear at first glance, but monofoliate. The larger lateral zooecia are also found in the other species of *Arcanopora*, where they reflect a dimorphism among the ordinary zooecia. They are also found in most bifoliate cryptostomateous bryozoans, but here they only reflect the various stages of growth of the zooids. (The apertures of the zooecia are wider because the vestibulum is shorter, and the calcification of the frontal wall has not reached so far in the younger, lateral zooecia).

Usually, the non-celluliferous band of *A. wimani* is not straight, parallel with the direction of the branches, but more or less curved, often in a steep, irregular spiral.

The internal structure is badly preserved in this species. Several attempts were made at obtaining good, thin sections, but in vain. No real difference could be observed between the lateral zooecia and the frontal ones. No diaphragms and hemisepta were found in either of them, but this might be due to the bad state of preservation. The zooecia, at least the frontal ones, seem to be of a normal cryptostomateous type (Textfig. 4c). The rhizooecia are continuations of zooecia, which makes it probable that they are homologous with the ordinary zooecia, just like the rhizoids of the recent bryozoans.

Remarks. This species was referred to as "Species no 1" by Wiman (1901), and as supposed to be identical with *G. strigosa* Billings by Bassler (1911). However, from the description of the latter species by Bassler in Twenhofel (1928, p. 161, pl. 14, figs

8–9), it is obvious that the two species are not identical. The surface sculpture and the way in which the zooecia are placed is quite different. The Ojl Myr-species is therefore referred to a new species. This species is referred to *Arcanopora*, though it is questionable whether this is correct, because of the differences in the zoarial growth, and even more because the sharp distinction between the lateral and frontal zooecia is not found in the new species. The species differs from *Nematopora* in having a non-poriferous band, and in the structure of the base. The irregular appearance of the zooecial rows might indicate that this species as an intermediate stage in some evolutionary series, but it is difficult to say which.

Arcanopora wimani is not recorded from other localities than Ojl Myr.

Superfamily PTILODICTHYOIDEA Astrova & Morozova 1956

As mentioned above (under the suborder Cryptostomata) this superfamily is an artificial and polyphyletic unit. The most deviating group is the pachydichthyids, characterized by having the apertures surrounded by a histologically distinct wall, median tubuli in the mesial lamina, and a typical wall structure (described by Ross (1964), and further refined and subdivided by Karklins, 1969). This group deviates in anatomical and histological characters, and in its geological history from the other bifoliate bryozoans, and may be quite different from the central section of the cryptostomes.

The *Stictopora*-group has unjointed zoaria, a characteristic wall structure and a well-defined frontal wall, with or without mesopores, and generally with hemiseptae. The frontal walls are either massive, or with mesopores. The related stictoporellids have a slightly different wall structure (Karklins, 1969), and abundant mesopores. They may form a transitional link to the trepostomes.

The typical ptilodichthyids are centered about the nominal genus, which has rectangular apertures, because of slight development of the frontal walls, no hemiseptae and an escharopodid wall structure. The colonial shape is variable, ranging from the lanceolate, unbranching form found in *Ptilodictya lanceolata* to the reticulate-bifoliate form found in *Clathropora*. All have articulated bases. The base has been used as a unifying character, and the anatomy of the articulated base (see below, under General Remarks) indicates an origin from rhabdomeside forms.

The phaenoporids, which were placed in a sepa-

rate subfamily by Astrova (1965), were raised to family rank by Kopajevits (1975), have mesopores in the walls between the zooecia, normally triangular in cross-section.

Escharopora comprises forms with the escharoporida wall structure, articulated base, and a peculiar arrangement of the zooecia. This has been described as zooecia arranged in diagonal rows, but detailed studies show that also in these species the basal parts are rectangular, in longitudinal rows. The basal parts are long and narrow, and the upper part of the zooecia widen laterally, alternatively in adjoining rows, to give the impression of diagonally arranged zooecial apertures at the surface.

Graptodichya resembles *Stictopora* in surface features, but has escharoporida wall structure, articulated base, and normally hemiseptae.

When the anatomical features used for classification of this group of bryozoans is examined critically, it appears that the feature which is most distinctive is the wall structure. This is not only because it is easily observed in well preserved material, but also since it is generally supposed that differences in the process of deposition of calcium carbonate reveals fundamental differences in biochemical and genetic setup. The wall structure has been used as a basis for classification by Ross (1964 a.o.) and Karklins (1969). An alternative classification, based on morphological characters have been suggested by Astrova & Morozova (1956) and Kopajevich (1975).

The budding pattern is also important, but seems to be of the same general type in all the ptilodichthyids, although there are some exceptions, such as the trepostome-like pattern found in some stictoporellids, and the irregular one found in *Escharopora angularis* (Ulrich, 1893, pl. XII, figs. 1–4).

The mesopores found in the ptilodichthyids are of three different types. In the stictoporellids they seem to occur in the same place in the budding pattern as in many trepostomes, and may indicate a relationship to that group. In the phaenoporids the mesopores are restricted to the interzooecial walls in the longitudinal rows of zooecia. Generally they are (at least in the basal part) triangular, bordering the two zooecia, and the longitudinal wall separating the rows of zooecia. They are rarely in contact with one another, except in the maculae-like situation where whole areas are covered with mesopores. They are normally open, only rarely filled with secondary tissue, and in some very rare cases (observed in *P. lindstroemi* from Gotland, Sweden) they are tabulated. In *Stictopora*, *Graptodichya* and related genera, more or less polygonal depressions in the frontal wall, which has also been described as mesopores. They are usually shallow, often obscured by deposition of secondary calcareous

tissue, and in some cases extremely variable in appearance.

All these three types are probably systematically different, and the important point is whether the mesopores contained kenozooids, which had a genetically fixed position in the budding pattern of the colony. This seems likely in the phaenoporids, and probably also in some of the stictoporellids, judging from the growth lines in the walls, but the structures found in most species of *Stictopora* and *Graptodichya* are probably ornamental, without a real kenozooid. This is supported *i.a.* by the extreme variability in the appearance of these mesopores, both among colonies, and within one colony, as described from *Graptodichya bonnemai* by Toots (1952, pp. 126–7, pl. 9, figs. 2a–d).

Hemiphragms are plates in the immature part of the zooecium in the ptilodichthyids. Two types occur, the external hemiseptum, which grows out of the lower-distal edge of the frontal wall, and the internal hemiseptum, which grows from the basal lamina or the lower part of the distal wall in the immature part of the zooecium. The external hemiseptum may be straight or curved (normally inwards), it may have a sharp edge, or a blunt or swollen one. Histologically it may be an extension of the frontal wall, or it may consist of a double layer of finely parallel laminated calcareous tissue. In some cases it is hard to recognize it, because of the difficulty to discriminate between a sharply angular corner of the frontal wall, and a real hemiseptum.

The internal hemiseptum is more uniform both in shape (normally a straight, simple plate) and histology (identical to the mesial lamina, and double).

In some cases, with long vestibulum, there are several pairs of hemiseptae. It is not quite clear how these extra hemisepta relate to the ordinary ones, and to the hemiphragms found in trepostomes like *Hemiphragma* and *Esthoniopora*.

Unfortunately, the anatomy, geometry and ontogeny of the hemiseptae are known only in very few species, and it is therefore difficult to appreciate the exact systematic value of this feature.

Several and widely different attempts have been made to model the phylogeny of this groups (Ross, 1962, 1963, 1964a; Astrova, 1965). From a modern systematic point of view, the lack of distinctive and exclusive (apomorphic) characters is striking. All the features used in the present classification seem to be prone to homeomorphism and parallelism. Even such an apparently distinctive character as the median tubuli of the pachydichthyids is found in the bifoliate trepostome genus *Peronopora*, and in a slightly different form in the strictoporids.

The wall structure and budding pattern seem to be the best candidates for useful systematic characters.

Two models can be suggested for the origin of the group. One from rhabdomesids, by suppression of all but one pair of radial laminae, to the bifoliate median lamina, and another from incrusting forms like *Paleschara*, rising to form a bifoliate colony in the manner known from many modern bryozoans. The transition from the typical stenolaematous budding pattern to the regular, cheilostome-like found in this group may have taken place both before (some of the rhabdomesids and partly in *Paleschara*) and after (the stictoporellids) the bifoliate colony-forms was established. The geologically oldest representatives, such as "*Stictoporella*" *gracilis* (Eichwald) from the Lower Ordovician (Middle-Upper Arenig) of Estonia and Scandinavia, and *Phyllo-dichtya cristallaria* Hinds from the Whiterock of Utah have long strongly inclined and tabulated vestibules, giving a distinct trepostome appearance. There are, however, more typical looking members from beds only slightly younger (Llandvirn-Llandeilo), and much more studies of these earliest cryptostomes are necessary in order to evaluate their importance for the phylogeny.

As mentioned above (and discussed further below, under Budding and Classification in General Remarks), the present classification of the group must be regarded as artificial, and detailed studies on better preserved material are needed in order to obtain a more modern classification, which may reflect the phylogeny of the group.

Ptilodichtyoidea incertae sedis

Genus STICTOPORA Hall 1847 (*sensu* Ross 1966)

Stictopora (?) sp.

Plate 4, fig. 5.

Material. Two small specimens from Porkuni. Some of the specimens from Ojl Myr which have been entirely silicified may belong here.

Description. Sharp-edged branches, 4.5 to 5.5 mm wide with broad nonporiferous margins, and elliptical zooecial apertures, 0.30 to 0.50 mm long, and 0.20 to 0.32 mm wide, arranged in 7–9 rows. The fact that there is a non-poriferous margin distinguishes this species from *Pachydichtya bifurcata*, which has similar dimensions both as to the branches and the zooecial apertures. The internal structures are unknown. Since the presence and nature of the median tubuli is unknown, the generic position is uncertain. Similar looking species have been reported from beds of the same age in the Baltic region i.a. by Kiepurā (1962, p. 407, pl. LX, figs. 2–3, as *Rhinidichtya exerta* (Eichwald). This material comes

from an erratic boulder in Poland (0.204, Mochty) which carries a fauna similar to that of Ojl Myr.

Genus PACHYDICTYA Ulrich 1890

Pachydichtya bifurcata (Hall 1883).

Pl. 7, figs. 1,6; Textfig. 5A–B.

1860 *Stictopora scalpellum* Lonsdale, Eichwald, p. 390, pl. 24, figs. 15a–c.

1883 *Stictopora bifurcata* sp. n., Hall, p. 267, pl. 13, figs. 3–4.

1911 *Pachydichtya bifurcata* (Hall), Bassler, p. 143–5, textfig. 67.

1962 *Pachydichtya bifurcata* (Hall), Kiepurā, p. 407.8, pl. IX, figs. 2–3.

1975 *Metadichtya bifurcata* (Hall), Kopajevits, p. 62.

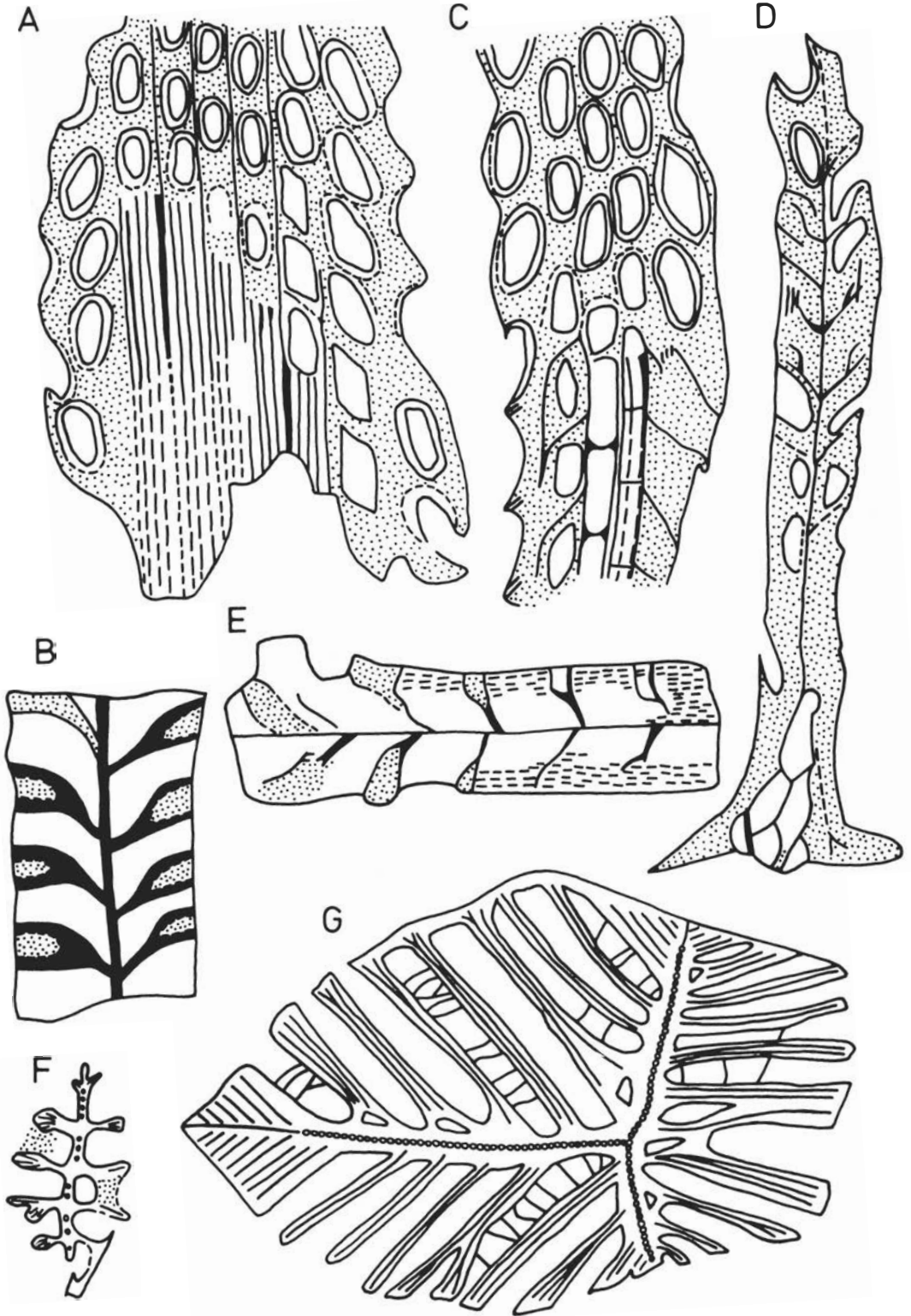
Material. 17 fragments, most of which are badly preserved, all from Ojl Myr.

Description. Since all the fragments are comparatively short, nothing can be said about the branching of the zoarium. The fragments are 2.5 to 4.0 mm wide, and semi-elliptical in cross-section, with rounded edges and no non-poriferous margins. The zooecia are arranged in 7–8 more or less longitudinal rows. The apertures are circular, or slightly elliptical (0.37 to 0.50 mm long and 0.17 to 0.24 mm wide), the marginal ones can also be pyriform and larger than the central ones.

The sections show that there are no hemisepta or diaphragms, and that the comparatively thick median laminae and zooecial walls have median tubuli. For some reason the space between the peristomes, which usually is filled with vesicular tissue, is not calcified (or silicified) in this and the following species, so that the specimens seem to have mesopores. This results in the species quite resembling *Stictoporella*. But the presence of median tubuli, and the fact that the extra-zooecial rooms are closed, clearly indicate that the species belong to *Pachydichtya* and not to *Stictoporella*.

Remarks. Because of the incomplete and badly preserved material of this species, there is some doubt as to whether the identification is correct. According to the scattered information obtainable from the literature, however, it seems to be identical with *Pachydichtya bifurcata* Hall. It is closely related to *Pachydichtya borkholmensis* (Wiman). The differences between these two species and their generic position are mentioned in the description of the latter.

Occurrence: *Pachydichtya bifurcata* Hall has a long vertical range. It is recorded from the Silurian of U.S.A. and from the Porkuni stage of Estonia (Bassler, 1911, p. 145).



Pachydichtya borkholmensis (Wiman)

Pl. 4, figs. 1,3,4,8, pl. 7, figs. 2–5,7; Textfig. 5C–F.

- 1901 *Rhinidichtya borkholmensis* sp. n., Wiman, p. 180, pl. 6, figs. 1–7.
 1911 *Pachydichtya bifurcata* (Hall), Bassler, p. 143–5, textfig. 68.
 1962 *Pachydichtya bifurcata* (Hall), Kiepurá, p. 407.
 1975 *Metadichtya bifurcata* (Hall), Kopajevits, p. 62.
 1978 *Stictoporella borkholmensis* (Wiman), Brood, p. 54.
 1980 *Metadichtya borkholmensis* (Wiman), Brood, p. 163.

Material. 760 specimens. In many cases the base is preserved. This species is the most common among the bryozoans of the Ojl Myr fauna, contributing 59% of all specimens. There are also some specimens from Porkuni. The lectotype, nr. bz 1048, is the specimens figured by Wiman, p. 6, fig. 5 and in this paper pl. 4, fig. 3. It is from boulder nr. 53.

Description. Thin, sharp-edged branches in the higher parts of the zoarium. In the basal parts, the branches are rounded. The zoaria branch frequently with 3 to 6 mm interval, and in most cases form a steep spiral. The branches are 1,9 to 2,3 mm wide, except near the base, where they are narrower, and more circular in cross-section. The base is incrusting, and in a few instances, it has a small circular disc. This is also the case with the lectotype. The base is usually tube-shaped, as e.g. in *Enallopora oeilensis* and *Thaminscus orusus*. In a very few cases, the incrusting base shows transitions to a rhizoecial one. Some of the zooecia in the base are considerably prolonged in a horizontal direction, and resemble the rhizoecia of *Arcanopora wimani*. The great variability of the base indicates that this part of the zoarium might be adapted to different types of bottom, and that its shape is not genetically fixed.

A thin section of the base of *Pachydichtya borkholmensis* (Textfig. 5D) shows that there is no bifoliate symmetry in the basal parts of the zoarium. On the other hand, there is a gradual transition from bifoliate to polyfoliate-radial symmetry or asymmet-

ry. Because of the small number of normal zooecia in the base (6–9), and the often drastic changes of the shape of the base due to environmental responses, it is difficult to trace the symmetry of the primary plane of budding. Judging from what can be seen in the ptilodictyonids (both *sensu stricto* and *incertae sedis*), there has probably been a radial symmetry, although what is believed to be traces of it in this species, can hardly be taken as a proof of this assumption.

The zooecial apertures are circular, or slightly elliptical (0.29 to 0.48 mm long and 0.20 to 0.30 mm wide) in the central rows, and pyriform in the marginal ones. In some cases there are mesopore-like holes in the surface of the stem, giving the zoarium a *Phaenopora*-like appearance. This is due to the exceptional state of preservation of this species and of *P. bifurcata*, described from the latter.

The observable internal structures are the same as those of *P. bifurcata*. The dimensions of the zooecia are also rather similar. The number of rows of zooecia, however, are different in the two species. *P. borkholmensis* has 4 to 6, while *P. bifurcata* has 7 to 9. Consequently the branches of the latter species are broader and often thicker and more rounded at the edges than those of *P. borkholmensis*.

Remarks. Bassler (1911) referred this species to *P. bifurcata*, and the author does not deny that the two are closely related. However, the author believes that they are two separate species, since there are no intermediate forms in the Ojl Myr fauna, this in spite of the large number of specimens. Both species have their range of variation, but there is no overlap. *P. borkholmensis* might, of course, be taken for young specimens of *P. bifurcata*. If this really was the case, the number of zooecial rows would increase with age, (in higher part of the zoaria), but this is not observed even in the largest colonies of *P. borkholmensis*. The admittedly few specimens of *P. bifurcata* where the base is observed, also indicate that also the basal parts of the zoaria had 7–9 rows of zooecia in this species.

Fig. 5. *Pachydichtya*. All figures are magnified 22x.

A–B. *Pachydichtya bifurcata* (Hall). A. Tangential section showing large marginal zooecia and smaller central ones. In the middle, lower part of the drawing, the section cut through the mesial lamina and shows the median tubuli, apparently three to each row of zooecia. B. Vertical section, showing thick walls, and untabulated interspaces. From two different fragments, boulder nr. 1, Upper Ordovician, Ojl Myr (Bz 1065 and Bz 1066).

C–F. *Pachydichtya borkholmensis* (Wiman). C. Tangential section showing peristomes around the apertures, and median tubuli. Specimen Bz 1067, boulder 6, Upper Ordovician, Ojl Myr. D. Longitudinal section through the basal part of a zoarium, showing the irregular arrangement of the zooecia in the base (This specimen is spiral-shaped, so that some of the zooecia are obliquely cut in the section). Specimen Bz 1068, boulder 45, Upper Ordovician, Ojl Myr. E. Vertical section from the same specimen (nr. Bz 1067) as in fig. C. F. Cross section of a young branch showing median tubuli. Thin section z. 455, boulder 95, Upper Ordovician, Ojl Myr.

G. *Pachydichtya holmi* Hennig. Cross-section of *Trigonodichtya*-like basal part of zoarium. Note the presence of median tubuli in the primary part of the mesial laminae only, not in the secondary, thickened edges. Silurian (Wenlock?), Visby Gotland, Sweden. Redrawn from Hennig 1905, fig. 32, with the aid of the original thin section (unnumbered).

In all cases where the base of *P. borkholmensis* is preserved, the zoaria have 5, or even 4 rows of zooecia. Even in the largest zoaria, there is neither increase nor decrease in the number of zooecial rows. It is not likely that *P. borkholmensis* is an ecological type of *P. bifurcata*, as it is unusual that two different ecological types occur in the same biotope. The fact that there is no vesicular tissue preserved makes it difficult to compare *P. borkholmensis* to other pachydichtyas. Kopajevits (1975) and Brood (1978, 1980) have placed this species (and *P. bifurcata*) in other genera, but considering the unresolved classification of the pachydichtyid bryozoans, and the lack of really diagnostic characters in the present, silicified, material, the author prefers to place them in *Pachydichtya* (*sensu lato*).

Occurrence. *P. borkholmensis* is found in Ojl Myr, in the Porkuni stage, and in the upper part of the Saaremoisa stage in Estonia, and in the Boda limestone in Dalarna, Sweden. Brood (1978, 1980) has reported this species from the Upper Ashgillian of Borensult in Sweden, and Ullerntangen in Norway.

Ptilodichtyoidea sensu stricto

Genus PTILODICTHYA Lonsdale 1839

Ptilodichtya sp.

Plate 4, fig. 6; Textfig. 6F, I, L.

1901 *Phaenopora* cf. *ensiformis* Hall-Wiman: p. 180, pl. 6, figs. 25–28.

1911 *Phaenopora ensiformis* Hall-Bassler: pp. 118–119, textfig. 45 (reproduced from Wiman 1901).

Material. 7 specimens. In one case (boulder 45) the base is preserved.

Description. Long, slender non-branching zoaria, with a needleshaped base. The largest (still fragmentary) specimen, is 15 mm long and the greatest width

is 0.85 mm. The zooecia are arranged in longitudinal rows, from four (at the base) to seven. The walls between the rows are protruding and swollen in the upper part, above the apertures. The apertures are rectangular, 0.26 to 0.30 mm long, and 0.09 to 0.13 mm wide, and the transversal walls are oblique and very thin. No mesopores can be seen even with a high magnification. (200x).

The internal structures of this species are not well preserved. The transversal walls are very thin and do not bend. There are no hemisepta and diaphragms.

Remarks. Two species can be discerned in the material labelled *Phaenopora* cf. *ensiformis* by Wiman. The figured specimens all belong to *Ptilodichtya* sp., and the others to *Graptodichtya perelegans*. The extremely strong longitudinal walls distinguish *Ptilodichtya* sp. from all other ptilodichtyas. It belongs to a common group of ptilodichtyas in the Upper Ordovician and Lower Silurian, with slender zooecia, very elongate zooecial apertures, which is in part due to the swollen edges of the longitudinal walls. These overhanging walls may also obscure the phaenoporid mesopores, which are found in some of these species. The systematic relationship of the group is not clear, the typical ones, like *Ptilodichtya* sp., are here regarded as a section of the genus *Ptilodichtya*, whereas those with phaenoporid mesopores should be regarded as belonging to the phaenoporids, probably in the genus *Ensipora* Astrova (cf. Kopajevits, 1975, pp. 67–81).

Because of the restricted material, and the confused systematics at the species level (cf. Ross, 1960, 1961) of this group, the present material is not named, even if it may cover a discrete systematic unit. This species is only found in Ojl Myr, but a detailed study will probably show that a number of specimen listed as "*Phaenopora ensiformis*" and "*Ptilodichtya gladiola*" Bill. must be referred to this species, such as the specimen figured by Kiepurä (1962, pl. XI, fig. 1).

Fig. 6. *Graptodichtya* and *Ptilodichtya*. All figures are magnified 22x.

A. *Oanduella bassleri* Männil (= *Graptodichtya proava* of Bassler 1911). Vertical section of a specimen from zone D3 at Uxnorm, Estonia. Redrawn from Bassler 1911, fig. 50c.

B. *Proavella proava* (Eichwald) (= *Graptodichtya obliqua* Bassler 1911). Vertical section of a specimen from the lower part of zone F1 at Kertel, Dagö, Estonia. Redrawn from Bassler 1911, fig. 51c.

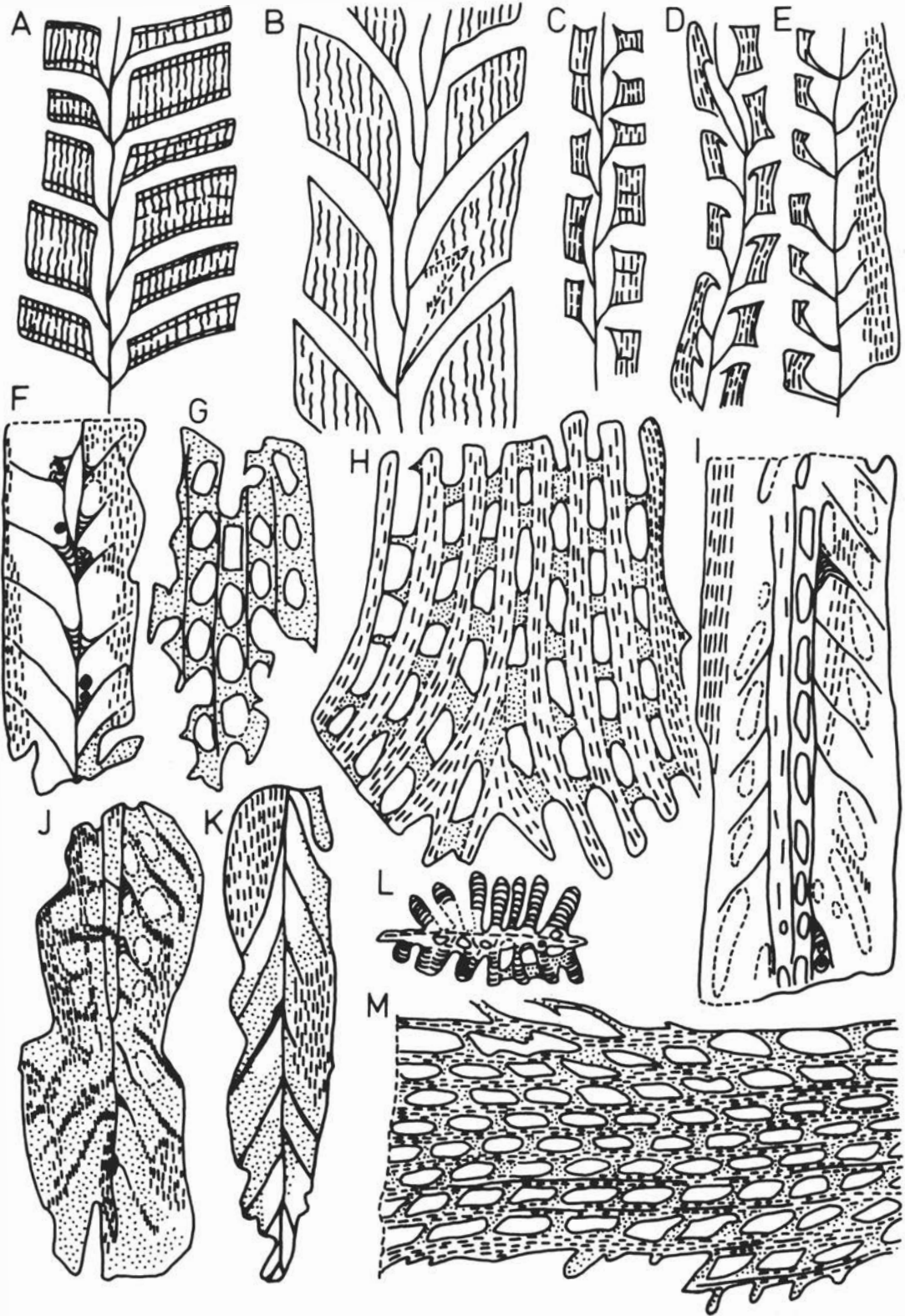
C–E–G. *Graptodichtya perelegans* (Ulrich). C. Vertical section from the Richmond Group (Upper Ordovician) of Clarksville, Ohio. Redrawn from Bassler 1911, fig. 47c. E. Vertical, and G. Tangential section of a specimen, bz 1059, from boulder 53, Ojl Myr.

D. *Graptodichtya bonnemai* Bassler. Vertical section of a specimen from zone C2 (Kukruse Formation), Kukruse, Estonia. Redrawn from Bassler 1911, fig. 48e.

F–I–L. *Ptilodichtya* sp. F. Vertical section showing phosphatic linings and globules. The structures in the surface are destroyed by silicification. From specimen Bz 1060, boulder 6, Ojl Myr. I. Deep tangential to vertical section showing phosphatic linings. Specimen Bz 1061, from boulder 6, Ojl Myr. L. Cross section of a branch, specimen Bz 1062, from boulder 45, Ojl Myr. (This thin section is also the type for Wiman's figure 1901, pl. 6, fig. 25.)

H–K. *Ptilodichtya* cf. *nitidula* Billings. H. Tangential section. K. Vertical section. Specimen Bz 1063, from boulder 53, Ojl Myr.

J–M. *Ptilodichtya irregularis* sp.n. J. Oblique vertical section showing phosphatic lining. M. Tangential section. Specimen Bz 1064, from the Upper Ordovician Porkuni horizon at Porkuni, Estonia.



Ptilodictya irregularis sp. nov.

Plate 4, fig. 2; Textfig. 6 J, M.

Material. Two specimens from Porkuni. In both cases the base is missing. The holotype, figured on pl. 4, fig. 2, is no. bz 1011.

Diagnosis. *Ptilodictya* species with rather narrow branches. The sides of the zoarium are "wavy".

Description. Broad zoarium with irregularly wavy margins, so that the branches have a zig-zag outline. The branches are up to 2.5 mm wide. The waves are formed by small nodes on the sides, possibly aborted lateral branches. The zooecia are placed in 12–14 longitudinal rows with thick, elevated longitudinal walls in between. The marginal zooecia are of the same size as the central ones, (0.26 to 0.31 mm long, and 0.11 to 0.13 mm wide).

The internal structure is fairly well preserved, compared to that of the other species in this fauna. The thick longitudinal walls have no median tubuli, and the transversal ones are very thin and inclined. There are no hemisepta, diaphragms or mesopores.

Remarks. This species resembles *Ptilodictya* sp., but differs from that species in having a greater angle of the transversal zoecial walls, and in the fact that the longitudinal walls are more pronounced. The numerous and equal-sized longitudinal rows of zooecia and the irregular margins, separate this species from all other contemporaneous species of the same genus. However, further studies may show that the latter feature is subject to great variations, and of little taxonomic value.

Ptilodictya cf. *nitidula* Billings 1866

Plate 4, fig. 7; Textfig. 6 H,K.

cf. 1866 *Ptilodictya nitidula* sp. n. – Billings p. 9.cf. 1889 *Dicranopora nitidula* (Billings) – Miller, p. 300.cf. 1900 *Dicranopora nitidula* (Billings) – Nickles and Bassler, p. 233.cf. 1928 *Rhinidictya nitidula* (Billings) – Bassler in Twenhofel: p. 165.cf. 1961 *Ptilodictya nitidula* (Billings) – Ross. p. 336, pl. 43, fig. 6.

Material. 3 specimens from Ojl Myr. (Boulder 53).

Description. Infrequently branching zoarium with 8–10 strictly longitudinal rows of zooecia. The greatest width of the branches is 2.4 mm. The base is missing. The zooecia have thick longitudinal walls and very thin transversal ones. The apertures are of a rectangular shape, 0.33 to 0.37 mm long and 0.13 to 0.17 mm wide, and directed obliquely to the surface of the zoarium. No median tubuli can be

seen in the thin sections of this comparatively well preserved species.

Remarks. The systematic position of this species is somewhat doubtful. The pointed base, which would have given the conclusive proof, is missing both in the specimens from Anticosti, and in those from Ojl Myr. On the other hand, the marked difference in thickness between the longitudinal and transversal walls, and the fact that there are no median tubuli, indicate that the species belongs to the ptilodictyids. The latter feature may, however, be due to the bad state of preservation. In that case the species would have belonged to the rhinidictyids, near *Stictopora exerta* (cf. Bassler, 1911, textfig. 57, p. 133). However, when taking into consideration that the median tubuli have been found in the much more damaged *Pachydichtya bifurcata* from the same locality, and that even a systematical search for median tubuli in *Ptilodictya* cf. *nitidula* gave no result, the author thinks it is justified to believe that the species in question had no median tubuli at all. Due to this, it is referred to the ptilodictyids.

Occurrence. This species is recorded from the English Head Formation of Anticosti Island, and from Ojl Myr. A similar specimen was described from the Upper Ordovician Portrane Limestone of Ireland by Ross (1966, pp. 125–126, pl. 7, fig. 1) as *Ptilodictya* sp. A.

Graptodictya perelegans (Ulrich)

Plate 4, figs. 9, 10; Textfig. 6 E,G.

1878 *Ptilodictya perelegans* sp. n. – Ulrich. I, p. 94, pl. 4, fig. 16–16a.1882 *Graptodictya perelegans* (Ulrich) – Ulrich, p. 165.1882 *Graptodictya nitida* sp. n. – Ulrich, p. 166, pl. 7, figs. 8–8a.1900 *Graptodictya perelegans* (Ulrich) – Nickles and Bassler, p. 280.1908 *Graptodictya perelegans* (Ulrich) – Cummings, p. 836, pl. 29, fig. 8.1911 *Graptodictya perelegans* (Ulrich) – Bassler, pp. 121–122, textfig. 47.1960 *Graptodictya perelegans* (Ulrich) – Philips, pp. 19–23, pl. 7, figs. 1–3 and 7, pl. 8, fig. 4.

Material. Three fragmentary specimens, two from Ojl Myr, and one fragment from Porkuni. In all cases the pointed base is preserved.

Description. The zoaria bifurcates, but the insufficient material makes it impossible to say anything about the frequency of the branching. The zooecia are arranged in 7–9 longitudinal rows, the branches are 4–6 mm broad and the surface is not sculptured. The specimen from Porkuni is apparently a young one, as it has sharp-edged margins and only slightly

calcified zoecial walls at the margin. The specimens from Ojl Myr have more rounded margins and comparatively thicker branches. However, these differences are probably due to difference in age. The zoecial apertures are 0.17 to 0.22 mm long, and 0.08 to 0.11 mm wide at the surface.

The internal structure is almost identical with that of American specimens of this species as described by Philips (1960). The shape and direction of the hemisepta are exactly the same, and so are the other features. The Ojl Myr specimens may be a little larger than the American ones.

Remarks. As these specimens are almost identical as to internal structure, they believed to belong to *G. perelegans*, the type of *Graptodichya*. The differences in external sculpture (the typical specimens have a sculptured surface) are probably due to the state of preservation of the Ojl Myr material. As shown by Toots (1952), the surface features of *Graptodichya*-species may be extremely variable.

Occurrence. Besides having been found in Ojl Myr and Porkuni, this species is also recorded from Upper Ordovician (Richmond) beds of North America.

Superfamily RHABDOMESONACEA

As the nominal genus is somewhat atypical, it is not convenient to use the subdivision into "*sensu stricto*" and "*incertae sedis*" in this superfamily.

It consists by definition of the ramose, more or less cylindrically branching cryptostomes, and, in the author's opinion, it is a rather heterogenous, distinctly polyphyletic unit. In the following review, it has been subdivided into informal groups, most of which are supposed to be, if not monophyletic, at least morphologically and genetically related.

The feature which distinguishes the ramose cryptostomes from the other ramose bryozoans (trepostomes and cyclostomes) is the radial symmetry of budding (see below, in the chapter "Budding and classification").

Group 1 includes *Rhabdomeson*, *Coeloconus* and *Hyphasmopora*, which all are genera with zoaria consisting of hollow branches. The base is presumed to be incrusting in all genera except *Coeloconus*, where it seems to be articulated (Ulrich, 1890, pl. LXXII, fig. 3–4).

The zoarial shape found in this group – hollow, ramose branches – is found in almost all types of bryozoans with incrusting zoaria. In several cases it has been reported from otherwise incrusting species, and the systematic value of this character is therefore negligible. The group, as defined there, is

probably highly polyphyletic, related to a number of independent incrusting cryptostome types, and not particularly interesting for the further discussion of the relationship of the real ramose (cylindrical) cryptostomes. The author has no material of these genera at his disposal, and consequently cannot give any new information on them.

Group 2 includes *Rhombopora* and a number of closely related genera (*Orthopora*, *Acanthoclema* and others). The members of these genera have a similar structure, consisting of a ramose zoarium, with zoecia growing from a filiform axis, with radial symmetry. The zoecia are arranged in longitudinal segments, which are usually separated from the neighbouring ones by walls thicker than between the zoecia in the segments. The zoecia are usually surrounded by strong acanthopores, but judging from the descriptions and figures of the internal structure given in the literature, they vary considerably as to shape and dimensions. Some species, such as *Orthopora tonolowayensis* Bassler 1926, have zoecia of a strictly cryptostomateous type, arranged in longitudinal rows, and with two different types of interzoecial walls. (See chapter: "Budding and Classification"). Both superior and inferior hemisepta are strongly developed. Other species, such as *Goldfussitrypa esthoniae* Bassler 1911, can hardly be distinguished from the trepostomes, as they have gradually tapering zoecia, and the mesopores apparently are filled with secondary calcareous tissue. This peculiar resemblance between some of the rhabdomesids and the batostomellids has already been pointed out by Ulrich (1890, pp. 342, 364). In some cases (*Megacanthopora* Moore, see Bassler 1935, p. 144) it is even difficult to place the genera in the correct suborder. A great number of species can easily be referred to either *Batostomella*, *Lioclema*, *Hemiphragma* or *Rhombopora*. An example of these intermediate forms is *Lioclema* (?) sp. (pl. 2, figs. 2, 3, 5). In this species the major stem has tabulated mesopores, which in connection with untabulated zoecia and strong acanthopores points in the direction of *Lioclema*. However, the monofoliate secondary branches show the zoecial type of *Rhombopora*, with a massive body instead of mesopores.

The fundamental difference between the trepostome and cryptostome types, the radial symmetry in the budding of the ramose cryptostomes, is discussed below, in the chapter "Budding and classification". In some of the transitional cases it may be very difficult to see if there is a radially symmetric budding, either due to imperfect preservation, or due to the presence of forms which are really transitional. The *Lioclema* (?) sp. referred to is – in this respect – not quite typical, as the secondary

branches are monofoliate, and not ramose with radial symmetry.

This probably indicates that the systematic gap between the genera in question is not very great. They seem to form a link between the Cryptostomata and the Trepostomata. (For instance, *Trematopora granulifera* Hall, which has been referred to *Rhombopora* by Ulrich (1890, p. 647) and to *Batostomella* by Bassler (1906, p. 28). There are also a number of cases described in the literature, and in the author's material, where such species show a strong calcification of the mesopores in the basal part of the zoarium, more typical trepostome mesopores in the distal, younger parts, and indistinct symmetry in the budding. This seems to indicate that a gradual transition exists from typical trepostomes to cryptostomes with radial symmetry, and calcified "frontal wall" instead of mesopores. It is not clear from the meagre evidence available if this transition has taken place only once, or if it has occurred several times.

As for the genus *Rhombopora* itself, the type species *R. lepidodendroides* Meek has mesopores, hemiphragms and two types of acanthopores. (Ulrich, 1890, p. 84, pl. 1, fig. 1a–b). Other species of *Rhombopora* have complete diaphragms, others again resemble species of *Batostomella* or *Lioclema*, except for the mesopores being filled with calcareous tissue. Complete diaphragms and wedged-shaped "frontal wall" are characteristic features of these species.

The other genera of this group show similar features as far as their internal structures are known (except *Orthopora tonolowayensis*). The genera all seem to have been distinguished by the surface ornamentation, sinuous ridges and zooecia in longitudinal or diagonal rows (Nickles and Bassler, 1900). The zooecia appear to be irregularly distributed in most species, so that it may look as if they are arranged both in longitudinal and diagonal rows. The symmetry of budding is radial in the admittedly few cases where it has been observed.

The ornamentation of the surface is subject to great changes, not only because of differential secondary corrosion of the fossils, but also because of the age of the zoaria and the ecology. The generic definitions applied in this group is therefore not very useful, and the systematics and nomenclature of the group is ripe for a thorough revision.

Group 3 includes the genus *Bactropora* Hall and Simpson 1887, which mainly differs from the genera of group 2 in having an articulated base. The articulated base might have indicated a relationship with the ptilodichthyids. This resemblance seems to be strengthened by the radial symmetry in the articulated base of the ptilodichthyids. However,

Bactropora does not have the complicated secondary structures which are characteristic of the base of *Phaenopora* and other ptilodichthyids. Since the internal structure of *Bactropora solida* sp. n. is the same as that of the "Lioclema-group" of *Rhombopora*, *Bactropora* probably is related to *Lioclemella* in the same way as *Rhombopora* is to *Lioclema*. This is also indicated by the *Bactropora*-like basal part found in *Lioclemella* (?) *ramosa* (Bekker, 1921, p. 41, pl. VI, fig. 18) compared to the typical *Lioclemella*-structure in the upper part of the same species (Bekker, 1921, pl. VI, fig. 16). This indicates that colonies of *Lioclemella* which have an articulated base, can, as they grow older, attain a *Bactropora*-like structure, by deposition of calcareous tissues in the mesopores.

The symmetry of the budding is not known from the typical members, and in the Ojl Myr material, the preservation is far from being perfect. It seems to be transitional, but under the present circumstances the groups (as the family Bactroporidae) are left in the Trepostomata. It may be an independent line, in the development of the cryptosome "level" from trepostomes, which apparently took place in several lineages, independently during the Ordovician.

Group 4 includes the genera *Nemataxis* Hall and Simpson 1887, *Nematotrypa* Bassler 1911, *Cyclophaenopora* gen. nov., *Streblotrypa* Ulrich 1890, *Nikiforoviella* Nekhoroshev 1956, *Linotaxis* Bassler 1953, and possibly also some others, which are not sufficiently known. In the oldest genus, *Nematotrypa*, the apertures are irregularly distributed on the surface of the branches (not strictly arranged in longitudinal rows). In accordance with their relative geological age, *Nematotrypa* has open mesopores, which are filled in the geologically younger *Nemataxis*. It has been suggested that the base was incrusting in this group (cf. Nickles & Bassler, 1900, p. 43), but as far as I can see from descriptions and figures, the base has actually only been observed in one species, *Nematotrypa spiralis* Bekker (1921, p. 57, pl. VII, figs. 32–37). In this species the base is articulated. It is therefore possible that also the other species of this genus had an articulated base, such as *Cyclophaenopora*.

The genera in this group also have a tendency for unbranched zoaria. Branching does occur, but is conspicuously less common than in many other groups both of trepostomes and cryptostomes. Another empirical feature, found especially in this group, but also in others with a radially symmetrical budding, is that the zoaria have a tendency to split along the thicker, double walls of the segments, much in the same way as the bifoliate zoaria may split along the mesial lamina. This indicates that the

intersegmental walls in the ramose, radially symmetric forms are homologous with the mesial lamina in the bifoliate cryptostomes. The structure of the basal part of the ptilodictyids (see below) and other bifoliate cryptostomes, where a radial symmetry, with multiple mesial laminae are found, can be taken as a support for this hypothesis.

The affinities of these genera are somewhat uncertain. They might either be interpreted as trepostomateous-like derivatives of an originally cryptostomateous stock, or specialized trepostomateous bryozoans. Because of the hemisepta (hemiphragms) and the numerous, closely tabulated mesopores, it is tempting to believe the latter theory to be correct. In that case, the genera of this group are probably not derived from the same stock as group 2. It is very likely that they come from *Dittopora*, which has reduced diaphragms, numerous small mesopores with closely placed diaphragms, and large macula consisting of mesopores arranged in more or less regular bands around the stems. All these features are found in most species of *Nematotrypa*, *Nemataxis* and *Cyclophaenopora*.

At least one Middle Ordovician species of *Dittopora*, *D. magnopora* Bekker (1921, pp. 46–48, pl. VI, figs. 1–8) has an articulated base, a fact which very much supports the author's theory on the relation between *Dittopora* and the genera of group 4. The microstructure of the base of *Dittopora magnopora* has not been studied in detail, but judging from the figures given by Bekker (1921, pl. VI, fig. 2), the base may have been of the same type as that of the Ptilodictyidae, and not like that of the Bactroporidae. (The presumably corroded cone of the base shows openings of pores (mesopores?) which indicates that the pores were directed perpendicularly against the surface of the cone, not parallel to it, as in the Bactroporidae). The symmetry relations in the *Dittopora* species are not clear, because most specimens are recrystallized in the central part. The few ones in the author's material, where the axial features could be observed, are intermediate.

Most of the genera in the group differ from *Nematotrypa* in that the zooecia are placed in longitudinal rows with strong ridges between them. This affects the distribution of the mesopores, which are found in more or less constant numbers between the zooecia. We therefore have a fairly continuous line of development from the early Ordovician species of *Dittopora* via transitional forms like *Dittopora magnopora* and *Nematotrypa*, and from this genus to *Cyclophaenopora*. In the oldest species of the latter genus, the way in which the zooecia are arranged in longitudinal rows, is not so regular as in the later species of that genus. In *Nemataxis* (and

Streblotrypa and other advanced genera), the zooecia are always placed according to a regular pattern. The development in this group therefore seems to lead from irregular forms with high variability both as to the shape of the zoaria and the arrangement of the zooecia, towards forms where both the shape of the zoaria and the pattern of the zooecia are genetically constant.

The way in which the zooecia are placed in the later genera of this group, indicates that they may be related to the ptilodictyids. The external and internal differences between a species of *Cyclophaenopora* and the basal, ramose part of *Phaenopora*, is very small. However, the internal structures are slightly different in the two genera. In *Phaenopora*, the mesopores are very rarely tabulated, and there is only one pair of hemisepta, in spite of the vestibula being just as long as in specimens of *Cyclophaenopora*, which have a large number of hemiphragms. The structure of the hemiphragms are also very different.

It was previously assumed that *Streblotrypa* had an incrusting base, but no definite statements concerning this base can be found either in descriptions or figures of the species of this genus. The internal structures are only known from *S. nicklesi* (Ulrich, 1890, pl. 71, fig. 9c). This species seems to be closely related to *Cyclophaenopora*. However, it differs from this genus in the longitudinal ridges between the rows of zooecia being more strongly developed, and the hemisepta were probably different, too.

Like the other genera of this group, *Cyclophaenopora* has an articulated base. The base of two of the three species known so far, has been studied (the type species, *C. robusta* and *C. minor* from Ojl Myr). The zooecia are placed alternatively on the right and left side in the longitudinal rows, something like the way they are arranged in *Dichotrypa* (Ulrich, 1890, pl. XLII, figs. 1c, 2d). The structure of the mesopores are quite similar, too, but there are no lunaria in *Cyclophaenopora*.

As mentioned above, this group has both trepostomateous and cryptostomateous affinities. The trend of development suggested here indicates that it originates from the Trepostomata, but the structure of the zooecia, especially of the younger members, are very like those of the Cryptostomata, as they are short and wedge-shaped (instead of box-shaped), while the trepostomateous zooecia are long and thicker in the proximal parts. The group might therefore represent a parallel to the Celleporidae, which have a similar zoarial growth, (ramose developed from bifoliate/incrusting zoaria), in spite of belonging to the Cheilostomata. In that case, *Orthopora tonolowayensis* might belong to the Nematrypiidae, or to an independent parallel line of develop-

ment. It is evident, however, that the geologically oldest genus (*Nematotrypa*) is more like the Trepostomata than the younger ones, and according to the last mentioned theory, the opposite should have been expected.

In conclusion, it must be admitted that the actual knowledge on the phylogeny of the rhabdomesids is very fragmentary. The author's opinion is that the group is an entirely artificial one, where some of the lineages, identified above have developed independently from various trepostome groups. The typical rhomboporoids may have developed from batostomellids, or similar trepostomes, in one or more lineages. The bactroporids (retained here as a family, provisionally placed in the Trepostomata) seems to have developed from *Lioclemella* after this genus acquired a pointed, articulated base. The family Nematotrypidae (new) is made for the group with numerous, open, but closely tabulated mesopores. It may have originated in *Dittopora*, and developed through *Nematotrypa* into forms where the longitudinal segments were more clearly defined.

The relationship of this group to the trepostomes, and to the bifoliate cryptostomes is further discussed below, in the chapter "Budding and Classification".

Family NEMATOTRYPIDAE fam. nov.

Definition: Ramose cryptostomes, with radial symmetry, strong longitudinal walls, and numerous, open mesopores, which may be arranged in spot- or ring-like maculae. In most species the branching is sparse, or non-existent. The base is articulated in most forms, and hemiseptae may occur.

Genus CYCLOPHAENOPORA gen. nov.

Type species: *C. robusta* sp. nov. from the Kullberg limestone in Dalarna, Sweden, and corresponding

strata (Middle Ordovician) in other parts of Scandinavia, Range of genus: Middle to Latest Ordovician.

Diagnosis. Zoarium consisting of ramose, cylindrical, unbranching stems with pointed base for articulation. The zooecia, which rise from a filiform axis, are placed in longitudinal rows, separated by comparatively thick walls. There are two or more tabulated or vesicular mesopores between each zooecium. Generally there are macula consisting of clusters of mesopores, arranged without breaking the longitudinal walls.

Remarks. The affinities of this genus are discussed in the chapter: "Superfamily Rhabdomesonacea". It is related to *Dittopora* and *Nematotrypa* when it comes to the structure of the mesopores, the incomplete diaphragms and the pointed base. This genus differs from the other genera of the family, apart from *Nematotrypa*, in the way the zooecia are placed in distinct longitudinal rows. In this feature it resembles the Ptilodictyonidae (*in casu Phaenopora*). However, the existence of any actual relationship has not been proved, and it must be remembered that there are typical bifoliate phaenoporas in older layers than *Cyclophaenopora*, (the Kukruse stage (C2) in Estonia), even if the difference in time is not so great. Therefore, according to our present knowledge, *Cyclophaenopora* cannot be regarded as the direct predecessor of *Phaenopora*.

Species of this genus are common in the Middle and Upper Ordovician of Scandinavia, and probably also of Estonia. Some of the Middle and Upper Ordovician specimens referred to *Dittopora* from these areas, should probably be referred to *Cyclophaenopora*.

Cyclophaenopora robusta sp. nov.

Plate 2, fig. 1; Textfig. 7C, D.

Material. Several hundred specimens from the type locality and other localities in Scandinavia, particularly in Dalarna, Sweden.

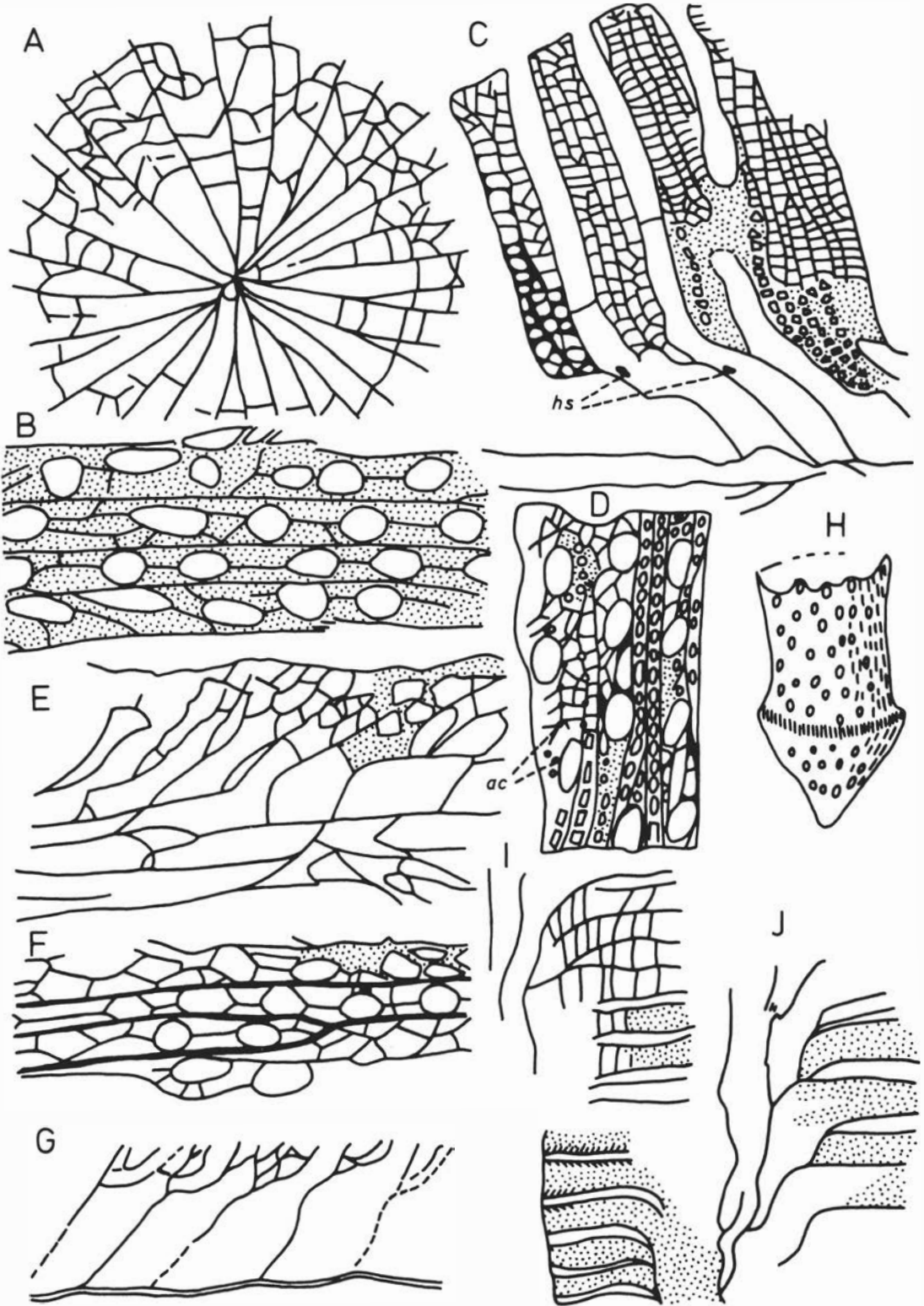
Fig. 7. *Cyclophaenopora* and *Dittopora*. All figures 22x.

A–B, E. *Cyclophaenopora annulata* sp.n. A. Cross-section of a stem showing that the zooecia emanate from a filiform axis. From Boulder 24, Upper Ordovician, Ojl Myr (Bz 1074). B. Tangential section. E. Vertical section. The structures of the central part of this species are badly preserved, and it is difficult to get good thin sections. Figure E shows half the stem, from the axis to the surface, but is oblique. From boulder 17, Upper Ordovician, Ojl Myr (specimen By 1004, the holotype of this species, cf. plate 2, fig. 6).

C–D. *Cyclophaenopora robusta* sp.n. C. Longitudinal section, showing closely tabulated mesopores and the peculiar shape of the hemiseptae (hs) Thin section Z401. D. Oblique tangential section showing both the features near the surface of the stem (to the left), with small acanthopores (ac) and irregular distribution of the mesopores, and (to the right) a deeper section, where the zooecia and mesopores are arranged in longitudinal rows. Thin section Z400. Both sections are made from the holotype, By 16872, from the red and green beds lateral (mostly lower than) the Kullberg Limestone at Amtjärn, Dalarna, Sweden (Middle Ordovician).

F–G. *Cyclophaenopora minor* sp.n. F. Tangential section. G. Longitudinal section (dotted walls are reconstructed). Both sections from specimen Bz 1006, from boulder 24, Upper Ordovician, Ojl Myr.

H–J. *Dittopora* (?) *magnopora* Bekker (1921). H. The pointed base of this species, showing apertures (of zooecia or mesopores) on the cone-shaped basal part. I. Part of a vertical section of the upper, young part of the zoarium. J. Part of a vertical section of the lower, older and heavily calcified part of the same zoarium. From zone C2 (Middle Ordovician) in Estonia. Figs. H–J are redrawn from Bekker (1921), pl. 6, figs. 2, 3 and 5).



Type data: The holotype is By 16872, the specimen figured on pl. 2, fig. 1. It is from the Kullberg Limestone (Middle Ordovician), from the red layers below the lower reef limestone (Middle Ordovician) in the S-E part of the quarry at Amtjärn, Dalarna, Sweden.

Diagnosis. Medium sized *Cyclophaenopora* with irregularly placed longitudinal walls, macula as irregular patches and small acanthopores in the peripheral zone.

Description. In spite of the abundant material available, there is not a single case of the ramose stems branching off. The zoaria are usually regularly cylindrical, a few are irregularly cylindrical, (2.6–3.1 mm in diam.) and one single zoarium is irregularly compressed and 2.3 to 3.8 mm in diam. This probably represents a pathological specimen. The longest specimen observed is 11.5 cm long. The base is pointed for articulation. In spite of the large material, there are only two well preserved bases, one from the type locality, and one from a corresponding layer, the *Macrourus*-marl at Fjäckå, Dalarna. The zoecia are placed in longitudinal rows, but they cannot always be seen clearly on the surface. They are 0.19 to 0.24 mm in longest diameter. The mesopores are irregularly, rounded polygonal in outline, and 0.028 to 0.055 mm in longest diameter. The longitudinal walls between the rows of zoecia are slightly irregular. This indicates that the arrangement of the zoecia in longitudinal rows was not yet fully established in this species. Within the rows, the zoecia and mesopores are arranged somewhat irregularly. There are macula consisting of irregular patches of mesopores, placed so that they do not break the longitudinal walls. The mesopores are closely tabulated, and sometimes vesiculose. The walls between the zoecia and the mesopores are stronger than the walls between the mesopores themselves. The zoecia emanate from a filiform axis, and after a short immature zone, they are directed perpendicularly to the surface of the stems. There is a number of mushroom-shaped hemiphragms (textfig. 7C) which are placed alternatively in the zoecial tube. Some small acanthopores can be seen near the surface (or in textfig. 7D).

Remarks. The author has introduced the description of this species here, because the two species of *Cyclophaenopora* found in Ojl Myr, are not so well preserved so that they are suitable for type species. The somewhat irregular appearance of the longitudinal rows and the distribution of the zoecia suggest that this species is a primitive one. The two other species of *Cyclophaenopora* are geologically younger, and in these, the zoecia are placed more regularly.

This species is very common in the Middle

Ordovician of Dalarna, and it can be found in contemporaneous beds in other parts of Scandinavia.

Cyclophaenopora minor sp. nov.

Plate 2, figs. 7–8; Textfig. 7F–G.

Material. Four specimens from Ojl Myr, one of which has a pointed base.

Type data: The holotype is nr. bz 1005 from boulder nr. 24 Ojl Myr, Gotland.

Diagnosis. Small *Cyclophaenopora* with regular longitudinal walls, no macula and no acanthopores.

Description. Thin, non-branching stems, with needle-shaped base. No macula is found in the comparatively limited material. Diameter ab. 1.45 mm, the longest specimen (fragment) is 15 mm long. The internal structures are principally like those of *C. robusta*, but the way in which the zoecia are placed in longitudinal rows is more regular in this species. The zoecia are placed alternatively on the edges of the longitudinal rows, which makes the species resemble *Dichotrypa*. In vertical sections, this species is also very much like *C. robusta*, but the zoecia are slightly shorter, due to the stems being so small. The zoecia are 0.185 to 0.22 mm in longest diameter. The hemiphragms are very small, if present at all.

Remarks. This species differs from the two others of the same genus in being so small, and in the apparent absence of macula. It is found in Ojl Myr, and in the Boda Limestone of Osmundsberget, Dalarna (Uppermost Ordovician to Lowest Silurian).

Cyclophaenopora annulata sp. nov.

Plate 2, fig. 6; Textfig. 7A, B, E.

Material. Four specimens from Ojl Myr. In none of them is the base preserved.

Type data: The holotype is no. bz 1004, from boulder 17, Ojl Myr, Gotland.

Diagnosis. Thick *Cyclophaenopora* with regular longitudinal walls, no acanthopores, and macula forming annulations.

Description. Zoaria consisting of comparatively coarse (2.3 to 3.7 mm in diameter), cylindrical stems with annulations composed of more or less irregular areas consisting of mesopores only. The longitudinal walls are not broken or disrupted in these areas. The characteristic shape of these macula probably indicates the relationship between *Cyclophaenopora* and *Dittopora*. The internal structure is the same as that of the preceding species, except for the zoecia being longer, and the hemiphragms more de-

veloped. The zoecia are 0.20 to 0.26 mm in longest diameter.

One of the specimens from Ojl Myr seemed to be branched. A closer study of the point of contact between the "branches" revealed that two fragments were fused secondarily, probably by the process of silicification. As mentioned above, no species of *Cyclophaenopora* have branching zoaria.

Remarks. This species is found in the Ojl Myr fauna, and probably also in the Boda Limestone of Dalarna.

7. General remarks

Budding and classification

The different ways of budding of the calcareous parts of the recent bryozoans, have been thoroughly described i.a. by Borg (1926) and by Silén (1944).

There are two main types of budding. In the first, the new zooids are separated from the preceding ones by the formation of a septum in the latter. This septum is the future external wall of the new zooid. The walls are all calcified behind the common bud (see Borg, 1926, fig. 21–22). This type of budding is found in the Cyclostomata, and probably (acc. to Borg 1926, p. 482, in addition to the author's observations) also in the Trepostomata. In the bryozoans which bud in this way, there is only one type of calcareous interzooidal wall. A characteristic feature is the fact that the zoecia formed by this type of budding, are proximally tapering due to the generally small angle of divergence between the septum and the wall of the parent zooid.

In the other type, the new zooids are separated from the very long distal zooid, in each row (Silén, 1944, textfig. 44–45, p. 58). The transverse walls are therefore formed later than the lateral ones, and are thin and single. The longitudinal walls between the rows of zooids are double, each row having lateral walls of its own (Silén, 1944, textfig. 47, p. 59). The difference as to histological structure between the transverse and lateral walls, is due to the manner of growth. The transverse walls are formed very rapidly, and are thin and straight with no visible growth-lines. The lateral walls are formed by continuous distal growth, and show distinct growth-lines when well preserved. Later on, both types may be thickened by deposition of secondary calcareous matter.

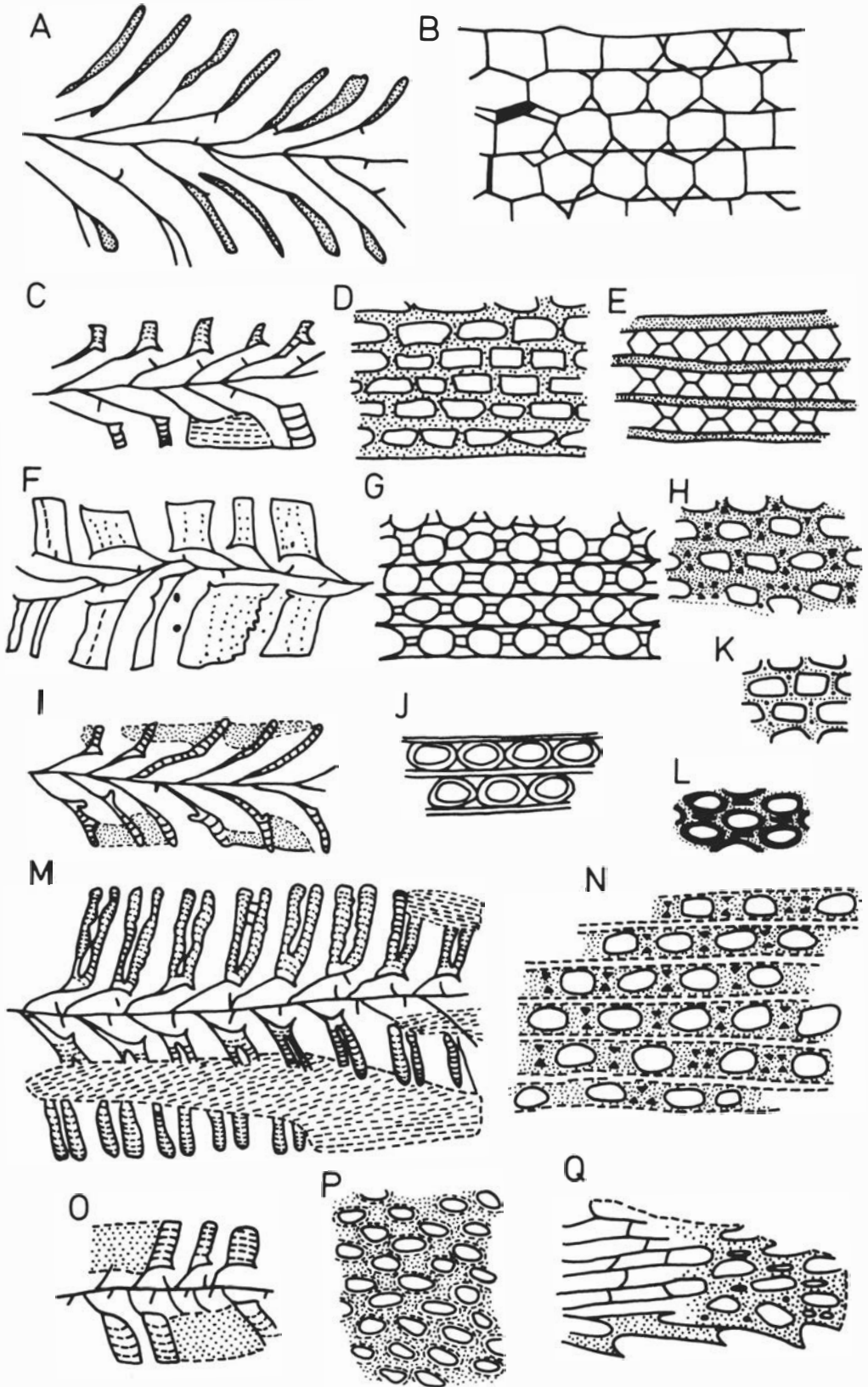
This type of budding is found in the Cheilo-Ctenostomata and partly in the Cryptostomata. The histological differences between the transverse and lateral walls can be seen in many cases in the latter suborder. The normal cryptostome zoecium, therefore consists of a box-like lower part, bounded by

thick longitudinal walls, and thinner transversal ones. It is covered by a "frontal wall", with a vestibulum, leading to the aperture. The "frontal wall" may have different histological structure, and the box-like shape of the zoarium proper is often accentuated by the presence of hemiseptae at the angle between the "frontal wall" and the vestibulum.

Twitchell (1934) tried to refer the Trepostomata to the entoproct bryozoans, comparing them to *Urnatella gracilis* Leidy. His assumptions as to the budding and structure of the Trepostomata are interesting, in spite of the fact that some of them seem to be based on misinterpretations of the microstructures. He presumes that the space between the tabula was filled with kenozooids, forming a stolon. The autozooids lived in the space above the last tabulum. Most of the reasons given by Twitchell for referring the Trepostomata to the Entoprocta, can, however, also be used in favour of placing them with other stoloniferous groups of bryozoans, such as Ctenostomata Stolonifera (see Silén, 1944). The presence of various types of heterozooids in the Trepostomata (mesopores, acanthopores) and also the early development of the zoaria (see Cummings & Galloway, 1915), indicate that they belong to the Ectoprocta.

Twitchell's theory seems to be based on the fact that the tabula of the Trepostomata correspond histologically to the transverse walls in the calcified Gymnolaemata. The zooids of the Trepostomata may therefore be interpreted as a row of kenozooids forming a stolon, terminating in an autozooid. However, the very short space between the tabula in some species, contradicts this theory, as does also the fact that the tabula continue to be formed during the mature stage of the zooid. At this stage, it is very probable that the distal part of the zoecial tube was filled by an autozooid. The tabula (diaphragms) observed in recent bryozoans, are all formed in connection with periodical degenerations of the zooids, either individually, or all at the same time (see Borg, 1933, p.301 and following). Even if it has not been proved that the tabula of all trepostomateous bryozoans are formed in this way, it does seem to make Twitchell's theory rather improbable.

A detailed survey of the budding of the Trepostomata by means of serial sectioning and comparison between young and old parts of the same zoarium will be the only way of solving these problems. Some few studies have been made (Boardman & Cheetham, 1969; Boardman & McKinney, 1976, McKinney, 1975, 1977) and it is obvious that a number of important questions regarding the systematics and relationship of the trepostome bryozoans must wait for more studies along these lines.



The question relevant for the present discussion, how the radial symmetry of the rhabdomesids may have developed out of a stenolaematous budding pattern, is one of them. At present our knowledge about the details and regularity (pattern) of budding is too scattered and sparse to form the base for far-reaching conclusions. As mentioned above, it seems, from what we know at present, that the Trepostomata are closely related to the other Stenolaemata.

In the older classifications of the fossils bryozoans (i.a. Bassler, 1953), the Cryptostomata were placed together with the Cheilo-Ctenostomata. Borg's introduction of the order Stenolaemata, and further work, especially on the wall structure of the Cryptostomata, have led to a reconsideration, and they are now generally placed in the Stenolaemata, with the Trepostomata, Cystoporata and Cyclostomata (Ryland, 1970).

The classification of the smaller units will not be discussed here, as many of them were not represented in the available material. However, it is worth mentioning that there are fewer real Cyclostomata in the Palaeozoic than what it appears from Bassler (1953). A number of the forms referred to this suborder, and they obviously belong either to the Trepostomata or to the Cryptostomata. The most numerous Palaeozoic group of "cyclostomateous" bryozoans is the ceramoporids and the fistuliporids, which belong to Borg's Division Calyptrastega of the Trepostomata (Borg, 1944, pp. 18–19) – are now placed in the Cystoporata.

The relationship between the budding, phylogeny

and astogeny seems to be rather clear in the Cheilostomata. Both the most primitive forms (like *Labiodostomella* cf. Silén 1944) and the earliest fossil representatives have uniserial branches. As shown by Pohowsky (1973) the lateral pore chambers are already developed in these Jurassic forms, indicating that this is not a secondary feature developed after the coalescence of the branches.

The incrusting zoaria can be modelled as a series of parallel, joined uniserial stripes, which also explains the marked lateral budding found in these bryozoans. Bifoliate and hollow, ramose zoaria is formed by upwards expansion of incrusting zoaria. In many cheilostomes these zoarial shapes are found together in one single species.

The vinculariform zoaria may be regarded as a bundle of uniserial stripes, either radially symmetric, or more or less one-sided, with a nonporiferous back-side. In some of the fine-branched forms, such as the retetporids, the geometry of the colony seems to be strictly fixed genetically, and in others it may vary rather widely, with ecology.

In the groups with jointed zoaria, they have probably developed from the vinculariform, by reduction of calcification, or by other modification (see below, chapter on the articulated base in the ptilodictyonids). The lunulitiform zoaria have probably developed from incrusting ones, although the process is not obvious.

The budding pattern and astogeny of the massive ramose branches, such as in the celleporids, is not known in detail. Frontal budding seems to have taken place, and radial symmetry, which was to be

Fig. 8. *Phaenopora*. All figures are magnified 22x.

A–B. *Ph. twenhofeli* Bassler (1928). A. Vertical section. B. Tangential section showing the comparatively small number of mesopores. Silurian (Beccscie Formation) Anticosti Island, Canada. Redrawn from Bassler, in Twenhofel (1928, pl. 11, figs. 3–4).

C–D. *Ph. ensiformis* Hall 1852. C. Vertical section. Note the position of the inferior hemisepta. D. Tangential section, showing absence of mesopores. Silurian (Rochester Shale) Grimsby, Ontario, Canada. Redrawn from Bassler (1906, pl. 27, figs. 8–9), with the aid of thin sections of specimens from the Rochester Shale at Lockport, N.Y.

E. *Ph. aperta* Bassler 1928. Tangential section showing the large mesopores, and thick walls between the rows of zooecia, Silurian, Jupiter Formation Anticosti Island, Canada. Redrawn from Bassler in Twenhofel (1928, pl. 12, fig. 3).

F–G. *Ph. superba* (Billings). F. Tangential section. G. Vertical section showing the superior and inferior hemisepta. Silurian (Beccscie Formation) Anticosti Island, Canada. Redrawn from Bassler in Twenhofel (1928, pl. 9, figs. 9–10).

H. *Ph. fimbriata* James. Tangential section. Silurian (Clinton Limestone) Dayton, Ohio, U.S.A., Redrawn from Bassler (1906, pl. 21, fig. 20).

I–J. *Ph. lonsdalei* (Vine) I. Vertical section showing small number of hemisepta. J. Tangential section. Silurian (Wenlock Shale) England. Redrawn from Vine (1884, textfigs. 1, 2, 4).

K. *Ph. fimbriata canadensis* Bassler (1906). Tangential section showing very small mesopores. Silurian (Rochester Shale), Grimsby, Ontario, Canada. Redrawn from Bassler (1906, pl. 21, fig. 19).

L. *Escharopora* (?) *limitaris* Ulrich 1894. Tangential section, showing elongate mesopores. Middle Ordovician ("Trenton Shale"), Minneapolis, Minnesota, U.S.A. Redrawn from (Ulrich 1893, textfig. 9b).

M–N. *Ph. lindstroemi* Ulrich 1890. M. Vertical section. Note that one of the mesopores is tabulated. This is very rare in this species (and other phaenoporids), occurring in less than one in 2500 colonies. N. Tangential section near the surface of the specimen. Silurian (Visby Marl) Gotland, Sweden. Redrawn from Hennig 1905, textfig. 5, with the aid of the original thin sections.

O–P. "*Hemidichtya*" *lebanonense* Coryell 1921. O. Vertical section showing both inferior and superior hemisepta. P. Tangential section. The figures of this species (which should probably be referred to *Stictopora*, cf. Ross 1961, p. 336) are introduced for comparison. Redrawn from Coryell (1921, pl. 14, figs. 2–3).

Q. *Ph. incipiens* Ulrich 1884. Tangential sections showing the arrangement of the zooecia in longitudinal rows near the mesotheca. Ordovician (Trenton Limestone) Montreal, Canada. Redrawn from Ulrich (1883, pl. 13, fig. 16).

expected because of the method of budding, is not apparent.

In the stenolaemateous bryozoans the budding pattern is somewhat different, as the new zooids bud from the common bud, at a low angle from another zooid. The incrusting zoarium is the "typical" form, and its development into more massive lumps, and to solid, cylindrical branches is easily explained. Transitions between these zoarial types are found, often within a single species. Also thin-branched (vinculariform) zoaria, and articulated ones (such as the crisiids) are natural derivatives of the stenolaemateous type of budding.

It is more difficult to explain the box-shaped zooecia, with a thick "frontal wall", and a more or less circular aperture in the cryptostomes. In many of the advanced cryptostomes, the longitudinal walls are thicker than the transversal ones, and the latter are definitely formed later than the longitudinal ones. This strongly recalls the budding pattern of the cheilostomes, and is difficult to explain in terms of the budding pattern of the other stenolaemates.

It looks as if the common bud was separated into "tongues", one for each of the longitudinal rows of zooids, but there is not other evidence in the skeleton of the cryptostomes for this. In contrast, the occurrence of isolated zooecia in secondary basal parts (cf. pl. 5 fig. 5) and the varied protuberances and accessory structures indicate that the cryptostome colonies were surrounded completely or almost completely by coelom, and that new individual could bud outside the regular pattern from this common bud.

In contrast to the cheilostomes, where the fossil evidence point to an origin from uniserial forms, the oldest known cryptostomes are large, multiserial, heavily calcified, and often with complex zoaria. It may be that some of the supposed early Palaeozoic cyclostomes (such as *Corynotrypa*), which Brood (1965) has shown to be nonporiferous, in reality are generalized primitive stenolaemates. In that case the evolution of the budding pattern, and the zoarial shapes must have taken place long before the first known appearance of the cryptostomes (in the Arenig).

The early cryptostomes seem to have more inclined zooecia, longer vestibules and more tabulae in the vestibules than the younger, more typical forms. This is seen independently in several lineages, such as in the pachydichtyids (i.a. "*Rhinidichtya*" *tabulata* Coryell (1921, pl. XII, fig. 5) and *Phyllodichtya crystallaria* Hinds (1970, pl. 6, figs. 3 and 5), which may have developed from *Peronopora*, which is also bifoliate, and have median tubuli.

Some early species of *Escharopora* (i.a. *E. angularis* Ulrich, textfig. 9K) have an irregular pattern of

budding, and polygonal zooecia, without any apparent linear pattern. In other species of *Escharopora*, this irregular budding is restricted to the basal part, whereas the upper, younger parts show the normal arrangement of the zooecia.

This may indicate that the ancestors of these forms may be among incrusting stenolaemates, with irregularly polygonal zooecia, and without a distinct lineal pattern. In the genus *Paleschara* Hall there are some possible candidates. This genus appear, according to the author's unpublished studies of a number of species, to be a complex one, including a mixed bag of forms with primitive zooecial structure, but highly variable wall structure. It is probably highly polyphyletic, and may include a variety of different stenolaemates, and possibly even other groups.

In order to solve these problems, detailed studies by means of serial sections of critical species is needed, in order to map the distribution and development of the various budding patterns, and the development of the zoarial types.

The few and fragmentary observations at hand indicate that the cryptostomes are polyphyletic, and have originated along several independent lines during the Ordovician, or even earlier. Some of these lineages, or rather glimpses of them, have been mentioned above, in the Rhabdomesonacea, and others may be found in the *Peronoporella-Pachydichtya* connection, and the possible *Paleschara-Escharopora* link.

Specialized zooecia and "zoarial appendices"

In most bryozoans there are several types of zooecia. The *ordinary ones*, the autozooecia, in which the ordinary zooids lived, and the others, the mesopores, acanthopores, nanozooecia, and possibly cystiphragms. These zooecia are all included in the pattern of budding of the zoaria formed either by lateral, or by frontal budding. Although the number and size of these zooecia often vary within the same species, and even in a single zoarium, they are normal parts of the zoaria at all stages of growth, and they often occur so regularly that they may be used for identifying the species.

Beside these specialized zooecia, which occur in the ordinary pattern of budding, we also find other, irregularly specialized zooecia. They are just as important as the regular ones, but seem to be formed by a transformation of ordinary zooecia which are already developed, or by occupying the place of such a zooecium in the pattern of budding. The irregularly specialized zooecia, which are referred to as zoarial appendices because some of them are of a doubtful origin, are: rhizooecia (see below), secondary bases, supposed gonozooecia and prob-

lematic structures. The latter includes some formations which may be the remains of parasites or commensals.

Some of the rhizoecia and the zooecia which are transformed into chitinous joints in the articulated specimens, have an intermediate position between these groups, since they may occur regularly, but, at least in some cases, they are formed by a transformation of already developed autozooecia. The zooecia of the joints, which are not preserved in fossil specimens, might be called arthrozoecia.

The rhizoecia described here are those found in the Ojl Myr, and similar materials. The arthrozoecia which are a regular part of the colony, such as in crisiids and cellarids, are not included here. They are generally autozooecia, where the zoecial apertures are considerably prolonged, often several millimetres (pl. 6, figs. 5–9). The long, thread-like tubes have acted as roots, so that the zoaria may have been "planted" in the mud of the bottom, or, more probably, they have enabled them to cling to some protruding body. Those zooecia are usually found at the base of the zoarium, but they can occasionally be seen higher up. In these cases the rhizoids have probably stabilized the zoarium by uniting it to other organisms, or they have supported zoaria which have been secondarily tilted (pl. 6, fig. 9).

The formation of the rhizoecia seems to be subject to phenotypic variation, at least in some cases, such as *Pachydichtya borkholmensis* (pl. 4, figs. 1,4). This species usually has a discoid or cylindrical base, but in some specimens from Porkuni, the zooecia forming the base are prolonged into long tubes. On the other hand, a few specimens of *Arcanopora (?) wimani*, a species which usually is provided with a rhizoidal base, have a discoidal base (pl. 6, fig. 8). Consequently there is some doubt as to the systematical value of the presence or absence of rhizoecia in these cases.

There are also rhizoecia-like structures of another type in *Pachydichtya borkholmensis*. They consist of thin, cylindrical, apparently massive protruberances rising up between the zooecia, and especially from the non-poriferous margin (pl. 4, fig. 8). They appear quite sporadically, and are only found in less than 10 % of the specimens available. Generally several occur together, when they do occur. These structures probably had the same purpose as the rhizoecia, but they were not formed by a transformation of one of the ordinary zooecia. They differ from the rhizoecia in being massive, in addition to the fact that they do not occupy the place of an ordinary zoecium in the pattern of budding. These structures may also resemble acanthopores, but are massive, without a central pore, and are

apparently formed by calcification of the same tissue which calcified the "frontal wall". Similar structures are common in many cryptostomes, but are, because of their fragility, best observed on silicified material. In some groups, especially fenestellids, they are a regular feature of the colonies, and have been described under the name *Palaeocoryne* by Young & Young 1874. Because of their regular forms, but apparently accidental distribution, these structures have been ascribed to synoecic algae (such as *Microweedia* Toots 1952a). In fact all of them seem to be made by the bryozoans themselves, and there is a smooth transition from the gradual thickening and strengthening of the colonies in old specimens, to the architectonically more sophisticated structures mentioned here.

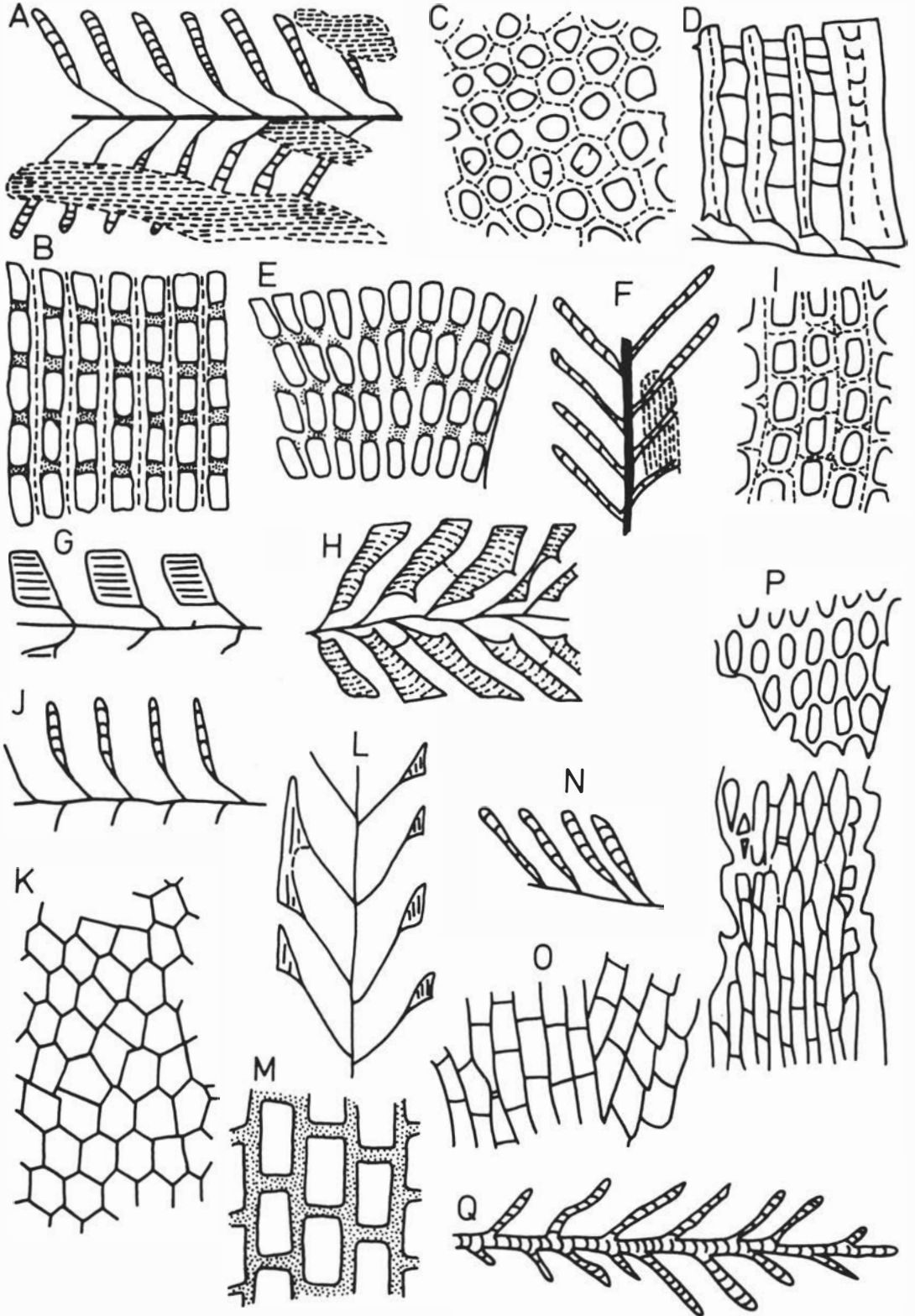
Such structures may occur also in cheilostome bryozoans, but they are conspicuously rarer, and generally much less developed. This is just what would be expected if the cryptostomes had a stenolaemateous type of budding, and were covered almost completely with coelom, from which both new zooids could bud, and accessory calcareous structures could be formed, in response to ecological influences.

It is possible that at least some of the zooecia forming the rooted base of *Arcanopora (?) wimani* really are heterzoecia, and not secondary transformed autozooecia. However, the pattern of budding can not be seen clearly in the base, due to the secondary structures, and the problem must therefore remain unsolved for the time being.

In the case of *Arcanopora (?) wimani* (rhizooidal base), and some species with a more or less discoid base (*Pachydichtya borkholmensis*, *Arcanopora plumula* and others), the ecological value of the rhizoids might seem overestimated, but a closer study of the "discoid" bases, shows that in most cases they are incrusting on cylindrical objects, and consequently have not grown directly from the bottom. Other specimens show that they have grown on a surface with a marked, and often regular relief, probably shells or fragments of shells of brachiopods or trilobites. The species with rooted base probably attached themselves to the same cylindrical bodies by means of rhizoecia.

It is worth mentioning that the state of preservation of the different groups of animals in the Ojl Myr fauna varies considerably. For some reason, the bryozoans are far better preserved (or rather silicified) than most of the other fossils. This fact explains why the bases of the bryozoans are preserved, but not the originally hard objects, to which they were attached.

The secondary bases resemble the real ones as to external shape, and they probably had the same



functions, too. However, they are placed fairly high up on the zoarium. In most cases, the secondary bases helped to support the zoarium, in the same way as the rhizoids. They are either discoid or cylindrical, like the real base. Secondary bases are found in all abundant species in the Ojl Myr fauna, and are common in *Pachydichtya borkholmensis* and *Enallopora oeilensis*. They are also present in silicified cryptostomes from a number of other Ordovician and Silurian faunas. Both the secondary bases, and the other structures mentioned here are therefore of no taxonomic value. They may occur in most, if not all cryptostome species as the result of ecologic influences, and may be used in interpretation of ecological and hydrological conditions. Care must be taken in not transferring experiences from the recent cheilostomes to the cryptostomes without due regard for the differences in budding pattern.

Beside these structures, which can be comparatively easily explained, there are also some which are of more uncertain origin. Some of them might be gonozoecia or broodchambers, others the remains of parasites and commensals, or be due to some pathological feature. They are found in the following species:

Arcanopora plumula. In this species, the appendices consist of tubularly prolonged zooecia, circular in cross-section, and gradually tapering towards the base. The tubes emanate from the apertures, and bend over to the non-celluliferous side of the zoarium. The apertures of the tubes are generally broken because of the very thin and fragile walls. In one case (pl. 5, fig. 6), the aperture (of the tube) seems to have a deep sinus. No constrictions have been found on the tubes, but transversal growth-lines have been observed in one case. The tubes vary

as to size, the larger ones being nearer to the base. There can be up to three tubes on one zoarium, but one or two is the usual number. About half of the specimens of this species, which still have their base, have appendices, while only a few small ones are found on fragments of the higher parts of the zoarium. The substance of the walls of the tubes cannot, in the present state of preservation, be discriminated histologically from the tissue of the zoarium itself.

In the author's opinion, this type of structure might be interpreted either as zooecia transformed to serve reproduction, gonozoecia, or as remains of parasitic or synoecic animals. The animals which lived in the tubes might, according to similar recorded cases, have been annelids (*Polychaeta Tubicola?*), hydrozoans or rugose corals.

Among the arguments supporting the interpretation of the tubes being gonozoecia, is the fact that they are different in the different species (see description of the appendices of the other species below). If each species of bryozoans did not have a different species of parasitic animal, this would mean that the structures in question were intimately connected with the structures of the bryozoans. As it will be seen from the description of the appendices, only one type occurs in each species. It is also interesting to note that closely related species (as for instance *Arcanopora plumula* and *A. wimani*) have similar appendices, while more distantly related species have different ones. The available material is, however, much too small to be statistically significant.

All tubes of this type (in *A. plumula*) emanate from one zooecium, just like the gonozoecia of recent cyclostomateous bryozoans.

The position of the tubes on the zoaria also

Fig. 9. Ptilodichthyonids. All figures 22x.

- A-B. *Ptilodichthya lanceolata* (Goldfuss). A. Vertical section from Hennig (1905, textfig. 12). Silurian (Wenlock) Visby, Gotland, Sweden. B. Tangential section just below the surface of the specimen. From Hennig (1905, textfig. 9). Silurian (Wenlock), Fårö, Gotland, Sweden.
- C-D. *Ptilodichthya clathratulus* (Nicholson) (= *P. pavonia* auct., non d'Orbigny) C. Tangential section. D. Vertical section. From Ulrich (1882, pl. 7, figs. 3a-c). A typical, Upper Ordovician, trepostome-like species.
- E-F. *Ptilodichthya triangularis* Hennig. E. Tangential section just below the surface of the specimen. F. Vertical section. From Hennig (1905, textfigs. 15, 18). Silurian (lower Wenlock), "the Waterfall", Visby, Gotland, Sweden.
- G, P. *Escharopora subrecta* Ulrich. G. Vertical section. P. Tangential section showing the arrangement and shape of the zooecia at different levels. From Ulrich (1893, pl. 2, figs. 25-26, 28). "Middle third of Trenton Limestone" (Middle Ordovician) St. Paul and Minneapolis, Minnesota, U.S.A.
- H-I. *Clathropora frondosa* Hall. H. Vertical section. I. Tangential section. From Bassler (1906), pl. 21, figs. 6.7. Silurian, Rochester Shale, Lockport, New York, U.S.A. (compare fig. Q).
- J-K. *Escharopora angularis* Ulrich. J. Vertical section. K. Tangential section showing irregular arrangement of the zooecia. From Ulrich 1893, pl. 12, figs. 30-31.
- L-M. *Taenodichthya* (?) *schucherti* Bassler. L. Vertical section. M. Tangential section. From Bassler (1906, pl. 27, figs. 10, 12) Silurian, Rochester Shale. Grimsby, Ontario, Canada.
- N-O. *Ptilodichthya flabellata* Eichwald. N. Vertical section. O. Deep tangential section. From Hennig (1905, textfigs. 20, 21). Silurian (Lower Wenlock), "The Waterfall", Visby, Gotland, Sweden.
- Q. *Clathropora* (?) *alcicornis* Hall. Vertical section of specimen A 20369 (Paleontological Museum, Oslo). Silurian, Rochester Shale, Lockport, New York, U.S.A. Note the difference between this species and *C. frondosa* (figs. H-I).
- The figures taken from Hennig (1905), A-B, E-F and N-O, have been redrawn with the aid of the original thin sections.

support the theory of them being gonozooecia. As mentioned above, they are usually placed in the basal, older part of the colony. At least all the large tubes are found in this part of the zoaria. This corresponds to the position of the gonozooecia of recent cyclostomateous bryozoans, where they occur in the oldest parts of the zoaria. The fact referred to here is important, as it clearly indicates that the tubes have grown together with the zoaria. Consequently the supposed parasites must have been nearly as old as the zoaria. The possibility of the animals having fixed themselves to dead colonies, is therefore excluded in this case. The animals must have killed a single zooid, or simply entered the empty place of a dead zooid in the zoarium, preferably one of the marginal ones, which are the largest. While growing the animal must have bent over to the non-celluliferous side instead of incrusting, and thereby killing the neighbouring zooids. All these facts strongly indicate that the animals in question were highly adapted to living on the bryozoans.

Comparing the tubes to the gonozooecia of recent cyclostomateous bryozoans, it is evident that those of *Arcanopora plumula* are very like the initial stages of the gonozoids of *Hornera lichenoides* (Borg, 1926, p. 393, see textfig. 10F, G). In both species they turned over to the non-celluliferous side of the zoaria.

Very few gonozooecia have until now been reported from Palaeozoic bryozoans. Kettner (1913) described some large pores in a trepostomateous bryozoans from Bohemia, which he interpreted as gonozooecia. McNair (1937) described anomalous, large protruding pores from a *Sulcoretepora* from the Devonian of Michigan. He gives no definite opinion of the purpose of the structures, and only indicates that they might either be due to parasites, or be reproductive organs. The pores in question occur on the old, basal part of the zoaria. They are, like those of Kettner, quite unlike the structures described here, and more resemble the macula of the ceramoporids and fistuliporids.

Borg (1965) regarded these maculae to be brood-chambers, of the same type as that found in some recent stenolaemateous bryozoans. In many old specimens, the maculae appear to be perforated, or there is a pattern of holes, resembling the pattern of maculae in younger specimens. Borg (1.c.) believed this to be brood-chambers where the "roof" had

been broken or resorbed to let the larvae escape. In most cases studied by the author – both on the material used by Borg, from the Silurian of Gotland, and other Ordovician and Silurian materials – the holes appear to be due to boring organisms. Most of these borings are short, straight, and rather unspecific, but some of them are more complex, U-shaped, and in one particular case, from *Diplotrypa petropolitana* (Nicholson, non Pander) in the Middle Ordovician, the borings are due to an *Hicetes*-like worm (cf. Hekker, 1928) similar to that found in the Devonian coral *Pleurodichyum problematicum* (Schindewolf, 1958).

Vine (1889–1890) described some structures, which he interpreted as gonozooecia, from several species of bryozoans from the Permian of Yorkshire. The species belong to sulcoreteporids and rhabdomesids. The supposed gonozooecia of these species are small, bulbous swellings, with an aperture. These, too, are quite different from the structure described by McNair (1937), even if some of the species are related to them. If the bulbous structures in the Permian species are gonozooecia, they definitely are of a cyclostomateous (stenolaemateous) type, whereas the families to which they belong, are regarded as belonging to the Cryptostomata.

Brood (1971) described a similar supposed ovicell in an Ordovician cryptostome. More enigmatic structures, unlike those seen in recent bryozoans, have been described by Ross (1960, *Ptilodichtya* and Dunaeva (1968, a trepostome) as possibly related to reproduction.

In the fenestellids, there are descriptions of two different types of supposed reproductive structures, by Taverner-Smith (1966), which resembles those of cyclostome bryozoans, and by Stratton (1975) which are more like those of the cheilostomes.

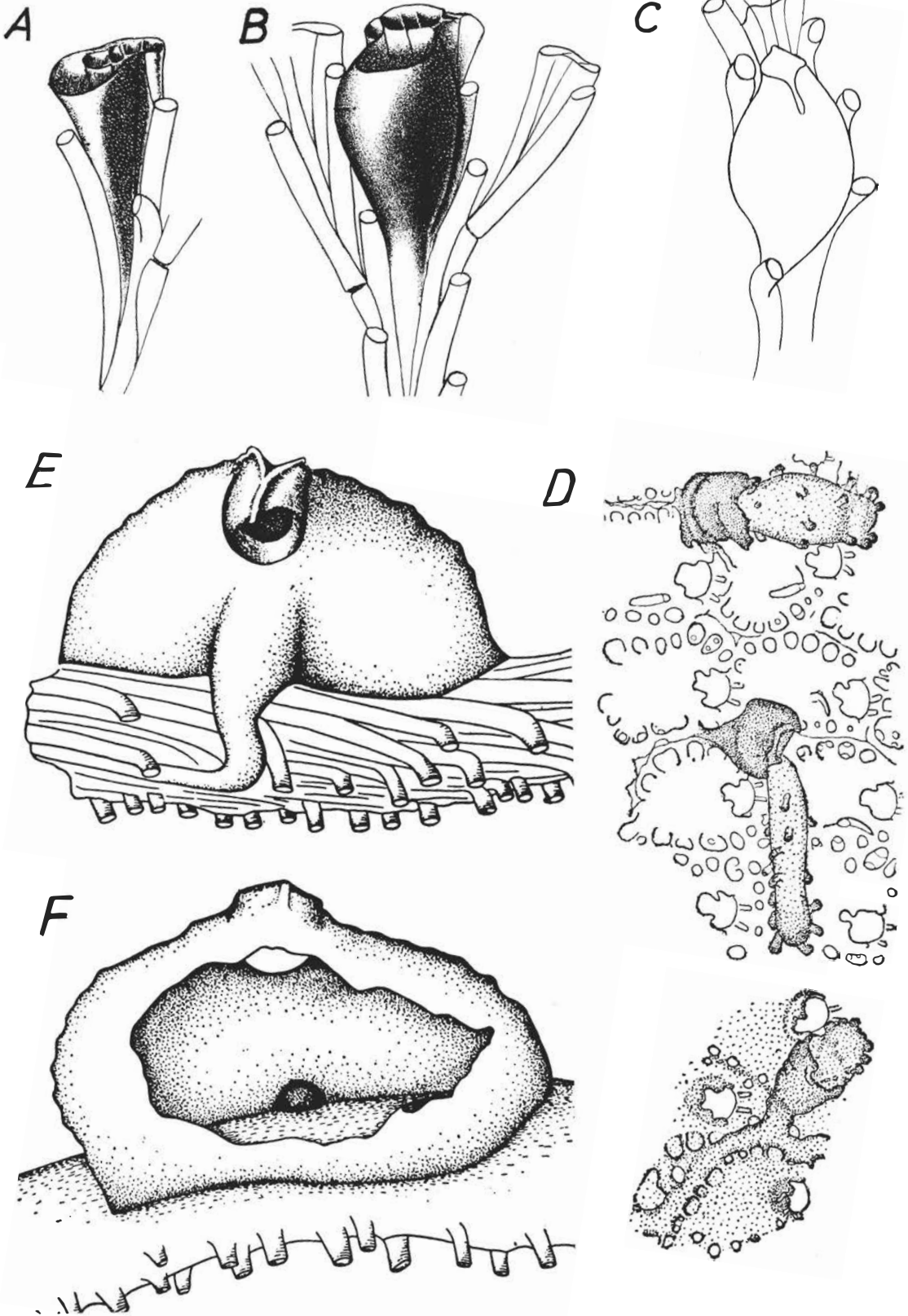
If the structures discussed here are reproductive structures, they are mostly similar to those found in recent cyclostomes, and different from those found in cheilostomes. At present the cryptostomes are referred to the stenolaemates, and not to the gymnolaemates, in spite of their superficial resemblance to the cheilostomes in budding pattern. It may be tempting to use the supposed reproductive structures as further evidence for the present classification, but as mentioned above, there are alternative interpretations, and until the structures have been further studied, they should not be used as evidence for any classification.

Fig. 10. Structures compared to the zoarial appendices.

A–C. Development of the gonozooecia in *Crisia eburnea*. Ab. 25. x. Recent. From Harmer 1893.

D–E. Calcareous tubes formed by the frontal wall of the bryozoans to house the hydroid *Zanclaea protecta*. 50 x. Recent. From Hastings 1930.

F–G. Two early stages in the development of the gonozooecia of *Hornera licheoides*. 25 x. Recent. From Borg (1926, figs. 95–96).



If the tubes are regarded as being remains of other animals, it is difficult to decide whether the animals were parasites or commensals. Since the growth of the bryozoans was at least not visibly retarded by the presence of the tubes, it might have been commensalism. Symbiosis is another possibility, because of the intimate intergrowth, but with no knowledge of the biology of these animals, all suggestions in this direction will be mere guesswork. The more neutral term, synoecic animals, is therefore used in the discussion below.

Only very few data can be found in the literature about similar structures. Hastings (1930) described synoecy between a hydroid, *Zanclaea protecta* Hastings, and several cheilostomateous bryozoans. The hydroids live in a calcareous tube formed by the frontal wall of the bryozoans. These calcareous tubes show some resemblance to the tubes discussed above, but differ from them in being formed by the frontal wall, and not by the apertures. They are also of a more irregular shape than the tubes described from *Arcanopora*. This indicates, that even if these tubes were formed to house hydroids, the relationship between the hydroids and the bryozoans was different to that described above, and probably it was closer in the case of the fossils.

In silicified material it is next to impossible to ascertain if the skeletal material was secreted by the bryozoan, or by an synoecic organism. As seen from Hastings (l.c.) this is not of great importance, since there is evidence for the bryozoans forming the skeleton (tube) for the synoecic organism. Only the cases where the tissues were formed by another animal (cf. pl. 7, fig. 6), would be of interest.

Another interpretation of the structures in question, is that they are remains of synoecic rugose corals, which have lost their septa and tabula secondarily, when they became part of the bryozoan. This interpretation might seem rather hypothetical, but it is supported by the occurrence of amalgamated growth of different bryozoans and rugose corals showing all transitions from accidental growth to real synoecy.

Fischer and Fay (1950, p. 1459) have described a case which may have been symbiosis between a trepostomateous bryozoans and a rugose coral. They state that the septa are only slightly developed in the coral, probably due to the conditions under which it lived.

The author's own unpublished observations on this point, show that *Phaenopora lindstroemi* from the Silurian of Gotland, in some cases has grown together with a structure resembling a rugose coral. The tabula and septa of the supposed coral are very much reduced, and are only found in the lowest part of the animal. In the upper part, the coral tissues are

replaced by similar structures of bryozoan tissue, even forming septa for the coral. This type of synoecy is, however, much more complicated than that from Ojl Myr, since the structures of the supposed coral are replaced by bryozoans tissues, and not simply reduced, as in the zoarial appendices. The structures described here (from *P. lindstroemi*) to house the supposed coral, are formed by a large number of zooecia and mesopores. If the coral tissue was not observed, this structure may have been mistaken for a complex type of brood-chamber (cf. Spjeldnaes, 1981).

An argument supporting the assumption of the zoarial appendices being annelid tubes, is the presence of transversal growth-lines (cf. Pl. 6, fig. 2). Such growth-lines are common among the Tubicolous annelids, but to the authors's knowledge, they are not found in gonozooecia.

Usually annelid tubes are well calcified, even at the apertures. At first, the thin walls of the tubes on the bryozoans therefore seemed to be an important point against the assumption that they were annelid tubes. The extremely thin apertural walls remind one of those of gonozooecia. Theoretically it was possible that a proximal part with an oecistoma which was not calcified, had existed. The proximal part of the gonozooecia is usually calcified last, and not so strongly as the rest of the zoarium. However, one specimen which obviously is an annelid tube, had been found growing on the base of a specimen of *Pachydichtya borkholmensis*. Apart from the spiral growth which is like that of the recent genus *Spirorbis*, this specimen resembles the tubes found on some of the bryozoans both as to the structure of the walls and the dimensions. However, it is possible that the tubes were formed by the bryozoans themselves, and not by the synoecic animal, since no histologic differences can be observed in the structure of the walls. This is the case with some of the similar, recent structures.

Since the biology and soft tissues of the animals are unknown, it is very difficult to give any definite conclusion as to the structures discussed above. If they are found in other localities, the problem might be solved. If the same structures are found on species of *Arcanopora* from different localities of different age and environment, it is probable that they belong to the bryozoans, and must be interpreted as gonozooecia. If, however, the structures are also found on other species, which are not related to *Arcanopora*, they are probably the remains of synoecic animals of some kind.

Arcanopora (?) *wimani*. Only one tube has been found in this species. It is just like those of *Arcanopora plumula*, and is discussed with that species.

Pachydichtya bifurcata. Two tubes were found on a fragment belonging to this species (pl. 7, fig. 6). They differ considerably from the bryozoan as to colour and apparent histological structure. They do not fill the whole aperture. All this, in addition to the resemblance to the *Spirobis*-like annelid tube mentioned above, clearly indicates that the tubes in question are the remains of two Tubicolous annelids, which have settled on a dead zoarium. They evidently have no biological connection with the bryozoan, as they only used it as a substratum. An intermediate case between this simple fixation, and the appendices described above, consisting of bryozoans tissue, is described by Voigt (1956).

Thamniscus orosus. The zoarial appendices in this species (pl. 5, fig. 4) are cup-like, hemispherical, and placed at the end of comparatively short branch near the base of the zoarium. In all well preserved specimens there is a thin, often slit-like aperture at the bottom of the cup. This indicates that the structure was connected to the zooecium at the very top of the branch. In most specimens, the edges of the cup are not preserved, so that the original margin can not be studied. As mentioned above, this type of structure is only found on specimens where the base is preserved, and not on fragments of higher parts of the zoaria. (The specimen on pl. 5, fig. 4 was originally joined to that on pl. 5, fig. 5).

A similar type of zoarial appendices can be found on *Chasmatopora tenella* from Porkuni, Estonia. They differ from those on *Thamniscus orosus* in being of a more elongated, ellipsoidal shape, besides being placed on the celluliferous side of the reticulated zoarium, growing perpendicularly from it. The margin of the apertures are well preserved in some of the appendices in this species, too. The cups are slightly constricted at the mouth, and like the structures on *Thamniscus orosus*, they are generally placed near the base and mostly on old zoaria.

In the same way as with *Arcanopora*, there is no proof of the structures described from the two last species, being gonozooecia or tubes of some synoecic animal. However, it is evident that the shape of the cups, and the constricted apertures in *Chasmatopora*, excludes the possibility of them being annelid tubes. The slit at the bottom of the cups in *Thamniscus orosus* and probably also in *Chasmatopora tenella*, might indicate that these structures really were gonozooecia. However, also in these cases more material from other localities will be required in order to prove that the structures are not the remains of synoecic animals. It is also worth mentioning that the cups, especially those of *Chasmatopora tenella*, are like the initial stages in the development of the gonozooecia of *Crisia* (Textfig. 10, A–C).

Pachydichtya borkholmensis. (pl. 7, figs. 2,5,7). The zoarial appendages found in this species, are fundamentally different to those previously mentioned. They consist of elevated layers of zooecia surrounding an open, deep cup with semi-parabolic outline. The walls are composed of one layer of zooecia, apparently like the normal ones. The mature part of the zooecia have probably been developed after the formation of the cup, since some of the cups have rather thin walls, consisting only of the immature parts of most of the zooecia. One or two of the zooecia are usually larger, than the others at this stage of development, but later on, when the mature parts of the zooecia are completely calcified, too, all the zooecia seem to be of the same size, except for one or two near the base of the structure. These zooecia generally deviate from the normal ones in having a wider aperture. All structures are found on well calcified fragments, and there are none in the less calcified parts higher up on the zoaria. However, only a few of the structures are found in close connection with the base.

These structures might have been brood-chambers (not gonozooecia, since they are composed of many zooecia), housing for some synoecic animal or have served some other purpose. Brood-chambers, consisting of many zooecia, are known from a number of recent bryozoans described by Borg (1926, *Lichenopora*, 1933, Heteroporidae, 1943 *Fasciculipora*), but they all differ considerably from the structures described here. In most of the species described by Borg (l.c.), the brood-chamber is formed inside the zoarium by resorption. In this case, however, the cup was formed outside an already established zoarium by addition of new material.

The possibility of synoecic animals can not be excluded in this case either, even if no similar instances have been described from recent species.

It is also possible that the cup fitted on to a massive object, and that the whole structure therefore acted as a secondary base, supporting the zoarium.

The same type of structure – thin vertical cups, gradually covered by frontally budding zooecia – is found not only in the Oj1 Myr material, but also in a number of pachydichtyids, silicified or not, from the Ordovician and Silurian of both Europe and North America. Regardless of the functional interpretation, it seems to be a stable, and characteristic feature of this group of cryptostomes. Together with other evidence, this will strengthen the author's hypothesis that the pachydichtyids are a separate group, not closely related to other cryptostomes, and possibly with an independant origin within the trepostomes, perhaps from forms like *Peronopora*.

The Articulated Base of the Ptilodichthyonidae

Articulated zoaria are found in several groups of the bryozoans (*Ptilodichthyonidae*, *Arthrostyliidae*, *Cellaridae* and others).

The descriptions given below are, however, chiefly of the feature of the Silurian ptilodichthyonids. The termination of the articulated segments are in some cases hemispherical but usually pointed conical. In young specimens, the pointed base is usually thinner than the rest of the zoarium. As they grow, the articulation is strengthened by a deposition of calcareous tissue, in some cases consisting of transformed mesopores. In the old specimens the pointed base is not confluent with the rest of the zoarium, but separated from it by a ring-like swelling just above the cone (Textfig. 12, C-G).

At least in the Ptilodichthyonidae, the cone is always radially symmetrical. As the cone grows upwards, it also conceals originally bifoliate, slightly higher parts of the zoarium. The upper part of the cone will therefore have a bifoliate central part, and a radial marginal part. The base has radial symmetry only (Textfig. 12, A-B).

Above the cone-ring, the zoarium is usually not so strictly bifoliate, in old specimens it is roughly rounded with irregular longitudinal ridges. In thin sections these ridges are homologous with the basal lamellae of the bifoliate zoarium. This homology is proved not only by their identity in histology, but also by the fact that the specimens split up along the planes formed by these ridges, in the same way as they split along the basal lamellae.

Since the Ojl Myr material is not fit for histological studies, the author has undertaken a detailed study of the basal parts of the Silurian species *Phaenopora lindstroemi* Ulrich, which is introduced for comparison. This species has been described by Ulrich (1890) and Henning (1905).

The cone of the upper, free part of the zoarium is finely longitudinally striated. Usually the cone is not absolutely straight, in most cases the axis is slightly

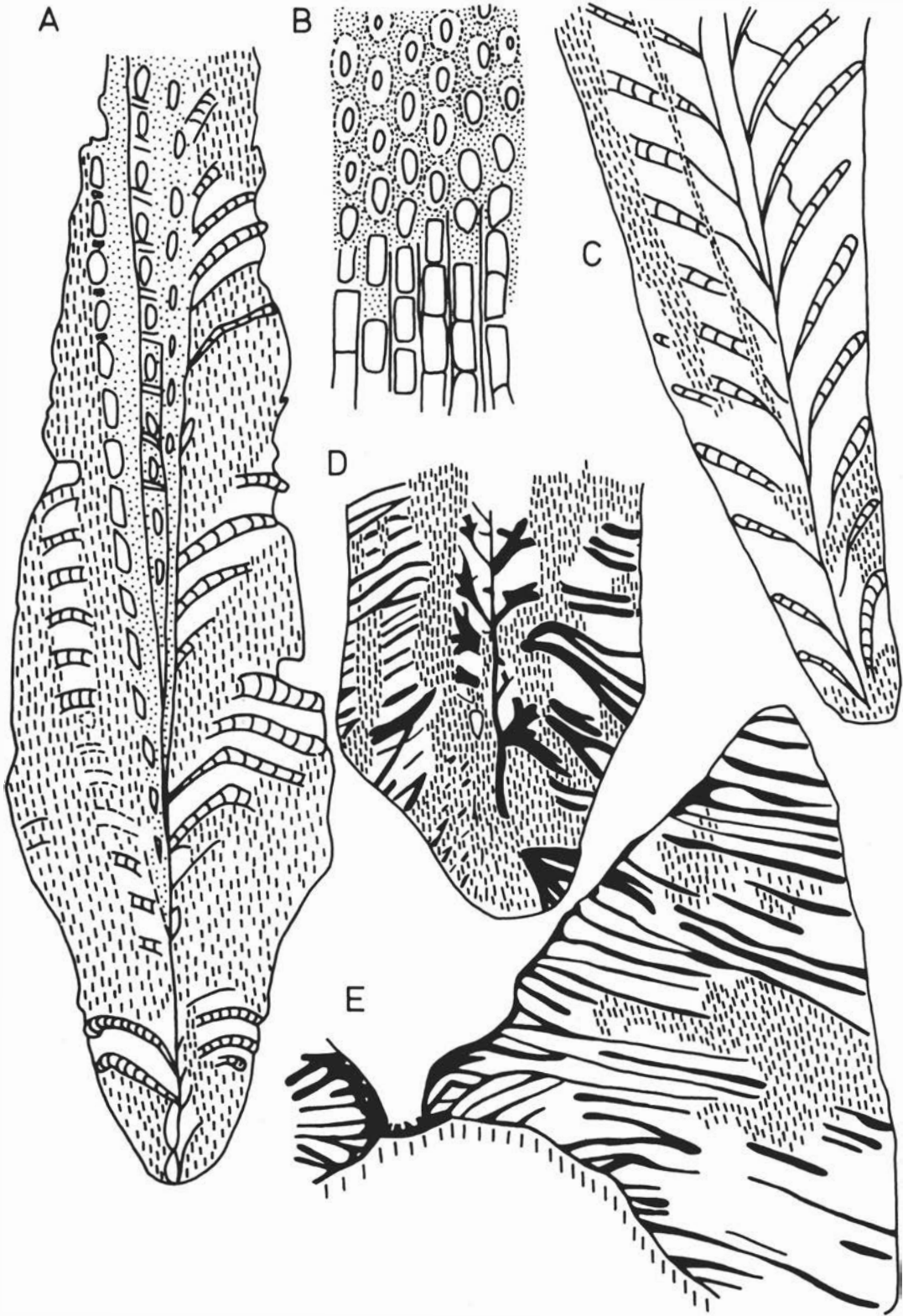
bent (Textfig. 12, C-G). Above the cone-ring, which is developed in mature specimens only, the apertures are obscured. In their place there is a number of mesopore-like openings. It has not been proved that these mesopores are homologous with the ordinary ones. These secondary mesopores evidently had the function of mechanically strengthening the zoarium, and were perhaps formed by specialization of ordinary zoecia. They branch frequently, in contrast to the ordinary mesopores, and form a spongy tissue, which conceals the ordinarily built central part of the zoarium. No ordinary mesopores can be discerned in this secondary tissue.

A study of the pointed base by means of serial sectioning shows that the extreme basal part of the cone is formed by a comparatively small number of zoecia (5–8), placed radially. In small (young) specimens, the bifoliate growth might be discerned some 0.8–1.2 mm above the base. In older specimens, the distance from the basal point to the cone-ring, might be 4–5 mm. The microstructure of the cone is seen from Textfig. 12, A–B, where A is a section through the zoarium just above the cone-ring, and B is a section just below it.

The longitudinal walls have growth-lines. In most cases the number of growth-lines is the same in all walls, both those continuing the basal laminae, and the other ones. (This cannot be seen from textfig. 12 A–B, where only clearly distinguished lines are drawn). Some very prominent lines can be followed all around the zoaria, both in the longitudinal walls and the interspaces. These lines probably correspond to a (seasonal?) change in the rate of growth of the zoarium, or to a periodical regeneration of the secondary mesopores. The latter alternative is quite probable, because of the fact that the degree of obliteration of the structures is remarkably different on both sides of the prominent growthlines. This can especially be seen in Textfig. 12 B, where the mesopores are almost obliterated in the central part, while they are clearly visible in the marginal part, outside the growth-line.

Fig. 11. *Ptilodichthya* and *Phaenopora*. All figures are magnified 22 times.

A, C. *Ptilodichthya lanceolata* (Goldfuss). A. Longitudinal section of a comparatively small and old specimen. Note how the zooecia have turned over (downwards) in the proximal part. The zooecia of this specimen are to a large extent filled with phosphatic matter. Silurian (probably lower Wenlock), Visby, Gotland, Sweden. Thin section Z380. C. Longitudinal section of the basal part of a large specimen with only slightly developed constriction above the pointed base. Note that the lowest zooecial walls are turned downwards, and the tabulae seen in three zooecia (this is a rare feature in this species). This specimen has larger zooecia than that in fig. A., reflecting the increase in size of the zooecia in younger beds. Silurian (uppermost Wenlock) Mulde Marl, Fröjel, Tegelbruket, Gotland, Sweden. Thin section Z269. B. *Ptilodichthya pulmaria* James. Oblique tangential section showing the arrangement of the zooecia in longitudinal rows in the basal part, close to the mesial lamina, and in diagonal rows near the surface (upper part of the drawing). Note also the decrease in size of the apertures higher up, due to the deposition of calcareous tissue. Upper Ordovician (Cincinnatian) Cincinnati, U.S.A. Specimen By 17228. D–E. *Phaenopora lindstroemi* Ulrich. D. Longitudinal section of a free, jointed part of a zoarium. Silurian (uppermost Llandovery or basal Wenlock), Visby, Gotland, Sweden. E. Longitudinal section of the basal incrusting part of a zoarium. Silurian (Wenlock?) Rute Stormyr, Gotland, Sweden (the provenance of this specimen is somewhat doubtful). Figs. D and E are redrawn from Hennig (1905, figs. 7–8), with the aid of the original thin sections.



A remarkable difference between the cone (Textfig. 12 B) and the part just above the cone-ring (Textfig. 12 A), is that the mesopores are much more numerous, smaller and more closely placed in the cone than higher up. The zooecia are filled with clear calcite, indicating that the zooids have grown to a definite size, and then have been transformed more or less abruptly into, or been replaced by secondary mesopores.

Here we come across one of the most intricate problems of the growth of this type of bryozoans. How did the transformed zooids in the basal parts get their supply of food and oxygen? Judging from recent bryozoans, they were probably not able to supply themselves, since they did not have tentacles and intestine. No communication pores have been found between the zooecia, such as in most recent bryozoans. Even if they existed, they were probably very small, and placed in the transversal walls only (Ross, 1960a). The hypotheses that the transportation of food and oxygen took place through a thin ectodermal soft tissues on the surface of the zoarium, is not probable.

The transfer of nutrients and oxygen may have taken place through an external coelom, or through the presumably perforated secondary mesopores (including the spongiöse connecting ring). The rather extensive volumes of calcareous tissue deposited without active zooids, both in the basal part of the free colony, and in the incrusting basal part, may indicate that an external coelom was present.

The question of communication pores in the Palaeozoic Stenolaemata has not been adequately solved. Brood (1965) maintains that there are no communication pores in most Silurian cyclostomes, and the "pores" observed and described from trepostomes are – as far as the author's observations go – due to borings by algae or other small organisms. Ross (1960a) has reported communication pores in the transversal walls of *Ptilodictya lanceolata*, but the author has not been able to duplicate these observations. There are an observation on phosphatic linings in this species which may be taken as an indication of communication between the zooecia in this species (see below, "Phosphatic bodies in bryozoans"), but generally it seems as if the communication between the zooids in the cryptostomates (and perhaps most primitive stenolaemates) took place through an external coelom.

The structure of the incrusting base is the same as that of the lower part of the free portion of the zoarium of old specimens. There are no ordinary zooecia, only secondary mesopores. The ancestrula itself has not been seen, but if we presume that it is placed in the centre of budding, it will be found in the bottom of the inverted cone (Textfig. 13D). No sharply defined longitudinal walls can be seen in the incrusting part, the mesopores are arranged radially or nearly so, from the bottom of the cone. The mesopores bud from the inner surface of the cone, directed outwards and downwards, so that they are in uniformity with the lowest mesopores of the pointed base, which are turned downwards, terminating perpendicularly against the inner surface of the conical part of the free zoarium. Usually the mesopores of the free part are directed upwards in the central parts, and horizontally in the marginal parts of the zoarium.

It appears from Textfig. 11 E, that a certain amount of budding of secondary mesopores also takes place from the basal part of the incrusting base itself. These mesopores have probably budded from the ordinary zooecia in the central part of the incrusting base. The amount of budding of mesopores in this part of the zoarium seems to depend on the topography of the substructure. If the base incrusts a comparatively high point, and consequently grew downwards when the diameter increased, the amount of budding is rather extensive. The mesopores formed in this way, are always placed lower than those formed from the upper, free part of the zoarium. Histologically they are identical, and they also have the same dimensions.

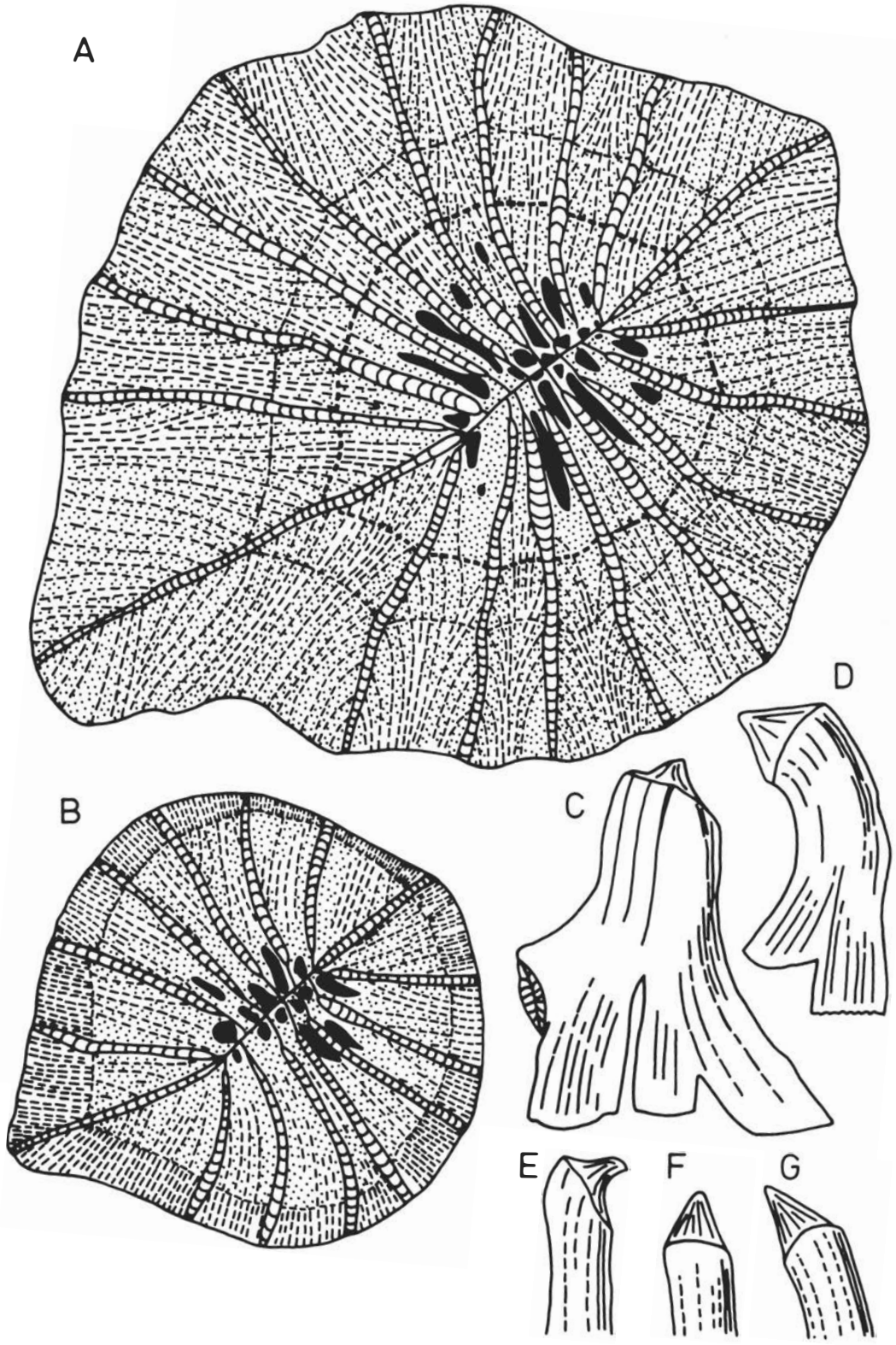
The ptilodictyids will therefore have the following stages of growth: the basal part (incrusting) is radially symmetrical or assymetrical. The corresponding pointed base is radially symmetrical, and the zoarium is polyfoliate or subcylindrical just above the cone, and bifoliate in the higher parts.

Similar features are found in other bifoliate species. In *Pachydichtya holmi* Hennig 1905 (Textfig. 5 G), the bifoliate zoarium is *Trigonodictya*-like in the lower part. In the incrusting base, the zoarium is polyfoliate or radially symmetrical. Some of the species referred to the genus *Trigonodictya*, are probably only the basal parts of *Pachydichtya*. Judging from the figures published of most species of *Trigonodictya*, only comparatively short, thick

Fig. 12. The pointed base in *Phaenopora lindstroemi*.

A–B. Two cross sections of a pointed base A. Section taken just above the cone-ring, B. section taken just below the cone-ring. Note the concentric growth lines, and the radial to polyfoliate symmetry of the marginal parts, where the mesial lamina and the interzooecial walls have the same structure. Silurian (uppermost Llandovery or basal Wenlock), Gustafsvik, Gotland, Sweden. 22x.

C–G. Five sketches of pointed bases, showing variation. C. is a gerontic specimen, D, F and G. are quite normal ones, and E. is a strongly bent specimen. Specimens By 16758a–e. Silurian, (basal Wenlock?) Västkinde, Gotland, Sweden. 3.5 x.



fragments are found of this genus, a fact which supports the author's theory.

Probably the longitudinal ridges correspond to the walls between the primary zooecia in the cone-base of the young specimens. The number of interspaces between the ridges corresponds to the number of zooecia in the primary base, and the formation of the ridges from a limited number of longitudinal zooecial walls (Textfig. 12–13) also supports this theory.

The fact that the radial symmetry moves upwards, might be a purely mechanical adjustment, but it might also be of some genetical significance, either reflecting a tendency towards developing ramose forms, or indicating that the bifoliate bryozoans emanated from ramose ones. In the opinion of the author, the latter view seems to be the most probable, since the base is radially symmetrical (ramose), and the structure of the base is likely to reflect primitive features. However, the base is highly specialized in this group. Its members might descend from ramose forms, but the possibility cannot be excluded that the tendency to forming a radial symmetry in the basal parts of the ptilodichthyids is a secondary one.

This is similar to the situation in graptolites, where in some cases the new character appear in the early astogentic stages, to be suppressed later, or there may be a repetition of the phylogeny in the ontogeny (astogeny). Since the basal, cylindrical part was also mechanically stronger than the bifoliate upper one, this may involve not only phylogeny, but also an element of function and strength.

On the other hand, the radial symmetry is also found in other bifoliate species which do not have a pointed base (*Stictopora*, *Stictoporella*), and in species which are not bifoliate, but have a pointed base (*Bactropora*, *Lioclemella*, *Cyclophaenopora*). Altogether, the author believes that this conical base, even if it has no direct genetical significance, gives the clue to the formation of the bifoliate zoaria, at least among the Cryptostomata.

The bifoliate zoaria probably developed from ramose ones with radial symmetry through the predominance of one pair of the longitudinal zooecial walls. That the basal lamellae are homologous with these longitudinal walls, is also indicated by the fact that there are median tubuli in both of them in the pachydichthyids.

The *Trigonodichtya*-type is probably formed by a similar reduction of the longitudinal rows, resulting in three, instead of one (or two) permanent rows. The fact that there are two types of growth (bifoliate and trifoliate), which both easily might be interpreted as products of reduction of the radially

arranged elements, corroborates the author's theory on the formation of the bifoliate zoarium.

Regarding the mechanics of the pointed base, some peculiarities were discovered in the course of the author's studies. It is evident that the articulations in most cases do not correspond to the movable joints of the vertebrates. This needs a spherical or hinged joint, which is only found in some of the Arthrostylidae, where it may be a secondary feature. The movements of a cone-shaped joint will, of course, be restricted to rotation around its axis, it will not be able to bend to the sides if it is fixed to a corresponding base. However, this is not the case in the ptilodichthyids. After having studied a large number of incrusting and conical bases, chiefly of *Phaenopora lindstroemi* and *Ptilodichtya lanceolata*, the author discovered that the angles of the incrusting base and the zoarium did not correspond. Individual variations occur, but generally the hollow cone of the incrusting base has a larger angle of opening (80–100°), and is usually rounded at the bottom. The cone-bases have a smaller angle (60–80°) and are in many cases acutely pointed. This indicates that the two calcareous parts of the joint did not fit directly into each other. Probably there was a connecting ring between them.

Judging from the recent joint-bearing bryozoans, this ring consisted of an elastic, chitine-like substance, and in that case the joint would be able to move in all directions. Probably the bryozoans were not able to move on their own accord, but the joint certainly acted as a spring, absorbing strong external movements (wave-action, currents and collision with swimming animals). Even if the bryozoans were not able to move on their own accord, they could probably respond to a continuous pressure, and slowly compensate tilting of the body to which the base was attached. The latter feature is indicated by the common occurrence of cones which are bent up to 60° (Textfig. 12 C–E). It is possible that these movements took place by absorption of calcareous and soft tissues in one part of the ring, and deposition on the opposite side, until the zoarium again was established in a vertical position.

The formation of the articulation in the ptilodichthyids is difficult to explain on the basis of the fossil material, because only the calcareous parts are preserved, but studies on recent articulated bryozoans will throw some light on this problem.

Among the recent articulated bryozoans, the joints are usually formed by transformation of the basal parts of one or a few zooids into chitinous tubes (Crisiidae and Scrupocellaridae). The calcareous parts of the transformed zooids are absorbed so that the joint can move freely. From the Cellaridae (*Cellaria salicornia*) Marcus (1940, p.

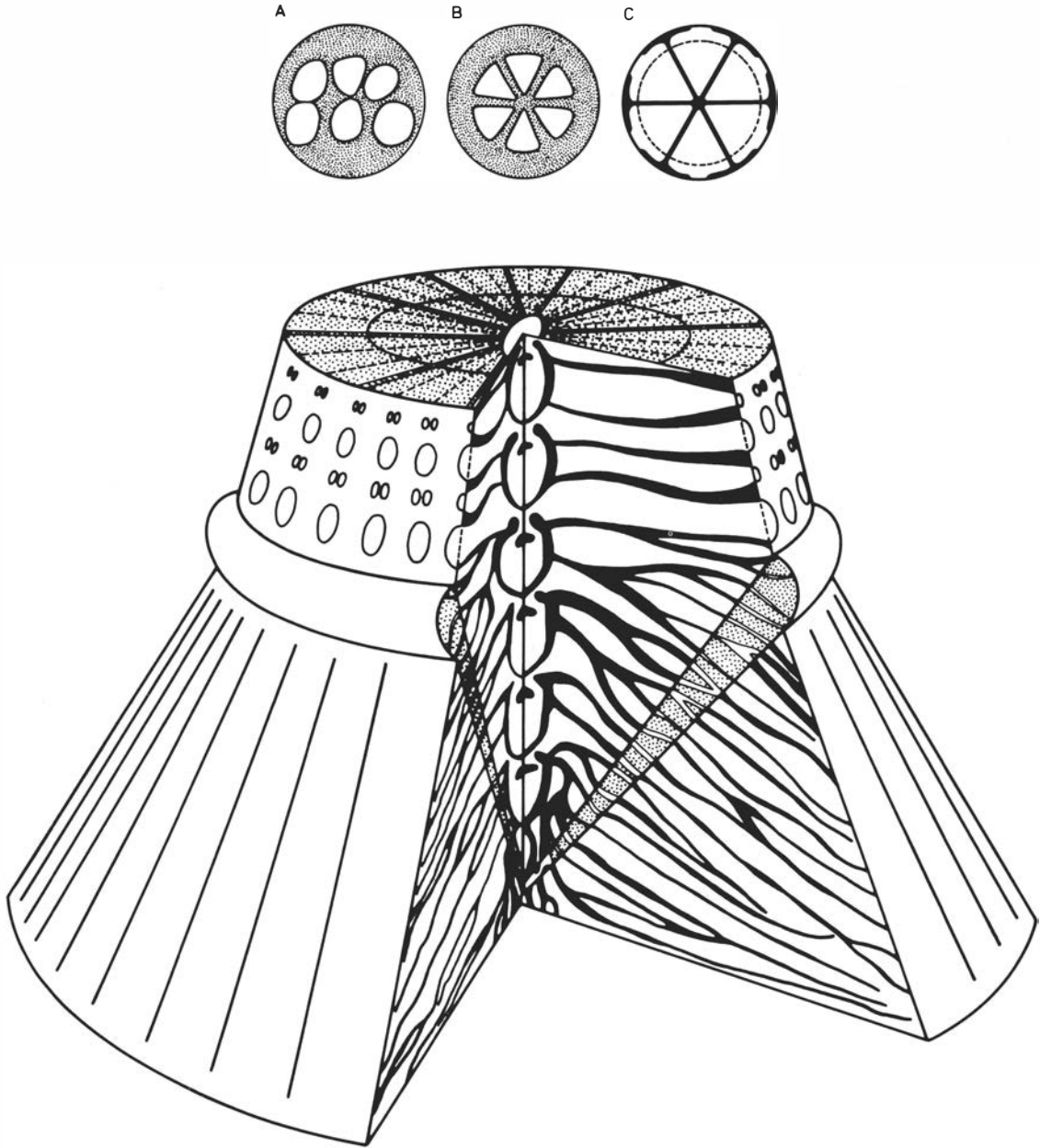


Fig. 13. Reconstructions of the basal parts of *Phaenopora lindstroemi*.

A–C. Hypothetical sections through a young zoarium. A. is a section through the incrusting base, showing the irregular arrangement of the zooecia. B. is a section through the supposed connecting ring between the calcareous parts, showing more regularly arranged zooecia, transformed into chitinous tubes. C. is a section through the apical part of the cone-shaped base of the free part of the zoarium, showing radial symmetry, and the hemisepta (dotted line). The number of zooecia (6) is an average. The actual number observed vary between 5 and 9.

D. Block-diagram of the three parts of the base, the incrusting and the cone-shaped calcareous parts, and the elastic connecting cone-ring. The upper surface of the block is just below the thickening at the base of the cone. In order to make the diagram as clear as possible, the inclination angle of the incrusting part of the sides of the base, is exaggerated. For the same reason, the angle between the cone and the inner surface of the incrusting base is excessively reduced. The cone-ring (dotted on the figure) is drawn as if the individual mesopores continued through it. As mentioned in the text, the cone-ring may as well have consisted of irregularly spongiöse tissue.

The reconstruction is based on specimens from the Lower Visby Marl (uppermost Llandovery) at various localities near Visby, Gotland, Sweden.

157) describes the formation of the joint as follows. The original segment, which was rounded polygonally in cross section with 4–5 rows of zooecia in the basal part, was at first not jointed. The 4–5 rows of zooids grow upwards and increase in number. After a while, the calcareous parts of the basal zooids are split transversally, and the zooids are transformed into short chitinous tubes, forming the connection between the segments.

Returning to the ptilodichtyids, the whole appearance of the pointed base indicates a similar origin. It will explain the different angles of the cones, and thereby also the movements of the articulation (Textfig. 11, D–E).

The elastic ring which united the two parts of the base, probably consisted of short chitinous tubes, partly formed by the splitting of a ring of zooecia, such as in *Cellaria salicornia*. These tubes formed the central part of the ring, uniting the ordinary, radially arranged zooecia in the top of the cone with the ancestral part of the zoarium. This part is seen in the successive diagrammatic cross-sections in textfig. 13 A–C.

The rest of the chitinous tubes were formed by the secondary mesopores, emanating from the higher ordinary zooecia of the cone-shaped base. It is impossible to say whether each mesopore had a separate tube, or if the body fluid passed through spongy tissue, which united all or several mesopores. In fact no mesopores has been observed on either the surface of the cone or the incrusting base. However, the calcareous lamellae coating the contact surfaces, are thin and seem to be perforated by numerous pores. This is probably also the case with the inner surface of the incrusting base. This observation may indicate that the connecting ring was spongy, and composed of separate tubes only in the central part.

These data give the impression that the ptilodichtyids started off as a small ramose stem with incrusting base. The zoarium obtained its bifoliate symmetry through the predominance of one pair of the longitudinal zoecial walls, and by the splitting up of one of the lowest rings of the zooecia, and the transformation of the zooids into chitinous tubes, the zoarium became articulated at the base.

Although there is no doubt as to the taxonomic value of the pointed base, it must not be overestimated. Among the Palaeozoic bryozoans, it is found not only in the Ptilodichtyidae, Arthrostylidae, Nematotrypidae and other cryptostomateous families, but also in Bactroporidae, which may belong to the Trepostomata. In the recent bryozoans, articulation of the same structural type is also found in families belonging to different groups (for instance Crisiidae and Cellaridae).

The existence of the articulation in the different groups, both in recent and fossil ones, makes it very probable that it has developed independently in several groups, and does not indicate any relationship between these groups. On the other hand, the presence of articulated zoaria must also be regarded as an adjustment to life under certain ecological conditions (see chapter "Palaeoecology of the Ojl Myr fauna"), and can therefore be of great value when it comes to interpreting the conditions under which the bryozoans have lived.

Another thing worth mentioning, is that the deposition of elaborate secondary tissue in connection with the articulated base described above, seems to be characteristic of the ptilodichtyids. No other family studied by the author showed the change in direction of growth of the secondary mesopores. In most other cases the increase in size of the pointed base is obtained by distal growth of the ordinary zooecia above and below the joint in the ordinary direction (obliquely upwards).

Phosphatic bodies in bryozoans

Phosphatic "pearls" or globules have been described first from the Silurian species *Favositella interpuncta* (Quenstedt), and has later been found in a number of other species. Earlier authors (Edwards & Haime, 1854; Bassler, 1911) presumed that the globules were siliceous, Sollas (1879) showed that they are phosphatic. The best description of the globules is by Oakley (1934, 1966). They were called "Oakleyit" by Eisenach (1965). The author's studies show that they are rather widely distributed, in all they have been found in 16 species, most of which are cystoporates (ceramoporoids), and cryptostomes. Only three trepostome species have occasional globules, and two of them are constellarids, which form an isolated group among the suborder. Besides the globules there are also other phosphatic bodies in Ordovician and Silurian bryozoans, as described below.

Description of the globules:

Oakley (1934, 1966) has given a detailed description of the globules of the ceramoporids, and only a few new observations can be added to his descriptions. The globules are often of a rather irregular shape, two or more may unite to form a large one. The larger globules are usually of a darker colour. The author has previously (Spjeldnaes, 1950) pointed out the possibility of confusing the globules with corroded fish scales. Like the fish scales, the globules are easily stained by organic dyes, such as malachite green, methylene blue, fuchsine and others. This is a

great advantage both when it comes to identifying the globules with the naked eye, and when studying the microscopical structure, which can be much more clearly seen in the stained specimens than in the unstained ones. As pure apatite does not stain in this way, the colour may reside in remains of the organic matrix such as in the globular calcified cartilage of the lower vertebrates (see below).

The optical data are the same in my material as in that of Oakley, refractive index 1.61, the sphaerolitic cross gives adductor colours in I and III quadrants when the gypsum plate is inserted. Oakley presumes that this proves the birefringence really to be negative, and that the globules are radially cryptocrystalline. This is confirmed by some slightly altered globules, where the radial arrangement of the crystals can clearly be seen (pl. 8, fig. 2). The optics of these globules are the same as the ordinary ones, and as these globules prove to be radially crystallized, the substance forming them definitely has a negative birefringence.

In some cases, the globules are partly dissolved, so that only the central part is left (pl. 8, fig. 7). Because of the optical data and X-ray diagram, Oakley concluded that the globules consisted of dahllite, the carbonate apatite. However, the dahllite is definitely contains fluorine, since it was deposited under marine conditions. This is the case with the dahllite of the conodonts, too (Hass 1944), the conodonts having approximately the same birefringence (1.61–1.6149) as the bryozoan globules.

Most of the globules which the author has studied, are from thin sections, but some have been loosened from the fossils by etching with dilute acetic acid. Some of the material of this type, were originally "by-products" when dissolving limestones from the Silurian of Gotland while searching for vertebrate remains. Among the sectioned material is the type material of Hennig (1906), and sections of approximately 150 zoaria of *Helopora lindstroemi*. A large number of thin sections were made of foreign (non-Scandinavian) bryozoans, chiefly ceramoporids. Out of more than 100 sections of North American ceramoporids, only one single of *Favositella epidermata* contained some circular bodies which might represent dissolved globules (cf. the partly dissolved globules of *Favositella armata* pl. 8, fig. 7). The rock in which the fossil is embedded, is partly dolomitised, and this change in chemical composition might have a connection with the absence of globules. It is probable that many of the globules have been dissolved after the death of the bryozoans, because the concentration of phosphorous ions was so low that the apatite was unstable and therefore was dissolved. In the English material, which chiefly comes from the Wenlock Shale, the

globules are well preserved. From this locality I have seen *Favositella interpunctata*, and possibly also some other species of the same genus.

Types of globules. There are two types of globules. The first type is found in the ceramoporids, and probably also in *Dianulites* sp., a trepostomateous bryozoans from Dalarna. It is the same type as the one which was described by Oakley (1934). The author has attempted to find some rules for the distribution of the globules within the zoaria, and in order to obtain representative material, 8 parallel thin sections were made of one single zoarium of *Favositella armata* from the Silurian of Gotland. The effective thickness of the sections (for counting the globules), is approximately 50 μ , and the distance between each section is 2 mm on the average. Approximately 10 % of the zoarium is left unsectioned, and since 300 globules are found in the sections, the total number of globules in this, avaragely sized zoarium, will be approximately 13 000, with an estimated weight of about 0.55 g. This is about 15 % of the weight of the fossil, and must have been considerably above 20 % of the live-weight of the colony.

The globules observed in the thin sections, were divided into three groups, according to their position in the zoarium. Group I is found at the bottom of the zoarium, below the lowest diaphragm. Group II is on the surface, above the second diaphragm from the surface. Group III is found between the two first groups. The position of the globules in relation to the diaphragms (lying on top of them, below them or between them), was also studied. The globules were again divided into groups, this time according to the type of nucleus, that is whether it was simple or complicated, if it could be seen at all. The results of the studies are shown in table 1:

The table shows the fairly even distribution of the globules in groups I–III, but since group III covers a much larger area than the two other groups together, it is justifiable to conclude that they are concentrated at the bottom and in the surface layers of the zoarium.

Another fact, which cannot be seen from the table, is that the globules found near the surface, generally are smaller than those at the base, and they often occur together (unfused) in one zoecium, while practically all fused globules are found in the basal part. This also indicates that the globules have been formed and grew while the bryozoan was still alive.

The distribution of the globules in relation to the diaphragms, shows that they mostly rest directly upon a diaphragm, and more rarely between or below the diaphragms. The table does not give a true impression of the extent of this, since some of the

Table 1.

Thin section	Number of globules	Positional group			Relation to diaphragms			Nucleus	
		I	II	III	above	below	between	simple	complicated
303	4	0	3	1	3	0	1	—	—
304	36	15	7	14	19	6	11	19	6
305	32	12	14	6	18	6	8	13	4
306	54	20	18	16	28	9	17	13	6
307	35	11	13	12	21	2	12	17	10
308	38	11	17	10	24	3	11	21	7
309	47	12	21	14	27	6	14	21	6
310	54	12	20	23	35	5	14	23	9
Sum:	300	93	111	96	175	37	88	127	38
% :	100	31	37	32	58.3	12.3	29.3	77	23

globules counted as being between and even below diaphragms, really rest upon other globules, which in their turn rest on a diaphragm.

The table shows that most of the globules have simple nuclei, but this is partly due to the fact that some are cut tangentially, with the nucleus outside the section. The author has not undertaken any advanced statistical analyses to correct these figures, but supposing the thickness of this section nearly corresponds to the main diameter of the globuli, the complicated nuclei are underrepresented by approximately 100 %, so that the number of complicated and simple nuclei will be nearly the same. Among the complicated nuclei, are both large, irregular, brown bodies, the "aborted embryos" of Oakley, pl. 2, figs. 9–10, and fused globules, with several nuclei. Other forms of globules have mentioned and figured by Eisenach (1964, 1965). The supposed amoebocytes described by Eisenach (1965, fig. 6) have not been observed in the author's material.

The second type of globules is found in a number of cryptostomateous bryozoans and in *Hallopore varians* and *Fistulipora corticae*. They are much smaller than the globules of the first type, and usually they do not have a concentric structure. In some cases, however, there are up to three, broad concentric bands of different colour. The nuclei are comparatively large, and the globules are often no more than thin shells on the nuclei. The nuclei of this type of globules may be brown bodies, since all transitions between free bodies and globules can be found. They often occur in bryozoans without diaphragms, and there can be up to 20 in each zoecium. They have the same optics as the larger globules, and show the same microchemical reac-

tions of phosphorus. The distribution of the globules of this type was studied on a large number of specimens of *Helopora lindstroemi*, from the Silurian of Gotland. All the primary segments showed globules, sometimes filling a considerable part of the volume of the zooecia. Globules were also found in the secondary and tertiary segments, but not in all of them, and generally there were not so many as in the primary ones. The globules are also generally smaller in the younger segments.

In addition to the globules, the author has found other phosphatic bodies in bryozoans. Some of the cryptostomateous bryozoans which have been studied, show a lining of apatite on the inside of the zooecial walls. This can be clearly seen in *Ptilodichya lanceolata*. In old specimens of this species, the whole basal part of the zooecia is filled by the phosphatic material, which is laminated like the globules, and has the same optical and chemical properties. They are regarded as being homologous with the globules. These phosphatic bodies can be dissolved from the bryozoans, and give casts of the interior of the zooecia, showing muscle impressions (?) and other anatomical features, which cannot easily be seen in thin sections. These linings were described by Eisenach (1964) as a problematic organism, *Phosphatoconus dentiformis*, but Martinsson (1965) realized both their bryozoan nature, and relation to *Ptilodichya lanceolata*, the most common species in the Silurian in Gotland having such linings. It is also important to note that in some cases, the phosphatic linings are confluent, when the zoarium is dissolved in acetic acid. This indicates that there are communication pores between the zooecia, even if they cannot be seen in thin sections.

Ross (1960a) reported communication pores from *Ptilodichtya lanceolata*, but the author has been unable to find them in thin section. The confluent lining must therefore be studied in detail in order to reveal the nature of the connections, which may also be diagenetic.

In *Ptilodichtya* sp. from Ojl Myr, there are both globules and linings, as well as intermediate structures (textfig. 6.F). Similar features are also found in some specimens of *P. lanceolata*.

In *Revalotrypa gibbosa* from the upper Arenig in the Oslo Region, the lining is restricted to the mesopores. No phosphatic linings have been seen in the zoecia themselves.

The formation of the globules. The author agrees with Oakley that the globules are internal products, formed while the bryozoans were alive, but he is not so sure that Oakley's theory on the buffer-effect on the body liquids of the bryozoans explains their formation. This theory was chiefly based on the occurrence of the globules in a single family, and the fact that they are found in many groups, makes it more disputable. However, the possibility of the globules being formed inorganically can be excluded, on the basis of Oakley's convincing arguments, which are confirmed by the author's observations.

Due to the organic matrix, presumably preserved both in the globules and in the linings, it is reason to believe that they were formed by a mechanism resembling that of bone formation, by deposition of apatite on a protein (collagen) matrix.

There may be some doubt as to whether this was a regular feature, a pathological or perhaps gerontic one. In the genus *Favositella* globules are a regular feature, found in all species and all specimens, and both in young and old ones. There can be no doubt that they were a normal part of the physiology in this genus. The same is the case with the linings in a number of Silurian and Ordovician cryptostomes, of which *Ptilodichtya lanceolata* is best studied. In these species, the linings are found in the basal (old) part of most, but not all zoaria, but is regularly absent from the distal (young) part of the zoaria. There are also gradual transitions from linings to globules (cf. textfig. 6.F.). This indicates that the linings grew with the colony, and may be regarded as a gerontic, but not senile character.

In a number of the species where linings and globules have been deposited, they are rare, being found only on one or a few specimens, and they may also be restricted to one locality. Some of these rare, and irregular occurrences may be due to pathological features, or be diagenetic artefacts.

Some recent bryozoans (Silén, 1947) have a considerable concentration of phosphoric acid,

which is used for boring calcareous shells. In some figures, Silén (1947, fig. 57) shows that the phosphorus is concentrated in small rounded bodies, which, however, are smaller than most globules. This indicates that at least some bryozoans might concentrate and incorporate considerable quantities of phosphorus in their metabolism.

Studies of similar bodies in other animal groups for comparison, have given some interesting results. Besides resembling pearls and simple oolites, which consists of calcium carbonate instead of phosphates, the globules are quite like the globular calcified cartilage found in some primitive vertebrates (Örving, 1951, Textfig. 17, 18; pl. 4, fig. 1–2, pl. 8, fig. 3–4). As mentioned above, this resemblance also includes the similar mineralogy and – because of the similar staining – equivalent organic matrix. Also the otoliths of *Chimaera monstrosa* have a similar structure, consisting of clusters of small globules. The globular form is possibly the most simple and primitive manner of deposition of phosphatic matter in the vertebrates.

An interesting point is that the globules must have been deposited mesodermally, and not ectodermally, like the calcareous skeleton. Since a phosphatic, mesodermal skeleton is characteristic of the vertebrates, this may have some information value in the discussion of the phylogeny of the bryozoans. Marcus (1940) mentioned the prochordate affinities of some bryozoan larvae, but most authors (Marcus, 1940; Lemche, 1963; Nielsen, 1979 and others) have stressed the resemblance to annelids or molluscs.

Until the physiological basis for the phosphatic bodies is better known, they may reasonably be regarded as an unexplained peculiarity, rather than the phylogenetically reduced mesodermal skeleton. The only fact which give support to the latter theory, the occurrence of phosphatic bodies in many different systematic groups, and over large time-spans, may be explained as an enzymatic character common to all stenolaematous bryozoans, but expressed only in a restricted number of them.

The linings have been formed in contact with the calcareous wall (the contact is not always precise, as seen in Martinsson, (1965, textfig. 2, bottom), in many cases there are "corners" or calcareous deposits between the primary walls and the lining) and this poses some problems as to the physiology of deposition. The gradual transition between the linings and the globules makes it evident that they were formed by the same physiological mechanism.

The large quantity of phosphate deposited in these bryozoans pose another, ecological problem. They must have acted as veritable "phosphate sinks", and captured a considerable part of the phosphorus in circulation in the environment in which they lived.

As phosphorus is the limiting factor for organic production in many environments, especially the tropical ones, it is possible that the deposition of much phosphate in the bryozoans may have limited the growth of other, competing organisms.

The globules may also be regarded as homologous with the "brown bodies". This theory is supported by the fact that brown bodies and globules never are found in the same zoecium in the large material which was studied by the author. The small type of globules also shows transitional types from pure brown bodies to globules. The globules might fill a considerable part of the volume of the zoecia. This explanation does not contradict, but supplements the suggestions made above. At present, the phosphatic bodies must be regarded as unexplained physiologically and phylogenetically, but of considerable potential value for the study both of the origin, and life-style of the bryozoans.

Palaeoecology of the Ojl Myr fauna

The age of the Ojl Myr fauna does not pose any problems. Wiman (1901) regarded it as belonging in the Estonian Porkuni stage (= Borkholm in his terminology), and this has, with good reason, been accepted by most subsequent authors. Thorslund & Westergård (1938) supposed that it was more related to the underlying Pirgu horizon, but this is probably due to the fact that a number of the characteristic Porkuni species (among them *Pachydichtya borkholmensis*) made their first appearance at the Pirgu level. Both among the bryozoans, as well as other animal groups, there is a dominance of species which are restricted to the Porkuni horizon in Estonia, and there can be no doubt that this is the age of the Ojl Myr fauna.

The species reported from Ojl Myr are, besides Estonia, also known from other Upper Ordovician localities. The formation which shows the closest resemblance is the Upper Ordovician to Lower Silurian Boda Limestone of Dalarne in Sweden. Seven species appear to be in common (*Cyclophaenopora minor*, *C. aff. annulata*, *Hallopora elegantula*, *Enallopora oeilensis*, *Chasmatopora tenella*, *Pachydichtya borkholmensis* and *P. bifurcata*), but these species do not occur together in the Boda Limestone. Brood (1978, 1980) has mentioned some of the Ojl Myr species from other Upper Ordovician localities in Sweden and Norway. His *Hallopora solbergensis* may fall within the limits of variation of the material described as *H. elegans* here, as the variability within the halloporid species is not too well known.

In the author's material, there are also several species, either identical to, or closely related to

those found in Ojl Myr, from the Upper Ordovician of Scandinavia and Britain. There are some species in common with North America, as could be expected from the homogenization of faunas found at the end of the Ordovician (cf. Spjeldnaes, 1978). From the old description of the bryozoan faunas of the Anticosti Island (Bassler in Twenhofel, 1928) there appear to be a striking resemblance with the Ojl Myr fauna. Following the modern description of the Anticosti bryozoans by Ross (1960c, 1961) this resemblance is somewhat less apparent.

The palaeoecology of the Ojl Myr fauna has been studied in detail. The zoarial shape of the bryozoans has been used to determine depth, water movement and sedimentation rate. Stach (1936) was the first to do this systematically. He divided the zoarial forms found in Recent and Tertiary bryozoans in a number of types, with ecological characteristics. This has been refined and extended by Lagaij & Gautier (1965) and Schopf (1969), and the method has been used successfully by i.a. Labracherie (1972, 1972a, 1973, 1973a), Lagaij (1963), Flor (1972), and Thomsen (1976).

Work on the hydrodynamic effects on colony form in related organisms have also been valuable for the interpretations of the ecological features of bryozoan colonies (Abel, 1959; Riedl, 1964, 1966), and this is also the case with recent work on the mechanical properties of the bryozoan skeleton, and its effect on colony shape (Cheetham, Hayek & Thomsen, 1980, 1981).

The depth indicated by the zoarial growth will be minimal, because of the ability of at least some Arctic and Boreal bryozoans to escape climatical changes by migrating to deep waters, where the temperature is fairly constant (cf. Nordgaard, 1918).

It is also evident that in an environment with changing conditions, the zoarial shape will reflect the most stressing condition (sedimentation rate, water movement). A special case is changes which are irregular, and with long intervals (in relation to the growth of the bryozoan colonies), such as heavy storms with 2–5 years interval, which uproot the sessile benthos at a sublittoral level which normally is characterized by moderate water movement. The results of such storms are well known, as large numbers of specimens are thrown up at the beach, both of bryozoans and other animals. These mass mortalities do often hit communities with a low diversity, "pioneer" fauna, very rich in specimens. It appears as if the denuded area is repopulated by the "pioneer" species, in great number. If the interval between the storms is very long in relation to the average age of the bryozoan colony (or other animals), the fauna will normally be a more diverse one, approaching a "climax" community.

It must be expected that the same physical agents have been active in the Palaeozoic, as at present and that therefore the same criteria might be used also when it comes to studying the palaeoecology of the Palaeozoic strata by means of the zoarial growth of the bryozoans found in them. It is evident, however, that the results cannot be as exact as with the Recent and Tertiary ones, since the biology of the animals are practically unknown; most of them belong to extinct suborders.

Since there are some differences between the Ordovician-Silurian bryozoans, and the Recent ones, both in systematics, and budding pattern, it has been necessary to "translate" the ecological groups used by Lagaaij & Gautier (1965) and Schopf (1969). Besides the author's unpublished studies, there are few analyses of zoarial patterns in Early Palaeozoic bryozoa. One of the examples is Bretsky (1970).

1) *Membraniporiform I*. This is the common incrusting form, mostly one-layered. Both in the Recent-Tertiary and old material there are forms which are strictly attached to a solid substrate with the whole under-surface, and forms which have the ability to "roof over" irregularities in the substrate, which may be rather loose, consisting of several different particles. In this way the bryozoans may act as a sediment-binder. This is rare, and occurs only in coarse sediments.

This colonial form is known from environments with considerable water movement, either waves or currents. It is also found in restricted spaces, such as caves under stones and shells, and in cavities in coral reefs (Spjeldnaes, 1975, Cuffey, 1972) and, in fact at any depth, and under almost all conditions. In itself it has a low information value, but combined with a detailed faunal analyses, it may give interesting information, as shown by Thomsen (1976).

The numerous old forms with this zoarial growth do not pose any problems, but there are gradual transitions to massive colonies, either by formation of multi-layered zoaria, or with long zooecia. Some of these massive forms seems to be equivalent to the simple incrusting ones, and others are specialists on less solid bottom. For the purpose of the old forms this group may be subdivided in three, *IA* – strictly incrusting forms, *IB*, "roofing over" forms, and *IC*, multilayer, massively incrusting forms on a solid substrate.

2) *Setoselliniform*. This group with zoaria incrusting in spiral growth on small foreign objects which do not become incorporated in the adult zoarium, has not been positively identified in old material. The few specimens seen are interpreted as juvenile zoaria, either of forms with lunulitiform zoaria, or those belonging to group 1B.

3) *Membraniporiform II*. This group includes the unilamellar zoaria incrusting on flexible, usually flat substrates, possibly algae. It is very common in the recent littoral, but has a low preservation potential, and is rare in fossil material. It has been reported by Voigt (1956, 1981) from the Upper Cretaceous, and the author have seen specimens from an Ordovician black shale, which may belong here. This group consists strictly only of the forms with flexible joints in the walls, but the forms which grew on flexible seaweeds, even if they had no such joints, but small buttonshaped colonies (a mode of growth resembling that of the *Spirorbis*-like worms also growing on sea-weed) are also included here, because they are ecologically equivalent.

4) *Celleporiform*. Lagaaij & Gautier (1965) restricted this group to irregular multilamellar masses on or around a flexible substratum. The old, fossil material is much more diverse, and consists partly of the irregular masses, mentioned under group 1C, those with massive ramose branches, and those with hollow branches. There is, especially among the trepostomes, many forms belonging to this group. Transitions are found from the incrusting masses (group 1C) to ramose forms with a very small incrusting base. As with the vinculariform group, there is a good ecological response to water movement in the type of branching, from very high, thin forms in very quiet water, to short, stubby colonies in more agitated water, as described by Riedl (1966).

There are also dense colonies forming a low, spherical "bush", planar ones, and cork-screw-like spiral ones. The dense colonies are resistant to stress, and the planar ones appear to be adapted to areas with weak currents of uniform direction. The ecological meaning of the spiral ones is unknown.

The hollow ramose branches are often found in species with highly variable zoarial shape, and appear to indicate more agitated water than the massive ones. There is a gradual transition between the perfectly cylindrical, hollow branches, to the irregular ones, often funnel-shaped. The latter can be found in combination with the reteporiform group.

In this group there are also forms which may be related to a flexible substrate. Modzalevskaia (1955) described some sphaerical trepostomes with this type of substrate, quite similar to that found in some of the Ojl Myr forms.

The forms adapted to loose sediments, are mentioned below, under group 11.

As in some of the other groups (5, 6 and 7) there are fossil forms with a basal articulation. Among this group are particularly the nematotrypids, and bacroporids. The ecology of this type is mentioned below.

This group may be divided into four subgroups, 4A. The large, irregular masses, grading into 1C, but being higher, 4B. is the massive, ramose forms, which may be called the *Halloporiform*, 4C. is the more or less regular hollow, ramose forms, and 4D. is the massive, ramose forms with a basal articulation, the *Bactroporiform*.

5) *Adeoniform* is the bifoliate form, which is met with in many cryptostomes, and a few cystoporates and trepostomes. Generally, the group is found in quiet water, but as in many other, there is a gradual transition from the loose, planar or spiral zoaria, where the bifurcations are few and at low angle, to the denser almost spherical, bushy colonies able to resist more mechanical stress. The extreme forms are irregular, with numerous anastomosing branches, forming a complex three-dimensional framework. The latter type is generally found in the high sublittoral, where intermittent wave-action is a problem.

There is also a subgroup with basal articulation. The ecological importance is difficult to estimate, because of the lack of recent analogues. They have probably not swayed with the waves like sea-weeds, but the articulation has probably acted as a shock-absorber, in case of sudden water movements, or collision with swimming animals. The type is generally found on objects protruding over the bottom surface (such as dead corals), as dense marginal "forests" around hard "islands" in otherwise soft bottom areas (mini-reefs, or small coquina heaps), and on hard-grounds. In all cases they are associated with moderately resistant forms (hollow-ramose, incrusting, and low, bushy bifoliate), but not with forms indicating strong agitation.

A further subgroup is the forms with a large, reticulate planar frond, and basal articulation. Those which have the same frond, but an incrusting base, can be regarded as a special case of the ordinary, bushy bifoliate colony, and do not seem to differ from them in ecological requirement. The type with articulated base, which is quite common in some horizons in the Middle and Upper Ordovician, appears to be indicative of highly agitated water. They are found in areas where the sedimentary structures indicate much turbulence and sediment movement. Some of them had a long "shaft" below the planar frond. This would seem to be hydrodynamically inexpedient, but may be a response to sediment movement. One of the few recent bryozoans with a similar, bifoliate-reticulate colony, *Retiflustra* Levinson, is weakly calcified, flexible, and also adapted to life in agitated water, together with lunulitiform species.

The group may therefore be subdivided into: 5A (*Stictoporiform*), normal bifoliate, solidly

attached. 5B (*Ptilodictyiform*), articulated basally bifoliate, often sparsely branching. 5C (*Proaveliform*) a planar, bifoliate reticulated frond with basal articulation.

6) *Vinculariform*, with erect zoarium consisting of dichotomous subcylindrical branches, firmly attached by a calcareous base. This form is generally indicative of deep and quiet water, with low sedimentation rates. Both among the recent and fossil forms, there are low, bushy subsphaerical colonies (rarer than in groups 4B and 5A), and planar, arborecent (three-dimensional, loosely branching) and spiral colonies. The models introduced by Riedel (1966) are particularly useful in this group. Systematically but not ecologically, there are differences between the forms with radial symmetry, and those which have zoecia only on one side.

This group is more diverse, and numerous than it may appear from the literature, since these small forms have been overlooked in many faunas. They are more apparent in silicified faunas-like the Ojl Myr, and are ecologically equivalent to the recent ones. Also in this group, there are forms with an articulated base. The information available at present is insufficient to see if the articulated forms lived in more agitated waters than the rigidly attached ones. The available material seems to indicate a normal ecological association.

The group may be subdivided in 6A, the *thamnisciform*, which are rigidly attached to a solid substrate, and 6B, the *nematoporiform*, with an articulated base, but otherwise like the rest of the group.

7) *Reteporiform*, with erect, strongly calcified zoarium, fenestrate or reticulate, firmly attached to a solid substratum by a calcareous base. Almost all recent representatives belong to one single systematic group, whereas the fossil ones are much more diverse. The group is supposed to indicate more agitated water than the vinculariforms (Group 6). In most cases, the colonies are found in agitated environments, but in sheltered places within them, such as below dense sea-grass vegetation, in crevasses and caves, or below sheltered cliffs.

The fossil representatives are especially the fenestellid, which are less folded and contorted than the recent ones, but more strengthened by appendages and extra calcareous tissue. There are also a number of different forms, belonging to three suborders, which are generally placed in the "family" Phylloporinidae. Some of the species in this group have a rigidly fixed colonial growth pattern, but in others, a transition to the vinculariform type can be seen even within one single colony. This, and the association in which the fossil representatives are found, indicates that they are indicative of somewhat quieter waters than the recent representatives. There are very few

representatives in this group with an articulated base, and they may rather be aberrant representatives of group 9.

8) *Petraliform*. This growth form has not been positively identified from Early Palaeozoic bryozoans, and is therefore not considered here.

9) *Cellariform*, with erect, flexible-jointed, calcareous zoaria, internodes consisting of numerous zoecia. The recent ones are said to be attached by rootlets. In the fossil forms the mode of attachment is unknown; it may be similar to the basal attachments of the ptilodictyids. The fossil representatives seem to be ecologically precisely equivalents of the recent ones. The group is not often met with in the Early Palaeozoic, but when it occurs, it is often found in enormous numbers, indicating these bryozoans formed dense growths, such as the recent ones.

Most of the fossil forms are radially symmetric, but there are also examples of one-sided forms, and bifoliate ones.

10) *Catenicelliforms*. This growth form has not been positively identified among Early Palaeozoic bryozoans, and is therefore not considered here.

11) *Lunulitiform*. These bryozoans have normally a biconvex, one-layered zoarium which is free on the sediment surface. The recent representatives form a closely knit group, with a peculiar ecology, and mode of life (cf. Lagaaij, 1963; Cook & Chimonides, 1978 – further references herein). The fossil forms are not so advanced, but are more diverse, and the diagnosis of the group is extended to include all bryozoans which are free on the sediment surface. Some Ordovician trepostomes like *Mesotrypa lens* (McCoy) have biconvex, thin zoaria, and is generally found in dense, monospecific populations in clean sand or silt, indicating a mode of life resembling that of the recent lunulitids. Other forms, with a flat base, and variable colonial shape, from thin, flat to "hemispherical", or rather bun-shaped, are common, also as monospecific, but rich faunas occurring in shales. This indicates that these forms were able to live on clay surfaces, under conditions in which other bryozoans could not live, either because they were unable to attach themselves to the bottom, or because the sedimentation rate was too high. The most common species of this group in the Scandinavian Middle Ordovician, is *Diplotrypa petropolitana* Nicholson, which is also highly variable in shape and size.

It is evident that only a statistical study of a comparatively large material from one single layer (time horizon) will give reliable results with this method. Many modifications might occur, and considerable detailed studies on the distribution of both fossil and recent bryozoans will be required to obtain

sufficient material for comparison. A number of successful examples (Labracherie, 1972, 1972a, 1973, 1973a, Lagaaij, 1963, Flor, 1972, and Thomsen, 1977) show how these methods can be used for material from the Cretaceous to the Recent. According to the author's experience, the method will in most cases give the same results as a careful study of the lithology of the sediment. The method is therefore regarded as being useful also for faunas from the Early Palaeozoic, when the reservations mentioned above are considered. There has been much discussion – especially among older authors – of the systematic value of the zoarial shape. The author's observation supports the really rather trivial conclusion, that the zoarial shape is rigidly genetically fixed in some species, restricting them to the environments in which this shape is optimal, or compatible. In most other species, the zoarial shape is flexible, often drastically so, and reflects the ecological conditions under which the colony has grown. One of the results of this is, that it is possible to make an ecological analysis of a bryozoan fauna based on zoarial shape, even if the systematics of the fauna is incompletely known. This can be done as a first approximation, but when a more detailed analysis is demanded, the systematics must be studied, in order to obtain a maximum of ecological information.

The composition of the bryozoan fauna of Ojl Myr, is as follows:

The picture of the ecology obtained from these studies, is as follows: Undoubtedly calm waters. Only 3,5 % of the specimens could have endured more than very slight currents or wave-action.

Most of the colonies have a loose, open pattern of branching, most of them are spiral, and a few planar. The depth must have been deeper than the wave-base with a good margin, but if the stems on which a number of the bryozoans were attached was of algal origin, the fauna must have lived in the photic zone. The depth was therefore probably moderate, but more than 20 metres. The bottom was soft; 75 % of the specimens were fixed to protruding cylindrical bodies; 8 % were specially adapted to life on soft bottom, and the remaining 17 % were attached to hard parts of other fossils.

The factor which limited the direct settlement on the bottom may either be the softness, or a high sedimentation rate, or a combination of both. *Ceramopora corniforme* appears to have an adaptation to a high sedimentation rate, but the generally thin sediments in the Baltic Upper Ordovician do not indicate that this was a common feature.

At this point, the "stems" on which the major part of the bryozoan grew, must be mentioned. The diameter of the stems varies from 0.2 to 1.5 mm. They seem to be circular in section. None of the

Table 2.

Species	Number of specimens	%	Type of zoarium	Type of base
<i>P. borkholmensis</i>	757	59	5A	incrusting
<i>Arcanopora plumula</i>	139	11	6A	„
<i>Hallopora elegantula</i>	101	8	4B	„
<i>Arcanopora wimani</i>	99	8	6A	rhizoidal
Ramose Trepostomata	56	4,5	4B	incrusting
<i>Thamniscus orosus</i>	35	3	6A	„
<i>Enallopora oeilensis</i>	27	2	6A	„
Incrusting species	27	2	1A	„
Species with pointed base	18	1,5	5B	articulated
Reticulated species	3	0	7	incrusting

other fossils described from the Ojl Myr fauna seems to have produced these tubes. They might not have been silicified, and have been dissolved when the bryozoans were etched out of the rock. The author suggests that the tubes are the remains of algae corresponding to modern sea-weed. Voigt (1956, 1981) has used the basal parts of bryozoans for a study of the fossil marine plants which they used as a substratum, and Modzalevskaia (1955) has reported similar, tube-like attachments by other Ordovician bryozoans, and suggested that they are of algal origin. The stems were not flexible, since they were covered by the thin calcareous membrane of the base for several millimetres (up to six times the diameter of the tube). Branching of the tubes has not been observed. The tubes have helped to support the bryozoan, which could not settle directly on the mud of the bottom. If they were algae, they may have supplied the bryozoans with oxygen. The species with a rhizoidal base, probably did not live directly on the calcareous ooze forming the bottom. They seem to have attached themselves by means of the radicles to the same cylindrical objects on which the other species incrustated. This method of attachment might have been an advantage if the cylindrical bodies or parts of them were flexible.

Many of the specimens are complete, and this, in addition to the evidence of the sedimentology, indicates that most of the specimens were broken by diagenetic pressure, or by accidents during life, and not by transportation, predation or wave-action.

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PLATES

Plate 1

- Figs. 1–3. *Enallopora oeilensis* (Wiman).
1. Fragment of holotype (Bz 1018), showing heterozooecia (hz) and ordinary zooecia. 27 x. Ojl Myr, boulder 17.
 2. Zoarium of the spiral type (Bz 1020), 6,2 x. Ojl Myr, boulder 58.
 3. Zoarium with the usual type of branching (Bz 1019), and with a secondary attachment (sb). 6,2 x. Ojl Myr, Boulder 53.
- Figs. 4–5. *Ceramopora corniforme* sp.n.
4. Holotype (Bz 1002) seen from the side, 5 x.
 5. Holotype seen from above, 10 x. Porkuni Stage, Porkuni, Estonia.
- Fig. 6. Indet. cyclostomateous bryozoan, showing free, tubular zooecia. (specimen Bz 1022) 7 x. Ojl Myr, boulder 73.
- Fig. 7. *Ceramopora* sp. Showing the structure of the walls. 24 x. Specimen Bz 1003. Ojl Myr, boulder 73.
- Fig. 8. *Ceramopora hennigi* sp. n. Holotype (Bz 1001). Complete zoarium with eccentrically placed initial part. 6 x. Ojl Myr, boulder 73.

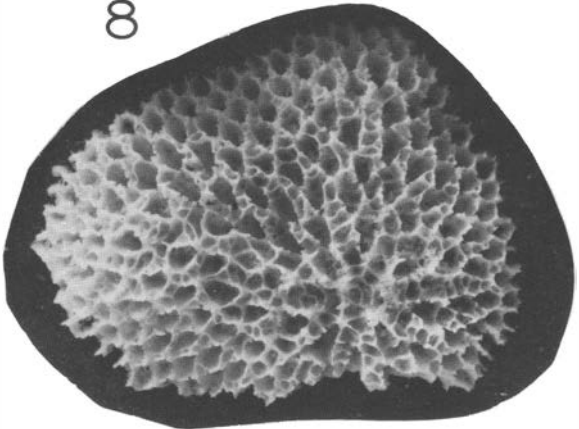
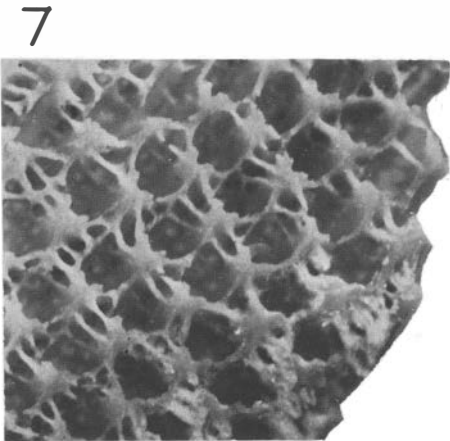
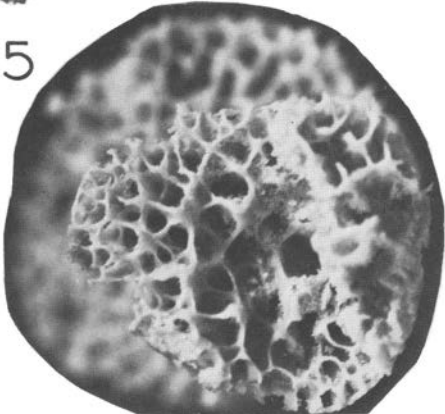
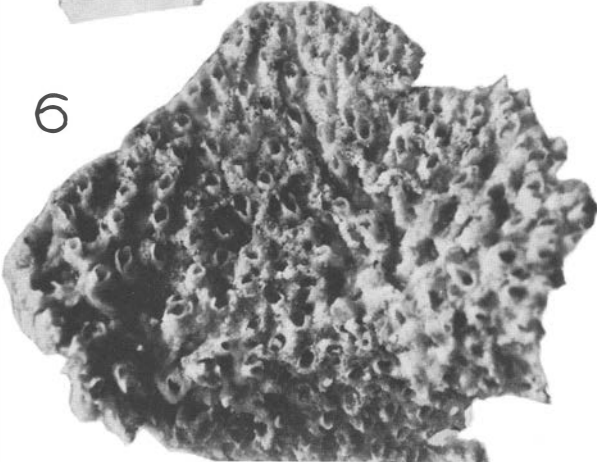
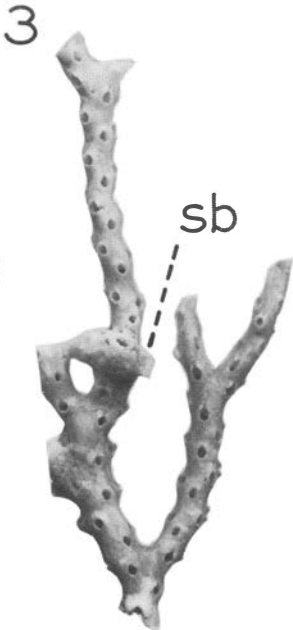
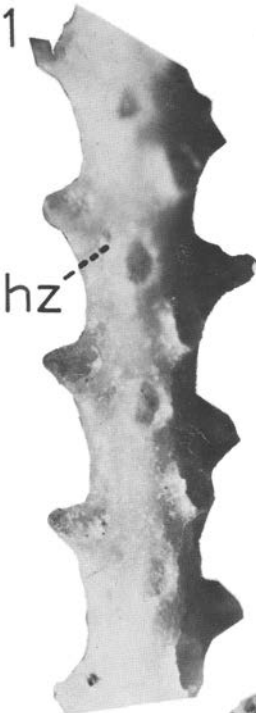


Plate 2

- Fig. 1. *Cyclophaenopora robusta* sp.n. Holotype (By 16872). A fragment of a stem with the adhering basal part of a young rugose coral. 7 x. From the Middle Ordovician Kullsberg Limestone, at Amtjärn, Dalarne, Sweden.
- Figs. 2-3, 5. *Lioclema* (??) sp. (specimen Bz 1007).
2. The celluliferous side of one of the monofoliate branches. 7½ x.
 3. The surface of the main stem. 7½ x.
 5. The whole specimen, showing the manner of branching, and the non-celluliferous sides of the branches. 4 x. Ojl Myr, boulder 29.
- Fig. 4. *Bactropora solida* sp.n. Holotype (Bz 1008), showing the pointed base, and small apertures surrounded by acanthopores. 6½ x. Ojl Myr, boulder 7.
- Fig. 6. *Cyclophaenopora annulata* sp.n. Holotype (Bz 1004), a fragment of a stem, showing the badly preserved surface, and annulations consisting of bands of mesopores. 6½ x. Ojl Myr, boulder 17.
- Figs. 7-8. *Cyclophaenopora minor* sp.n.
7. Fragment of a specimen (Bz 1006), where the surface is well preserved. 6½ x. Ojl Myr, boulder 24.
 8. Holotype (Bz 1005), showing the pointed base. 6½ x. Ojl Myr, boulder 24.
- Figs. 9-10. Irregular phosphatic globuli from *Favositella armata* (Hennig). 33 x. From the Silurian of Gotland, probably from the Visby Marl (lowest Wenlock). For discussion of provenance, see explanation to plate 8, figs. 7-8). Thin section Z311.

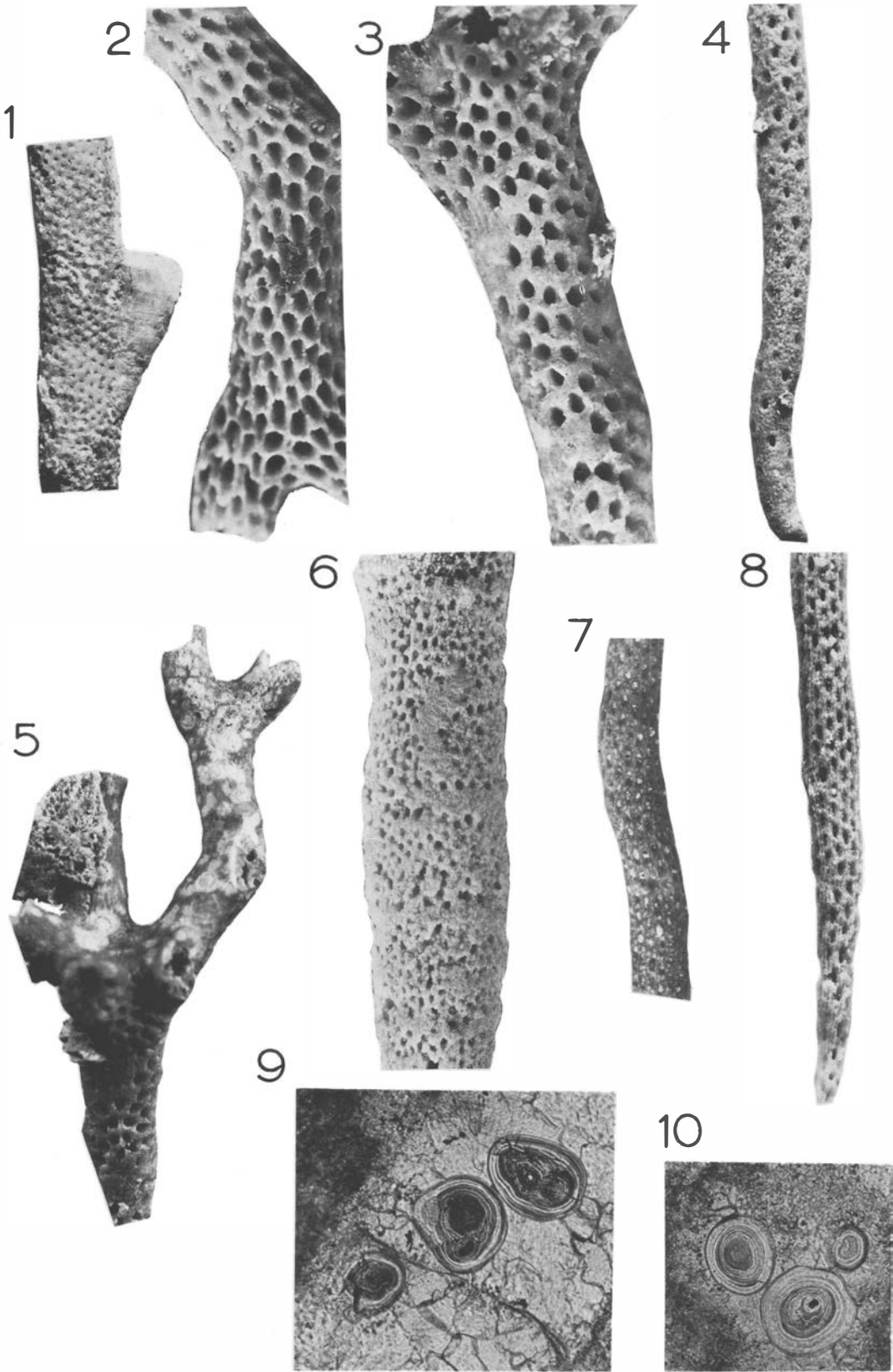


Plate 3

- Figs. 1–2, 6. *Hallopore elegantula* (Hall).
1–2. Fragments of stems showing the branching, and numerous mesopores. 5 x. Ojl Myr, boulders 45 (fig. 1, specimen Bz 1009) and 6 (fig. 2, specimen Bz 1010).
6. A young incrusting specimen, probably belonging to this species. 5½ x. specimen Bz 1011. Ojl Myr, boulder 53.
- Figs. 3–4. *Homotrypella* sp. a.
3. Type, part of a zoarium showing the branching. Specimen Bz 1012.
4. Young, club-shaped zoarium, showing the base. Specimens Bz 1013. Both specimens 5 x., from the uppermost Ordovician Porkuni Stage at Porkuni, Estonia.
- Fig. 5. *Homotrypella* sp. b. Type, specimen Bz 1014. 5 x. From the uppermost Ordovician Porkuni Stage at Porkuni, Estonia.
- Fig. 7. Indeterminable trepostomateous bryozoan. The largest specimen found, which show the celluliferous side, and the shape of the zoarium. 4 x. Specimen Bz 1015. Ojl Myr, boulder 45.
- Figs. 8–9. *Eridotrypa peculiare* sp. n. Two views of the holotype (Bz 1016), showing the noncelluliferous band, which is rather broad on this specimen, and the manner of branching. 4½ x. Ojl Myr, boulder 73.
- Fig. 10. *Orbignyella* (?) *expansa baltica* Bassler. Surface of the only specimen preserved, which shows the angular apertures of different sizes. 5.5 x. Specimen Bz 1017. Ojl Myr, boulder 6.

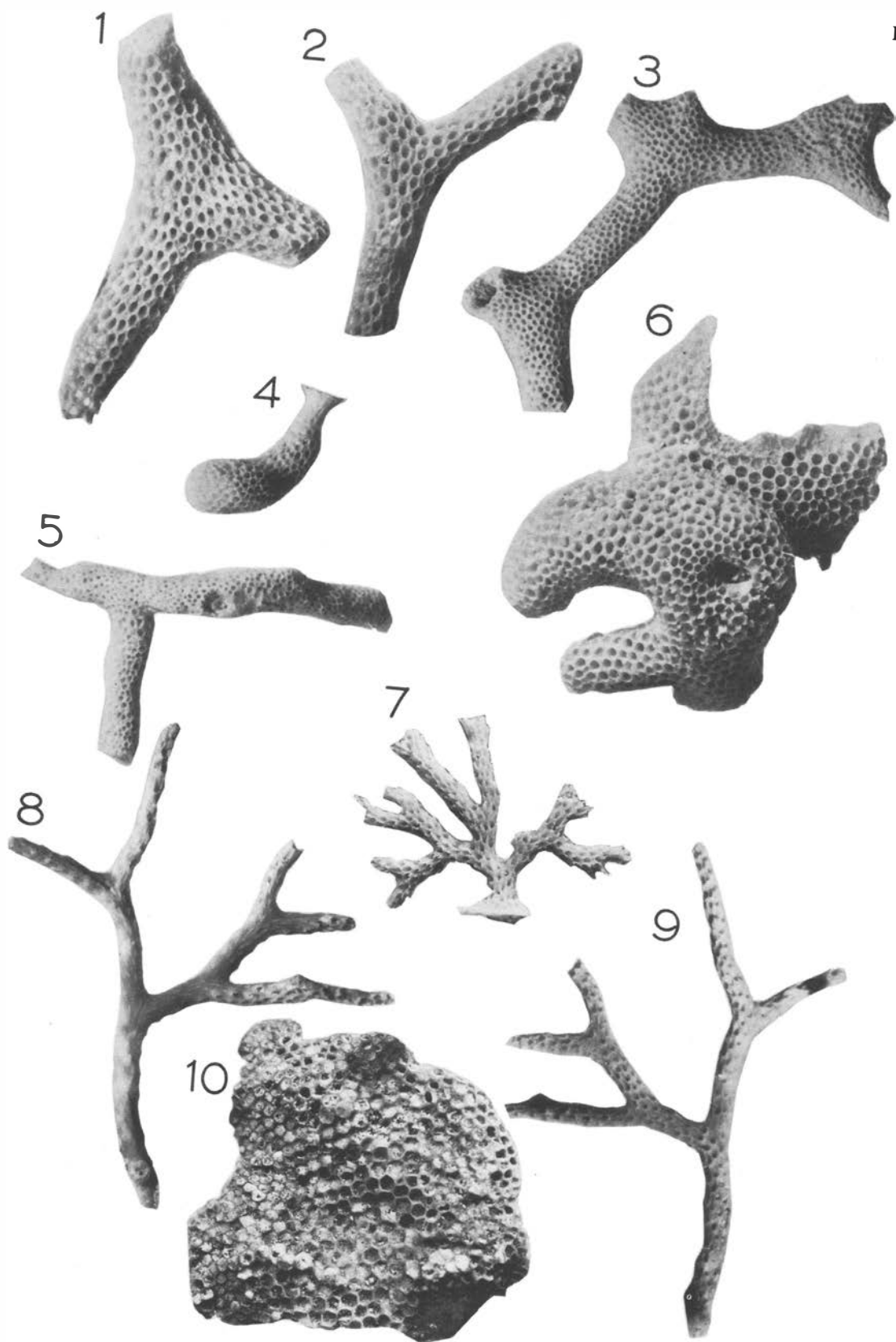


Plate 4

- Figs. 1, 3, 4, 8. *Pachydichtya borkholmensis* (Wiman).
- 1, 4. Specimen with root-shaped bases, formed by long, noncelluliferous tubes, possibly extensions of zooecial apertures. The upper part of the specimen in fig. 1., is overgrown with base of another bryozoan. 5 x, specimens Bz 1044 (fig. 1) and bz 1045 (fig. 4). From the uppermost Ordovician Porkuni stage at Porkuni, Estonia.
 3. Lectotype, showing the manner of branching, and the disc-shaped base with irregularly scattered zooecia. 5 x. Specimen bz 1048. Ojl Myr, boulder 53.
 8. Young specimen showing growing edge with only slightly calcified transversal (single) and longitudinal (double) walls, and solid protuberances, mostly from the non-poriferous margins. 5 x. Specimen bz 1018. From the Uppermost Ordovician Porkuni Stage at Porkuni, Estonia.
- Fig. 2. *Ptilodichtya irregularis* sp. n. Holotype, showing the undulating edges of the branch. 5 x. Specimen bz 1011. From the uppermost Ordovician Porkuni Stage at Porkuni, Estonia.
- Fig. 5. *Stictopora* sp. Fragment of branch, showing large non-poriferous margins, and many rows of zooecia. 5 x. Specimen bz 1020. From the uppermost Ordovician Porkuni Stage at Porkuni, Estonia.
- Fig. 6. *Ptilodichtya* sp. Specimen, showing the narrow branches, and the thick longitudinal walls. 6 x. Ojl Myr, boulder 45. Specimen bz 329.
- Fig. 7. *Ptilodichtya* cf. *nitidula* Billings. Comparatively well preserved specimen, showing branching. 5 x. Ojl Myr, boulder 53. Specimen 1021.
- Figs. 9–10. *Graptodichtya perelegans* (Ulrich).
9. Young specimen. 5 x. Specimen bz 1023, from the uppermost Ordovician Porkuni Stage at Porkuni, Estonia.
 10. Mature specimen, 5 x. Specimen bz 1024, Ojl Myr, boulder 45.

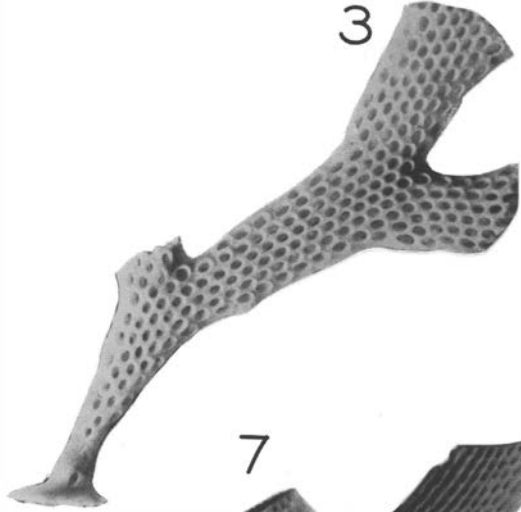
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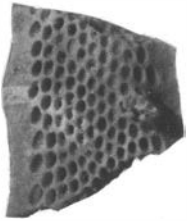
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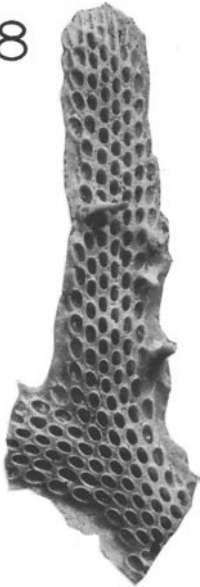
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Plate 5

- Figs. 1–5. *Thamniscus orosus* Wiman.
- 1–2. Both sides of the lectotype, showing the keel on the reverse side, and the arrangement of the zooecia on the frontal side. 5 x. Specimen bz 327. Ojl Myr, boulder 53.
 3. Well preserved specimen showing slightly elevated zooecial apertures, with small acanthopores at the edges. 10 x. Specimen bz 1025. Ojl Myr, boulder 37.
 4. Non-celluliferous side of a specimen, showing only slightly developed keel, and zoarial appendage (ap). 6 x. Specimen bz 1026. Ojl Myr, boulder 37.
 5. Specimen with tubularly incrusting base, with scattered zooecia on the incrusting part (*iz*). 6 x. Specimen bz 1027. Ojl Myr, boulder 37.
- Fig. 6. *Arcanopora plumula* (Wiman). Specimen with three more or less fragmentary zoarial appendages (ap), showing their shape, and position in this species. 7 x. Specimen bz 1028. Ojl Myr, boulder 53.
- Fig. 7. *Chasmatopora* sp. Fragmentary zoarium with cardiform fenestrules. 7 x. Specimen bz 1027. Ojl Myr, boulder 6.

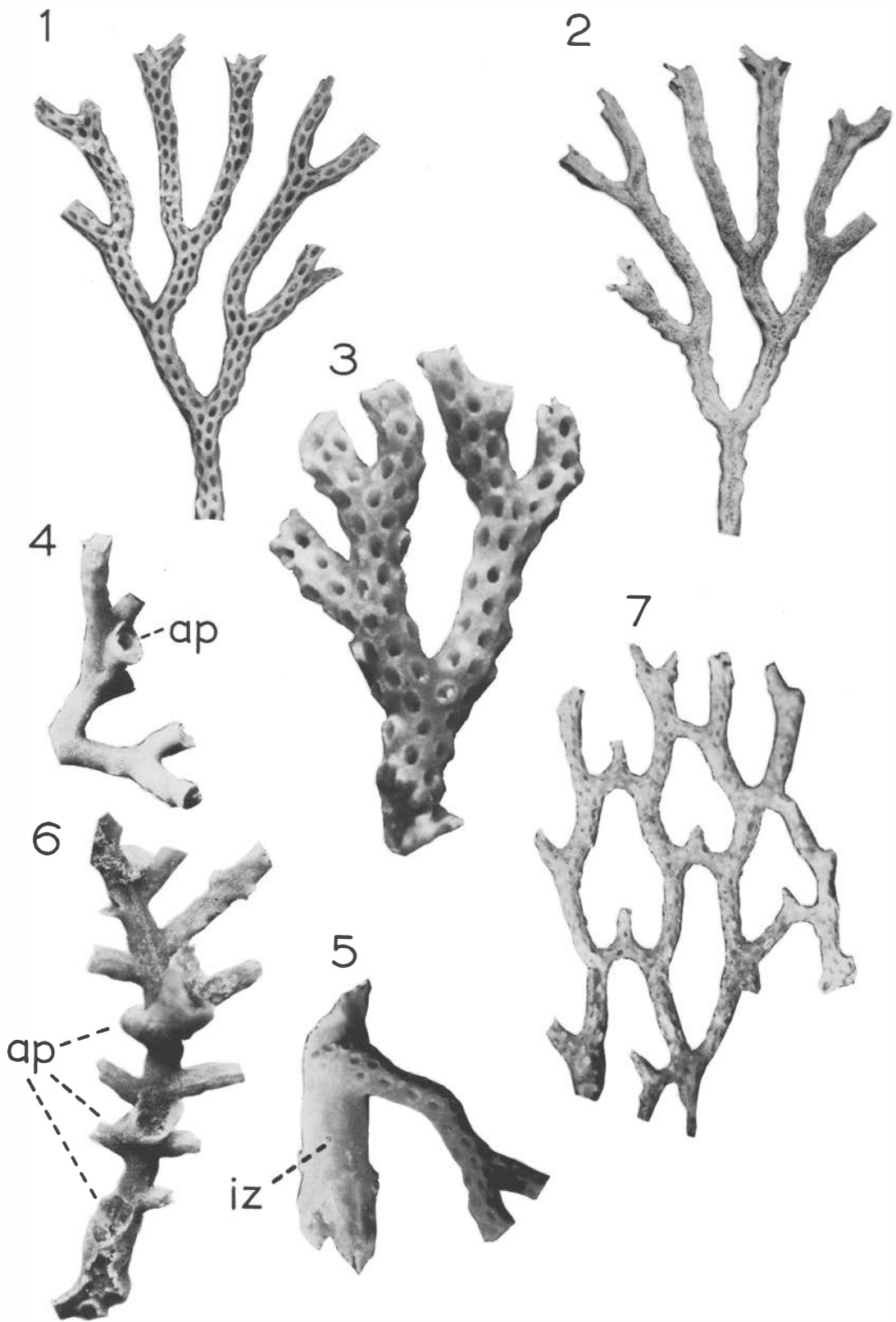


Plate 6

Figs. 1–4, 10. *Arcanopora plumula* (Wiman).

1. The lectotype, the largest specimen preserved, showing secondary branching, five rows of zooecia, and secondary calcareous incrustations on the base. 3 x. Specimen bz 336. Ojl Myr, boulder 85.
- 1–2. Two specimens from the uppermost Ordovician Porkuni Stage at Porkuni, Estonia, showing the more slender branches of the specimens from this locality. One of them (fig. 2) has a zoarial appendage (*ap*). Specimens bz 1046 (fig. 2), 6.4 x, and bz 1047 (fig. 3). 7.2 x.
4. Typical, young specimen of this species. 5 x. Specimen bz 1030. Ojl Myr, boulder 45.
10. Young specimen, showing incrusting base, secondary attachments (*sb*) and secondary branching. 5 x. Specimen bz 1031. Ojl Myr, boulder 45.

Figs. 5–9. *Arcanopora* (?) *wimani* sp. n.

5. The base of two stems (originally separate zoaria?), x. Specimen bz 1035. Ojl Myr, boulder 77.
6. Young specimen, showing basal "roots", and root formation starting from two zooecia. 13 x. Specimen bz 1036. Ojl Myr, boulder 77.
7. Basal parts of zoarium. 5 x. Specimen bz 1033.
8. Holotype, showing long, slender main stems with few secondary branches, rootlike base, and an incrusting secondary attachment (*sb*) 5 x. Specimen 1032. Ojl Myr, boulder 53.
9. A root-like attachment formed on the middle of a stem. 7. x. Specimen bz 1034. Ojl Myr, boulder 77.

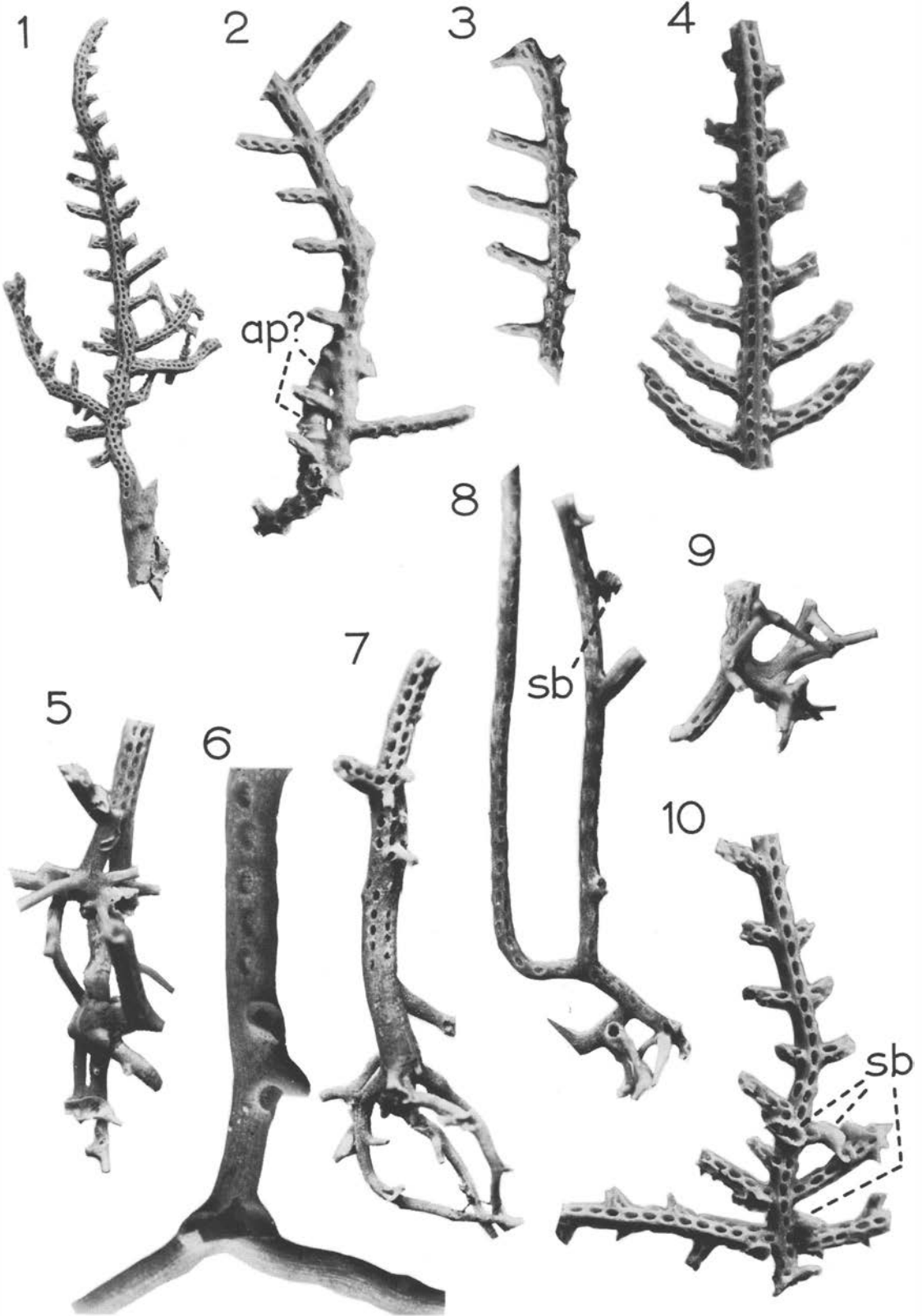


Plate 7

- Fig. 1. *Pachydichtya bifurcata* (Hall). Normal specimen (Note the difference in magnification between this figure, and the others on this plate). 4.5 x. Specimen bz 1037, from the uppermost Ordovician Porkuni Stage at Porkuni, Estonia.
- Figs. 2–5, 7. *Pachydichtya borkholmensis* (Wiman), with zoarial appendages of various types.
2. Specimen with tubular extensions of some zooecia. 12 x. Specimen bz 1038. Ojl Myr, boulder 24.
 3. Specimen with an extra, oblique zooecium (or symbiont?). 12 x. Specimen bz 1039. Ojl Myr, boulder 24.
 4. Specimen with secondary incrusting base, probably composed of several heterozooecia. 12 x. Specimen bz 1040. Ojl Myr, boulder 53.
 5. Specimen with cup-shaped expansion of one zooecium, with secondary zooecial apertures in the walls of the cup. This is an intermediate stage between the structures seen in figs 2 and 7. 12 x. Specimen bz 1041. Ojl Myr, boulder 72.
 6. *Pachydichtya bifurcata* (Hall). Fragment of a zoarium with two incrusting annelid tubes (?). 12 x. Specimen bz 1043. Ojl Myr, boulder 53.
 7. Specimen with a zoarial appendage consisting of a cup-like extension of a zooecial aperture, surrounded by a layer of secondary zooecia. See also figs. 2 and 5. 12 x. Specimen bz 1042. Ojl Myr, boulder 29.

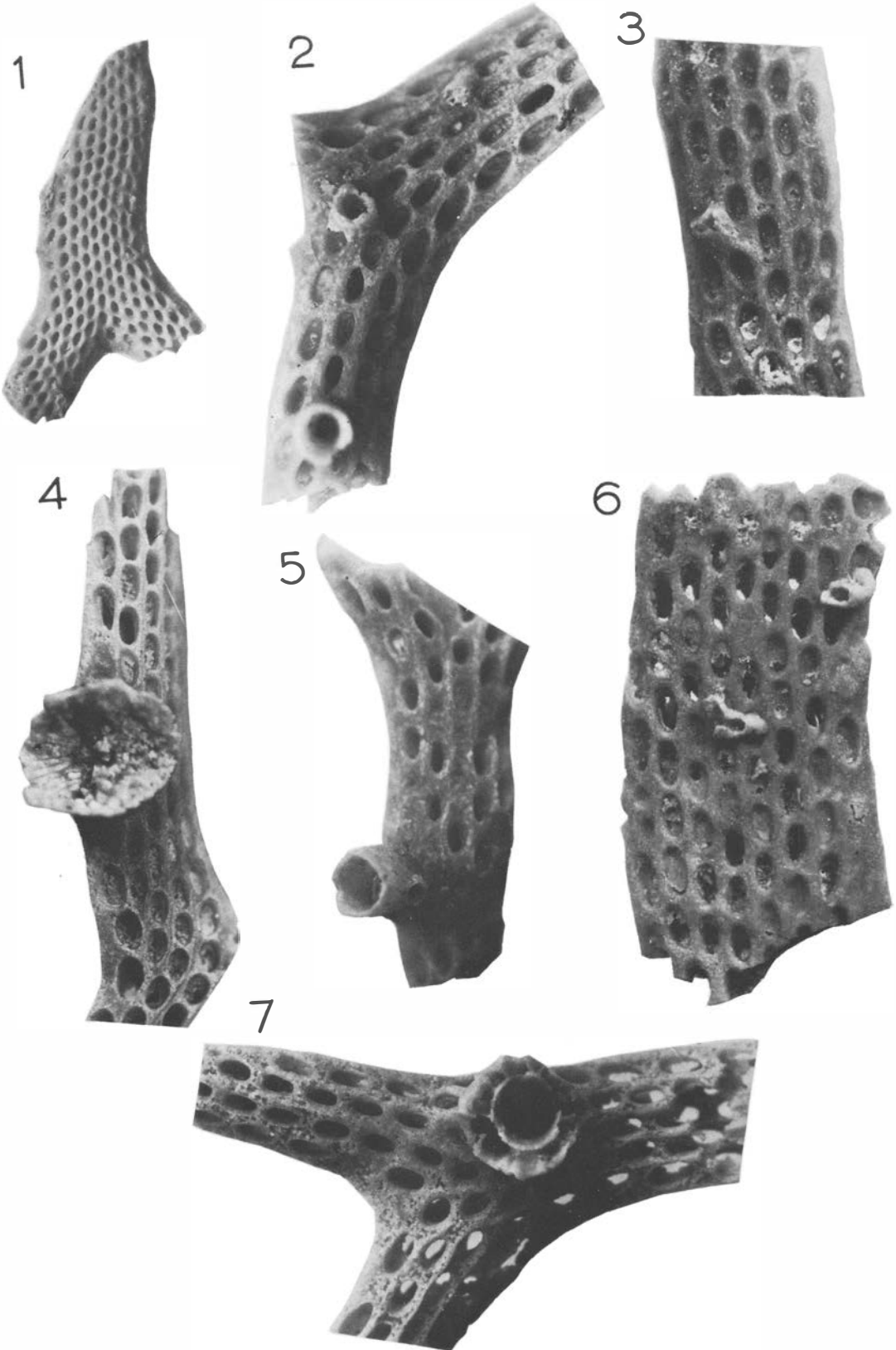


Plate 8

- Phosphatic bodies in bryozoans.
- Figs. 1–2. *Helopora lindstroemi* Ulrich. The globules found in this species. Both figures from the thin section figured by Hennig (1906, textfig. 16), from the Upper Visby Marl, Visby, Gotland, Sweden.
1. shows the distribution of globules in four successive zooecia. Normal light, 66 x.
 2. One of the globules show in fig. 1, in polarized light, crossed nicols. 133 x.
- Fig. 3. Phosphatic bodies in *Ptilodichtya lanceolata* (Goldf.). (*pb*). This is the usual form of phosphatic deposit in this genus. From the thin section figured by Hennig (1905, textfig. 12.), from Gotland, Sweden. 66 x.
- Figs. 4–5. Globules from strongly recrystallized constellarid bryozoan, from the Middle Ordovician Kullsberg Limestone, at Amtjärn, Dalarna, Sweden. Thin section z294, 200 x.
- Fig. 6. *Phaenopora lindstroemi* Ulrich, showing the small globules in this species. From the thin section figured by Hennig (1905, textfig. 5). From the Lower Visby Marl (Uppermost Llandovery or Lowermost Wenlock), at Visby, Gotland, Sweden. 50 x.
- Figs. 7–8. *Favositella armata* (Hennig), with globules. Thin section Z307. The specimen from which this series of thin sections was made (cf. Table 1) is numbered no. By 16990-1, "Westlands in Hablingbo". According to this, it should be from the Upper Ludlovian Hamra Group. It is, however, obviously mislabelled, as indicated both by the rugose coral, on which the bryozoan is incrusting, and the fact that *F. armata* otherwise is restricted to the Visby Marl, and lower part of the Högklint group.
7. Partly decomposed globules, on polarized light, crossed nicols. The dark line around the globules possibly correspond to their original outline. 133 x.
 8. A well preserved, large globule from the basal part of the zoarium. Normal light. 50 x.

