Studies in carboniferous bryozoa

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STUDIES IN CARBONIFEROUS BRYOZOA

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ABSTRACT

Morphological investigations of some British Carboniferous bryozoan taxa has allowed aspects of their palaeobiology and systematics to be revised.

Forty-one taxa, representing seventeen genera of nine families in the extinct Palaeozoic orders Cryptostomata, Fenestrata, Trepostomata and Cystoporata, are redescribed. Lectotypes have been established wherever necessary. Three new species are described and holotypes have been selected for these.

Ordinal, familial and generic assignments have been made and diagnoses emended. Significant aspects of ordinal, familial and generic morphological characters have been discussed. Skeletal ultrastructures have been analysed in most forms studied and the function of a number of morphological characters has been reviewed. Evidence of the double walled concept of growth in the four extinct stenolaemate orders has been reviewed.

Extensive quantitative studies have allowed precise assessment of taxa, and the accurate definition and quantification of some unusual aspects of skeletal morphology, notably in Rhabdomeson rhombifera (Phillips). Combined with the quantitative studies there are extensive photographs and illustrations of the new and redescribed taxa.

Geological ranges have been established for all taxa described.

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DECLARATION

The content of this thesis is the original work of the author (other people's work is acknowledged by reference). It has not been previously submitted for a degree at this or any other university.

A. J. BANCROFT
Durham
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CHAPTER I

INTRODUCTION

The Bryozoa are a phylum of sedentary, colonial, aquatic filter feeding organisms. Three classes are recognised: Phylactolaemata, Gymnolaemata and Stenolaemata.

The phylactolaemates are uncalcified freshwater forms ranging from the Cretaceous to present, and are found only very rarely as fossils. The Gymnolaemata are subdivided into two orders the Ctenostomata and the Cheilostomata, and these constitute the dominant marine bryozoan faunas of today. Traces of the generally uncalcified ctenostomes range from the Ordovician and the calcified cheilostomes range from the late Jurassic.

The marine Stenolaemata is the only class of calcified bryozoans recorded from the Palaeozoic. Five stenolaemate orders are recognised: Cryptostomata, Fenestrata, Trepostomata, Cystoporata, and Cyclostomata. The first four orders range from the Ordovician to the Permian (? Triassic), with the Cyclostomata range from the Ordovician to the present.

In the Carboniferous, Fenestrates and rhabdomesid cryptostomes were at their zenith and dominate bryozoan faunal assemblages. Trepostomes and cystoporates were generally less diverse or numerous, and cyclostomes were extremely rare.

History of Research

Past research on Carboniferous bryozoans has received only scant attention in this country and most work has been wholly concerned solely with their systematics. Little work has been undertaken in the last seventy years.

In the first half of the nineteenth century, taxa were described by Phillips (1836) and McCoy (1844). In the second half of the century valuable research was carried out by Prof. J. Young and J. Young of Glasgow and between 1874 and 1893 they published over twenty-five papers on Carboniferous Bryozoa. They collected widely in the Lower Carboniferous strata of the Midland Valley of Scotland and their papers concentrated on taxonomy, especially on the many species of fenestrate and pinnate acanthocladiid forms notably Penniretepora, Diploporaria, and Synocladia. They erected also the cryptostome genus Rhabdomeson describing two species (1874b, 1875c) and species of the cystoporate Sulcoretepora. Their descriptions though entirely qualitative, were very good, and were accompanied by high quality illustrations.

Etheridge (1873a,b) described and figured some Carboniferous Bryozoa, erecting two new Fenestella species, the cystoporate genus Carinella (= Goniocladia) and the rhabdomesid cryptostome genus Hyphasmopora (1875). He also published two papers with Nicholson (1879, 1881) describing several trepostome species from abroad. Nicholson also described several species of trepostomes in British Carboniferous strata (1881, 1883), and combined with Foord to describe several species of the cystoporate Fistulipora (1885).

Shrubsole worked on fenestellid fenestrates and was interested in the Cryptostomata in general. In his first paper (1879) he reduced twenty-six British species of Fenestella to five, and later reviewed this work (1881).

Vine worked on Carboniferous Bryozoa in the late 1870's and throughout the 1880's and was primarily interested in cryptostomes. In 1883 (b) he formally diagnosed the suborder Cryptostomata for those Palaeozoic Bryozoa whose orifice lay at the base of a tubular vestibular region. Most of his work was taxonomic and he named and described many Yorkshire forms (1885) and attempted a redescription of Phillips species (1884). His descriptions and illustrations of new species and taxa originally described by Phillips, and Young and Young are extremely poor, lack figures or are accompanied by only poor illustrations. Consequently, doubt surrounds the validity of his taxa.

Lee (1912) monographed British Carboniferous Trepostomata accurately describing and illustrating many species of _Tabulipora_, _Stenopora_ and _Dyscritella_.

After Lee there was a long time lapse of about 50 years in any research on Carboniferous Bryozoa in Britain. Abroad, during this period, the situation was very different. In the United States since the classic work of Ulrich (1890) there was a host of workers on Carboniferous Bryozoa, e.g. Moore (1929), Condra and Elias (1944), Elias and Condra (1957), Easton (1943), McFarlan (1942), Koenig (1958), Burkle (1960) Perry and Horowitz (1963). Likewise in the U.S.S.R. the work of Nikiforova (1933, 1938), Nekhoroshev (1926), and Shulga-Nesterenko (1951, 1955) greatly increased our knowledge of Carboniferous species. Advances were made in the methods of examining bryozoans, with emphasis being placed on quantification and internal morphological detail.

In the last twenty years in Britain there have been some workers on Carboniferous Bryozoa. Miller 1961, 1962a, b, 1963) redescribed many of McCoy's fenestrate species and Graham (1975) redescribed Young and Young's, and McCoy's species of pinnate and fenestrate acanthocladiid Bryozoa. These redescriptions were poor, almost entirely qualitative and Miller used only the type material for his redescriptions without examination of any comparative method.

Limited work on bryozoan faunas has been carried out by Wilson (1961) who described four Carboniferous Scottish trepostome species, and Owen (1966, 1969, 1973) who described taxa from Derbyshire, Ireland and Scotland. Work of a very high standard carried out on a bryozoan faunal assemblage is that of Tavener-Smith. In several short papers he described individual species from one locality in Northern Ireland (1965a, 1965b, 1966a) and also monographed thirty-five species from this locality (1973). Olaloye (1974) described the pinnate acanthocladiid taxa from this locality.

The Present Study

From the previous discussion it is apparent that there is a lack of any comprehensive work on known Carboniferous bryozoan taxa in this country. The present study has been developed as a complete revision of many of our established British species. Although the descriptions of taxa by McCoy (1844), and Young and Young (e.g. 1874a, b, 1875a) for example, are very good with illustrations of high quality, these are not up to the standard required by today's emphasis on quantification and the examination of internal skeletal features.

The recent revisions of some British fenestrates by Miller (1961, 1962b, 1963) and Graham (1975) have done little to improve our knowledge of these species. Their descriptions are very poor lacking in both detail and quantitative data and the necessary examination of comparative material. In order to revise the systematics of the taxa studied, all available type material has been examined and additional comparative material has been collected in the field from more than twenty localities in Britain.

The systematic revisions included in this thesis owe much to the collections of Prof. J. Young and J. Young at Glasgow and the Griffith Collection of type and figured McCoy material. In the nineteenth and early twentieth centuries authors did not select holotypes or syntypic series for new species, consequently it has been necessary to establish lectotypes for most of the taxa studied.

This thesis is primarily a systematic revision of many British Carboniferous Bryozoa, so consequently the main body of the text is concerned with taxonomic studies. Thus following a chapter on materials and methods (II) and a chapter on cyclostome double-walled growth and structures of special interest (III) the following five chapters are devoted to systematic descriptions. These chapters are arranged in ordinal sequence, Chapter IV is concerned with cryptostomes, Chapters V-VI with fenestrates, Chapter VII with trepostomes and Chapter VIII with Cystoporates.

Considerable discussion is incorporated of significant aspects of skeletal morphology displayed at ordinal and familial levels, based on previously published work and on personal observations. Additionally special studies have also been made of taxa displaying morphological characters of special interest.

At the end of the systematic descriptions for each order there is a section on the evidence of double-walled growth of that order. This is followed by a discussion of the calculated values of the coefficients of variations for the various parameters used in the quantitative analysis of taxa in that order.

Chapter IX is concerned with the stratigraphical ranges of the taxa examined and a brief resume of the field localities. Chapter X contains the conclusions of the present research and suggestions for further research.

TAXONOMIC PROCEDURE

Among the stenolaemate Bryozoa the classification of taxa within the four extinct orders is hindered by our total ignorance of the living animal. Although this situation renders a true phylogenetic classification impossible, a classification of these Bryozoa has been built up based in part on phylogenetic and sound biological principles.

This classification is based primarily on the establishment of valuable taxonomic criteria such as the constancy of characters or structures in a number of forms. As bryozoans are colonial organisms they possess an abundance of morphological characters and structures that can be used in such a classification. Such character states should be genetically controlled, however in practise many such characters are subject to strong ecophentypic variation. However, the ability of colonies to attain a variety of morphological states suggests that such ecophenotypic variation is itself genetically controlled. In taxonomy a satisfactory number of characters used can be obtained only if such environmentally variable characters are involved.

The recent proliferation of published names of living and fossil Bryozoa taxa increasingly requires the use of detailed measurement and recording of as many independent characters as possible. In the taxonomic analysis of a species a large number of individual conspecific colonies need to be examined. This is because the range of morphological variation of a character within a colony may not be typical of the species to which it belongs and thus may have only limited taxonomic value. The analysis of a number of colonies allows the range of morphological variation of the character states within a species to be determined. The measurement of a standardised series of independent parameters and their numerical analysis facilitates very precise description and assessment of morphological variability within and between species. The standardised series of independent parameters measured involves the analysis of both external and internal zooecial and zoarial characters.

In the present study a number of colony fragments have been selected for analysis for each taxon examined from each locality. A series of measurements (at least 9) were made on each specimen for each variate under consideration and the specimen mean, variance and coefficient of variation calculated. The series of measurements was repeated on each specimen examined. The total number of colony fragments examined comprises the sample needed for numerical analysis. The sample mean, variance and coefficient of variation was then calculated for each variate. It is the number of colony fragments, the sample mean and variance that are the basic statistics necessary for numerical analysis to allow a detailed assessment of the morphological variability exhibited by a species in a population, or between different populations of the same species, and to allow detailed comparison between species.

The taxa within the four orders of stenolaemate Bryozoa examined exhibit great morphological variety. It has often been necessary only to develop measurement schemes at a family level since genera within a family have many morphological characters in common. However, many genera within families do exhibit additional unique diagnostic morphological features and, where necessary, appropriate other parameters have been added to the standard measurement scheme used. The general familial taxonomic procedure used will be described prior to the sytematic descriptions of taxa arranged in families. Where a genus or even species does possess additional unique diagnostic morphological characters the method of measurement of these will be discussed prior to the systematic description of that genus.

The selected morphological statistics are arranged so that comparisons with other samples may be made by using standard significance tests.

Coefficients of Variation

The Coefficient of Variation (C.V.) is the ratio of the spread of values about the mean (the Standard Deviation, S.D.) expressed as a percentage of the mean value ($\bar{X}$).

$$CV = SD \div \bar{X} \times 100$$

It is a useful measurement of the relative variability of observations which may have widely differing mean levels and is independent of units of measurement as the Standard Deviation and mean are both expressed in the same units.

For the purposes of the present study coefficients of variation have been calculated to facilitate the analysis of within and between colony and between population variations of parameters selected for measurement on taxa. This allows the identification of parameters which are useful aids in taxonomic discrimination. Additionally the total colony coefficients of variation have also been calculated. This involves the summation of the mean values of each parameter measured for every specimen of a taxon examined from different stratigraphical horizons. Comparisons between the values of the between colony and the total population coefficients of variation is a useful measure of combined ecophenoptyic and evolutionary variation of the morphological characters measured in a taxon.

For biological data coefficients of variation in the order of 8 to 15 are very common, for a very homogenous sample this may be reduced to 2 or 3. Coefficients of variation in excess of 20 indicate very considerable variability. Research has shown that parameters related to the nature of the individual zooecium exhibit the lowest within and between colony coefficients of variation as their development is subject to strong genetic control. Zoarial morphological characters are subject to strong ecophenotypic influences and exhibit constantly higher within and between colony coefficients of variation.

Taylor (1977, p. 121) discussed some of the causes of perturbations in the calculated values of within-colony coefficients of variation. This may result from sampling biases, measurement error and differential preservation. However, it is thought that these effects are not significant.

Because values of coefficients of variation vary proportionally with the scale of measurement, the comparison of the taxonomic value of different parameters which have greatly differing mean levels becomes difficult. However, coefficients of variation are taken as being a true reflection of the magnitude of genetically and environmentally induced variation within and between colonies in a species

ABBREVIATIONS

(A) Mathematical

SD = Standard Deviation

CV = Coefficient of Variation

CV^{W}= Within Colony Coefficient of Variation

CV^B = Between Colony Coefficient of Variation

CV^T = Total Colony Coefficient of Variation

N = Number of colonies on which determinations were made.

NM = Number of Determinations

Mn = Minimum observed colony mean value

Mx = Maximum observed colony mean value.

$\bar{X}$ = Mean Value.

(B) Locations of Specimen Collections

BMNH	British Museum of Natural History (Department of Palaeontology)
AB	A. Bancroft Collection
AUGD	Aberdeen University Geology Department
BOM	Bolton Museum
DUGD	Department of Geological Sciences, University of Durham
GAGM	Glasgow Art Gallery and Museum
GSE	Institute of Geological Sciences, Edinburgh
HM	Hunterian Museum, University of Glasgow
NH	Hancock Museum, Newcastle
NMI	National Museum of Ireland, Dublin
OUM	Oxford University Museum
RSM	Royal Scottish Museum, Edinburgh
YM	Yorkshire Museum, York.

CHAPTER 2

MATERIALS AND METHODS

MATERIALS

The bryozoan material studied in this project was obtained from two sources; museum collections in Britain and Ireland, and field collecting in the British Isles.

The project has involved a revision of many British Carboniferous Bryozoa and thus a strong emphasis has been placed on the study of type material preserved in museum collections. Type and comparative material of all taxa systematically studied has been borrowed for examination whenever possible. Material has been examined in and borrowed from the British Museum of Natural History (BMNH), the Royal Scottish Museum, Edinburgh (ERSM), the Art Gallery and National Museum, Glasgow (GAG), the Hunterian Museum, Glasgow (GH), the National Museum of Ireland (NMI), Bolton Museum (BOM), the Hancock Museum, Newcastle (NH), Oxford University Museum (OUM), and York Museum (YM).

Much of the material contained in museum collections was acquired in the late nineteenth and early twentieth centuries from private collections. Though usually well preserved, the material is frequently erroneously labelled, with names of taxa often incorrect, and the citation of localities inadequate. However, the examination of museum material proved extremely important, as some of the material studied was obtained from localities now no longer accessible, and some rare taxa are represented solely in museum collections where reasonable quantities of material are often available.

Over twenty localities in England, Wales and Ireland were visited in the field to collect fossil bryozoans. Wherever possible material was collected in situ for processing in the laboratory. However, this was often difficult and sufficient quantities of material could only be made by collecting from loose blocks on the quarry floor, or talus debris below an exposure. At several localities large samples of unconsolidated sediment were collected in the field for processing in the laboratory from spoil heaps adjacent to disused quarries. Large adnate, fenestrate and erect bryozoa were often recovered from debris in the field. It was possible to correlate the loose blocks and unconsolidated debris collected with the actual beds by lithological and faunal comparisons.

Adnate bryozoans usually encrust such macrofossils as corals, crinoids and brachiopods, and although it was normally possible to separate those specimens with a bryozoan epifauna, it was usually necessary to bulk sample macrofossils, and to clean and search them in the laboratory for encrusting bryozoans.

With the present understanding of Carboniferous stratigraphy, most localities could be correlated only to stage level. This, together with the present state of Carboniferous bryozoan studies and the fact that many species have long stratigraphical ranges, means that determination of absolute stratigraphical ranges is only provisional at present.

METHODS

Cleaning and Preparation

Bryozoans in unconsolidated sediment were recovered by wet sieving or picking through the sample. Very delicate ramose erect specimens were then cleaned ultrasonically for a few minutes in a beaker of water with a small amount of detergent added. Larger, more robust adnate, erect and fenestrate bryozoans were initially lightly scrubbed with a toothbrush to remove dirt and less cohesive rock matrix and were then cleaned ultrasonically. A dissecting needle and very fine wire titanium needles were used to remove more difficult matrix. By carrying out this technique under water, any adhering matrix quickly softened and could be removed more readily.

A technique described by Bassler (1953, p.G16) for removing adhering argillaceous sediment from the surface of specimens was tried out on some adnate bryozoans. This involves placing pellets of potassium hydroxide (KOH) on the zoarial surface using forceps, and then leaving for a few hours until the KOH has deliquesced. To deliquesce, the KOH removes water from the clay minerals destroying their cohesiveness and thus breaking them down. Afterwards specimens treated in this manner were thoroughly rinsed in water and cleaned ultrasonically.

Although good results were often attained and the clarity of surface detail enhanced occasionally the zoarial surface, especially with adnate trepostomes, was damaged. A thin white layer remains adhering to the surface of the specimen and has the same effect as an ammonium chloride coating for photography. The technique was used only on expendable specimens, i.e. small, generally poorly preserved colony fragments.

At several localities, bryozoans were collected from fine grained soft fissile mudstones. Fenestrate bryozoans were especially abundant in this lithology. In most cases the celluliferous surface (the obverse) of planar fronds was found face down adherent to the matrix in which they are embedded. This is because morphological features such as upraised rims around apertures, and nodes along the midline of branches give this surface a rougher surface enabling it to adhere to the matrix better. On the other hand, non-celluliferous surfaces (the reverse) are comparatively smooth, hence much less adherent to the matrix and are thus usually exposed.

A method described by Young (1877a) involving the use of asphalt fixed to the reverse surface to reveal the detail of the obverse surface was tried out on such material. The procedure was as follows:

The selected specimen is heated to drive off any moisture before applying the layer of asphalt. This makes the asphalt adhere more firmly to the specimen than when it is cold and damp. Pure asphalt, of a type used in street pavements and roofing which is free from any impurities, was heated over a bunsen burner in a container for several minutes until it had completely melted. The molten asphalt is then poured onto the specimen surface using a previously heated spoon. This ensures that the asphalt spreads evenly over the specimen surface without adhering to the spoon. Enough asphalt is spread on to form a layer between 3 and 5 mm thick. A thin piece of strong plastic is pressed onto the rapidly cooling asphalt to strengthen it, so minimising the possibilities of cracking and bending of the asphalt which may occur with handling. The asphalt cools and hardens within a couple of minutes.

The specimen is then placed in water to allow the matrix covering the obverse surface to soften and break up. In most cases the shales completely broke away from the fronds within a few minutes. In harder shales the process may be hastened by picking away the shale with a fine needle point as the shale softens in water.

The newly exposed surface of the frond can then be ultrasonically cleaned for a couple of minutes for the final removal of matrix from branch surfaces, without loss of the branches from the asphalt backing.

This method of preparation was extremely successful and excellent results were obtained on all specimens on which the technique was carried out. Detailed examination of obverse surface morphological characters are extremely important in the taxonomic differentiation of fenestrate bryozoans so the asphalt preparation technique is valuable. Additionally, the grey-white colouration of branches contrasts extremely well with the black background, enhancing photography.

Examination of External Morphology

The bryozoans were examined with a Leitz binocular microscope offering a range of magnifications between X8 and X150. Detailed quantitative taxonomic analysis of morphological characters was undertaken at magnifications of X64 and X96. Specimens were mounted on glass slides with plasticine to facilitate their easy manipulation.

Measurement of the various morphological parameters was made by using a graticule fitted into the eyepiece of the microscope. A micrometer graticule graduated into 100 divisions was used. Measurements were made to an estimated precision of ± 1 division, which at magnifications of X64 and X96 represented 0.0085 mm and 0.0057 m

As values were subsequently expressed to two decimal places, this source of error was negligible in biometric analysis. A graticule with a grid pattern was used in determining the concentration of zooecial apertures on the zoarial surface of adnate and more robust erect ramose bryozoans. A protractor graticule was used to measure the angle of branching in pinnate fenestrate bryozoans.

Photography of External Morphology

A large photographic record has been built up of all types and comparative material examined in the present study. In the photography of external morphology two arrangements were used.

In small scale and low magnification photography of large zoaria to show colony shape and size, the camera used was a Pentax ME Super. This is a 35 mm S.L.R. camera with aperture preferred automatic exposure. To the standard Pentax M 1:1.7 50 mm lens a Varioprox adjustable focal length lens was attached. Small lens apertures up to f 16 were used in the photography of large conical and foliaceous fenestrate colonies to obtain the maximum depth of focus.

For the high magnification photography of zooecial details, a Pentax S La camera was used to which was added 3 extension tubes and a Leitz 24 mm 'Summar' Lens. The Summar lens is a short focus magnifying lens. Adnate bryozoans encrusting flat surfaces, planar fenestrate and robust erect ramose zoaria were photographed satisfactorily. However, delicate erect ramose zoaria were less easily photographed due to the small depth of focus at the high magnifications used. It was necessary to close down the aperture as far as possible to increase the depth of focus.

The lighting arrangement most commonly used consisted of two lamps set quite close to the specimen, one from top left and the other, with slightly less intensity, from bottom right.

For small scale photographs of very large zoaria, and for photographs of large blocks with bryozoans on, the following arrangement was used. Two high voltage flectaiux quartz halogen lamps were set up about 1.5m away on either side of the specimen and illuminating at an angle of 45°. This lighting arrangement gave a bright even light over the large area of the specimen to be photographed.

Ilford Pan F extra fine grain and FP4 medium fine grain black and white film was used throughout. These films have slow speeds of ASA 50 and ASA 100. Because photography was by artificial lighting, the ASA setting was adjusted to slightly below the actual film speed which is set for natural sunlight outdoor conditions. For small scale and low magnification photographs, exposure times ranged between ½ and 2 seconds, and between 4 and 7 seconds for high magnification photographs.

Drawing External Morphology

Drawings are necessary, as many of the morphological features are too small to be adequately reproduced by photography. Drawings were made using a grid graticule in the eyepiece, and with a similar grid pattern marked on graph paper beneath plain white paper or tracing paper. Most drawings were made at a scale magnification of X77 that of the actual specimen. Drawing was made easier and quicker by the use of a camera lucida fitted onto the eyepiece of the binocular microscope.

Although the resulting drawings were accurate, it was sometimes difficult to ascertain some of the more subtle and minute morphological features when using the camera lucida. Both the apparent level of lighting and the clarity at which the specimen could be seen were somewhat subdued by placing the camera lucida over the normal eyepiece.

Thus when a drawing was inked in, reference was made at high magnification to more subtle morphological features of the specimen under the binocular microscope not picked out clearly using the camera lucida.

Internal Morphology

Analysis of internal morphological characters is extremely important in the taxonomic study of stenolaemate bryozoans and in the present study over 1,300 thin sections and acetate peels have been prepared. A few specimens have also been studied with the scanning electron microscope.

Resin Encapsulation

Most very delicate erect ramose, fenestrate and adnate bryozoans were embedded initially in resin blocks prior to thin sectioning and acetate peel preparation for the following reasons.

(a) It is very difficult to prepare accurately orientated sections from small unmounted specimens. Resin mounted specimens are easily manipulated and allow single or multiple accurately orientated cut or ground sections to be made.

(b) On the subsequent preparation of a thin section or acetate peel, the outer part of a specimen is not lost.

(c) Embedment increases the rigidity of fragile specimens which may otherwise break up during cutting and grinding.

(d) Resin may impregnate the interior air spaces in a specimen. This diminishes the problem of trapping air between the specimen and glass slide during thin section preparation, or between the acetate sheet and specimen during the preparation of acetate peels.

Peels produced from unmounted specimens tend not to reproduce morphological detail so well. This was especially true of fenestrate bryozoans. Owing to irregularities of matrix between branch surfaces it was difficult to get rid of all air bubbles beneath the acetate sheet rolled onto the ground down branch surface. As a result lateral branch margins often do not replicate very well. However, when embedded in resin, there is a perfectly flat surface for peel presentation, the air bubble problem is eliminated and perfect replicas may be produced of the whole of the exposed etched surface.

Unless embedded, smaller erect ramose bryozoans may not replicate at all due to the very small surface area over which the peel is required to adhere.

The following method was used to embed specimens. A thin layer of a pre-activated polyester resin (Trylon EM 306) was mixed with catalyst and poured into each of the 8 compartments (35 x 45 x 25 mm in size) contained in a plastic mould. After the resin had hardened, the specimens to be embedded were placed in the compartments and a fresh batch of resin, thoroughly mixed with catalyst, was then poured over all the specimens covering them completely. The plastic mould was then placed in a bell-jar which was then evacuated. The electric pump used developed a vacuum of about 1000 mm/Hg, and was left running for about 20 minutes. In this way, air was removed from the specimen allowing resin to fill the spaces remaining. The resin was then left to harden, and after about a day had hardened sufficiently to be cut.

Thin Section Preparation

Thin sections were prepared in the standard manner. In some lithologies bryozoans were so abundant that randomly orientated sections were made. Prior to sectioning resin mounted specimens, as much of the resin as possible around the specimen was ground away. This is because the polyester resin expands when heated and may break away from the glass slide when it cools as the Lakeside cement solidifies.

Thin sections of unmounted specimens of very small erect ramose, adnate and fenestrate bryozoans were extremely difficult to prepare. However, the following technique was successfully used for longitudinal sections of erect ramose bryozoans and tangential sections of fenestrate and adnate bryozoans. The specimen was mounted on a glass slide in Santolite or Lakeside resin. The specimen surface was ground down until the desired plane of section was reached. The glass slide was then heated, melting the resin, and the specimen was inverted and the ground surface laid flat on the glass slide. The specimen was then ground down to the required thickness.

Transverse sections could also be prepared of small erect ramose bryozoans using a similar technique. A colony fragment was chopped up with a sharp razor blade to a length of 1 mm. The specimen was then mounted and orientated on a glass slide and ground flat until the exact plane of section was obtained. The glass slide was then heated and the specimen inverted, with the ground surface placed on the glass slide, and then ground down to the required thickness.

In larger, more robust erect ramose bryozoans, a surface could be ground down by hand on a glass plate until the desired plane of section was reached, and then mounted on a slide.

Acetate Peels

Acetate peels were usually made in preference to thin sections for the following reasons:

(a) They could be made more rapidly.

(b) Duplicate peels could be made.

(c) Problems of attaining the right thickness were eliminated.

(d) Very closely spaced serial sections could be prepared to elucidate zooecial budding patterns in erect ramose zoaria, this being impossible in the preparation of thin sections.

(e) In mounted specimens peels could be prepared from a single specimen, in various precise orientations.

(f) In all cases a specimen is never totally destroyed.

To obtain a replica the procedure was as follows:

A properly orientated specimen face was ground down using a fine abrasive (F.600-F1200), and then polished using 1 micron alumina powder. The polished surface was then etched with dilute hydrochloric acid (10% HcL) for 10 to 15 seconds. Immediately after etching the specimen was washed in water to stop any further destructive action by the acid, and then dried.

The etched surface was then flooded in acetone and the acetate sheet was smoothly rolled over the surface with minimum pressure to ensure that no air bubbles were trapped between the acetate sheet and specimen. On small unmounted specimens it was easier to pour acetone onto the acetate sheet and then to press the specimen onto the sheet. Peels required between 5 and 15 minutes to dry (the drying time depending on the size of the specimen). The specimen was then removed from the acetate mount with a quick snapping action. The resulting peel was then placed between two glass slides sellotaped together to keep the peel flat.

The definition of peels produced by this method is extremely good and revealed details of the skeletal microstructure at magnifications of up to X400 under the light microscope.

The Examination and Recording of Internal Morphology

In the examination and quantification of internal morphological characters, acetate peels and thin sections were studied with the same Leitz binocular microscope used to study external morphology. For the detailed examination of skeletal microstructures a Swift polarising microscope was used to examine thin sections and acetate peels at magnifications of up to X400.

The examination and quantification of internal morphological characters is frequently difficult. Any slight inaccuracies in section orientation may have a profound effect on the dimensions measured and in the identification of certain morphological characters.

Photographs of thin sections and acetate peels were taken with a Zeiss Ultraphot II Microscope equipped with an automatic exposure camera. Although magnifications up to X450 could be used, low magnification photographs with a field of view in excess of 2.5 x 3.5 mm could not be taken. Medium fine grained Ilford FP4 film was used.

Scanning Electron Microscope

Some specimens were examined and photographed with a scanning electron microscope. Only external morphologies were scanned, though this helped to indicate and clarify the nature of skeletal microstructures. Specimens were scanned using a Cambridge 600 S.E.M. The working voltage used was between 20 and 40 K.V. Large specimens were mounted on plasticine and very small specimens by double sided sellotape onto stubs. This provided quite a good dark, even background to specimens, though there was a tendency for the sellotape to become electrically charged after prolonged scanning. Magnifications between X10 and X800 were used.

CHAPTER III

ORDER CYCLOSTOMATA Busk, 1852

The extant Cyclostomata play a key role in facilitating our interpretation of fossil forms. They are the source of reconstruction of soft parts and the generalised mode of growth for fossil forms as they are considered to be the closest living relatives to taxa within the extinct orders Cryptostomata, Fenestrata, Trepostomata and Cystoporata.

The skeletal morphology and anatomy of cyclostome Bryozoa has been considered elsewhere and will not be reviewed here (see Borg, 1926,1933, Neilson, 1970; Ryland, 1970; Boardman, 1973; Silén and Harmelin, 1974; Taylor, 1977).

The double-walled growth concept applied to recent lichenoporid and hornerid cyclostomes by Borg (1926 , pp. 195-198, pp. 305-319) is followed for the arrangement of soft parts and the generalised mode of growth in the four extinct orders.

The Double-Walled Growth Concept

In recent lichenoporid and hornerid cyclostomes the living layers of the secreting epithelium (that secretes the calcified zooecial and zoarial skeleton) which lines the zooecium continues onto the zoarial surface as a double investment separated by a narrow extension of the exosaccal coelom and covers the entire colony.

The zooidal epithelium lining the zooecial chamber, which is responsible for secreting the zooecial skeleton, is continuous onto the zoarial surface as the hypostegal epithelium, responsible for secreting the adjacent calcareous skeleton. Above the hypostegal epithelium is a thin layer of peritoneum, followed by a thin eustegal coelom responsible for nutrient distribution throughout the colony and which is continuous with the internal zooecial exosaccal coelom. Above this layer lies another thin layer of peitoneum followed by the outer epithelium termed the eustegal epithelium. This was responsible for the secretion of the external cuticle tissue which covered the entire colony (see Fig. 1).

Application to Fossil Forms

Borg (1926) first described the double walled nature of lichenoporid and hornerid cyclostomes and suggested (p. 482) that this could be applied to Palaeozoic trepostomes.

Following Borg's work, research on skeletal structures and the zooecial microstructure of skeletal elements outside the immediate calcareous investment of the zooecial cavity in Palaeozoic bryozoans suggests that the deposition of such elements took place commonly on the outermost surfaces of zoaria. In these Palaeozoic forms there must have been a continuous coelomic cavity outside of the depositing epidermis around the living colony in order to nourish the depositing epidermis everywhere comparable to that in recent lichenoporid and hornerid cyclostomes.

Elias and Condra (1957 , pp. 37-38) suggested that the calcified skeleton of fenestrates and trepostomes were deposited in the same manner as in hornerid and related cyclostomes. Tavener-Smith (1969a) used the double-walled model of growth as a basis for construction of a double-walled model for fenestellid growth. Boardman and Cheetham (1969, p. 209, 213) suggested that the double-walled concept of Borg could be extended to most fossil tubular bryozoans. Boardman (1971) gave a detailed account of the double-walled model as applied to trepostomes and Utgaard (1973) applied the model to Cystoporates.

In the present study, following the systematic descriptions of taxa for each order, there is a discussion of the evidence for double-walled growth in each order. The evidence discussed is based in part on present observations and on all available published evidence.

Of primary importance to the concept of zoarial growth in fossil stenolaemate Bryozoa is the assumption that their calcified skeletons consisting of granular, granular-prismatic or laminated material is assumed to have been secreted by an orally situated epidermis which lined zooecial cavities. In the case of laminated skeletons, individual lamina are composed of minute tabular units of calcite 1-5μm thick and are straight to normally gently flexuous and of variable length.

Individual laminae are orientated parallel to the assumed position of the depositing epithelium and are interpreted as zoarial growth surfaces (Boardman and Cheetham 1969, p.211). Growth lines separating laminae represent pauses in the secretion of successive calcareous laminae by the overlying epithelium.

In fossil cystoporates the same assumption applies, and the granular and granular-prismatic skeleton are assumed to have been secreted in a plane parallel to the assumed position of the overlying depositing epithelium.

STRUCTURES OF SPECIAL INTEREST IN PALAEOZOIC BRYOZOA

BASAL DIAPHRAGMS

Basal diaphragms are very commonly developed in stenolaemates and in the present study have been found to occur in the rhabdomesid cryptostome, trepostome and cystoporate taxa examined.

The basal diaphragms observed form thin transverse imperforate partitions in autozooecial chambers. All were secreted by an epithelial tissue situated on their oral sides because the diaphragms are orally flexed at their junctions with vertical interzooecial walls and continuous with laminae or skeletal tissues lining interzooecial walls distal to them (Fig.2). Basal diaphragms vary in thickness and composition: in the rhabdomesid cryptostome and trepostome taxa examined they are composed of skeletal laminae identical in nature with zooecial wall laminae, while in cystoporates they are composed of a pale-grey granular-prismatic layer identical with the outer secondary granular-prismatic layer lining zooecial chambers. In the taxa examined their distribution may be sporadic but more commonly they occur at similar levels in adjacent autozooecia (e.g. Pl.164, fig. b). Basal diaphragms possibly formed the floors of autozooidal living chambers raising the zooid nearer to the colony surface and their intermittent nature suggests a possible relationship with degeneration-regeneration cycles of feedings zooids (Boardman, 1971). During the degeneration of an autozooecium vertical zooidal walls still continued to grow and the development of feeding organs of the next cycle was displaced by the amount of wall growth which occurred during degeneration. The development of new basal diaphragms, which may serve as floors to the new living chambers, will also be displaced outwardly by the amount of vertical wall growth achieved during degeneration. If the length of the living chamber remains about the same from cycle to cycle, this leads to the equidistant spacing of basal diaphragms in autozooecial tubes. The occurrence of basal diaphragms at similar levels in adjacent autozooecial tubes suggests a semi-colony-wide or colony-wide control of regeneration-degeneration cycles (Utgaard, 1973).

Boardman (1971) described the occurrence of fossil-brown deposits, possible remnants of brown bodies, in every abandoned chamber in one species of trepostome suggesting a one to one relationship of degeneration-regeneration cycles with the formation of basal diaphragms.

In these taxa communication pores are absent in vertical walls and the segments of autozooecial chambers enclosed by skeletal diaphragms are assumed to have been sealed physiologically and to have contained no living tissue. The absence of preserved diaphragms does not preclude the possible former presence of non-calcifield diaphragms.

HEMISEPTA

Hemisepta are minute shelf-like curved skeletal projections, which may occur singly in the proximal sides of autozooecia, or in one or two pairs in alternate positions on proximal and distal sides of zooecia. Following the usuage of Bassler (1953) superior hemisepta project from the proximal side of tubes and inferior hemisepta from the distal sides of autozooecial tubes.

Hemisepta occur in some of the rhabdomesid cryptostomes and fenestrates examined in the present study and all are situated in the lowest exozone region at the orificial limit of the vestibular region (e.g. Pl. 10, fig, b). They may be calcified from one or both sides and are formed by a narrow inflection of the wall laminae into the autozooecial chamber. Hemisepta have been one of the main polythetic characters in the cryptostomes, and have only recently been discovered in living (Harmelin, 1974) and fossil tubuliporate cyclostomes (Hinds, 1973).

Newton (1971, p. 33) suggested that the hemiseptum acted as a support and pivot point for an hypthesised structure. However, as Ryland (1970, p. 123) suggested, the length of the vestibular region in some cryptostomes precludes this idea in that it would demand the presence of a very long introvert tentacle sheath and a remarkably efficient hydrostatic protrusion mechanism. Ryland suggests that the hemiseptum was possibly involved with the mechanism of tentacle eversion, and provided a locus point for the attachment of muscles.

Hinds (1973, p. 302) described hemisepta in an Eocene cyclostome species of the Genus <u>Filisparsa</u>, and suggested that because of their location near the apertural ends of zooecia it is possible that their function is closely related to the lophophore - gut complex of autozooids. He suggested that the similarity in the spatial relationships of hemisepta in this species and cryptostomes in autozooecial chambers suggests a similar function, despite differences in their skeletal structure.

The fact that feeding organs are retracted behind the hemiseptum in some recent cyclostomes suggests that the function of the hemiseptum was primarily associated with tentacle eversion. This hypothesis is supported by the fact hemisepta are situated in fairly constant positions in autozooecia in taxa possessing them, and are always situated close to autozooecial apertures.

EXILAZOOECIA

Exilazooecia are the only form of polymorphic zooecia developed in rhabdomesid cryptostome and stenoporid and dyscritellid trepostome taxa examined in the present study. Exilazooecia, which are restricted to exozone walls, are small, irregularly shaped features of variable size forming short very narrow cavities of variable depth. The cavities may have rounded or subangular proximal extremeties and often expand slightly distally, and are never divided by diaphragms.

Their distribution is extremely variable, and they may be isolate, scattered over the zoarial surface, or contiguous with each other commonly with several occurring in clusters at interzooecial junctions or they may be numerous enough to isolate autozooecia. Additionally, clusters of exilazooecia occur as maculae in the stenoporid and dyscritellid trepostomes examined. They may comprise clusters up to 2 mm in diameter, commonly of regular shape, circular to slightly elongate or they may occur in irregular linear tracts which may be elevated above, flush with or depressed below the general level of the zoarial surface. The term maculae is used here to describe those clusters that are flush or depressed relative to the general level of the zoarial surface, and monticule to describe those clusters that form elevated prominences above the general level of the zoarial surface. Maculae and monticules may be irregularly or regularly arranged, and in erect ramose forms there appears to be a correlation with colony diameter, distance apart and regularity of arrangement. Maculae are typical of more slender colonies and may be irregularly or regularly arranged, while monticules are more typical of robust colonies and are regularly arranged, in a hexagonal pattern on the zoarial surface. In erect ramose forms, the distance between regularly arranged clusters of exilazooecia forming maculae and monticules increases in proportion to the zoarial diameter.

Functional Interpretation

Boardman and Cheetham (1973, p.154) suggested that the living chambers o many exilazooecia are large enough to house a small polypide other than normal autozooecia despite the fact that such polypides are not known in modern cyclostomes. Although they noted that it is not possible to speculate about the possible functions of organs in Palaeozoic forms, the great variability in chamber shape, size and depth in a single colony would seem to preclude the presence of a small polypide in exilazooecia.

Exilazooecia are morphologically similar to the common polymorphic zooecia in the gymnolaemates and Post-Palaeozoic cyclostomes termed kenozooecia. Kenozooecia are morphologically variable, but may form small empty chambers. They are essentially zooids without polypides containing only some funicular strands and parts of communication organs, but empty of alimentary canal, and mostly without musculature and are thus incapable of feeding.

Boardman and Cheetham (1973) suggested that mesozooecia, common in Lowe Palaeozoic Trepostomata may be kenozooecia, as they lacked both feeding and any sexual reproductive ability, because their living chambers (which were crossed by many closely spaced imperforate diaphragms) oral to the outermost diaphragm were too small to house even a small polypide such as a nanozooid. It is quite possible that some kenozooecia with a cavity are also homologous to exilazooecia as described previously.

The sporadic occurrence of exilazooecia in some taxa suggests that they performed no function other than to occupy space which was too small for an autozooecium to fill. Their development possibly resolved overcrowding of autozooecia in a zoarium (Taylor, 1977, p. 95) and may have increased the structural rigidity of erect ramose zoaria (Newton, 1971, p. 35). It was probably beneficial to the colony to fill spaces with exilazooecia with no active function, rather than leave small vacant spaces on and within the colony framework which may have weakened the zoarial structure in erect ramose forms. In dyscritellid trepostomes, the common contiguity of exilazooecia between often isolate autozooecia suggests this interpretation (see, Pl.161, fig. a).

The occurrence of exilazooecia in clusters as maculae and monticules may agree with this latter interpretation, although their commonly uniform spatial distribution suggests that they may have been intra-colonial centres for some function or process. These clusters of polymorphic zooecia are assumed to have been isolated from each other by areas dominated by normal feeding autozooids.

The morphological prominence of monticules especially has long attracted attention. Ulrich (1890, p. 940) suggested a reproductive function, an interpretation referred to by many subsequent authors. However, such a function does not seem probable, with reference to the morphology of exilazooecia as previously described, and the fact that in a single taxon, their arrangement is extremely variable. They may be absent, or irregularly arranged in slender colonies, while being regularly arranged in more robust colonies.

Banta, McKinney and Zimmer (1974) interpreted monticules as excurrent water outlets based upon the analogy with excurrent structures in extant bryozoans. They observed colonies of the living cheilostome *Membranipora* with regularly arranged regions of outwardly leaning tentacle crowns which bend away from areas of excurrent flow. The distal portions of autozooecia diverge centripetally away from monticule summits, and autozooid tentacle crowns adopt a similar orientation and are directed towards intermonticular regions. Tentacle crown orientations of this nature cause inhalent currents to be focussed on intermonticular regions while exhalent currents depart from the colony surface above monticular summits.

Boardman and McKinney (1976, p. 63) observed that extant Lichenoporid cyclostome colonies are morphologically comparable to individual monticules. Dome-shaped colonies of *Lichenopora* possess radial fasicles of autozooids with tentacle crowns leaning centripetally away from the colony summit. When protruded in the feeding position cilia of the tentacles set up pronounced currents which sweep over the colony surface from the periphery, gaining speed as they travel to the elevated colony centre and jet away from the colony at the summit. Cook (1977) found that inhalent currents are passed to interafasicular regions, occupied by kenozooids, and channelled toward the colony apex for discharge.

Banta, McKinney and Zimmer (1974) suggested that most, if not all, monticules acted as excurrent water outlets, and suggested several lines of evidence supporting this interpretation in fossil taxa.

(a) Monticules are common in many taxonomically unrelated Bryozoa with robust erect ramose zoaria, and in adnate zoaria forming large sheet-like expansions.

(b) Intermonticular distances are fairly constant among Palaeozoic taxa.

(c) Monticules are arranged in a hexagonal pattern in virtually all taxa possessing them.

(d) Monticular diameters are fairly constant within a species and only vary slightly among taxa.

(e) Autozooecial or intra-autozooecial structures are commonly radially orientated around monticular centres.

In adnate fistuloporid cystoporates enlarged autozooecia are commonly arranged in a radial pattern around a centre devoid of polymorphic zooecia (e.g. Pl.167, figs.b,c). Lunaria, crescentic hood-like projections which partly occlude apertures, are radially arranged on the side nearest the monticular centre. These outward facing lunaria probably caused autozooid tentacle crowns to be similarly orientated, thus establishing chimneys of exhalent extra-zooidal flow analogous to those described in *Membranipora*. In some monticuliporid trepostomes living chambers of presumed feeding autozooecia are delineated by cystiphragms arranged around a monticule relative to the monticular centre. In some stenoporid trepostomes enlarged autozooecia occur around monticular centres (e.g. Pl.141, figs.a,c). Although structurally the same as normal autozooecial tubes, it is quite possible that polypides of a larger than average size occupied these tubes and aided excurrent water outlet.

The fact that monticules are normally present in robust erect ramose colonies, while maculae most commonly occur in more slender colonies, suggests that monticules were necessary to filter or remove waste material in robust colonies with a larger surface area. The occurrence of monticules in most adnate fistuliporids suggests this interpretation.

Maculae, usually flush with the normal zoarial surface, are typical of more slender colonies, where filtered and waste material was more readily removed from the colony surface and there was no need of elevated monticular areas to increase the force of excurrent outflow.

The low concentration or common absence of feeding autozooids on maculae and monticules would aid their function as exhalent current outlet loci, as outcurrent flow was unopposed over the colony surface in these areas. The occurrence of exilazooecia in maculae and monticule centres in stenoporid and dyscritellid trepostomes, had no particular function (Anstey, Pachut and Prezbindowski, 1976), but were developed rather than leave large vacant areas on and within the colony framework which may have weakened the zoarial structure, and left large areas more readily open to predation.

STYLETS

The term stylet is used here to describe the morphological features which have been termed acanthopores, stylets, acanthostyles and paurostyles.

Stylets are very common in all Carboniferous trepostome and rhabdomesid cryptostomes examined in the present study. They are elongate cylindrical spinose structures projecting above the zoarial surface, and originate in either the endozone or exozone. Internally they may possess a differentiated axial structure (the core) enveloped by skeletal laminae which are orally deflected in a cone in cone pattern. Some laminae may extend across the core, or the space usually comprising the core may be composed entirely of orally flexed nests of skeletal laminae. Skeletal laminae comprising sheaths around the central cores of stylets, or entirely comprising stylets, are continuous with the laminae of zooecial walls.

Stylet Morphology

Most early workers interpreted all stylets as hollow tubes occupied by heterozooecia or by young zooecia during the life of the colony (Nicholson, 1883; Waagen and Wentzel, 1886; Ulrich, 1890; Cumings and Galloway, 1915; Bassler, 1953; Cuffey, 1967).

Cumings and Galloway (1915, p. 363) distinguished a hollow central lumen surrounded by a thin primary wall of skeletal laminae, buttressed by extensive secondary deposits laid on it by adjoining zooecia. Bassler (1953, G7) described some of the hollow cores as being crossed by minute diaphragms, while Cuffey (1967) interpreted the hollow cores as being lined by a thin dark coloured zone of laminae separating the stylet tissue from that of interapertural walls.

Recent work (Tavener-Smith, 1969b; Brood, 1970; Blake and Towe, 1971; Blake, 1973b) has unequivocally shown that stylet cores were infilled with skeletal material during life, and that they are internally complex and diverse, and are the products of specialised areas of zooidal epithelium. Several lines of evidence support this concept.

(1) Tavener-Smith (1969b) and Blake and Towe (1971) used the high magnification and resolution of the electron microscope to study the morphology of stylets with central cores in two genera of Palaeozoic Bryozoa. They showed that the boundary between the core and enclosing laminae may be obscure, ragged and even intergrown (Brood, 1970). Tavener-Smith proved the existence of some of the skeletal laminae continuing across the core. He suggested the boundary may be indefinite because the core was secreted as the bryozoan grew and not as a secondary cavity infilling. The absence or rarity of skeletal laminae across the core may be due to more or less continuous calcite deposition and not to the original presence of a central hollow space.

(2) In stylets which had differentiated homogenous cores, sheath laminae converge on the cores at very low angles and may be sub-parallel to the core orally. Laminae were added to the outer surfaces of sheaths and are continuous with the surrounding laminae of zooecial walls. A solid core was necessary to deflect the depositing epithelium orally to develop the stylets.

(3) The existence of sheath laminae crossing the cores in certain stylets suggests the presence of resistant material in the core during zoarial growth. Blake (1973b, p. 427) stated that in some Palaeozoic bryozoa there is evidence of apparent organic material draped across cores and typically following the sheath laminae beyond the core. As Blake suggested, if this material represents organic tissue of the bryozoan

preserved along a growth surface, then it suggests the contemporaneous formation of the core and surrounding sheath laminae.

(4) There is a tendency towards optically parallel orientation of the cores, seen best in subparallel to parallel extinctions under cross polars. As Blake (1937b,pp426-427) stated, this is found in widely diverse taxa and it would seem unlikely that this would be the case if the core was a secondary diagenetic filling.

(5) Armstrong (1970, p. 584) showed that the chemical composition of cores in two Permian species of Stenopora consisted of primary calcite and was the same as zooecial walls. However, the secondary fillings in zooecial tubes included calcite, ferroan calcite and ferroan dolomite. Many cores have been found to contain minute grains of pyrite thought to be indicative of organic rich skeletal material.

(6) In the present study no terrigenous material has been observed in the cores of any stylets. If cores were originally hollow they certainly would have become infilled with terrigenous material after death, as zooecial tubes commonly are.

Blake (1973b) does describe some rare instances where brown, apparently organic material may be concentrated along the core, however, in general it appears that stylets were solid, and were infilled with skeletal material during life.

Many workers have tried to classify stylets generally using size as the most important diagnostic character. Cumings and Galloway (1915) erected a seven fold classification based on size, with each class .05 mm larger in diameter than the preceding one. Moore (1929) suggested a simple two-fold division, large and small, and introduced the terms microacanthopore and megacanthopore. Boardman and Utgaard (1966) utilised position and size in recognising two classes of stylets in the trepostome genera Heterotrypa Nicholson and Dekayaia Milne-Edwards-Haime. Endacanthopores arose in either the endozone or exozone and are situated at zooecial corners. Exacanthopores are smaller and are restricted to the exozone. However, these definitions are not mutually exclusive, as both types may originate in the exozone.

The problem with these classifications is that stylets can vary greatly in size, and the ones situated at interapertural angles are not always larger than those occurring along interapertural walls. The height which stylets may attain above the zoarial surface is a function both of the angle of deflection of sheath laminae away from the normal orientation of zooecial laminae and of the angle of intersection of the sheath laminae with the core. A secondary consideration is the amount of sheath laminae deflection, and this is largely dependent on the level in the endozone or exozone at which stylets originate. Obviously, the lower down in the exozone wall stylets develop the more laminae are deflected orally, and stylets will be larger. Variations in the amount and angle of deflection of sheath laminae produces variations in diameter and height of stylets. In a single zoarium much variation in stylet diameters is due to these features.

Boardman and Utgaard (1966) were the first to utilise internal morphology in their classification. Blake (1973b), working on the family Rhabdomesidae, recognised three types and one subtype of stylet entirely on the basis of internal morphology.

Type 'A':- These have differentiated central cores which usually form continuous homogenous calcite rods enveloped by a sheath of laminae continuous with the skeletal laminae of the zooecial wall and orientated subparallel to the cores. These stylets may originate in either the endozone or exozone.

Type 'A' variants:- As in typical type 'A' stylets, a central core is surrounded by sheath laminae. However, differentiated cores may be incomplete or lacking, and core crossing laminae commonly occur. They differ from Type 'A' stylets s.s. in that sheath laminae curve orally for a relatively short distance and core outlines are very irregular.

Type 'B':- The central cores are composed of orally flexed cones of axial laminae, though very small granular cores may also occur. The axial laminae may be deflected laterally forming prominent axial spines. Sheath laminae are deflected to the zoarial surface for only short distances and are not deflected around the axial spines but appear to terminate against them. Sheath laminae are possibly slightly discontinuous with the axial laminae. Although distinct cores occur in some which originated in the exozone they are of the type described above.

Type 'C':- The cores consist of intervals of laminae continuous with the surrounding sheath laminae which alternate with well defined intervals of granular calcite. Peripheral spines are lacking and they originate in the exozone region. Some are very similar to type 'A' variant stylets.

Blake (1975, p. 214) ackowledged the variation in terminology for acanthopore-like structures and suggested a new terminology based on his 1973 (a, b) classification. He called type A acanthopores-acanthostyles, type B acanthopores-akinotostyles, type C acanthopores-heterostyles and type 'A' variant acanthopores-paurostyles.

Blake's tripartite classification of stylets is the most useful one. He was the first to utilise internal morphological detail as the most important diagnostic character to determine quite complex divisions. However, as he stated, some overlap does occur between these divisions.

In the present revision of some British Carboniferous Bryozoa several trepostome and rhabdomesid cryptostome genera and species have been examined. It has been possible to recognise three types of stylets, using internal morphology as the principal criterion for the divisions. Although the overal classification is based on that of Blake (1973b) the internal structure of the divisions are slightly different.

Tavener-Smith (1969b)questioned the use of light microscopy in studying the detailed morphology of stylets, but Blake and Towe (1971) showed it is possible to recognise even a few laminae crossing the cores of stylets using the light microscope. In the present study the light microscope has proved satisfactory in the recognition of the complex and variable internal morphology of stylets.

Type A Stylets

Type A stylets correspond to the form of stylets envisaged by Nicholson, 1881; Ulrich, 1890; Cumings and Galloway, 1915; Bassler, 1953; Cuffey, 1967 and others, i.e. they were hollow tubules surrounded by orally deflected skeletal laminae.

Type A stylets correspond in all respects to the Type 'A' stylets of Blake's (1973b) classification. They have well defined homogenous granular calcite cores (termed rods by Blake, p. 423) varying in diameter from 0.005 to 0.025 mm (Pl. 1 fig.a).Core diameters are fairly constant along the entire length of a stylet (Pl. 1, fig. b) but considerable variation in the diameter of cores occurs in the same zoarium. Under the cross polars of the light microscope the cores behave as a single crystal of calcite with subparallel extinction along their entire length and have optically sharp boundaries (Pl. 1, fig. c).

The surrounding sheath laminae are continuous with normal zooecial wall laminae but never continue into the core. Sheath laminae converge on cores at low angles, distally along their length as additional laminae is deflected orally around the cores laminae are tightly packed and become orientated parallel to the length of the core (Pl. 1, fig. b). The surrounding sheath laminae never bend into cores at all. The amount of sheath laminae orally deflected around cores decreases distally, so that stylets form very high spine-like protuberances (e.g. Pl. 7, fig. c). Stylet diameters range from 0.04 to 0.11 mm and may extend up to 0.2 mm above the zoarial surface.

Type A stylets usually develop in the upper endozone or lower exozone regions (Pl. 2, fig. b). They may be gently curved following the angle of divergence of zooecial walls (Pl. 1, fig. b) but along most of an exozone wall length they are straight and orientated perpendicular to the zoarial surface (Pl. 2, fig. b).

In taxa examined where Type A stylets occur, they are regularly situated. In stenoporid trepostomes they are situated at interzooecial angles with some present along the interzooecial walls, (Pl. 3, fig. a) while in some rhabdomesid cryptostomes they have established positions relative to autozooecial apertures (e.g. Fig10;Pl. 7, fig. c). In stenoporid trepostomes with moniloform exozone walls, there is no reduction in the diameter of the core and surrounding sheath laminae in very thin walled portions between the thicker monilae, and their outer margins may protrude beyond the interzooecial walls and into zooecial tubes slightly (Pl. 3 , fig. b).

Type B Stylets

Type B stylets are morphologically comparable to the type B stylets of Blake (1973b). They have narrow, poorly or quite well defined axial cores, crossed irregularly be skeletal laminae (Pl. 4 fig. a). The surrounding sheath laminae are continuous with the normal zooecial wall laminae, and are deflected orally towards the zoarial surface for relatively short distances. They are not deflected against the axial cores but appear to terminate against them (Pl. 4, fig. a). Axial cores range from 0.002 to 0.01 mm in diameter, and their diameters are fairly constant along the length of the stylet. The diameters of the stylets range from 0.02 to 0.05 mm and they form quite prominent spinose protuberances up to 0.12 mm above the zoarial surface. They originate in the lower exozone region and are usually straight, orientated perpendicular to the zoarial surface.

Type B stylets are rarely developed in the taxa examined but when present they are fairly irregularly arranged. In the rhabdomesid cryptostome Rhabdomeson gracilis (Phillips) they occur in a plane between autozooecial apertures in the same longitudinal row, distal to the larger type A stylets (e.g.Fig.12,Pl. 8, fig. b). Considerable intra- and inter-colonial variation occurs, and they may be absent or up to three may occur in the position described. In the rhabdomesid cryptostome Rhombopora similis (Phillips) and in the dyscritellid trepostome Dyscritella miliaria (Nicholson) they are closely spaced, and quite irregularly arranged on the flat interapertural walls between autozooecial apertures.

Type C Stylets

Type C stylets as interpreted in the present study are synonymous with structures which have been termed granules (Cuffey, 1967, p. 47) and mural tubuli (Karklins, 1969, p. 7). They exhibit many of the characteristics of Blake's (1973b) type A variants and type C stylets in his classification.

They are usually very small, but of very variable diameter (0.005 to 0.05 mm) and are composed of tightly packed orally flexed nests of skeletal laminae, without any defined cores (Pl. 5, fig. a), though very small lenses of granular calcite may be defined. The sheath laminae of type C stylets is continuous with zooecial wall laminae and their development is restricted to middle and upper exozone regions (Pl. 5, fig. a). Skeletal laminae are abruptly deflected orally for only a very short distance before bending over forming narrow cone-in-cone type structures of orally convex skeletal laminae, extending above the zoarial surface as small round projections up to 0.05 mm in height.

In the taxa examined in the present study type C stylets usually occur in association with type A stylets being usually more abundant and often exhibiting high intra- and inter-colonial variation. In stenoporid trepostomes they are usually closely spaced situated in well defined single rows along the midline of interzooecial walls between the large type A stylets (Pl. 5, fig. b) but may be sporadically distributed, and even absent along short distances of interzooecial walls. In stenoporid trepostomes with moniliform exozone walls they occur in the outermost thick walled portion. In the rhabdomesid cryptostome Rhadbdomeson gracilis although their occurrence is usually restricted to the narrow interzooecial walls between diagonally adjacent autozooecial apertures (e.g. Fig. 12f) they may be closely spaced or absent in the same zoarium. In Rhabdomeson rhombifera (Phillips) only type C stylets are present. They are regularly situated, in closely spaced uniserial rows on interzooecial walls, (Pl. 14, fig. b).

Growth of Stylets

The development of stylets reflects a difference between the growth rates of the developing zooecial walls and accelerated growth in localised areas. Stylets are unique in their manner of deposition (Armstrong, 1970). In stenoporid trepostomes for example, normal zooecial wall growth in exozone regions was achieved by both successive and edgewise growth of skeletal laminae. However, sheath laminae were added to the outer surfaces of cores, as indicated by their proximal thickening and by their structural continuity with the laminae of surrounding zooecial walls (Pl. 1, fig. b). The growth of stylets will be discussed with reference to the three types recognised in the present study.

Type A stylets (see Fig. 3); these typically develop in the upper endozone or lower exozone of interzooecial walls. They develop initially from localised orally rounded flexures of normal zooecial wall laminae. Distally the flexures become sharper, the spacing between laminae becomes wider and the axial zone becomes defined. Laterally, skeletal laminae are more closely spaced than at earlier stages and they become progressively more steeply inclined against the new well defined central core. Because the increase in the spacing of laminae is restricted to the core, decreasing on either side of it, it seems that the increase in growth rate was restricted to the axial zone. The result of this differentiated growth causes the development of the central core with the surrounding sheath laminae developing a cone-in-cone pattern around it.

The next stage of development shows evidence of further accelerated growth. In the axial region the absence of growth lines implies that calcite deposition was virtually continuous. The sheath laminae become tightly packed, and the angle of the sheath laminae around the core decreases and near parallelism may be attained.

Type B stylets (see Fig. 4); these display a similar mode of growth to type A stylets however the sheath laminae bend into the core at a low angle and some laminae cross the core. Calcite deposition was not always continuous in the cores and was subject to rhythmic pauses shown by the presence of growth laminae across them.

Type C stylets (see Fig.5); these are entirely composed of orally deflected nests of skeletal laminae, and their development is restricted to the exozone region. They developed from a very narrow oral deflection of normal zooecial wall skeletal laminae. This deflection is exaggerated distally, the angle of deflection becomes very steep and laminae are very tightly packed. The sheath laminae bend towards the zoarial surfaces for very short distances only before bending over gently and becoming slightly less packed.

The Function of Stylets

Interpretations of the function of stylets are very diverse. While early authors interpreted all stylets as being hollow, recent work has shown that stylets were infilled with skeletal material during life.

Early interpretations of stylet functions were based on the assumption that they were unoccupied by skeletal material during life, and housed young zooecia (Waagen and Wentzel, 1886) or small heterozooids (Nicholson, 1881; Ulrich, 1890; Bassler, 1953; Ross, 1964; Cuffey, 1967). Cumings and Galloway (1915, pp. 363-364) surmised that they were hollow, thick walled tubules and that in accordance with their number and relationship to zooecial apertures, they had a protective function stating though that different kinds of stylets had different functions. Nicholson (1881, p. 47), Ulrich (1890, p. 301) and Bassler (1953, G.7) suggested that stylets were structures that supported appendages possibly of a nature and function analogous to avicularia or vibraculae found on other Bryozoa. Ulrich (1890, p. 301) restricted this interpretation to the largest types of stylets, stating (p. 302) that smaller and more closely arranged ones were occupied by different but homologous appendages. Ross (1964) suggested that certain stylets were involved in brooding. Cuffey (1967, p. 55) suggested that the small heterozooids kept the zoarial surface free from sediment and settling larvae, or were involved in some way with sexual reproduction or care of larvae.

Recent authors (Tavener-Smith, 1969b; Armstrong, 1970; Brood, 1970; Blake and Towe, 1971; Blake, 1971; Blake, 1973a, 1973b) have shown that stylet cores were infilled with skeletal material during life, and suggest that stylets possible played a supportive role for soft tissues combined with a protective function. Tavener-Smith (1969b, p.97) suggested that stylets were partly protective, acting as surface deterents to predators without interfering with the activities of the exerted polypides and also stabilising the frontal membrane of the colony. Armstrong (1970, p. 585) compared stylets to pseudopunctae in brachiopod shells. Individual pseudopunctae, termed taleolae are calcite rods surrounded by sheets of shell material deflected towards the interior of the shell to form cone in cone type structures. Armstrong suggested that taleolae were the loci of attachment of small tendons or tonofibrils, and because of the similarity of stylets and taleolae stylets may have served some attachment type function also.

Blake (1973a, 1973b) agreed with these recent ideas that stylets possibly played a supportive role for soft tissues. He (1973b) reviewed the various interpretations of stylets excluding previous interpretations based on the concept that stylets were hollow. Blake (1973a, b) inferred a cheilostome-like morphology described by Harmer (1902a,b) for rhabdomesid cryptostomes suggesting that soft tissues may have been supported at the tips of stylets. Harmer (1902a) described an extant cheilostome Euthyris (Euthyrisella) obtecta Hincks in which a layer of soft tissue is supported above the zoarial surface by calcareous papillae comparable in size to stylets which were situated along the margins of zooecial apertures. Harmer noted the presence of similar papillae in certain Cretaceous specimens and suggested that these species may have had such an epitheca.

As interzooecial communication was not possible in rhabdomesid cryptostomes, Blake (1973a, p. 368) suggested that the soft tissue layer which probably covered the entire surface of the zoarium was supported above it by attachment to the tips of stylets (1973b, p. 434) allowing an open channel of communication between zooids. The method of attachment is unknown. Blake also suggested (after Harmer, 1902a, b; Blake, 1973a, p. 368; 1973b, p. 434) that such a relationship might provide protection for the calcareous walls from predation by boring organisms.

Most Palaeozoic Bryozoa had non-porous walls, and there was no means of interzooecial connumication. If stylets supported the soft tissues which covered the zoarial surface as has been suggested, this may have aided interzooecial communication through an outer coelomic space as envisaged in Borg's (1926) double walled growth model which is applied to Palaeozoic trepostomes, cryptostomes, cystoporates and to fenestrate Bryozoa.

The hypothesis that stylets aided interzooecial connumication is supported by the fact that with the common development of communication pores in post Palaeozoic Bryozoa stylets are absent. In some species examined, for example members of the cystoporate family fistuliporidae, and in the rhabdomesid cryptostome family Hyphasmoporidae stylets are absent. In these cases the volume of the outer coelomic space was probably adequate to allow interzooecial communication in these colonies.

Any structures that acted as the loci of attachment for epithelial tissues would most effectively be regularly distributed over the zoarial surface. Blake (1973a, p. 367) stated that the largest stylets always occupied a stabilised position relative to zooecial apertures in rhabdomesid cryptostomes.

In taxa examined that possess stylets, type A stylets are present in most and are always of regular occurrence. In the stenoporid trepostomes examined they are usually situated at interapertural angles, and in rhabdomesid cryptostomes they occupy stable positions relative to autozooecial apertures, e.g. in Rhabdomeson gracilis a single type 'A' stylet is always situated immediately distal to each autozooecial aperture.

In most taxa examined usually two and rarely three, types of stylets occur. When more than one type occurs, type A stylets are always present together usually with type C stylets, and very rarely with type B stylets also. Type C stylets exhibit high inter- and intra-colonial variation when present with type A stylets. In the stenoporid trepostomes examined type C stylets may be close to each other and regularly spaced in well defined uniserial rows along interapertural walls between the large type A stylets, their occurrence however may be sporadic and they may be absent for short distances along interapertural walls in a single zoarium. In Rhabdomeson gracilis both type B and C stylets may occur with type A stylets. Although type B stylets are always situated in a longitudinal row between autozooecial apertures in the same longitudinal row, some intra- and considerable inter-colonial variation exists: they may be absent or up to three may occur in a single row. Type C stylets are restricted to the narrow interapertural walls between diagonally adjacent autozooecial apertures, again high inter- and intra-colonial variation exists and they may be absent or closely spaced in the same zoarium.

The presence of the same types of stylets in different taxa suggests that they had important and related functions while the presence of different types of stylets in the same zoarium suggests differentiation in their function (Cumings and Galloway, 1915, p. 364; Blake, 1973b, p. 431). There may be a relationship between the development of stylets and the mature polypides.

Type A stylets develop in the upper endozone/lower exozone regions. From their initial development they formed prominent projections above the zoarial surface. If the cores were the loci of the attachment of soft tissues their early development would have been necessary with the oncoming maturation of polypides to allow full interzooecial communication between zooecia through the outer coelomic space. Type A stylets are the largest stylets and they probably also had a protective function.

Type B stylets normally develop in the lower exozone region. They are slightly smaller than type A stylets, and their fairly irregular occurrence and the presence of laminated cores may preclude their function as loci of attachment for tissues, but their relatively large size and their early development suggests a protective function.

The small rounded form of type C stylets, and their normal closeness of spacing around zooecial apertures suggests that they helped stabilise skeletal tissues around zooecial apertures, thus retaining the individuality of feeding zooids. Such a function seems appropriate with their development in middle and upper exozone regions associated with the maturation of polypides. The lack of uniformity of type C stylet distribution in many taxa implies that their exact positioning was not important. Possibly the high intra- and inter-colonial variations in type C stylets was environmentally influenced.

Some taxa had only one type of stylet, and these are regularly distributed. In some specimens of Rhabdomeson gracilis only type A stylets occur, their positions are regular with one situated immediately distal to each autozooecial aperture. In Rhabdomeson rhombifera only type C stylets occur and they are regularly situated in closely spaced uniserial rows on interapertural walls. It seems likely that these closely spaced small round stylets served to keep outer skeletal tissues stable on the zoarial surface and help retain the individuality of feeding zooids, minimising competition during feeding. In R. rhombifera the volume of the outer coelomic space was sufficient to allow full interzooeical communication between zooecia. It is very unlikely, due to the small size of the type C stylets, that they had a protective function.

Some taxa of stenoporid trepostomes examined have moniliform exozone walls (i.e. walls with a bead-like appearance with alternating thick walled and thin walled portions) and type C stylets occur in the outermost part of thick walled portions. Thick walled portions are associated with periods of slower growth and maturation of polypides (see page 359), and the occurrence of type C stylets in this phase of growth agrees with the above interpretation of their function. (Note:- type C stylets are seen only in the outermost thick walled portion; there is no evidence of the former presence of type C stylets in older thick walled phases, as their outermost portion is usually resorbed after the degeneration of a polypide and prior to the oncoming period of renewed growth and development of a new polypide (see pages 359-360).

CHAPTER IV

ORDER CRYPTOSTOMATA Vine, 1883b

Diagnosis

Stenolaemata with erect, ramose, cylindrical or subcylindrical, bifoliate, rarely articulate dichotomous or pinnate zoaria. Autozooecia are tubular, quite short and of relatively constant length, diverging at a fairly constant angle from a well defined axial cylinder or bundle, linear axial zone or from a median wall. Autozooecial walls are compound with a variably defined thin primary granular layer, bounded on both sides by thicker secondary laminated skeleton; walls are thin in the endozone, thickening abruptly, and commonly changing orientation with development of the exozone wall. Autozooecia with a well faceted hexagonal cross-section in the endozone, become rounded in the exozone. The distal part of each autozooecial tube is defined by a vestibular region. Hemisepta are common, basal diaphragms are uncommon in autozooecia.

Autozooecial apertures vary in size, commonly oval to elliptical, closely spaced and usually opening around all sides of the zoarium, but apertures may be more common on one surface, or may rarely open on only one side of a zoarium; occasionally apertural dimensions may be graded around the zoarium. Metapores and exilazooecia are uncommon, with monticules and maculae of exilazooecia rarely developed; ovicells are very rare. Stylets are abundant and structurally very diverse.

Range

Ordovician to Permian.

Discussion

The suborder Cryptostomata was first proposed by Vine (1883b) for Bryozoa with tubular or subtubular zooecia, angular in cross-section, and having an orifice concealed by a vestibule (from which their name meaning 'hidden-mouth' originated). Only Five genera were assigned originally to the suborder, Ptilodictya, Stictoporella, Glauconomella, Rhabdomeson and one now assigned to the Cystoporata, Arcanopora (= Sulcoretepora).

Ulrich (1890) gave the Cryptostomata ordinal status and included additional families, among them the fenestellids. He stressed the importance of zooecial shape, presence of a vestibule, the presence of a well developed and abruptly arising exozone, and of hemisepta in many taxa. Ulrich recognised the need for a phylogenetic classification and was concerned with the evolutionary relationships of taxa.

MacNair (1937) recognised three distinct zoarial types of cryptostomes, a unilaminate group comprising the families Phylloporinidae and Fenestellidae, a cylindrical group including the Arthrostylidae and Rhabdomesidae and a bifoliate group including the Rhinodictyidae, Ptilodictyidae and Sulcoreteporidae. He did not believe the three groups were taxonomically or phylogenetically related. However, Astrova and Morozova (1956) called the three groups of MacNair's suborders, and considered them to be natural phylogenetic branches. Shishova (1966) included the family Hyphasmoporidae (Vine, 1885) within the suborder Rhabdomesoidea. Morozova (1966) added the suborder Timanodictyoidea to the order for some Permian Bryozoa similar to the Ptilodictyoidea.

The last twenty five years has seen the subdivision and removal of taxa into new orders. Elias and Condra (1957) segregated all the fenestrate cryptostomes into a new order Fenestrata. This was based on the homology of the colonial plexus (the primary wall of later authors, e.g. Tavener-Smith, 1969 b; Gautier, 1973) of fenestrates to the common bud of extant cheilostomes, and the fact that comparable structures are absent in other members of the Cryptostomata. Shishova (1968) further emphasised this subdivision noting the characteristic zooecial shape, budding pattern, microstructure, presence of peristomes, lunaria and ovicells in fenestrates. Shishova also established the Order Rhabdomesonata containing the families, Arthrostylidae, Hyphasmoporidae and Rhabdomesidae. She stressed the importance of the cylindrical zoarial shape, zooecial shape and budding pattern. She did not consider the three traditional cryptostome suborders to be closely related, and considered the Order Rhabdomesodonata to be closer to the Trepostomata than to the Cryptostomata differing from the former in the manner of budding about some form of axis, lack of maculae and nature of polymorphism. These subdivisions left only the bifoliate cryptostomes in the order. Utgaard (1973) removed some taxa within the bifoliate families Sulcoreteporidae and Rhinodictydae into the recently established Order Cystoporata (Astrova, 1964).

The new ordinal concepts have not been generally accepted. Tavener-Smith and Williams (1972) followed the classification of Astrova and Morozova (1966) and considered the three major groups as suborders. Blake (1975) suggested the retention of the Order Cryptostomata encompassing the bifoliates, rhabdomesids and fenestillids into a single phylogenetic entity. He used the stratigraphically early rhabdomesid family Arthrostylidae to unify the three groups. He stressed the similarities in skeletal development, the formation of primary granular zones bound by fine secondary skeletal laminae, regular budding patterns, zooecial and zoarial shapes. He attributed no importance to the vestibule, the traditional character for grouping the three cryptostome suborders together.

Recognition of higher taxonomic ranks he agreed to be very subjective and that it is possible to defend the ordinal status of the Fenestrata or Rhabdomesodonta as being different from the Ptilodictyoidea as from the Trepostomata or Cystoporata. However, he believed that the unifying ordinal characters, and the early coeval occurrence of distinctive Cryptostomata, Trepostomata and Cystoporata supports retention of the cryptostomes as a single ordinal group with the three main branches as suborders.

Many aspects of trepostome and cryptostome skeletal morphology are similar, and many rhabdomesid cryptostome genera seem to be transitional between cryptostomes and trepostomes. Indeed many workers now suggest the common phylogenetic ancestory of trepostomes and cryptostomes. Blake (1980, p. 459) believes that the evolution of a well defined locus of budding in the endozone was the innovative key to the establishment of the cryptostome clads which contrasts to typical trepostome budding which occurs throughout the endozone region in erect ramose forms.

The phylogenetic relationship of the three suborders of cryptostomes is uncertain. Tavener-Smith (1975) observed that since rhabdomesids and trepostomes have a similar skeletal arrangement, it seems unlikely that the ptilodictyids were more closely related to the rhabdomesids than was either group to the trepostomes from which both may have been independently derived. Tavener-Smith thus recognised the subjectivity of the morphological recognition of higher taxa. He suggested that study of the early astogeny of bryozoan colonies could yield valuable structural information and help assess phyletic relationships.

Early astogeny of fenestrate bryozoans contrasts with colony development in other stenolaemates. In fenestrates the protoecium is enveloped by the hypostegal coelom over the entire protoecial surface. In the trepostomata and cyclostomata the protoecium is not so enveloped. McKinney (1978) suggested that the pronounced difference in origin between fenestrates and other stenolaemates may indicate relatively great phyletic separation. Unfortunately, colony origins of rhabdomesids or ptilodictyids are very rarely preserved and the phyletic relationship between the cryptostome suborders remains uncertain.

Although there is some uncertainty, the many unique morphological characters of the Fenestrata currently favours the taxon as an order.

The phylogenetic relationships of the remaining two suborders in the Cryptostomata is also uncertain. Although some workers (Astrova, 1968; Shishova, 1968; Morozova, 1981) favour the ordinal status for the taxon Rhabdomesidae, in the present study the Order Cryptostomata is considered to consist of two suborders, the Rhabdomesoidea and the Ptilodictyoidea.

The Rhabdomesoidea comprises the families Arthrostylidae, Rhabdomesidae, and Hyphasmoporidae in which autozooecial arise from a well defined budding locus, an axis with zooecia normally opening on all sides of a narrow cylindrical stem.

The suborder Ptilodictyoidea is composed of the families Stictoporellidae, Rhinodictydae and Ptilodictydae which form bifoliate, occasionally trifoliate zoaria with autozooecia budded from a median wall.

In the present study some taxa within the suborder Rhabdomesoidea have been examined.

SUBORDER RHABDOMESOIDEA Astrova and Morozova, 1956

Diagnosis

Cryptostomata with erect, ramose cylindrical or subcylindrical dichotomous occasionally articulate or pinnate zoaria. Autozooecia are regularly budded from a quite well defined linear plane, central axis or bundle, or from a median plane, diverging at fairly constant angles and of comparable length. Hemisepta are quite common, basal diaphragms uncommon. Autozooecial apertures are of variable size, oval to elliptical usually opening on all sides of a zoarium and are relatively closely spaced, occasionally more common on one surface, and rarely opening on one surface only. Apertural dimensions may be graded around the zoarium. Metapores and exilazooecia are uncommon, monticules are rarely developed, ovicells are very rare. Stylets are very common and structurally diverse.

Range

Ordovician to Permian.

Discussion

The suborder Rhabdomesoidea is composed of three families, the Arthrostylidae, Hyphasmoporidae and Rhabdomesidae. Morphological comparisons between taxa within the three families shows that there are strong similarities between them (see Blake,1975, p. 214).

The existence of certain morphological characters such as articulation joints which were restricted to the Arthrostylidae and metapores in the Hyphasmoporidae (with one exception) serves to distinguish families. However, Blake noted (giving several examples, pp. 214-215) that while a taxon within a family might not possess this diagnostic familial character, it may occur within a taxon of another family. He suggested that the resulting morphological similarity between fossils assigned to different families may indicate a close phylogenetic link between them.

In the present study some taxa within the Family Rhabdomesidae have been systematically examined.

FAMILY RHABDOMESIDAE Vine, 1883b

Type Genus

Rhabdomeson Young and Young, 1874b

Diagnosis

Rhabdomesoidea with slender cylindrical dichotomous zoaria. Autozooecia are regularly budded in an annular or spiral manner from a quite well defined linear axial locus, central axial cylinder or axial bundle and diverge at fairly constant angles and are of comparable length. Hemisepta are common, basal diaphragms are uncommon. Autozooecial apertures are of variable size, oval to elliptical, quite closely spaced and arranged in a rhombic pattern, opening on all surfaces of the zoarium. Apertural dimensions are rarely graded around the zoarium. Exilazooecia occur occasionally. Stylets are abundant and structurally diverse.

Range

Ordovician to Permian.

SIGNIFICANT ASPECTS OF RHABDOMESID SKELETAL MORPHOLOGY

Budding and zoarial growth

Zoarial growth patterns and skeletal development within many taxa are very regular indicating a high degree of genetic control. Zoaria in many species are cylindrical, with slender branches of constant diameter. Budding patterns are very regular with autozooecia commonly arising from a well defined linear axis, axial cylinder or axial bundle (Pl. 6). Autozooecia are gemmated in well defined patterns and arise in a low spiral pattern about the axis (spiral budding), or in cycles, forming successive transverse tiers about the axis, (annular budding).

Autozooecial growth patterns following budding are relatively consistent within a species. Endozonal skeletal walls lie at approximately constant orientations to the zoarial axis, and autozooecia of many species are of relatively constant length (Pl. 6).

The change from thin walled endozone growth to thick walled exozone growth occurred at approximately constant endozonal diameters. This change was often accompanied by a significant change in growth patterns of skeletal laminae which bend abruptly becoming orientated parallel to the zoarial surface (Pl. 6).

The endozonal cross-section of autozooecia is typically a well faceted hexagonal shape, this becomes obscured with the development of the thick walled exozone and become rounded (e.g. Pl. 15, fig.a).

Autozooecial wall structure

Interzooecial walls are compound, typically three layered, with a very thin primary granular layer and thicker laminated skeletal layers on both sides. In some taxa the median layer may be continuous and well defined, but is more commonly intermittently developed or is rarely absent.

Terminal Diaphragms

These are situated near autozooecial apertures and are calcified diaphragms which sealed off the living chamber. They have been found to occur in Rhombopora similis (Phillips) where they form thin calcified laminate layers which are aborally flexed at the junction with interzooecial walls showing that they were secreted by an epithelial tissue on their proximal sides. In R. similis a single terminal diaphragm is situated very close to the autozooecial aperture (pl. 21, fig. c); in some taxa more than one may occur.

Silén and Harmelin (1974) showed that they were formed by the centripetal calcification of a laminate plate. Normally this calcification was complete, and the terminal diaphragm formed was imperforate, as those which occur in R. similis but occasionally a small central pore may remain. In R. similis the distribution of terminal diaphragms may be sporadic, but commonly all autozooecia in a branch fragment may possess one.

The function of terminal diaphragms is uncertain but it is possible that they were secreted by a degenerating polypide to protect the polypideless zooid, from parasitic or predatory organisms proliferating to other active parts of the colony (Taylor, 1977, p. 63). The occurrence of several terminal diaphragms in autozooecia are possibly associated with the saltatory proximal retreat of the zooid (Taylor, 1977, p. 60). Regeneration of the zooid at a later date possibly involved resorption of the terminal diaphragm.

Autozooecial apertures and interapertural walls

Autozooecial apertures are normally of constant shape and size, opening around all sides of the zoarium and, as a result of regular budding, are arranged on the zoarial surface in a rhombic pattern (e.g. pl. 7 , fig. c). Budding patterns may be elucidated by tracing ranks of autozooecial apertures around the zoarial surface. These ranks may be arranged in well defined alternating transverse tiers, or in a low spire around the zoarium with no tiering developed.

Due to the abrupt change in the orientation of skeletal laminae with the development of the exozone wall, which become orientated parallel to the zoarial surface often constricting zooecia, interapertural walls typically cover relatively large areas of the zoarial surface.

Stylets

Stylets are very abundant in rhabdomesids, and are structurally very diverse with types A, B and C stylets occurring. In many species stylets are regularly arranged around autozooecial apertures, or they may be concentrated in a particular area between apertures.

Branching

Two branching patterns are distinguished in the Rhabdomesoidea (Blake, 1976, p. 171). They are different because branching took place at different times in the life history of the individual parent branch.

(a) Bifurcation of a primary branch

When a budding axis of a branch dichotomises at the growing tip of the colony, two daughter branches are developed diverging at acute angles from one another (Fig. 6a). The two new branches may or may not be approximately the same diameter as the parent branch, and although daughter branches may be initially thinner, they commonly increase in dimension distally.

(b) Lateral branch development

A lateral branch develops on the surface of a mature stem (Fig. 6b). The exozone wall of the parent branch is completed before the lateral branch begins to develop, however growth laminae reveal that the branch is part of the parent colony and not an encrustation. Blake (1976, p. 171) suggested an analogy to modern Bryozoa, in that the actual time period between the completion of the exozone region of the parent branch, and the formation of the lateral branch may have been quite short. These lateral branches typically have smaller dimensions and rise at high angles, or perpendicular to the parent branch.

TAXONOMIC PROCEDURE

The general morphological parameters measured in the present examination of some rhabdomesid cryptostomes has been derived largely from the scheme outlined by Cuffey (1967, for the stenoporid trepostome Tabulipora) and utilised by Newton (1971) for some rhabdomesid cryptostomes. Newton's scheme involved the quantification of twenty individual parameters. However, in the present scheme only those characters which exhibit the least morphological variability and are of obvious taxonomic value have been utilised. Many of the morphological symbols used by Cuffey and Newton have been modified here. Measurements of apertural and interapertural dimensions were made on the zoarial surface of colonies. Figure 7. illustrates the dimensions measured for taxonomic purposes.

External morphological characters

Zooecial Parameters

(Z1): The number or range in the number of complete autozooecial apertures in one square millimetre.

(Z2): The number or range in the number of complete autozooecial apertures in a two millimetre line, measured parallel to the branch axis.

Autozooecial apertural diameter; in most rhabdomesids autozooecial apertures are oval or elliptical and their usual constancy in shape and size allows two measurements of apertural diameter to be made.

(AD1): Measured parallel to the direction of growth, between the inner rims of the interapertural walls.

(AD2): Measured transverse to the proximal-distal axis of the aperture, and to the direction of growth between the inner rims of the interapertural walls.

Interapertural Wall Thickness; the regularity of budding in rhabdomesids is accentuated on the zoarial surface and autozooecial apertures are usually regularly arranged in a rhombic pattern. It is thus possible to measure interapertural wall thickness in two directions.

(IWT1): Measured parallel to the direction of growth at the minimum point of separation of two adjacent apertures in the same longitudinal row.

(IWT2): Measured transverse to the direction of growth at the minimum point of separation of two adjacent apertures in the same transverse row.

Exilazooecia apertural diameter (ED): Exilazooecia apertural shape is very irregular and only one measurement of apertural diameter is made. This is measured across the maximum diameter between the inner rims of the interapertural walls.

Zoarial parameters

(ZD): The average diameter of the zoarium measured transverse to the growth direction.

Internal morphological characters

Zooecial parameters

(HZ): The number or range in the number of hemisepta in a mature autozooecium.

(TE): The thickness of the exozone region, measured transverse to the growth direction.

The axial ratio (AXR): is the ratio of the average thickness of the endozone region to the average diameter of the branch.

$$AXR = \frac{100\ (\text{total branch diameter}) - 2(\text{exozone wall thickness})}{\text{total branch diameter}}$$

GENUS Rhabdomeson Young and Young, 1874b

Type species

Rhabdomeson gracilis Phillips, 1836

Diagnosis

Rhabdomesid with very delicate, erect, ramose, cylindrical dichotomous zoaria. Autozooecia are regularly budded around a central axial cylinder in an annular or spiral manner. Hemisepta are common.

Autozooecial apertures are of variable size, usually elliptical rarely pyriform and are relatively closely spaced arranged in a rhombic pattern. Apertural dimensions are usually constant around the zoarium, rarely dimensions may grade around the zoarium, and apertures are more common on one surface as a result. Stylets are abundant and structurally diverse.

Range

Carboniferous to Permian.

SIGNIFICANT ASPECTS OF THE SKELETAL MORPHOLOGY OF RHABDOMESON

Axial cylinder

The genus *Rhabdomeson* is distinguished by the occurrence of a central hollow axial cylinder around which autozooecia are budded (Pl.6, figs.c,d). The nature, origin and function of the axial cylinder has long been a matter of debate.

Bassler (1929, p.69) suggested that the central axial tube was not an integral part of the zoarium because it was filled with material from the surrounding sediments. By comparison with many modern Bryozoa he believed that the zoarium was probably attached to the slender radicels of algae or similar organisms of a perishable nature which disappeared after death leaving a hollow space to be filled with mud or other material.

Elias (1957, p. 401) had reservations about the validity of *Rhabdomeson*, because he found some specimens which possessed an axial cylinder in their proximal parts, but which closed longitudinally with subsequent zooecia budded from a linear skeletal axis. Elias consequently erected the transitional phyletic subgenus *Rhabdomeson* (*Rhombopora*) for the three taxa in which this situation occurred. He did however, note that a number of species had been described (Moore, 1929) which could not have encrusted a foreign substrate, such as the slender radicels of algae or similar organisms of a perishable nature, as basal diaphragms extend across the axial cylinder.

Newton (1971) discussed and illustrated specimens of *Rhombopora lepidodendroides*, Meek which grew about brachiopod and echinoid spines and noted that algae too would have provided a suitable substrate. He suggested that the concept of *Rhabdomeson* is biologically untenable (p. 27) and that *Rhabdomeson* encompasses nothing but the zoaria of *Rhombopora* which grew about foreign substrates. However, Blake (1976) concluded that the structure of the axial cylinder shows that zoaria of Rhabdomeson did not encrust a rigid perishable foreign object. This is confirmed in the present study.

The axial cylinder has a compound wall, a three layered structure with a thin primary granular layer with, on both sides, thicker secondary laminated skeletal material (Pl. 17, fig. b). Such walls are secreted on both surfaces with growth extending in either direction from the central median zone. A secreting hypostegal epithelium and some coelomic space in which to grow must have been present on each side of the wall. There must have been a significant infold of the hypostegal epithelium inside the cylinder to secrete such a compound wall (see Fig. 8).

Supporting evidence lies in the occurrence of basal diaphragms which form thin transverse imperforate partitions in the axial cylinder. These have been recorded in many species of Rhabdomeson (e.g. Moore, 1929) and are observed in the two species of Rhabdomeson examined in the present study (e.g. pl.12, figs. a,b). These basal diaphragms were secreted by epithelial tissue situated at their oral side, because the laminae comprising them are continuous with the laminae lining the axial cylinder wall distal to them, and the diaphragms are orally flexed at their junction with laminae lining the axial cylinder (Fig. 8).

The amount of infolding of the hypostegal epthelium is uncertain, but basal diaphragms are usually secreted quite close to the growing tip of zooecial chambers. Thus it is possible that the infold of the hypostegal epithelium was only quite shallow (Fig. 8). The fact that many colonies examined do not have basal diaphragms across the axial cylinder does not preclude the possible former existence of a non-calcified diaphragm. On this interpretation it is evident that at least some coelomic space would have been present inside the cylinder. Therefore, as Blake stated, the bryozoan could not have been closely appressed to a foreign substrate.

Blake (1976, p. 171), in describing the two patterns of branching which characterise the Rhabdomesoidea, failed to apply these to the genus Rhabdomeson.

In the type of branching which involves the bifurcation of a primary branch, the axial cylinder of the parent branch dichotomises at the growth tip of the colony and continues without interruption in the two daughter branches diverging at acute angles. With the second type of branching a lateral branch develops on the surface of a mature stem, in which the exozone wall of the parent branch is previously complete. Obviously in this situation, the bifurcation and continuation of the axial cylinder of the parent branch into the lateral branch is impossible. As axial cylinders are present in lateral branches (see Blake 1976, Fig. 1, Fig. 2) it appears that a new axial cylinder could be gemmated with the development of a lateral branch, and was unconnected and unrelated to the axial cylinder of the parent branch. A longitudinal thin section of Rhabdomeson rhombifera (Phillips) of a primary branch and its lateral branch illustrates this (Fig. 9 ; Pl. 17, fig. a). It would seem from this evidence that the axial cylinder is a genetic feature derived from an autozooecium at the proximal extremity of the lateral branch. Thus the axial cylinder is not continuous throughout the entire colony as some authors have suggested (Gorjunova, 1975).

The present study has shown that although an axial cylinder originated in the earliest stage of colony development (Blake, 1976) the situation is more complex. Firstly the axial cylinder is continuous along the entire length of the zoarium to the growth tips of daughter branches derived entirely by bifurcation, and secondly additional unconnected axial cylinders could be independently gemmated with the development of lateral branches.

This discussion does not alter the basic taxonomic definition of Rhabdomeson which may be described as having an axial cylinder present along the entire length of branches in a colony. The axial cylinder usually has a constant diameter along the length of a branch, commonly of larger dimensions than autozooecia.

The function of the hollow axial cylinder is uncertain. Gorjunova (1975, p. 62) suggested that owing to the presence of diaphragms, as well as repeatedly observable bifurcation of the axial cylinder (he used the term primary zooecium, p. 61), that the cavity housed a peculiar zooid, differing in structure and function from autozooecia opening only on its top. However, in the light of the above discussion a structural interpretation seems more obvious. Blake (1976, p. 173) suggests that the cylinder would strengthen the living zoarium with a minimum expenditure of added skeletal material, and at the same time would increase the zoarial diameter and hence the number of polypides along a unit length of the branch.

Budding

The two types of budding, annular and spiral which characterise the Rhabdomesidae are most evident in the genus Rhabdomeson. This is because autozooecia are budded around a central axial cylinder and no polymorphic zooecia are developed which may obscure the regularity of apertural spacing on the zoarial surface. Budding patterns may be discerned by means of transverse and longitudinal sections through zooecia, and by means of tracing ranks of autozooecial apertures about the zoarial surface.

(a) Annular Budding

In annular budding, subsequent autozooecia are budded around the axis in a single transverse plane. Autozooecia rise up in cyclic tiers around the zoarium and are arranged in alternate transverse rows. The single transverse plane of budding may be perpendicular to or inclined at a low angle to the axial cylinder.

In longitudinal section beyond the axial cylinder, a marked bilateral symmetry is observed as autozooecia are budded in single alternate transverse planes about the axial cylinder (Fig.10a; Pl.13,figs. In transverse section successive tiers of alternately budded autozooecia are seen around the axis (Fig11a;Pl.13,fig.c). Each tier is compose of zooecial tubes of uniform size, and represent successive alternate transverse rows of budded autozooecia, the smallest lying adjacent to the axis, and the largest opening onto the zoarial surface.

The annular arrangement is accentuated on the zoarial surface by thickening of skeletal walls to form the exozone, and autozooecial apertures are arranged in closely spaced, well defined longitudinal and transverse rows.

(b) Spiral budding

In spiral budding, subsequent autozooecia are budded around the axis in a continuous low spiral.

In longitudinal section beyond the axial cylinder, no bilateral symmetry is evident about a median plane since autozooecia are budded in a low spire about the axial cylinder (Fig.10b,Pl.13, fig.c). In transverse section no tiering is developed (Fig.11b). The smallest autozooecial tubes lie adjacent to the axis, subsequent autozooecia increase in size around the zoarium, overlapping alternately with those adjacent to the axis, spiralling outwards until the largest in a section opens onto the zoarial surface, (Fig.11b, Pl. 9, fig. e).

Autozooecial apertures are arranged in closely spaced, well defined longitudinal rows, obviously no transverse rows are defined.

It should be noted that in a longitudinal section through the axial cylinder it is not always possible to tell whether autozooecia are annular or spirally budded. This is because annular budding may be accomplished with autozooecia being budded in horizontal or low angle transverse planes around the axial cylinder. In the latter case, longitudinal sections through the axial cylinder are indistinguishable from the same section produced from spirally budded autozooecia, with autozooecia offset at a low angle on opposite sides of the axial cylinder.

TAXONOMIC PROCEDURE

In addition to the series of measured parameters described for taxa of the family Rhabdomesidae, an additional measurement of axial cylinder width is measured (see Fig 7).

Internal morphological characters

Zooecial parameters

Axial cylinder width (ACW): measured transverse to the growth direction of the axial cylinder, between the opposite median walls of the cylinder.

Rhabdomeson gracilis (Phillips, 1841)

Figs.12,13,14; Pl.7, figs.a-g; Pl.8, figs.a-d; Pl.9, figs.a-e; Pl.10, figs.a-c; Pl.11, figs.a-b; Pl.12, figs.a-b; Pl.13, figs.a-c.

1841 Millepora gracilis Phillips, p. 20, Pl. 9, fig. 31

1844 Millepora gracilis Phillips; McCoy, p. 19

1854 Ceriopora gracilis (Phillips), Morris. p. 195

1874b Rhabdomeson gracile [sic] (nov.gen) (Phillips); Young and Young, p. 337, Pl. 16B, figs. 1-6,

1880 Rhabdomeson gracile [sic] Young and Young, Vine, p. 504.

1881 Rhabdomeson gracile [sic] (Phillips), Vine, p. 238.

1883a Rhabdomeson gracilis (Phillips), Vine, p. 173.

1885 Rhabdomeson gracile [sic] Young and Young, Vine, p. 92, Pl. 10, fig. 11.

1889 Rhabdomeson gracile [sic] Young and Young; Vine, p. 194.

1938 Rhabdomeson gracile [sic] (Phillips), Demanet, p. 51, Pl. 4, figs. 8 to 12.

Diagnosis

Rhabdomeson with very delicate erect ramose cylindrical dichotomous zoaria. Autozooecia are regularly budded from a straight axial cylinder in an annular or spiral manner. A single superior hemiseptum is situated at the base of each vestibular region. Autozooecial apertures are of moderate size, rhomboidal to elliptical, quite closely arranged in a rhombic pattern. Stylets are abundant, with usually one or two situated in a straight line between apertures in the same longitudinal row.

Description

External

Zoaria form delicate, erect ramose dichotomous cylinders ranging in diameter from 0.4 to 1.0 mm and may be up to 8 cms in length, with both irregularly and widely spaced branch birfucations and lateral branches occurring.

Autozooecial apertures are of moderate size, with apertural shape varying from pointed to well rounded ellipses of variable width, or a well defined rhomboidal shape. The zooecial orifice lies at the base of an adaxially narrowing vestibule which is normally quite well rounded, sloping at moderately to high angles relative to the zoarial surface. Autozooecial apertures are relatively closely spaced, regularly arranged in a rhombic pattern, and may be budded in an annular fashion with well defined alternately arranged transverse tiers developed around the zoarium, or budded in a low spiral fashion around the zoarium.

Interapertural walls vary from flat to well rounded, and have well rounded apertural margins. Interapertural wall dimensions vary considerably, although on average interapertural wall length is about the same as apertural length, and interapertural width is slightly less than apertural width. The relative dimensions are constant around the zoarium. The interapertural walls between autozooecial apertures in adjacent alternate longitudinal rows are usually narrow.

Usually stylets occur only along the median plane of interapertural walls, normally in a single line between autozooecial apertures in the same longitudinal row. A single large type A stylet (0.06 to 0.12 mm in diameter) is always situated close to the distal extremity of each autozooecial aperture. Rarely, only a single large type A stylet is situated in the position described above, but usually two stylets of similar or of very different sizes (type A or type B stylets) are situated close to the proximal and distal ends of the interapertural wall. Occasionally three or more stylets (type A, B and C stylets) of variable size may be positioned on the interapertural wall along the median plane, and very rarely additional very small type C stylets may occur on the side walls between autozooecial apertures in adjacent alternate longitudinal rows.

Internal

The axial cylinder is straight, present throughout the entire zoarial length, and its diameter is proportional to the zoarial diameter and is greater than that of any zooecial tube. The cylinder wall is very thin and compound, with the very thin median primary granular layer usually quite well defined, and bounded by thicker laminated skeletan. Very rarely a single thin transverse imperforate diaphragm may occur across the cylinder.

Autozooecia arise at regular intervals from the axial cylinder wall, and may be budded in an annular or low spiral manner. Compound interzooecial walls are continuous from the compound wall of the axial cylinder, and the very thin median primary granular layer is also usually quite well defined. Autozooecia arise at constant orientations relative to the axial cylinder and are of constant length. Arising from the axial cylinder interzooecial walls are thin in the endozone (about the same thickness as the axial cylinder wall) and diverge gently toward the zoarial surface at low angles of between 20° and 30°. Autozooecia gradually turn outwards at constantly increasing angles into the exozone region, and open onto the zoarial surface at angles between 40° and 60°. There may, however, be a sudden increase in the angle of divergence of autozooecia with the development of the exozone wall, and diverge at high angles up to 85° onto the zoarial surface. With the development of the exozone wall there is an abrupt increase in the thickness of the interzooecial wall, coupled with a corresponding abrupt change in the orientation of skeletal laminae which become orientated to the zoarial surface.

Autozooecia are initially rhomboidal in section adjacent to the axial cylinder, but rapidly develop a well faceted hexagonal cross-section, and become well rounded with the development of the exozone region. Autozooecial tubes are severely constricted at their distal extremeties due to the considerable lateral extension of the exozone wall distally. This may result in a fifty percent decrease in the dimensions of autozooecial tubes in the vestibular region. Orifices lie at the base of the adaxially narrowing, slightly sloping vestibular regions, and are orientated at a low acute angle relative to the aperture.

A single superior hemiseptum is situated at the distal extremity of the exozone wall at the base of the vestibular region, on the underside of the exozone wall close to its distal extremity, and usually projects as a simple curved or pointed short projection.

Type A, B and C stylets are present. Type A stylets form the largest projections above the zoarial surface, and form the most obvious skeletal structures in the exozone wall. One is always situated immediately distal to a zooecium and most appear to originate in the upper endozone wall. Rarely two may occur with one situated as described, and another immediately distal ot it, originating in the lower part of the exozone wall. Type A stylets have a well defined axial core, up to 0.03 mm in diameter, and cores are often slightly curved because they follow the external morphology of the distal wall of an immediately adjacent autozooecium.

Type B stylets are smaller, and are situated distally to type A stylets on interapertural walls between zooecia in the same longitudinal row. They originate low down in the exozone region, and have quite well to poorly defined axial cores across which some sheath laminae may cross.

Type C stylets are only very rarely developed, and when present are usually situated along the narrow, interapertural walls between autozooecial apertures in adjacent diagonal rows. They are very small, short and originate in the upper exozone wall.

Dimensions (N = 83)

	NM	Mn	Mx	$\bar{X}$
Z2	147	4.00	6.00	4.77
AD1	735	0.19	0.30	0.21
AD2	735	0.07	0.14	0.10
IWT1	735	0.16	0.36	0.24
IWT2	735	0.06	0.16	0.09
HZ	480	1	1	1
ZD	133	0.39	1.14	0.16
AW	79	0.10	0.31	0.16
TE	152	0.05	0.15	0.08
AXR	24	54.37	83.01	70.00

Discussion

Rhabdomeson gracilis (Phillips) is readily recognised by the regularly arranged acute elliptical to rhomboidal autozooecial apertures equally developed around the zoarium, the occurrence of a single superior hemiseptum at the base of the exozone region in each autozooecium, and the existence of a straight hollow axial cylinder from which autozooecia are budded.

Phillips (1841, p. 20) described *Millepora gracilis* from North Devon, listing three localities where it occurs: Croyde, Brushford and Pilton. However, two of the three localities are of Devonian age, and only the locality at Brushford Barton is of Carboniferous age. *R. gracilis* has subsequently been found only in Carboniferous strata and it is unlikely that the taxon from the Devonian localities is conspecific with the Carboniferous one. Unfortunately, Phillips original material is now lost and it is not possible to validate this point. In his description of the taxon Phillips described only the external appearance of zoaria, however his original description corresponds in all respects with zoarial surface appearance of material referred to *R. gracilis* examined in the present study. Following Phillips placing of the taxon in the genus *Millepora* there was considerable confusion over its systematic positon. Phillips placed *Millepora* among the Polypiaria together with true corals. However, Morris (1854, p. 102) placed *Millepora* among the zoophytes and placed the coralline genus *Ceriopora* Goldfuss in the phylum Bryozoa giving *C. gracilis* under that generic heading.

The generic name *Millepora* is invalid for a bryozoan because the type species *M. alcicornis* Linne, is a coralline hydrozoan. Young and Young (1874b,p.337) stated that the genus *Ceriopora* was founded on a coral and thus the generic name was untenable for *C. gracilis*. This left the taxon without a generic name so Young and Young (1874b, p. 337) established the generic name *Rhabdomeson* for the taxas with a central axis. They altered the species name *gracilis* to *gracile* without explanation, not stating their reasons why, and accordingly subsequent authors have used this name (e.g.s Vine, 1883a, 1885; Owen, 1969). However, such a change is considered to be untenable using present zoological nomenclature and consequently the original species name *gracilis* is used.

Material

ABCL 24	Calp Shale - Upper Limestone (Asbian), Carrick Lough, Co. Fermanagh.
ABL 2,-4,-5,-6,-9,-10,-12,-14,-16,-18.	Upper Grey Limestone (Brigantian), Eglwyseg Escarpment, Llangollen, N. Wales.
ABH 1,-9 to -11,-40.	Lower Limestone Group, Hosie Limestone (Brigantian), Hairmyres, E. Kilbride.
ABHR.1R.	Cavity slide with 32 specimens. Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABHR. -6,-7,-8,-12 to -18,-24,-25,-28,-39,-40.	Locality and horizon as above.
ABHR 200-218	Thin sections. Locality and horizon as above.
BMNH 60523	(Brigantian?) Capelrig, East Kilbride.
BMNH 60525	(Brigantian?) Trearn near Beith, Ayrshire.
BMNH D.166	Ingoe Shales (Asbian), Northumberland.
BMNH D.193	Holker Park (Brigantian), North Lancs. G.R. Vine Collection.

BMNH B2276	Lower Carboniferous series, Dalry, Ayrshire.
BMNH D.2583	Halkyn Mountain (Brigantian?), G. Shrubsole Collection.
BMNH E.235	Holker Park (Brigantian), Lancs. G.R. Vine Collection.
BMNH PD.931	Mid Millstone Grit, Cayton Gill beds Hampsthwaite. S.W. of Ripon, Yorkshire. E. Hawkesworth Collection 1906.
BMNH PD.1653-66	Gleaston, N. Lancs. and Hurst, N. Yorkshire.
DGUD MP.1211,-1223	Underset Chert (Brigantian). Mount Pleasant Borehole, Barnard Castle, Co. Durham.
DGUD MP.1232	Three Yard Limestone (Brigantian). Mount Pleasant Borehole, Barnard Castle, Co. Durham.
HM D.8	Carboniferous Limestone, Garpel Water, Muirkirk. Young and Young Collection.
HM D.9	Horizon and locality as above.
HM D.103	Multiple thin section showing longitudinal sections through 21 zoarial fragments. Lower Limestone Group, Hosie Limestone (Brigantian) Hairmyres, E. Kilbride. J. Young Collection 1884.
HM D.104	Cavity slide with 11 zoarial fragments. Lower Limestone Group, Hosie Limestone (Brigantian) Hairmyres, E. Kilbride, J. Young Collection.
HM D.105	Cavity slide with 14 zoarial fragments. Lower Limestone Group, Hosie Limestone (Brigantian), Hairmyres, E. Kilbride. J. Young Collection.

HM D.106	Multiple thin section through approx. 70 zoarial fragments. Capelrig (Brigantian?), E. Kilbride. J. Young Collection 1887.
HM D.107	Cavity slide with 12 specimens referable to *Rhabdomeson gracilis*. Roscobie, near Dumfermline. J. Bennie Collection 1881.
HM D.288	Auchensbeoch quarry, Dalry, Ayrshire. J. Young Collection.

Stratigraphical Range

Asbian - Arnsbergian.

Occurrence

Rhabdomeson gracilis is fairly common in the Lower Carboniferous of Britain and has a fairly wide geographical distribution, being recorded from strata in the Midland Valley of Scotland, North Yorkshire Northumberland, North Wales, Northern Ireland and the Derbyshire Reef Complex.

R. gracilis is very common in calcareous mudstones, where it lived in tranquil conditions in association with a dominantly suspension feeding community with a fauna of bryozoans, small chonetid brachiopods and crinoids.

Rhabdomeson rhombifera (Phillips, 1836)

Figs.15-21; Pl.14, figs.a-e; Pl.15, figs.a-d; Pl.16. figs.a-c; Pl.17, figs.a-b; Pl.18, figs.a-b.

1836 Millepora rhombifera Phillips; p. 199, Pl. 1, figs. 34,35.

1844 Millepora rhombifera Phillips; McCoy, p. 196.

1854 Ceriopora rhombifera (Phillips); Morris, p. 195.

1875b Rhabdomeson rhombiferum [sic] (Phillips); Young and Young, p. 333, Pl. 9.

1880 Rhabdomeson rhombiferum [sic] (Phillips); Vine, p. 504.

1881 Rhabdomeson rhombiferum [sic] (Phillips); Vine, p. 338.

1885 Rhabdomeson rhombiferum [sic] (Phillips); Vine, p. 92.

1889 Rhabdomeson rhombiferum [sic] (Phillips); Vine, p. 196.

1955 non Rhabdomeson rhombiferum [sic] (Phillips); Shulga-Nesterenko, p. 143, Pl. 23, figs. 1-3.

Diagnosis

Rhabdomeson with very delicate erect ramose cylindrical dichotomous zoaria. Autozooecia are regularly budded around a fairly straight axial cylinder in an annular fashion. Autozooecia diverge distally away from the axial cylinder at a very low angle which varies around the zoarium. Zooecial elements are graded around the zoarium. Autozooecial apertures are pyriform and are closely arranged in a rhombic pattern. Apertural dimensions grade around the zoarium and interapertural wall dimensions grade inversely to apertural dimensions. Small type C stylets are very abundant and situated in closely spaced single rows around apertures, their number around an aperture varies with apertural size.

Description

External

Zoaria are very delicate, and form short, erect ramose dichotomous cylinders ranging in diameter from 0.42 mm to 0.70 mm, and up to 3 cm in length. Branches have irregularly and widely spaced lateral branches and bifurcations. Lateral branches are usually perpendicular to the primary branch and bifurcating branches diverge at high acute angles from one another. Lateral branches are significantly narrower than primary branches.

Autozooecial apertures are closely spaced, and are regularly arranged in a rhombic pattern, and are budded in an annular fashion with well defined alternately arranged transverse tiers present around the zoarium. There is a gradation in apertural dimensions around the zoarium in a transverse row, and each well defined longitudinal row consists of apertures of similar dimensions. In a single transverse row there is a gradual increase in apertural size around the zoarium from a minimum size, then for about three apertures (on the opposite surface of the zoarium to the smallest apertures) apertural dimensions increase suddenly. The values of apertural length in a longitudinal row may increase up to 30% relative to adjacent apertural rows, while apertural width shows a more even gradation around the zoarium.

Since apertural size varies around the zoarium, apertures are more numerous on one side of a branch than the other, the number varies inversely with their dimensions. The smaller autozooecial apertures are narrow, oblong with rounded extremeties and polygonal to narrow pyriform in shape. With increased dimensions a broad pyriform shape is well developed, with well rounded proximal extremeties and narrowing distally often to a point. The proximal rounded margins of all apertures may be thickened by the presence of a low rounded narrow rim.

Vestibules in smaller autozooecial apertures are well rounded and quite steep sided, often slightly shallower distally and narrowing adaxially. In the largest autozooecial apertures vestibules are shallower, laterally and distally, with the position of the proximal wall of the succeeding interapertural wall often becoming ill-defined.

Zooecial orifices at the proximal extremeties of vestibules are inclined at a high angle, often perpendicular to the zoarial surface. The distance between successive zooecial orifices in the same longitudinal row stays fairly constant around the zoarium, however, due to variation in apertural dimensions the pattern of annular gemmation may be slightly obscured.

Interapertural wall length is inversely proportional to apertural size and interapertural wall width is directly proportional to apertural size around the zoarium. Between the smallest autozooecial apertures the interapertural wall length is equal to apertural length. With increasing apertural dimensions there is a gradual decrease in interapertural wall length, and this accompanies a very slight increase in interapertural wall width. Interapertural wall length decreases abruptly between the largest autozooecial apertures, it may be two to three times as short, while interapertural wall width increases suddenly and may be four to five times greater than the width measured between smaller autozooecial apertures.

Between the largest autozooecial apertures interapertural wall length may not be well defined. Often the pointed distal extremity of the pyriform apertures may extend almost to the proximal extremity of the succeeding aperture in the same row. Also a shallow trough often originates in the vestibular region of the largest apertures.

This trough is well defined, narrows distally, and may extend onto the succeeding interapertural wall forming a shallow division on the interapertural wall between the largest autozooecial apertures.

Type C stylets are very abundant, and are very small to moderate sizes, from 0.02 to 0.06 mm in diameter, and are short, well rounded, only up to 0.07 mm long. They are closely spaced on the top of the well rounded ridges of the interapertural walls. They occur in a very closely spaced single row around smaller autozooecial apertures, giving these apertures a superimposed rhomboidal to hexagonal appearance. Around the largest autozooecial apertures two rows may occur along the length of the interapertural wall between apertures in the same transverse row, these often separated by a narrow shallow trough. Rarely two stylets may be positioned between the two rows. Single rows of stylets still exist between the very narrow interapertural walls between these very large autozooecial apertures.

The number of stylets in a single row around an autozooecial aperture varies proportionally with apertural dimensions, with up to twenty-nine occurring around the largest apertures, but only 12 to 16 around the smaller autozooecial apertures.

Internal

A fairly straight central axial cylinder is present throughout the zoarial length, and may be crossed by extremely rare basal diaphragms. The diameter of the cylinder is greater than that of ordinary autozooecia and is proportional to the zoarial branch diameter. The walls of the cylinder are thin, compound and consist of a very thin, quite well developed primary granular layer bound on both sides by much thicker secondary laminated skeleton.

Autozooecia arise at regular intervals and diverge at a very low angle away from the axial cylinder, and are budded in an annular fashion. In the basal endozone autozooecia diverge from the axis at approximately the same angle between 8° and 10° around the zoarium. Away from the basal zone and extending into the exozone there is a gradation in the angle of divergence around the zoarium, reflected by the gradation of zooecial elements observed on the zoarial surface.

Where the angle of divergence is lowest, autozooecial apertures are largest on the zoarial surface. In the endozone, angles of divergence range from 8° to 12°. Towards the exozone there is little or no increase in the angle of divergence, and the distal interzooecial wall gradually bends to form the exozone wall.

Where the overall angle of divergence is higher, smaller autozooecial apertures occur on the zoarial surface. The angle of divergence of distal interzooecial walls increases gradually abaxially to the exozone reaching angles of 30° or more, with a more abrupt change in orientation of laminae to form the exozone wall.

Despite this variation in the angle of divergence of autozooecial tubes, all zooecia are of fairly constant length.

Interzooecial walls are compound and are continuous from the axial cylinder, and the median primary granular layer is usually quite well defined, and is bound by much thicker secondary laminated skeleton. Interzooecial walls are thin in the endozone (about the same thickness as the axial cylinder wall). Where the overall angle of divergence is less the skeletal walls thicken and bend gradually to form the exozone wall. Interzooecial walls thicken more abruptly where the angle of divergence is greater and laminae bend more suddenly to form the exozone wall. Exozone walls are of moderate thickness, and usually thin distally along their length, and often have quite well rounded, occasionally slightly upturned distal extremeties.

Zooecial orifices occur at the base of adaxially steeply sloping vestibules, deepest in the proximal region, shallower distally and are orientated at a high angle often perpendicular to the zoarial surface. Th distal shallowing of vestibules is most marked where the angle of divergence of autozooecia is lowest, as for the largest autozooecial apertures. In the exozone autozooecia having the steepest angle of divergence may be slightly constricted.

Autozooecia are rhomboidal in section adjacent to the axial cylinder, but soon develop a well faceted hexagonal cross-section with slightly increased dimensions abaxially. With the development of the exozone wall autozooecial tubes become well rounded, developing an oval cross-section.

Type C stylets are small to moderately sized, and are very closely spaced on interapertural walls. They originate in the middle and upper exozone wall, laminae are orally flexed for relatively short distances, and no core is usually defined but occasionally very small narrow intermittant cores may be developed.

Dimensions

So much astogenetic variability is shown by apertural dimensions on zoaria of Rhabdomeson rhombifera (Phillips) that a special study was made incorporating over 5,000 measurements on 15 colony fragments from one locality.

This entailed the measurement of dimensions of autozooecial apertures of similar size in the same longitudinal row, interapertural distances between autozooecial apertures of similar size in the same longitudinal row, interapertural distances between apertures in the same transverse row in a longitudinal line, and meristic counts of the number of stylets around apertures in the same longitudinal row.

The following five tables show the calculated values of these parameters and illustrate the astrogenetic variability of these parameters around the zoarium of R. rhombifera. Each of the tabulated values is an average value for that particular parameter measured in that specific longitudinal apertural row for that specimen.

Longitudinal Autozooecial Apertural Diameter (see Fig. 16)

Number of colony fragments examined	Number of Longitudinal Rows of Autozooecial Apertures										
	1	2	3	4	5	6	7	8	9	10	11
1	0.30	0.31	0.32	0.33	0.36	0.54	0.47	0.36	0.33	0.31	0.28
2	0.23	0.26	0.28	0.33	0.36	0.46	0.35	0.33	0.26	0.26	0.26
3	0.24	0.24	0.26	0.28	0.33	0.42	0.42	0.31	0.30	0.25	0.25
4	0.29	0.29	0.33	0.37	0.41	0.42	0.39	0.33	0.31	0.28	0.27
5	0.30	0.31	0.31	0.32	0.42	0.49	0.48	0.32	0.31	0.32	0.30
6	0.27	0.29	0.28	0.34	0.43	0.49	0.47	0.35	0.29	0.29	0.28
7	0.30	0.30	0.32	0.33	0.38	0.47	0.46	0.36	0.33	0.31	0.31
8	0.28	0.29	0.33	0.37	0.45	0.46	0.36	0.30	0.29	0.27	-
9	0.29	0.31	0.32	0.33	0.41	0.46	0.38	0.32	0.28	0.29	0.30
10	0.28	0.28	0.28	0.31	0.36	0.42	0.41	0.33	0.31	0.29	0.28
11	0.34	0.36	0.37	0.38	0.46	0.54	0.46	0.41	0.38	0.36	0.35
12	0.31	0.30	0.31	0.33	0.43	0.49	0.42	0.35	0.33	0.31	-
13	0.28	0.29	0.31	0.33	0.41	0.48	0.33	0.28	0.28	0.28	-
14	0.26	0.23	0.24	0.28	0.41	0.44	0.34	0.29	0.28	0.24	0.23
15	0.28	0.27	0.29	0.29	0.38	0.41	0.31	0.29	0.28	0.28	0.26
$\bar{X}$	0.28	0.29	0.30	0.33	0.40	0.47	0.40	0.32	0.30	0.29	0.28

Transverse Autozooecial Apertural Diameter (see Fig. 17)

Number of Colony Fragments examined	Number of Longitudinal Rows of Autozooecial Apertures										
	1	2	3	4	5	6	7	8	9	10	11
1	0.13	0.13	0.14	0.16	0.17	0.20	0.19	0.17	0.15	0.13	0.13
2	0.12	0.12	0.14	0.16	0.18	0.19	0.16	0.14	0.20	0.12	0.12
3	0.12	0.14	0.15	0.15	0.19	0.18	0.20	0.18	0.16	0.13	0.12
4	0.12	0.12	0.15	0.17	0.19	0.20	0.18	0.16	0.15	0.12	0.11
5	0.12	0.13	0.14	0.15	0.17	0.19	0.21	0.15	0.14	0.13	0.13
6	0.12	0.13	0.14	0.15	0.17	0.16	0.18	0.15	0.14	0.13	0.12
7	0.10	0.11	0.12	0.14	0.17	0.18	0.17	0.15	0.13	0.11	0.10
8	0.13	0.14	0.15	0.19	0.20	0.21	0.17	0.15	0.12	0.12	–
9	0.11	0.12	0.14	0.19	0.20	0.20	0.19	0.14	0.13	0.11	0.11
10	0.13	0.15	0.15	0.15	0.17	0.18	0.17	0.16	0.15	0.13	0.14
11	0.13	0.13	0.14	0.16	0.18	0.21	0.19	0.18	0.14	0.13	0.14
12	0.14	0.14	0.15	0.15	0.19	0.19	0.19	0.16	0.16	0.14	–
13	0.13	0.13	0.15	0.15	0.19	0.21	0.19	0.16	0.14	0.13	–
14	0.14	0.14	0.15	0.16	0.21	0.21	0.18	0.17	0.15	0.13	0.12
15	0.12	0.13	0.15	0.17	0.21	0.21	0.19	0.17	0.15	0.13	0.13
$\bar{X}$	0.12	0.13	0.14	0.16	0.19	0.19	0.18	0.16	0.14	0.12	0.12

Longitudinal Interapertural Wall thickness (see Fig. 18)

	Number of Longitudinal Rows of Autozooecial Apertures										
Number of Colony Fragments examined	1	2	3	4	5	6	7	8	9	10	11
1	0.40	0.39	0.38	0.37	0.33	0.18	0.29	0.33	0.39	0.38	0.40
2	0.59	0.53	0.45	0.45	0.36	0.37	0.45	0.45	0.50	0.54	0.52
3	0.41	0.42	0.39	0.35	0.28	0.26	0.26	0.36	0.39	0.42	0.41
4	0.48	0.48	0.39	0.41	0.34	0.29	0.38	0.44	0.46	0.44	0.45
5	0.50	0.45	0.45	0.41	0.33	0.23	0.22	0.42	0.46	0.49	0.49
6	0.43	0.42	0.40	0.35	0.21	0.21	0.24	0.36	0.41	0.41	0.44
7	0.51	0.50	0.46	0.45	0.43	0.26	0.29	0.48	0.51	0.56	0.55
8	0.34	0.32	0.30	0.25	0.14	0.11	0.22	0.23	0.24	0.24	-
9	0.50	0.49	0.48	0.44	0.33	0.19	0.29	0.41	0.47	0.50	0.50
10	0.38	0.37	0.36	0.35	0.30	0.26	0.26	0.35	0.39	0.39	0.39
11	0.44	0.44	0.44	0.40	0.33	0.21	0.33	0.38	0.43	0.48	0.45
12	0.39	0.39	0.38	0.36	0.21	0.12	0.15	0.31	0.39	0.36	-
13	0.36	0.38	0.36	0.35	0.25	0.16	0.25	0.33	0.33	0.36	-
14	0.35	0.39	0.36	0.34	0.22	0.26	0.28	0.36	0.37	0.39	0.40
15	0.42	0.43	0.40	0.38	0.31	0.29	0.38	0.41	0.42	0.42	0.44
$\bar{X}$	0.43	0.43	0.40	0.38	0.29	0.23	0.29	0.37	0.41	0.43	0.44

Transverse Interapertural Wall Thickness (see Fig. 19)

	Number of Longitudinal Rows of Autozooecial Apertures										
Number of Colony Fragments examined	1	2	3	4	5	6	7	8	9	10	11
1	0.06	0.06	0.06	0.07	0.08	0.21	0.19	0.09	0.07	0.07	0.06
2	0.07	0.06	0.07	0.10	0.15	0.18	0.14	0.09	0.08	0.06	0.07
3	0.07	0.07	0.07	0.08	0.11	0.15	0.14	0.07	0.07	0.06	0.07
4	0.06	0.06	0.07	0.09	0.15	0.16	0.11	0.08	0.07	0.07	0.06
5	0.06	0.07	0.06	0.07	0.11	0.19	0.21	0.09	0.08	0.07	0.07
6	0.07	0.07	0.07	0.10	0.18	0.21	0.16	0.09	0.07	0.07	0.07
7	0.06	0.06	0.06	0.06	0.07	0.16	0.13	0.07	0.06	0.07	0.06
8	0.06	0.06	0.06	0.09	0.17	0.18	0.10	0.09	0.08	0.07	–
9	0.06	0.06	0.07	0.07	0.12	0.19	0.11	0.06	0.06	0.06	0.06
10	0.07	0.07	0.07	0.08	0.12	0.16	0.16	0.08	0.07	0.06	0.06
11	0.05	0.04	0.04	0.05	0.07	0.12	0.07	0.06	0.05	0.04	0.05
12	0.06	0.06	0.06	0.07	0.15	0.23	0.19	0.09	0.10	0.06	–
13	0.06	0.06	0.06	0.06	0.14	0.20	0.09	0.06	0.05	0.05	–
14	0.07	0.06	0.07	0.09	0.20	0.19	0.10	0.08	0.06	0.06	0.06
15	0.07	0.07	0.07	0.07	0.13	0.14	0.08	0.07	0.06	0.07	0.06
$\bar{X}$	0.06	0.06	0.06	0.08	0.13	0.18	0.13	0.08	0.07	0.06	0.06

Number of Stylets in a single row around Autozooecial Apertures

(see Fig. 20)

	Number of Longitudinal Rows of Autozooecial Apertures										
Number of Colony Fragments examined	1	2	3	4	5	6	7	8	9	10	11
1	15.5	15.5	15.5	16.0	22.5	27	19.5	17.5	15.5	17.0	16.0
2	16.0	15.5	17.5	21.0	22.5	24.5	20.5	18.5	15.0	15.5	15.5
3	14.5	15.5	16.0	16.0	19.5	21.5	20.0	17.5	16.5	15.0	15.0
4	16.0	17.0	20.5	22.0	21.5	20.0	18.0	17.0	16.0	15.5	15.0
5	17.0	17.5	18.5	18.5	22.5	26.0	24.0	17.0	16.5	15.5	16.0
6	14.5	16.0	16.0	18.0	21.5	23.5	22.0	17.5	15.5	15.0	15.0
7	16.5	17.0	17.5	18.5	19.5	25.0	23.5	21.0	18.0	17.0	15.5
8	14.0	16.0	17.0	18.0	21.0	20.5	16.5	14.5	15.0	16.0	–
9	13.5	14.5	16.5	16.0	19.0	21.0	17.5	15.5	15.5	13.5	13.5
10	15.0	16.0	14.5	15.5	16.5	20.0	21.0	17.0	16.0	14.5	15.0
11	17.0	16.5	18.0	18.0	19.5	20.0	21.0	18.0	17.5	18.0	17.5
12	16.5	15.0	17.5	18.0	21.5	26.0	24.5	18.0	17.0	17.0	–
13	12.5	12.5	14.0	15.5	18.0	18.5	15.0	13.5	12.0	10.5	–
14	15.5	14.5	14.5	15.5	24.0	22.0	19.5	16.5	15.5	15.0	13.5
15	16.5	15.0	14.5	17.0	18.5	20.5	18.0	16.0	15.0	14.0	13.0
$\bar{X}$	15.28	15.64	16.61	17.55	20.50	22.54	20.26	15.89	15.81	15.31	15.17

The table below sets out the values of the other parameters measured on zoaria of R. rhombifera.

	NM	Mn	Mx	$\bar{X}$
Z2	30	3	4	-
ZD	19	0.42	0.58	0.49
AW	5	0.07	0.10	0.09
TE	15	0.05	0.08	0.06
AXR	5	72.92	76.44	74.90

Discussion

Rhabdomeson rhombifera (Phillips) is a very distinctive, extremely delicate rhabdomesid easily recognised by the gradation in the size of autozooecial apertures around the zoarium.

Phillips (1836) placed the taxon within the genus Millepora, as he did for M. gracilis (1841). However, Morris (1854, p. 102) placed Millepora among the Zoophyta and put M. rhombifera and M. gracilis into the coralline genus Ceriopora. Young and Young (1875b) redescribed Phillips' species of C. rhombifera and placed it in their new genus Rhabdomeson (1874b). Also they altered the original species name rhombifera to rhombiferum and subsequent authors have used this name. However, this usuage is strictly not correct and consequently the original species name has been used in the present study.

Rhabdomeson rhombiferum (Phillips) described by Shulga-Nesterenko (1955, p. 143, fig. 38 a-c) is not conspecific with R. rhombifera (Phillips). There is no gradation in apertural dimensions around the zoarium as in R. rhombifera, apertures are equally developed around the zoarium, and oval in shape. In R. rhombifera there is only one type of stylet (type 'C') present, these are closely spaced in well defined uniserial rows around apertures. In Shulga-Nesterenko's taxon two types of stylets occur; a single large (probably type A) stylet is situated midway between apertures in the same longitudinal row with small stylets (probably type C) closely spaced between.

Material

ABH 12 to 15	Lower Limestone Group, Hosie Limestone (Brigantian), Hairmyres, E. Kilbride.
ABHR.2R	Cavity Slide with 20 colony fragments. Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABHR 226-234	Thin sections. Locality and horizon as above.
ABR 1 to 6, 15 to 18,-25,-31.	Lower Limestone Group, Redesdale Ironstone Shale (Asbian), Ridsdale, Northumberland.
ABR 225-227	Thin sections. Locality and horizon as above.
BMNH D.166	Carboniferous Limestone Series, Ingoe Shales (Asbian), Northumberland.
BMNH D.184	Gleaston Castle near Dalton, North Yorkshire. G.R. Vine Collection.
BMNH D.250	Labelled as *Rhombopora vinculariformis* (Vine) Gleaston near Dalton, N. Lancs.
HM D.107	Cavity slide with 11 specimens referable to *Rhabdomeson rhombifera*. Roscobie near Dumferline. J. Bennie Collection 1881.
HM D.108	Cavity slide with 17 colony fragments. Capelrig (Brigantian?) E. Kilbride. J. Young Collection.

HM D.109	Lower Carboniferous Limestone, Loudon district Ayrshire. J. Young Collection.
HM D.288	Auchenskeoch quarry, Dalry, Ayrshire. J. Young Collection.

Stratigraphical Range

Asbian - Arnsbergian.

Occurrence

As for *R. gracilis*.

GENUS Rhombopora Meek, 1872

Type Species

Rhombopora lepidodendroides Meek, 1872

Diagnosis

Rhabdomesid with slender, erect, ramose cylindrical dichotomous zoaria. Autozooecia are regularly budded from a quite well defined linear axial region in a low spiral manner. Basal diaphragms are uncommon. Autozooecial apertures are large oval to round, quite closely spaced and arranged in a rhombic pattern. Exilazooecia are rare. Stylets are abundant and structurally diverse.

Range

Devonian to Permian.

Rhombopora similis (Phillips, 1841)

Figs.23-25; Pl.19, figs.a-e; Pl.20, figs.a-c; Pl.21, figs.a-c; Pl.22, figs.a-b; Pl.23, figs.a-b.

1841 Millepora similis Phillips; p. 21, Pl. 11, fig. 32.

1881 Ceriopora similis (Phillips); Vine, p. 338.

1885 Rhombopora similis? (Phillips), Vine p. 93

1889 Rhombopora similis (Phillips), Vine, p. 198

Diagnosis

Rhombopora with slender, erect, ramose, cylindrical dichotomous zoaria. Autozooecia are regularly budded from a quite well defined linear axial region in a low spiral manner. Autozooecial apertures are large, circular to oval, relatively closely spaced arranged in a rhombic pattern, and commonly have narrow low upraised rims with small stylets on. Exilazooecia are quite common. Stylets are abundant and structurally diverse.

Description

External

Zoaria form slender, erect ramose colonies ranging from 0.63 to 1.5 mm in diameter with branches usually cylindrical and irregularly dichotomising. Lateral branches are slightly thinner than the primary branches.

Autozooecial apertures are moderately large, circular to oval, quite closely spaced, and are arranged in a rhombic pattern. In delicate zoaria autozooecial apertures are arranged in quite well defined alternate longitudinal rows and the low spiral budding is evident. However, in more robust zoaria, where exilazooecia are more commonly developed, longitudinal rows are not so well defined and the spiral budding is difficult to ascertain. Narrow low rounded rims occur around all autozooecial apertures. Interapertural walls are flat and dimensions are extremely variable in a single zoarium.

Exilazooecia are quite common and are small, but may be up to 0.14 mm in diameter, and are irregularly shaped apertures without rims. Their size, positioning and number varies greatly between individual zoaria, they are irregularly distributed, with more robust zoaria having the highest concentrations on interapertural walls.

Stylets are abundant on the zoarial surface. On the narrow raised rims around autozooecial apertures closely spaced very small type C stylets occur. These range from 0.02 mm to 0.06 mm in diameter and may attain a height of 0.06 mm. The number on apertural rims varies considerably and ranges between 6 and 15, and when very closely spaced give apertural rims a slightly beaded appearance. Some small stylets may also be situated on interapertural walls. Larger type B stylets ranging from 0.04 to 0.10 mm in diameter and attaining a height of 0.12 mm are common on interapertural walls. These stylets are normally quite closely spaced, but their distribution is quite irregular.

Internal

Autozooecia are budded in a quite well defined central linear axial zone. Zooecia arise in a low spiral pattern around the axial zone and zooecial walls lie at fairly constant orientations from the axial zone, and are of relatively constant length. Initially diverging at very low angles between 15° and 30° in the endozone, the angle increases abaxially very rapidly at the top of the endozone, and zooecia diverge at very high angles in the exozone (between 60° and 90°) often becoming perpendicular to the zoarial surface.

Interzooecial walls are compound, the very thin median primary granular layer is usually only intermittently developed in a zoarium. Interzooecial walls are thin in the endozone, and laminae bend and thicken abruptly to form a quite thick exozone wall, with skeletal laminae changing orientation and becoming parallel to the zoarial surface. Exozone walls are of uniform thickness.

Autozooecia are initially rhomboidal, but soon develop a well faceted hexagonal cross-section, and increase dimensions gradually abaxially into the endozone region. With the development of the exozone wall autozooecial tubes become well rounded. Zooecial orifices are situated at the base of adaxially narrowing vestibules often perpendicular to the zoarial surface with orifices parallel to the zoarial surface.

Autozooecial apertures may be occluded by a single imperforate terminal diaphragm situated close to the zoarial surface. At their junctions with interzooecial walls they are aborally flexed and their distribution may be sporadic, but in a couple of colony fragments most zooecial apertures may be occluded.

Exilazooecia originate in the exozone wall, and have quite well rounded proximal extremeties and commonly increase dimensions orally. Normally only a single exilazooecium occurs very occasionally in an exozone wall between adjacent autozooecia.

Stylets are very common with both type A and type C stylets occurring.

Type A sytlets originate low down in the exozone wall, although some appear to develop in the uppermost endozone region. They have a well defined axial core up to 0.015 mm in diameter; axial cores may by curved, following the external morphology of the interzooecial wall.

Type C stylets are very small, narrow and short, originating in the upper exozone wall. Axial cores are not normally present, but if developed they are only intermittant.

Intrastylets are commonly developed in exozone walls. They are composed of very narrow, tightly packed, orally flexed nests of skeletal laminae continuous with normal exozone wall skeletal laminae, with laminae abruptly deflected orally for very short distances and lack an axial core. They are very short and while many are directed perpendicular to the zoarial surface, many are obliquely orientated and commonly bifurcate along their length. They are developed at any level within the exozone wall and may form minute projections above the zoarial surface.

<u>Dimensions</u> (N = 35)

	NM	Mn	Mx	$\bar{X}$
Z1	112	9	15	11.12
Z2	112	4	6	4.28
AD1	300	0.23	0.34	0.27
AD2	300	0.16	0.23	0.20
IWT1	300	0.21	0.30	0.25
IWT2	300	0.08	0.14	0.11
ED	81	0.04	0.13	-
ZD	28	0.63	1.53	0.89
ET	38	0.14	0.21	0.17
AXR	10	55.94	67.16	60.58

Discussion

Rhombopora similis (Phillips) is the only described species of Rhombopora Meek in British Carboniferous strata. It is a very delicate rhabdomesid characterised by its slender cylindrical zoaria, large oval autozooecial apertures, the common occurrence of exilazooecia, abundance and structural variety of stylets, and the development of autozooecia from a well defined axial locus.

Phillips (1841, p. 21, Pl. 11, fig. 32) described Millepora similis from Cannington Park, North Devon, and from Hope, near Torquay. Although the locality at Cannington Park is of Carboniferous age, the locality at Hope is of Devonian age. Rhombopora similis has subsequently been found only in Carboniferous strata, and it is unlikely that the taxon from the Devonian locality is conspecific with the Carboniferous one. Unfortunately Phillips material is now lost and it is not possible to validate this point.

In erecting the species Millépora similis, Phillips did not give a description of the taxon and his figures of the external morphological detail are poor. His illustrations (Pl. 11, fig. 32, b,c) show the occurrence of very closely spaced autozooecial apertures, that are markedly elliptical. From this brief description it is apparent that there is no similarity at all with the material examined in the present study labelled as Ceriopora similis or Rhombopora similis in the Vine Collection at the British Museum (Natural History), and the Young Collection at the Glasgow Art Gallery and Museum. Unfortunately it is not possible to check whether Vine's and Young's material is actually conspecific with Phillips' Millepora similis, because Phillips material is lost. The taxon described here as Rhombopora similis can only be tentatively assigned to Phillips' species.

Phillips placed *Millepora* in the true corals. Morris (1854) placed *Millepora* among the zoophytes and placed the coralline genus *Ceriopora* Goldfuss in the phylum Bryozoa giving *C. similis* under that generic heading. The taxon was referred to the genus *Rhombopora* by Vine (1885).

Material

ABHR.3R:1-16	Cavity slide with 16 zoarial fragments. Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABHR 239-251	Thin Sections, Locality and horizon as above.
HM D.110	Cavity slide with 14 zoarial fragments, labelled *Rhombopora (Ceriopora) similis* Phillips. Howood Quarry (Brigantian), Renfrewshire. J. Young Collection 1886.
HM D.118	Cavity slide with 9 zoarial fragments labelled *Rhombopora (Ceriopora) similis* Phillips. Gare near Carluke (Brigantian). J. Young Collection.
HM D.144	Cavity slide with 12 zoarial fragments, labelled as *Ceriopora interporosa* Phillips. Capelrig near E. Kilbride (Brigantian). J. Young Collection.
HM D.145	Multiple thin section of about 30 specimens, labelled as *Ceriopora interporosa* Phillips. Lower Limestone Series, Capelrig (Brigantian), E. Kilbride. J. Young Collection 1886.

Stratigraphical Range

Brigantian - Arnsbergian.

Occurrence

Rhombopora similis is fairly uncommon and has only been described from Brigantian strata in the Midland Valley of Scotland and in Brigantian and Arnsbergian strata in the Yoredales of North Yorkshire.

The double-walled concept of growth applied to rhabdomesid cryptostomes

All available evidence suggests that rhabdomesid cryptostomes were double-walled bryozoans. The main reasons for this are discussed below and are based solely on the material examined in the present study.

(a) Zoaria characteristically form irregularly dichotomising cylinders of constant diameter. Autozooecia are developed from a well defined axial locus such as a linear plane, central axial cylinder or bundle, and are budded in a well defined annular or spiral manner. In a zoarium autozooecia are typically of comparable length, and growth patterns following budding are constant in a taxon.

This regularity in the mode of growth suggests control probably by an orally situated colony wide depositing epithelium, rather than by a series of accretions of individuals.

(b) Skeletal laminae (interpreted as growth laminae) are continuous across fairly large interzooecial areas between adjacent autozooecia. This feature and the constant diameter of zoaria suggests the gradual addition of laminae continued across wide areas during the life of the colony. This regular at least semi-colony wide deposition of laminae suggests that the addition of skeletal material was subject to colony wide control, probably by orally situated depositing epithelium.

(c) Endozone interzooecial walls in the rhabdomesids examined are compound or at least intermittently compound. The occurrence of such compound walls suggests that they were secreted from both sides under and infolding of an orally situated depositing epithelium in a manner similar to the interior walls of recent double-walled cyclostomes.

(d) In the two species of Rhabdomeson examined in the present study, transverse imperforate diaphragms may occur across the central axial cylinder. These were evidently secreted by an orally situated epithelium because the diaphragms are orally flexed at their junctions with vertical interzooecial walls, and the laminae comprising them are continuous with laminae lining interzooecial walls distal to them. As axial cylinder walls are compound it is apparent that the epithelium that must have lined the cylinder orally to the diaphragm and must have been continuous with, and folded over into, adjoining autozooecia at the growth tip.

(e) With reference to the function of stylets (see pp.46-52) it is possible that the large type A stylets, which are typically arranged in stabilised positions relative to autozooecial apertures, acted as loci of attachment for the external colony wide epithelial tissue. The smaller type B and C stylets that are usually more irregularly arranged possibly had a protective function or stabilising function for the covering of soft tissues.

By applying the double-walled model of growth in recent hornerid and lichenoporid cyclostomes to rhabdomesid cryptostomes the above lines of evidence suggest the existence of an externally situated colony wide inner hypostegal epithelium. This and its internal equivalent (with which it was continuous), secreted all the calcareous skeleton. As interzooecial walls are non-porous in rhabdomesids (and in all cryptostomes) an externally situated hypostegal coelomic space above the hypostegal epithelium was probably responsible for nutrient exchange between autozooecia across the colony. An outer eustegal epithelium situated externally to the coelomic cavity was responsible for secreting only the cuticlar mantle covering of the colony including the terminal vestibular membranes of zooids.

Discussion of the Coefficients of Variation of selected parameters measured on taxa within the Family Rhabdomesidae

The calculated values of CV's in the present study are based on the measurement of parameters from parts of colonies which are typically small cylindrical fragments of zoaria which formed delicate quite large irregularly dichotomising branches. Complete colonies are very rare, because they are so delicate and easily fragmented, and consequently in the present study is has been necessary to undertake the measurement of set parameters on such small branch fragments.

As a consequence of measuring the parameters on small branch fragments it should be noted that the CV's of some of the parameters are not a true expression of the true within, between the total colony morphological variation which may be shown by colonies of a taxon. The degree to which the CV's may be inaccurate for these parameters is discussed below.

Zoaria typically form irregularly dichotomous cylinders with branches of variable diameter; although individual branches have a fairly constant diameter, lateral branches for example are only about half the width of parent branches. Obviously measuring zoarial diameter on such a colony would result in fairly high within colony CV's significantly higher than those stated in table 1, which reflects only measurements undertaken on a number of small branch fragments. The same is true also for exozone wall thickness, and for axial cylinder width in Rhabdomeson, where new axial cylinders arise with the development of lateral branches. The examination of a number of complete colonies involving the measurement of these parameters would

	ZD			Z2			AD1			AD2			IWT1			IWT2			AW			TE			AXR		
	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T
Rhabdomeson gracilis	5.41	15.00	21.89	3.31	7.38	10.76	5.88	12.33	13.51	7.29	11.88	11.91	9.01	13.61	15.46	19.72	15.32	20.80	2.80	23.56	32.80	3.15	20.29	44.55	3.01	12.01	12.46
Rhabdomeson rhombifera	3.21	9.24	20.24	3.15	5.43	6.84	14.31	10.39	14.31	12.31	7.70	11.89	21.45	18.05	24.01	20.45	16.04	23.45	2.41	17.51	21.50	2.90	20.34	31.54	2.19	10.85	11.03
Rhombopora similis	6.51	13.58	25.18	7.15	13.35	18.29	5.67	3.97	12.65	8.08	6.28	8.95	22.08	14.31	17.58	23.04	17.51	20.80	-	-	-	2.91	13.05	13.00	2.08	5.31	6.19
$\bar{X}$	5.04	12.61	22.44	4.54	8.72	11.96	8.62	8.90	13.49	9.23	8.62	10.92	17.51	15.32	19.02	17.74	16.29	23.45	2.60	20.53	27.10	2.99	17.89	29.70	2.43	9.39	9.89

obviously significantly alter the values of within, and between colony CV's. This would result in the within colony CV's for these parameters probably being elevated to values greater than those between colony CV's. Although in the following discussion the terms within colony, between colony, and total colony CV's are used, a better terminology in the light of the above discussion on certain parameters would be within, between and total branch CV's.

However, some parameters such as apertural dimensions, interapertural dimensions, and the axial ratio, show no significant variation when a complete colony is examined. Consequently the CV's given in table 1 are a true expression of within, between, and total colony morphological variation of those parameters.

External Morphological Characters

Zooecial Parameters

Number of Autozooecial Apertures in a 2 mm line (Z2): Rhabdomesids are characterised by their regularity in mode of growth of autozooecia which are budded from a well defined axial locus and from which the pattern of growth of successive autozooecia in a zoarium is identical. This regularity in the mode of growth is reflected by the regular arrangement of autozooecial apertures in quincunx on the zoarial surface, and in the very low values of within colony CV's for this parameter. In Rhabdomeson gracilis and Rhabdomeson rhombifera within colony CV's are extremely low, with an average of 3.23.

Rhabdomeson colonies are monomorphic with only autozooecia present, however, in Rhombopora similis exilazooecia occur, and the presence of these affects the regularity of the arrangement of autozooecial apertures. As a result within colony CV's are considerably higher ($\bar{X}$ 7.15) in R. similis than for the two species of Rhabdomeson.

Between colony CV's are considerably higher than within colony CV's and range from 9.24 to 15.00. This reflects the different mode of development of autozooecia (expressed on the zoarial surface in the shape size and arrangement of autozooecial apertures) between individual colonies in a population, and the effects of such exogenous factors as microenvironment.

Apertural Diameter (AD1, AD2): Owing to the different morphologies of the three taxa examined in the present study the calculated CV's for the parameters of Apertural length (AD1) and Apertural Width (AD2) are discussed individually for each taxon.

In Rhabdomeson gracilis autozooecia develop around an axial cylinder, budding is very precise and the pattern of growth of successive autozooecia in a zoarium is identical. Consequently apertural dimensions are comparable, and this high degree of regularity is expressed in the very low within colony CV's for apertural diameter (5.88 for AD1 and 7.29 for AD2). Between colony CV's are higher, 12.33 for AD1 and 11.88 for AD2, and these values express the genetic variation in the mode of development of autozooecia between colonies in a population.

In Rhabdomeson rhombifera because apertural dimensions are graded around a zoarium, the within colony CV is based on the average of the average CV of apertural dimensions in individual longitudinal rows (where apertures are of the same size) in a single zoarium. The between colony CV is based on the average of the average values of apertural dimensions measured on apertures of equivalent size in different zoaria in a population.

Within colony CV's are relatively high (14.31 for AD1 and 12.31 for AD2). This is due to the fact that the gradation in apertural dimensions with apertures of the same size occurring in the same longitudinal row is not clearly defined. A gradation in the angle of divergence of autozooecia away from the axial cylinder around the zoarium causes the gradation in apertural dimensions on the zoarial surface. Any local minor irregularity in the angle of divergence of autozooecia will obviously affect apertural dimensions and it is this factor which probably causes the relatively high average values of within colony CV's. Such variation is evened out when a number of colonies in a population are examined and consequently between colony CV's are lower (10.39 for AD1 and 7.70 for AD2).

In Rhombopora similis within colony CV's are slightly higher (5.67 for AD1 and 8.08 for AD2) than between colony CV's (3.97 for AD1 and 6.28 for AD2). This is due to the occurrence of exilazooecia which can affect the arrangement and hence the shape and size of autozooecial apertures. Between colony CV's are lower because when a number of colonies in a population is examined such within colony variation is evened out.

Interapertural Distance (IWT1, IWT2): As with apertural dimensions calculated CV's will be discussed individually for each taxon.

In Rhabdomeson gracilis within colony CV's are considerably lower (9.01 for IWT1 and 9.72 for IWT2) than between colony CV (13.61 for IWT1 and 15.32 for IWT2). This is due to the same factors as discussed for apertural dimensions where the same situation applies. The pattern of development of successive autozooecia away from the axial cylinder is identical for all autozooecia in a colony. This high degree of regularity is expressed in the very low within colony CV's for apertural dimensions, and this is also the case for interapertural distances. Between colony CV's are considerably higher than within colony CV's due to the genetic variation in growth patterns between individual colonies, and exogenous microenvironmental and other factors causing such variation in a population.

In Rhabdomeson rhombifera as apertural dimensions are graded around a zoarium so are interapertural distances. The within colony CV is based on the average of the average CV of interapertural dimensions calculated for individual longitudinal rows (where apertures are of the same size) in a single zoarium. The between colony CV is based on the average of the average values of interapertural dimensions measured between apertures of an equivalent size in different zoaria in a population. As for apertural dimensions within colony CV's are higher than between colony CV's (within colony CV's are 21.45 for IWT1 and 20.45 for IWT2, compared to 18.05 for IWT1 and 16.04 for IWT 2). The explanation for this is obviously due to the same factor as those inferred for apertural dimensions. Between colony CV values are lower because such within colony variation is balanced out when a number of colonies in a population are examined.

In Rhombopora similis within colony CV's are significantly higher than between colony CV's (22.08 for IWT1 and 23.07 for IWT2 compared to 14.31 for IWT1 and 17.51 for IWT2). This is due to the fact that the regularity of arrangement of autozooecial apertures on the zoarial surface is affected by the occurrence of exilazooecia, budding patterns may not be well defined on the zoarial surface and consequently interapertural distances are often quite highly variable. Between colony CV's are considerably lower, due to the fact that such variation expressed by individual colonies is balanced out when a number of colonies in a population is examined.

Zoarial Parameters

Zoarial Diameter (ZD): Within colony CV's are very low, ranging from 3.21 to 6.51 ($\bar{X}$ 5.04) and reflect the regularity in the mode of zoarial growth with the colony fragments being cylinders of constant diameter . Autozooecia are developed around a well defined axial locus, with the mode of development of autozooecia being comparable in all respects, and this leads to branches in a zoarium of fairly constant diameter. Between colony CV's are significantly higher, 9.24-15.00 ($\bar{X}$ 12.61). Although the within colony CV's are a true reflection of the regularity of budding and development of autozooecia in a branch, the values as previously discussed may not be applied on a colony wide basis since small colony fragments were examined in the present study. The same is true for between and total colony CV's.

Internal Morphological Characters

Zooecial Parameters

Axial Width (AW): This was recorded in the two species of Rhabdomeson examined in the present study. Within colony CV's are extremely low, ranging between 2.41 and 2.80 ($\bar{X}$ 2.60). These low values are a true reflection of the regularity in the mode of growth that characterises rhabdomesids, with autozooecia developed around an axial cylinder of constant diameter along the length of a branch.

Such an axial cylinder enables a zoarium of constant diameter to be formed with autozooecia comparable in their mode of development following budding.

Between colony CV's are significantly higher ($\bar{X}$ 20.53). As for zoarial diameter, axial width within colony CV's are a true reflection of the regularity of branch development. The values, as previously discussed, cannot be applied on a colony wide basis from only small colony fragments. The same is true for the between and total colony CV's.

Exozone Thickness: Autozooecia are budded from a well-defined axial locus, and, after budding, their mode of development is identical. The change in the mode of growth from endozone to exozone occurs at a constant distance from the locus. This high degree of regularity is expressed in the extremely low within colony CV's, ranging from 2.90 - 3.15 ($\bar{X}$ 2.99). Between colony CV's are significantly higher ranging from 13.05 to 20.34 ($\bar{X}$ 17.89). Although the within colony CV's are a true reflection of the regularity of autozooecia budding and pattern of development in a branch, again these values may not apply on a colony wide basis because only small colony fragments were examined. The same is true for the between and total colony CV's.

Axial Ratio (AXR): As would be expected with the extreme regularity in the mode of development of autozooecia from the well defined axial locus in a zoarium, within colony CV's are extremely low ranging from 2.08 to 3.01 ($\bar{X}$ 2.43). Between colony CV's are higher, ranging from 5.31 to 12.01 ($\bar{X}$ 9.39). The axial ratio appears to be fairly constant in an entire colony and the within and between colony CV's are taken as reflecting the true degree of variation in the mode of development of autozooecia within and between colonies. Between colony CV's are also affected by such exogenous factors as microenvironmental influences on colony growth.

In all parameters measured total colony CV's are higher, due to the combination of a number of factors, such as genetic, evolutionary and micro- and macroenvironmental factors.

All the parameters utilised in the present study of some British Carboniferous rhabdomesids are of high taxonomic value. Measurements of parameters such as interapertural distances which display higher within and between colony CV's is justified because it is taxonomically necessary to examine the whole range of morphological variance.

CHAPTER V

Order Fenestrata Elias and Condra, 1957

Diagnosis

Stenolaemata with reticulate expansions of branches, joined by dissepiments with or without apertures on, or by the coalescence of adjacent sinuous branches, or zoaria may be free, pinnate, dichotomous or foliaceous growths unconnected by dissepiments. Autozooecia are initially recumbent, becoming erect distally with a rounded vestibular region, the base of which is commonly defined by a shelf-like hemiseptum; autozooecial apertures open on one side of a branch only. Secondary nanozooids and ovicells are rare. Obverse and reverse surfaces are smooth, finely granular, pustulose, longitudinally striate or nodose. Internally branches have a three fold construction, with a thin granular layer flanked by inner laminated tissue lining the zooecial chambers, and thicker outer laminated layer traversed by numerous radiating skeletal ridges of the inner granular tissue from which skeletal ridges may extend.

Range

Ordovician to Permian.(? Triassic)

Discussion

Elias and Condra (1957, p. 35) suggested the seggregation of all fenestrate cryptostomes into a new order Fenestrata. This was based on the homology of the colonial plexus of fenestrates to the common bud in extant cheilostomes, and the fact comparable structures are absent in other members of the Order Cryptostomata in which fenestrates were then placed. They suggested the new order Fenestrata be included in the Class Stenolaemata.

The ordinal status of the Fenestrata is now widely recognised though not universally used in taxonomic studies. In the present study, on the basis of their diagnostic external and internal morphologies, the following families are recognised as lying within the Fenestrata, Fenestellidae, Polyporidae, Acanthocladiidae, Thamniscidiidae and Septoporidae.

SIGNIFICANT ASPECTS OF FENESTRATA SKELETAL MORPHOLOGY

Wall Structure

Branches have an internal three-fold construction (Elias and Condra, 1957; Tavener-Smith,1969a; Gautier, 1973): a thin granular layer (the colonial plexus of Elias and Condra) forms the basal and vertical walls of zooecial chambers, and is flanked by inner laminated tissue lining the zooecial chambers and a thicker outer laminated layer traversed by numerous skeletal ridges of the inner granular tissue from which skeletal rods may extend (see Figs. 26,27).

Dissepiments connect branches and in general where they too have zooecia, they have the same skeletal structure. Sterile dissepiments, i.e. dissepiments without zooecia, have a similar internal structure to branches but the inner laminated layer is absent.

Skeletal Growth

The growth of fenestrate Bryozoa has been discussed in detail by Tavener-Smith (1969a)and Gautier (1973) and will be only briefly reviewed here.

The studies have shown that the granular layer forming the basal and vertical walls of zooecial chambers developed prior to the surrounding laminated tissue and was of primary origin. The inner and outer laminated skeleton was secreted subsequently and is thus of secondary origin.

Tavener-Smith (1969a) applied Borg's (1926) double walled growth model for the morphologically comparable recent hornerid cyclostomes to fenestellids. He suggested that an inner hypostegal epithelium was responsible for secreting most of the fenestellid skeleton as is the case with hornerid cyclostomes. Growth of the colonial skeleton in fenestrate bryozoans probably followed the 'conveyor belt pattern' initially described by Williams (1956, 1968) for brachiopods and applied to fenestellids by Tavener-Smith (1969 a). This system is characterised by the ability of the secreting epithelium to vary its secretory product with time.

The hypostegal epithelium appears to have been proliferated at the tips of growing branches and to have secreted a thin cuticular covering in that area. As the branch tip advanced through growth and the conveyor belt moved to the rear the same epithelium seems to have laid down in successive phases, the primary and then the outer secondary layers of the calcareous skeleton (see Fig. 28).

Deposition of the primary granular layer was continuous and relatively rapid and the epithelium migrated outward during growth resulting in the primary wall being laid down. As the tip advanced through growth, towards the rear the same portion of the epithelium started to secrete the outer layers of the calcareous skeleton. There was possibly a decrease in the rate of secretion accompanied by a change from continuous to intermittent deposition, this being reflected by a transition between the primary and outer secondary skeleton. The outer laminated skeleton gradually increases in thickness by the regular addition of layers at the periphery as long as the colony lived. At the same time there was continued growth outward from the primary layer at a number of separate points resulting in the formation of rods piercing the laminated tissue. Such granular skeleton was possibly secreted by specialised areas of inner hypostegal epithelial tissues.

The laminated skeleton lining zooecial chambers was probably deposited by a zooidal epithelium and its development followed close on formation of the earliest granular tissue. Rythmic deposition resulted in a laminated wall structure, and the rate of deposition probably decreased with time.

Autozooecial Chambers

In the Fenestrata autozooecial chambers are very short, tubular typically flask-shaped, consisting of a proximal recumbent box-like portion that bends abruptly at a high angle at its distal extremity to form a characteristically short circular tube of reduced dimensions termed the vestibulum, at whose distal extremity is situated the aperture. The base of the vestibulum termed the orifice is quite commonly marked by the occurrence of a hemiseptum.

Autozooecial apertures all open on the same side of the colony - the obverse surface. In all taxa zooecial chambers in their proximal recumbent portion closely interlock. In taxa possessing two rows of zooecia, autozooecial chambers are identical in all respects and are mirror images of one another. However in taxa possessing three or more rows of zooecia there is considerable variation in basal chamber shape and size, for example while lateral rows may maintain a hemi-hexagonal shape, the median row has a typical rhombic shape.

Autozooecial Apertures

There is a large range in apertural dimensions and shape in fenestrate Bryozoa. However, apertural size and shape is fairly constant in a given taxon and is of considerable systematic value.

In fenestellids and acanthocladiids peristomes are commonly developed. These are very short low rim-like or more rarely, short tubular extensions of vestibular regions which raise the level of the aperture above the colony surface. Peristomes developed only after the vestibular region of zooecial chambers and the surrounding frontal wall was complete.

Peristomal rims are commonly only simple, consisting of a plain low rounded complete rim of the secondary skeletal laminae (e.g. Pl. 40, fig. b). However, quite commonly, peristomal rims are incomplete. Usually only a rim is developed around the distal and lateral margins of apertures, while in Penniretepora stellipora (Young and Young) the peristome is dissected by a proximal rimule (see Fig.59 , Fig.60).

In several species of Penniretepora and Fenestella examined in the present study, the inner peristomal rims are denticulated with eight small denticles (Young and Young, 1874a; termed 'septa' by Engel, 1975). These are spinose projections which taper toward the centre of the aperture leaving a small circular opening in the centre (e.g. Penniretepora spinosa (Young and Young), see Pl.98 fig.g). The denticles are composed of skeletal laminae continuous with laminae of the peristomal rims, and are developed from regularly arranged outfolds of laminae originating just below the crests of the rims and tapering upwards and outwards into the aperture. Denticulated apertures have been described in only very few fenestrate bryozoa, and in all cases there are eight denticles projecting out into the aperture.

Young and Young (1874a,p. 681) established a new genus Actinostoma and later (1875a,p. 327) a new subgenus Acanthopora for a species of Fenestella and Penniretepora based on the occurrence of the radially converging denticles and they believed such a condition to be of taxonomic importance. However they later altered their opinion (1879) stating that such a condition was the perfect unweathered state of apertures and later work showed that this feature is also present in other fenestellids and Penniretepora species, and Actinostoma and Acanthopora were placed in synonomy with Fenestella and Penniretepora by Nickles and Bassler (1900).

Engel (1975) established the new genus Septatopora based partly on the occurrence of strong denticulated apertures. Although he suggested that the occurrence of these septa indicate that the taxon has affinities with octocorals, examination of the internal skeletal morphology showed that Septatopora is inseparable from contemporary fenestellid Bryozoa. With reference to the denticulated apertures Engel suggested a possible mode of tentacle protrusion. The occurrence of the denticles obviously greatly restricted the ability of the polypide to extrude from the zooecial cavity. In their fully extended position the tentacles would have been placed between the denticle partitions and the mouth must have been located beneath the small central opening with the tentacle ring of the lophophore contained within the vestibule.

In Septatopora, Engel stated that the problem in assuming that the genus was a normal ectoproct is the fact that the anus, situated outside the lophophore, must also have been contained in the vestibule. In Septatopora there is a proximally situated auxially tube extending from the lower portion of the vestibular regions to the obverse surface. Engel suggested the function of this slit was to overcome this sanitation problem and would have been an essential requirement. The rimule dissecting peristomal rims in Penniretepora stellipora possibly had a similar function.

In Fenestella ivanovi Shulga –Nesterenko the peristomal rims of apertures are ornamented by round pustules, with one situated above the position of each of the denticles. In Fenestella ivanovi, Fenestella bicellulata Etheridge and in Penniretepora spinosa apertures are denticulated but there is no such rimule or auxillary tube present to function as anal openings (e.g.Pl. 28 , fig. c ; Pl.98 , fig.h). It is quite possible that the overall organisation of the polypide was different, but since there are no modern analogues it is not possible to postulate with any certainty modifications of soft part morphology which could have aided the removal of waste material. Many taxa examined do not have denticulate apertures, and although their presence is of taxonomic value, their possible phylogenetic significance cannot be ascertained, because the denticles are very delicate, and only very rarely preserved.

In the Polyporidae, peristomes are only very rarely developed, but apertured rims may occasionally be ornamented. For example, in Polypora dendroides McCoy every aperture is surrounded by a circlet of pustules. These are rods of the primary granular skeleton surrounding chambers extending up around the apertures (see Pl.80 , fig. a).

Polymorphic Zooecia

(a) Secondary Nanozooids

The term secondary nanozooid (Silén and Harmelin, 1974) is used here to describe those autozooecia whose apertures are sealed by a calcified terminal diaphragm perforated by a small open tubule. The opening is usually elevated above the general level of the terminal diaphragm by a low distally narrowing prominent peristome (e.g. Penniretepora elegans, Pl.24 , Pl.109, fig. f).

Silén and Harmelin (1974) first described secondary nanozooids in two species of the recent diastoporid cyclostome genus *Plagioecia*. In the fossil record they have been recognised in only a single species of the Carboniferous fenestrate bryozoan *Lyroporella* (McKinney, 1977). However, Young (1879, p. 212) described structures, considered here to be secondary nanozooids, in some Lower Carboniferous fenestrate taxa from Scotland. Young described the apertures (he used the term 'cell pore') covered by a thin calcareous disc or diaphragm pierced in the centre by a very minute pore. He described such structures in *Fenestella plebeia* McCoy, *F. ejuncida* McCoy; *Polypora tuberculata* Prout and *Penniretepora elegans* (Young and Young). Young believed the structures to be another condition of the perfect cell-pore in addition to the denticulated form of apertures he also described.

In the present study secondary nanozooids have been found to occur in six species of four genera of Carboniferous fenestrate bryozoans in addition to those mentioned by Young. These are *Penniretepora flexicarinata* (Young and Young), *Penniretepora pulcherrima* McCoy, *Fenestella ivanovi* Shulga-Nesterenko, *Fenestella polyporata* (Phillips), *Ptylopora pluma* McCoy and *Polypora dendroides* McCoy. No analysis of the distribution of secondary nanozooids was possible in the present study, because very few complete colonies were available. However it was noted that in fenestrate zoaria there appears to be a tendency for secondary nanozooids to be very abundant in proximal areas of colonies. In some small colony fragments examined of fenestrate and pinnate zoaria every aperture may be a secondary nanozooid. All the secondary nanozooids examined in different species are morphologically alike, and are comparable to the skeletal morphology of those described in *Plagioecia* by Silén and Harmelin (1974).

Secondary nanozooids are very unusual heterozooids; usually heterozooids are budded as separate individuals, however, the development of secondary nanozooids involves the transformation of an autozooid by its degeneration and the regeneration of a heterozooid. Although degeneration-regeneration cycles are common in bryozoans, the degeneration of an autozooid and the regeneration of a heterozooid in its place is an uncommon phenomenon, though quite common in cheilostomes. Silén and Harmelin (1974) described the mode of development and morphology of secondary nanozooids in two species of Plagioecia. They are developed in the central area of the colony, i.e. around the colony origin, where the oldest zooecia occur and their generation represents the ultimate stage of zooid development. The formation of a secondary nanozooid involves the transformation of an autozooid. Initially the membranous sac of the autozooecial polypide and the retractor muscle degenerated leaving the body wall of the remaining proximal part of the zooid unchanged with the atrial sphincter of the autozooid persisting. A centripetally calcified terminal membrane was then secreted leaving a small open tubule that served as a secondary aperture over the distal end. A different type of polypide with retractor muscle and membranous sac is then regenerated. All parts are smaller, the tentacle number is reduced to one, tentacle cilia are absent, and there is only a rudimentary alimentary canal. The tentacle emanating from the orifice of the tubule is very short, and extending straight and upright.

The function of secondary nanozooids in Plagioecia species is uncertain. Nanozooids s.s. although morphologically comparable have a much larger nonciliated tentacle which extends horizontally in a proximal position and performed a periodic proximal to distal or circular sweeping action. Silén and Harmelin showed that such movements facilitated the clearance of particles from the colony surface.

Silén and Harmelin excluded a cleaning function for the small tentacles of secondary nanozooids in *Plagioecia* as they are too small, and incorrectly orientated. The lack of cilia and the reduction of the alimentary canal also excludes feeding as a function and they did not find any sign of any sex (male) cells, and no other glands were observed. Silén and Harmelin did not suggest any function for secondary nanozooids only pointing out their obviously obscure nature.

As McKinney (1977) suggested, and the present study has also shown, fenestrate secondary nanozooids are morphologically comparable to similar sized and shaped perforate terminal diaphragms in *Plagioecia*. They may also have functioned as a heterozooid that extruded a single tentacle. McKinney suggested that the single tentacle polymorph may have functioned as male polymorphs as suggested for some cheilostome zooids with a reduced number of tentacles (Cook, 1968). Although this may be possible the soft part morphology of recent secondary nanozooids makes this interpretation seem unlikely. It may be that they performed some kind of defensive cleaning function as described by Silén and Harmelin for nanozooids s.s.

As in the recent cyclostomes in which they are found to occur they would have been an ephemeral stage in the ontogeny of any given zooid. Considering McKinney's (1977) suggestion that they were completely covered over by laminated skeletal deposits soon after their development; there is no direct proof of this in the considerable amount of material examined during the present study, although there appears to be a tendency for them to be abundant in the proximal area of colonies which are quite susceptible to secondary thickening of laminated skeletal deposits.

(b) Ovicells

In fenestrate bryozoans the skeletal indications of inferred brood chambers (here termed ovicells after Tavener-Smith, 1966a) have been recorded in only a few taxa (see Tavener-Smith 1966a; Stratton, 1975). The ovicells described in fenestrate bryozoans are comparable in position to those Gonozooecia described in extant cyclostomes (Borg, 1926) and in fossil cystoporates (Utgaard, 1973).

The ovicell in fenestrates consists of two chambers. The inner chamber is nothing more than an unmodified autozooecial chamber and is regarded as the gonozooid chamber. This is directly connected by a short vestibular region to the brood chamber, here termed the ovicellular inflation. Stratton (1975, p. 174) described the occurrence of a partition partly separating the gonozooid chamber from the brood chamber. The ovicellular inflations form elliptical or spherical globose inflated chambers with a small circular opening at their crests, through which larvae were liberated at the appropriate time.

The basal area of the ovicellular inflation is usually considerably depressed into the branch surface (e.g. Pl. 72 , fig. a), and is normally situated centrally above the vestibule of the chamber. The existence of an ovicell locally increases the height of a branch, and may affect the disposition of adjacent autozooecial apertures, but usually without any disturbance in their structure. The ovicellular inflations are usually of moderate size, located on one side of a branch (eg.Pl.25), but in some taxa may be very large and extend across the entire width of the branch even beyond branch margins (e.g. in Hemitrypa hibernica, McCoy, see Pl. 72, fig. a).

In the present study ovicellular developments of the above type have been found in Penniretepora spinosa (Young andYoung) and Penniretepora sp. nov. B, and are comparable in shape, size and structure to those described by Tavener-Smith and Stratton for fenestellids. In both taxa they form large oval inflations, and do not affect the disposition of adjacent apertures in the same row or the nature of the median carina (see Pl. 98, figs.e,f; Pl. 101. figs. b,c,d).

Ovicell walls are compound, continuous with the calcareous skeleton of the main branch and with a median primary granular layer, bound internally by a thin band of zooecial laminated skeleton and externally by a thicker secondary laminated skeleton.

Carinal Nodes

Carinal nodes are elongate spinose structures situated at regular intervals on a median carina or ridge centrally placed along the obverse surface of branches in fenestellids and acanthocladiids, and between the several rows of autozooecial apertures in polyporid fenestrates (e.g. Pl. 28 , fig. b , Pl. 91 , fig. b).

Carinal nodes consist of a central core of granular material surrounded by laminated tissues (see Fig. 27). Considerable confusion concerning the nature of carinal nodes has arisen because they are commonly broken and the granular skeletal core differentially weathers out giving nodes a hollow appearance. Until quite recently all stylets were thought to have been hollow originally, as a result of this interpretation several authors have considered carinal nodes and stylets to be homologous.

Ulrich (1890, p. 302) surmised that stylets (he used the term acanthopore) and carinal nodes supported appendages analogous to avicularia or vibraculae found in recent Bryozoa. Other authors (Bassler, 1953, G.120; Miller, 1961, p. 223) also suggested that carinal nodes, like stylets, housed heterozooecia.

Tavener-Smith (1969a, p. 302; 1969b, p. 97) showed that both stylets and carinal nodes are solid structures incapable of housing any soft parts, although they are similar in shape, size and internal structure they have a different ontogeny. The granular core of carinal nodes is of primary origin and was developed prior to the enclosing secondary laminated tissue, and arose as an extension of the primary granular skeleton surrounding autozooecial chambers. In contrast, with stylets the development of central cores and the surrounding sheath laminae was contemporaneous (see pp. 37-38). As Tavener-Smith (1969b, p. 97) stated, this distinction is fundamental and excludes homology between the structures.

Tavener-Smith (1969a, p. 302) suggested that carinal nodes may have had a protective function, to protect the obverse surface of a colony from predators and from larval encrustation. Many fenestillids exhibit irregular or geometrically regular outgrowths of the carinal nodes above the zoarial surface, for example in the genus Cervella numerous, closely spaced carinal nodes branch distally presenting a spiky appearance.

TAXONOMIC PROCEDURE

Taxonomic History in the Identification of fenestrate Bryozoa

Since the later part of the nineteenth century there has been an exponential increase in the number of recognisable species of fenestrate Bryozoa. Although a large number of species have been described, the detailed systematics remain in an unsatisfactory state. Systematics have generally been based on external zoarial morphological characters only. Despite the strong tendency for intraspecific morphological variation, it is only recently that it has become evident to establish series of detailed measurements involving zooecial and zoarial characters for taxonomic purposes.

Initially fenestrate Bryozoa were described entirely qualitatively. McCoy (1844), Shrubsole (1879, 1881) and Young and Young (1874-1886) were amongst the first to use any form of quantitative data on external morphological characters with descriptions. Shrubsole (1881) presented data in a tabulated form (Number of pores per fenestrule/ fenestrule shape/number of fenestrules in two lines transverse/number of fenestrules in two lines long) to facilitate comparison amongst species of Fenestella.

Ulrich (1886, 1890) popularised the technique of stating meshwork dimensions, and stating the number of branches, fenestrules, apertures and carinal nodes in a unit distance for taxonomic purposes. Both Shrubsole and Ulrich noted meshwork variability in species of Fenestella, and Ulrich noted differences in the internal morphology of different fenestellid taxa.

The need for refinement in identifying species was recognised in the early twentieth century by both Western and Russian workers, and measurement schemes were developed based on external morphological characters in order to achieve this. However, these schemes became so numerous and varied as there was no standard sequence of measurements that species comparisons became difficult. No account was taken of intra- or inter-colonial variation and new species were often erected on the basis of single small zoarial fragments. In some cases zoarial fragments on which a species was based were so small that the normal measurements such as statements of the range of the number of branches, apertures etc .... over the normal unit distance (5 mms') could not be made (e.g. Moore, 1929).

Some extremely unusual schemes were used for taxonomic purposes, e.g. Elias (1937) used a formula set out in the following manner as an aid in identifying Fenestella species, "Branch width/Zoarium size/Nodes per fenestrule/Internodal distance". Unfortunately, most of these parameters have no taxonomic discriminatory value, colonies are normally found in a fragmented state, and carinal nodes are quite irregularly distributed.

Nekhoroshev and Nikiforova in a series of publications from 1926 introduced a formula incorporating measurements they regarded as critical for species discrimination, and as an expression of meshwork variability in a species. Nekhoroshev (1928) also drew attention to differences in the internal structure of colonies of Fenestella species, and even distinguished groupings of species differing in the shape of zooecial chambers in section.

Condra and Elias (1944) adopted this formula which they termed the 'Meshwork Formula', later renamed by Miller (1961, p. 224) as the 'Micrometric Formula'. This stated the range in the number of branches, dissepiments, zooecial apertures and carinal nodes per unit distance in a single or series of specimens and was expressed in the following form:

'B10/D10/A5/N5'

The formula was widely adopted and great emphasis was placed on it as a means of species differentiation. New species were often erected on the basis of a single specimen of small size, with no account taken of meshwork variation (Elias, 1957; Koenig, 1958; Burkle, 1960; Miller, 1961). These workers used the formula as a basis for comparison of the same or similar species described by other authors. Elias (1957) even erected <u>Fenestella</u> groupings on the basis of the formula together with apertural spacing.

Some authors added extra parameters to the basic micrometric formula as an aid to taxonomic differentiation. Miller (1962a) extended the formula to include branch width, and zooecial chamber base shape. Malone and Perry (1965) suggested that the micrometric formula should include the following additions under each element, from left to right - the arithmetic mean, the standard deviation and the number of measurements as an aid for taxonomic analysis.

Tavener-Smith (1966b) showed that although the formula was useful as a means of indexing species on the basis of their meshwork characters, it is inadequate as a basis for taxonomic discrimination. As Miller (1961) stated, different species with a similar micrometric formula may differ markedly in certain structural elements. The visual comparison of species based on the micrometric formula, on the observed range of measurements per unit distance unsupported by other data is very subjective. Formulae founded on a single small zoarial fragment fail to reflect the range of intracolonial variation of meshwork dimensions which result from the different stages of growth, microenvironmental conditions or growth aberations.

The micrometric formula has thus produced some confusion in defining the limits of morphological variation of a species and has led to the proliferation of species names.

Although for many years workers have incorporated meshwork dimensions into their descriptions usually only the range of values have been stated, and the same parameter has been measured in different ways. For example fenestrule length has been recorded by measuring the actual length of the gap, or by measuring from the midpoint of adjacent dissepiments in one row. Even meristic counts have been recorded in different ways. Some workers have counted the actual number of zooecial apertures along one row of a branch over a unit distance, while others have used the space count method of Condra and Elias (1944) and recorded one less than the actual number.

Tavener-Smith (1966b)emphasised the need to make a direct series of standard measurements, to be repeated on a number of colony fragments of a species, and to derive from them statistics that would allow comparisons by a standard significance test. He established a measurement scheme consisting of a series of independent parameters necessary for species discrimination, utilising external zoarial and zooecial characters, together with some internal characters such as zooecial chamber base shape and dimensions. He retained the micrometric formula only as a means of indexing a species recording the variability of the meshwork.

Recently authors make a series of measurements on a number of colony fragments of a species to determine its morphological limits (Stratton,1975; Stratton and Horowitz, 1977a, b; Engel, 1975, 1979).

The results are set out to facilitate numerical comparison. However there is still no standard scheme of parameters utilised and the micrometric formula still dominates in some schemes (Termier and Termier, 1971; Simonson and Cuffey, 1981). It is only recently that Western workers have begun to realise the importance of internal morphological characters and now commonly state zooecial chamber base dimensions and describe chamber shapes for taxonomic purposes.

Russian workers still use a basic meshwork formula in their descriptions and quote only the range of values of zoarial and zooecial dimensions. Russian workers place a greater emphasis on the nature of zooecial chambers and internal morphological characters in taxonomy. They have built upon the work of Nekoroshev (1928, 1932) and Shulga-Nesterenko (1941, 49, 51, 52, 55) on the use of internal morphological characters in taxonomy, and Morozova (1974) for example, has subdivided the genus Fenestella partly on the basis of zooecial chamber shape.

Present Taxonomic Procedure

In the present study of some British Lower Carboniferous fenestrate Bryozoa, taxa belonging to the families Fenestellidae, Polyporidae and Acanthocladiidae have been examined.

The measurement schemes utilised in the systematic description of taxa within these families involve both external and internal, zooecial and zoarial parameters. Internally, in addition to analysing autozooecial chamber base shapes and their dimensions considerable attention has been focussed on the analysis of the nature of the surrounding skeletal tissues, occurrence of hemisepta etc... .

In the analysis of internal morphological details it is necessary to prepare sections in specific orientations (see Figs. 29, 26, 27).

(a) tangentially along the length of a branch.

(b) longitudinally along the length of a branch, and

(c) transversely perpendicular to the length of a branch.

Family Fenestellidae King, 1850

Type Genus

Fenestella Lonsdale, 1839.

Diagnosis

Fenestrata with zoaria which are planar, conical or foliaceous reticulate expansions of branches joined by sterile dissepiments; Autozooecial apertures are arranged in two rows opening onto one side of the zoarium, the rows separated by a median carina or ridge that commonly bears nodes; reverse surfaces may be granular, pustulose or nodose. Hemisepta are quite common. Secondary nanozooids and ovicells are uncommon.

Range

Ordovician to Permian.

TAXONOMIC PROCEDURE

In all taxa within the families Fenestellidae and Polyporidae examined, colonies form reticulate, fenestrate expansions with branches connected by dissepiments, and colonies may develop a planar, conical or foliaceous form.

Zoaria are developed from a single, thickened, short main stem from which branches in extreme proximal areas rapidly diverge to develop such colony forms. In extreme proximal areas bifurcation points are clustered due to the rapid divergence of branches, as the critical lateral distances involved in bifurcating occur simultaneously between several branches. This part of the zoarium is said to be immature, and as a result of highly irregular branch spacing fenestrule dimensions are extremely variable. Dissepiment and branch widths are subject to secondary accretion with increasing age of a colony and may vary considerably in proximal areas. Branches are commonly thickened, strengthening the basal areas of colonies.

Distally, bifurcations become scattered, the lateral divergence of bifurcating branches decreases, and a tuning fork type of divergence may develop. There is only a slight effect on adjacent branches when a branch bifurcates and branches may lie subparallel or parallel to one another. The meshwork is very regular in this, the mature part of the colony.

Zooecial related parameters exhibit extremely low levels of variation throughout a colony. Individual zooecia are asexually produced genetically alike clones, and do not display any variation related to the stage of colony development and only slight ecophentypic variation.

In contrast, as discussed previously, zoarial related parameters may display considerable variation relating to the stage of development of a colony and are also subject to greater ecophenotypic variation. However in the mature part of a colony (which is by far the largest area of the meshwork) where the meshwork is regular, the measurement of zoarial related parameters such as fenestrule dimensions are of significant taxonomic value.

Thus in taxa which are characterised by reticulate fenestrate expansions the measurement of zoarial and zooecial parameters is best undertaken in the mature portion of colonies to determine the precise morphological limits of a species. Specimens selected for examination need to be of such a size to allow the measurement of all the selected morphological parameters, and the analysis of morphological variation of these parameters within the mature parts of colonies.

The chief parameters considered in subsequent systematic descriptions are listed below, and are the principal morphological characters used in the analysis of taxa. The scheme followed in the present study is after that outlined by Tavener-Smith(1973)(see Fig 30).

External Morphological characters

Zooecial Parameters

Branch Width (BW) is measured across a branch transverse to its axis, away from dissepiments and branch bifurcations. Branch width increases considerably prior to bifurcation. After bifurcation newly developed branches are initially thinner than average, but rapidly increase in width within one or two fenestrule lengths.

The Number of Apertural Rows (AR) is recorded as the number of longitudinal rows of autozooecial apertures transverse to the growth axis of a branch. This is not recorded in areas of branch birfurcations where coupled with the increase in branch width, an additional row may develop for a short distance. The number of apertural rows is constant along branches, and in the Fenestellidae there are two rows situated on either side of a median carina or ridge.

Autozooecial Apertural Diameter (AD): measured between the inner sides of the rim. In circular autozooecial apertures, the diameter is measured parallel to the growth axis of a branch. Where apertures are oval the largest axes is measured.

Interapertural Distance (ID): In the Fenestellidae where only two longitudinal rows of autozooecial apertures occur along branches interapertural distance is measured between the centres of adjacent apertures in the same row.

Zoarial Parameters

Fenestrule Length (FL): measured parallel to the growth axes between the mid-points of adjacent dissepiments.

Fenestrule Width (FW): measured transverse to the growth axis between the midpoints of adjacent branches.

Dissepiment Width (DW): measured across the narrowest part of a of a dissepiment tansverse to its length.

Internodal Distance (IND): measured between the centres of adjacent nodes in the same longitudinal row.

Autozooecial Apertures per Fenestrule (ZAF): recorded as the number of complete zooecial apertures in a single row between the midlines of adjacent dissepiments.

The Micrometric Formula

This is a useful means of indexing the variability of the meshwork in a species.

It will be stated in the conventional manner following the tabulated data for each taxon examined, recording the range of colonial meshwork variation in the number of branches and dissepiments in a 10 mm line, zooecial apertures and carinal nodes in a 5 mm line. Readings were made in the following manner:

B10; The number, or range in the number of branches transverse to the growth axis in a 10mm line.

D10; The number, or range in the number of dissepiments parallel to the growth axis in a 10mm line.

A5; The number, or range in the number of autozooecial apertures in a single row parallel to the growth axis in a 5mm line.

N5; The number, or range in the number of carinal nodes in a single row parallel to the growth axis in a 5mm line.

Internal morphological characters

Zooecial parameters

Zooecial Chamber Dimensions; Although the zooecial chamber is a three dimensional sturcture, and its shape is not adequately represented by basal chamber measurements alone, basal chamber measurements are a useful means of quantifying chamber size and are taxonomically very useful.

In the Fenestellidae only two rows of zooecia occur along branches and basal chambers are of similar size and shape.

Zooecial Chamber Length (ZB1): measured between the proximal and distal extremeties where a chamber attains its maximum length parallel to the growth axis of a branch.

Zooecial chamber base width (ZB2): measured between the lateral extremeties where a chamber attains its maximum width transverse to the growth axis of a branch.

Measurements are not made in areas of branch bifurcation. Prior to branch bifurcation, branch width increases and an additional row of centrally placed zooecia may develop for a short distance. The zooecial chamber bases of the newly developed zooecia have a different shape and size than normal chamber bases of the two lateral rows and their development may affect the normal shape and size of the latter. Immediately after a branch bifurcation where the newly developed branches are initially thinner than normal zooecial chamber base shape and size may be modified.

The measurement of zooecial chamber base size and the analysis of chamber shape is best undertaken in areas away from branch bifurcation, chambers display only very limited genetic variability and are of similar size and shape.

Genus Fenestella Lonsdale, 1839

Type species

Fenestella antiqua Lonsdale, 1839.

Diagnosis

Fenestellids with zoaria forming planar, fan-shaped, conical or irregular foliaceous reticulate expansions of branches connected by regularly spaced sterile dissepiments. The obverse surfaces of branches have two rows of autozooecial apertures, separated by a median ridge or carina which usually bears a single row of nodes; reverse surfaces are smooth or striate and may be pustulose or nodose, all surfaces are usualy finely granular. Hemisepta are quite common; secondary nanozooids and ovicells are uncommon.

Range

Silurian to Permian (? Triassic)

Fenestella bicellulata Etheridge, Jun. 1873a

Figs. 31-33; Pl. 26, figs. a-c; Pl. 27, figs. a-b; Pl. 28, figs. a-c; Pl. 29, figs. a-b; Pl. 30, figs. a-b; Pl. 31, figs. a-b; Pl. 32, figs. a-c

1873a Fenestella bicellulata Etheridge, Jun. p. 101.

1874a Actinostoma fenestratum (gen. et spec. nov) Young and Young p. 681, Pl. 40, figs. 1-4, Pl. 41, figs. 12-16.

1888 Fenestella tenax, Ulrich, p. 71.

1890 Fenestella tenax, Ulrich, Ulrich p. 546, Pl. 51, figs. 2-2e.

1906 Fenestella tenax Ulrich; Cumings, p. 1279, Pl. 30, figs. 1-1b.

1944 Fenestella tenax Ulrich; Condra and Elias, p. 99, Figs. 1-3.

1957 Fenestella tenax Ulrich; Elias and Condra, p. 106, Pl. 16, figs. 1, 2.

1961 Fenestella bicellulata Etheridge; Miller, p. 235, Pl. 27, fig. 1.

1980 Fenestella tenax Ulrich; Simonsen and Cuffey, p. 9, Table 2; Figure 3B, 4B, 5B, 6B, 7B.

Type

Etheridge, Jun. (1873a) did not publish a figure of Fenestella bicellulata and as his original material is now presumed lost Miller (1961) erected a neotype for the taxon. The neotype (GSE. 1994) is a very small colony fragment 2 x 2 mm and comes from Etheridge's original collecting locality.

Emended Diagnosis

Fenestella with delicate, fairly close, fine textured reticulate planar and fan-shaped zoaria. Branches are thin, straight and subparallel; on obverse surfaces there is a narrow straight median ridge with a single row of very closely spaced nodes. Dissepiments are very thin, depressed, fairly short, and flare considerably towards dissepiment-branch junctions. Fenestrules are small, rectangular to oblong. Autozooecial apertures are small and circular with complete peristomes and closely spaced, set flush on branch sides with two or three per fenestrule.

Description

External

Zoaria form delicate small, fairly close, fine textured planar fan-shaped or slightly foliaceous recticulate expansions up to 4 cm in diameter.

Branches are thin, straight and subparallel. On the obverse surface of branches there is a narrow straight subangular median ridge on which a single row of closely spaced, quite small ellipsoidal nodes occurs. Branch sides slope steeply away from the median ridge, and reverse surfaces are well rounded. All surfaces are finely granular, and closely spaced small rounded irregularly distributed nodes occur on the reverse surface of branches. Prior to bifurcation branch width increases for up to three fenestrule lengths and may reach 0.4 mm in width.

Dissepiments are very thin, and normally relatively short. They are well depressed below the crests of branches on the obverse surface, less so on the reverse, and flare considerably towards dissepiment-branch junctions becoming less depressed as they do so. When dissepiments are very short they have a typical biconcave appearance. On the obverse surface dissepiments may be flat or well rounded with occasionally a low central ridge developed, while on reverse surfaces they are well rounded.

Fenestrules are small, typically rectangular to oblong, usually twice as long as wide, with well rounded extremeties and straight or gently curving lateral margins. The lateral margins of fenestrules occasionally may be slightly undulatory.

Autozooecial apertures are small, circular and with complete relatively thick low peristomes. They are closely spaced, slightly more than their own diameter apart with 2 or 3 per fenestrule and are usually set flush on branch sides. Occasionally outer peristomal rims of apertures may project slightly beyond branch margins when they may have slightly upraised outer peristomal lips. Normally one aperture is situated on a dissepiment-branch junction and faces away from fenestrules at a high angle.

Internal

Autozooecial chamber bases are hemi-hexagonal.

Dimensions (N = 42)

	NM	Mn	Mx	$\bar{X}$
BW	512	0.16	0.20	0.18
AD	351	0.05	0.08	0.07
ID	351	0.16	0.22	0.18
FL	523	0.32	0.50	0.42
FW	523	0.30	0.42	0.36
DW	475	0.06	0.12	0.08
IND	378	0.16	0.23	0.20
ZB1	25	0.15	0.19	0.18
ZB2	25	0.09	0.12	0.10

Micrometric Formula 25-35/23-32/25-31/23-37

Discussion

Fenestella bicellulata Etheridge, Jun. is the most delicate British Carboniferous Fenestella species and is extremely distinctive being easily recognised by its very fine, close reticulate meshwork, the occurrence of extremely closely spaced carinal nodes along the median ridge, and small prominent autozooecial apertures with usually about two per fenestrule.

Young and Young (1874a, p. 681) erected the new genus and species Actinostoma fenestratum based on the occurrence of denticulated autozooecial apertures which they thought were significant enough to distinguish it from the genus Fenestella. However, later work showed that this feature is also present in other fenestellids and Actinostoma was placed in synonomy with Fenestella by Nickles and Bassler (1900, p. 37, p. 245).

The syntype material of A. fenestratum has been examined in the present study and this has shown that the form is conspecific with F. bicellulata and not Fenestella frutex McCoy as Tavener-Smith (1973, p. 413) had suggested. A. fenestratum is a junior synonym of F. bicellulata described earlier. F. bicellulata is a more delicate species than F. frutex and has significantly finer meshwork characters with smaller measured parameters. Fenestrule dimensions are significantly smaller, branches are thinner, carinal nodes are considerably more closely spaced, and autozooecial apertures are smaller, closer spaced and with only about two per fenestrule on average.

As Miller (1961, p. 236) stated, there is little doubt that F. bicellulata is conspecific with F. tenax Ulrich (1888, p. 71) the widely distributed Upper Palaeozoic species, and F. tenax is here placed in synonomy with it. Both taxa are characterised by their very fine meshwork dimensions, high numbers of branches and dissepiments per unit distance (23-33 and 22-30 in a 10 mm line), extremely closely spaced carinal nodes (22-37 in a 5 mm line) and very small prominent closely spaced autozooecial apertures with only about two per fenestrule.

Material

ABHR 1F	Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABP -8, -101, -115 to 117, -119, -120, -122, -123, -125, -127 to 129, -133, -136, -140, -141, -143, -146 to 148, -152, -156 to 158, -162, -166 to 168, -178, -179, -182, -188.	Fifth Limestone (Asbian), Alston Group, Penruddock, nr. Penrith, Cumbria.
ABP 307	Thin Section, Horizon and locality as above.
GAGM 01-53 aaf	Syntype of *Actinostoma fenestratum* Young and Young. Dykehead Pit (Brigantian), High Blantyre. J. Young Collection.
GAGM 01-53 aah	Syntype of *Actinostoma fenestratum* Young and Young. Dykehead Pit (Brigantian), High Blantyre. J. Young Collection, 1875.
GAGM 01-53 aal	Labelled as *Actinostoma fenestratum* Young and Young. Hairmyres (Brigantian), E. Kilbride. J. Young Collection, 1881.
GAGM 01-53 aan	9 specimens on a cavity slide. Syntypes of *Actinostoma fenestratum* Young and Young. Boghead, Hamilton. J. Young Collection. F.K. McKinney prepared one thin section and one acetate peel from specimens on the slide.
GAGM 01-53 aao	4 specimens on a slide. Syntypes of *Actinostoma fenestratum* Young and Young. Boghead, Hamilton. J. Young Collection.
GAGM 01-53 aap	44 specimens on a cavity slide. Labelled as *Actinostoma fenestratum* Young and Young. Boghead, Hamilton. J. Young Collection. F.K. McKinney prepared three thin sections and

	five acetate peels from specimens on the slide.
GAGM 01-53 aaq	6 specimens on a cavity slide. Syntypes of *Actinostoma fenestratum* Young and Young. Labelled as *Actinostoma fenestratum* and *Fenestella* with star-like pores. Upper Limestone, Calderwood cement Limestone (Brigantian), Capelrig, East Kilbride. J. Young Collection. Specimen no. 3 was figured by Young and Young 1874a, Pl. 40, fig. 3.
GAGM 01-53 zt	3 specimens labelled as *Actinostoma fenestratum* Young and Young. Newfield, High Blantyre (Brigantian). J. Young Collection.
GAGM 01-53 zv	labelled as *Actinostoma fenestratum* Young and Young. Newfield Quarry. (Brigantian), High Blantyre. J. Young Collection.
GAGM 01-53 zz	labelled as *Actinostoma fenestratum* Dykehead Pit (Brigantian), High Blantyre. J. Young Collection.
GSE 1994	Neotype. Shale between First and Second Calderwood Limestone (Brigantian), Lower Limestone Group, Hoghead, East Kilbride. Neotype of Miller 1961, p. 235, and figured by him Pl. 27, fig. 1.
HM D51-2	labelled as *Fenestella nodulosa* Carboniferous Limestone, Halkyn Mountain (Brigantian?), G.W. Shrubsole Collection 1882.

Stratigraphical Range

Asbian - Arnsbergian.

Occurrence

Fenestella bicellulata is a very common species and in the Lower Carboniferous of Britain it has been recorded in strata in the Midland Valley of Scotland, Cumbria, Yorkshire and North Wales. Fenestella tenax, which is here considered to be conspecific with F. bicellulata, is a very well known taxon, and is widely distributed and has a long geological range being recorded in Upper Palaeozoic strata of America, Europe and the Soviet Union.

Fenestella ivanovi Shulga-Nesterenko, 1951

Figs. 34, 35; Pl. 33, figs. a-c; Pl. 34, fig. a; Pl. 35, fig. b.

1951 Fenestella ivanovi Shulga-Nesterenko, p. 100

1973 Fenestella ivanovi Shulga-Nesterenko, Tavener-Smith, p. 413, Pl. 2, figs 1-9.

Diagnosis

Fenestella with small, delicate, planar fan-shaped open reticulate zoaria. Branches are thin, straight or gently distally curving and subparallel; obverse surfaces have a narrow, straight subangular median ridge with a single row of moderately spaced nodes; reverse surfaces are well rounded and may be nodose. Dissepiments are long, thin and depressed. Fenestrules are small, squat, typically hour glass-shaped, with well rounded extremeties and slight or strong median constrictions. Autozooecial apertures are small, circular to oval, with complete often ornamented peristomes and have a petaloid appearance. Apertures are widely spaced, and apertural positions are stabilised, one situated at each dissepiment-branch junction and one midway between which usually project out into fenestrules. Secondary nanozooids occur.

Description

External

Zoaria form small delicate, open reticulate fan-shaped expansions up to 3 cm in diameter.

Branches are thin, extremely slender and are straight or distally gently curved and subparallel. The obverse surfaces of branches have a narrow, straight or gently sinuous median ridge on which a single row of nodes occurs. Nodes are of small to moderate size, and there is considerable inter-colonial variation in their spacing so that they may be very close or fairly widely spaced. Branch sides slope steeply away from the median ridge. The reverse surfaces of branches are well rounded, and may have several irregularly defined rows of closely spaced small rounded nodes on them. All surfaces are finely granular.

Dissepiments are long, thin and depressed below the crests of branches on both the obverse and reverse surface, usually more so on the obverse. They are typically biconcave, thinnest in the centre and flare considerably and become less depressed towards dissepiment-branch junctions. On the obverse surface dissepiments are usually flat, and a thin low median ridge may occur along their length, while on the reverse surface they are poorly or well rounded.

Fenestrules are small, typically squat and hour-glass shaped, with well rounded extremeties and slight or strong median constrictions that are commonly symmetrically opposed.

Autozooecial apertures are small, circular or oval, and with thin complete peristomes, which may be ornamented by eight small round pustules giving peristomes a petalloid appearance. The inner rims of peristomes may be denticulate and eight very small distally narrowing spines may project slightly into apertures. Apertures are fairly widely spaced, about one and a half diameters apart and their positions are stabilised, one at each dissepiment-branch junction, and one midway between set flush and low down on branch sides. These latter ones may project slightly or considerably into fenestrules giving branches a serrated outline. Where branches divide, an aperture is symmetrically placed in the angle of bifurcation. Secondary nanozooids occur.

Internal

Autozooecial chamber bases are trapezoidal.

Dimensions (N = 41)

	NM	Mn	Mx	$\bar{X}$
BW	384	0.16	0.19	0.18
AD	339	0.06	0.09	0.08
ID	339	0.23	0.27	0.25
FL	449	0.51	0.53	0.52
FW	449	0.44	0.50	0.47
DW	407	0.07	0.35	0.25
ZB1	25	0.23	0.27	0.25
ZB2	25	0.11	0.14	0.12

Micrometric Formula: 19-27/19-24/18-26/13-30

Discussion

Fenestella ivanovi is characterised by its open delicate scalariform meshwork, small squat commonly hour-glass shaped fenestrules, stabilised positions of autozooecial apertures with one situated at each dissepiment-branch junction and one midway between, and the occurrence of a single row of fairly small moderately spaced nodes.

The material examined in the present study corresponds well with F. ivanovi Shulga-Neterenko (1951) from the Upper Carboniferous of Russia and is assigned to that species. The only apparent difference is the occurrence of wider branches in the Russian form. Tavener-Smith (1973) described F. ivanovi from Asbian strata in Northern Ireland, and some of the material examined in the present study comes from that locality. In her original taxonomic description of the taxon, Shulga-Nesterenko described the occurrence of petaloid peristomes. Although this feature is not evident in the Carrick Lough material, the petaloid form of peristomes is very distinct in the Hurst material. Additionally, apertures are commonly denticulate, with the development of eight small spines extending from the inner rims of peristomes.

Material

ABCL 1	Cavity slide with seven zoarial fragments. Calp Shale - Upper Limestone (Asbian), Carrick Lough, Derrygonelly, Ireland.
ABCL 15	Cavity slide with two zoarial fragments. Horizon and locality as above.
ABCL 16	Cavity slide with two zoarial fragments. Horizon and locality as above.
ABHR -2, -6, -10, -18,-19,-20,-25, -26,-28,-29,-30, -34,-37,-42.	Shales above the Main Limestone (Arnsbergian). Hurst, No. Yorkshire.

Stratigraphical Range

Asbian-Arnsbergian.

Occurrence

Fenestella ivanovi has only been described from two localities in the Lower Carboniferous of Britain, in Asbian strata at Carrick Lough and in Arnsbergian strata at Hurst. Elsewhere *F. ivanovi* has only been described from the Lower Carboniferous of the Soviet Union.

Fenestella frutex McCoy, 1844

Figs. 36-39; Pl. 35, fig.a; Pl. 36, figs. a-b; Pl. 37, figs. a-b; Pl. 38, figs. a-b; Pl. 39, figs. a-b.

1844 Fenestella frutex McCoy, p. 201, Pl. 28, fig. 10.

1887 Fenestella limbata Foerste, p. 83, Pl. 7, figs. 10a - d.

1926 Fenestella limbata Foerste; Nikiforova, p. 175, Pl. 4, fig. 1.

1927 Fenestella limbata Foerste; Nikiforova, p. 246, Plt. 12, fig. 1.

1934 Fenestella aff. limbata Foerste; Likharev, p. 155.

1937 Fenestrellina limbata Foerste; Elias, p. 318, fig. 3 J,K.

1961 Fenestella frutex McCoy; Miller, p. 232, Pl. 25, figs. 1-4.

1973 Fenestella frutex McCoy; Tavener-Smith, p. 411, Pl. 1, figs. 1-9.

Type

Miller (1961, p. 232) cited McCoy's (1844, p. 201, Pl. 28, fig. 10) figured specimen the holotype. However, McCoy did not select a holotype, thus Miller's reference to a holotype is incorrect. In the present study only one specimen referable to Fenestella frutex has been found in the Griffith Collection of McCoy type material at the National Museum of Ireland, Dublin. This specimen (NMI F.6038) was figured in the upper of McCoy's two drawings of the taxon, and is here formally selected as lectotype. It is a small zoarial fragment (about 10 x 10 mm) and is the reverse surface of the extreme proximal part of a colony, with irregularly disposed close bifurcating branches originating from a thick root-like process.

Miller (1961, p. 232) also designated a syntype for the taxon from the McCoy type material in the Griffith Collection. This specimen (NMI F. 6041) is a poorly preserved small zoarial fragment (9 x 5 mm) revealing the obverse surface of a mature portion of a zoarium. The morphology and the measurement of selected morphological parameters show that the specimen is referable to Fenestella ivanovi Shulga-Nesterenko. Branch Width ($\bar{X}$ = 0.16) is considerably lower than for

F. frutex fenestrule dimensions are significantly smaller (FL $\bar{X}$ = 0.44; FW $\bar{X}$ = 0.43) and the specimen displays the most diagnostic character of F. ivanovi, i.e. the constant placing of autozooecial apertures with one situated above each dissepiment-branch junction and one between. In the latter, apertural rims project into fenestrules slightly giving fenestrules a typical squat hour-glass shape. Specimen (NMI F. 6041) is rejected as a syntype of F. frutex.

Emended Diagnosis

Fenestella with fairly close, rigid, planar fan-shaped expansions. Branches are of moderate width, straight and subparallel; the obverse surfaces of branches have a narrow median ridge on which a single row of fairly closely spaced nodes occurs; reverse surfaces are quite well rounded, occasionally nodose. Dissepiments are relatively short and depressed. Fenestrules are small, rectangular or oblong, with straight sides and well rounded extremeties. Autozooecial apertures are circular, small with complete peristomes and are closely spaced, two or three per fenestrule, and are set flush on branch sides, with one normally set on a dissepiment-branch junction.

Description

External

Zoaria form fairly close, planar, reticulate expansions up to 5 cm. in diameter.

Branches are slender, of moderate width, relatively rigid and usually straight and subparallel or parallel to one another, but may be gently curved distally. On the obverse surface of branches there is a straight, narrow sub-angular median ridge, on which a single row of quite widely spaced, fairly large ellipsoidal nodes occurs. Away from the median ridge branch sides are steeply inclined.

The reverse surfaces of branches are poorly to well rounded, and may have a slightly sinuous well rounded ridge or narrow median ridge along their length. A single row of closely spaced, irregularly distributed nodes may be situated on the crests of the reverse surface of branches. They are usually of small to moderate size and round to oval, however, occasionally very large inflated ellipsoidal nodes may commonly be situated above dissepiment-branch junctions, with smaller ones between. Branch surfaces are usually finely granular, but reverse surfaces may have a slightly coarser granular texture than the obverse surface of branches. Prior to bifurcation branch width may increase for up to three fenestrule lengths and may reach 0.5 mm.

Dissepiments are usually relatively short, of variable thickness, but normally very slender. On the obverse surface they are well depressed below the crests of branches, but only slightly depressed on the reverse surface. Dissepiments flare considerably towards branch junctions and become less depressed also. They may be well rounded or flat, or with a low narrow subangular median ridge along their length, usually better developed on the reverse.

Fenestrules are small, rectangular or oblong rarely elliptical, and of equal or of slightly greater width than branches, and normally two and a half to three times as long as wide. They have well rounded extremeties and straight or gently curving lateral margins only occasionally slightly indented.

Autozooecial apertures are fairly small, circular with complete thick low or upraised peristomes. They are closely spaced, less than their own diameter apart with usually three per fenestrule, and set flush on the steeply inclined branch sides. Occasionally the outer peristomal rims of apertures may slightly indent fenestrule margins. One aperture is commonly situated on a dissepiment-branch junction and faces away from fenestrules at a high angle. An incipient third row of autozooecial apertures may develop immediately prior to bifurcation of a branch.

Internal

Autozooecial chamber bases have a typically hemi-hexagonal shape.

Dimensions (N = 39)

	NM	Mn	Mx	$\bar{X}$
BW	416	0.20	0.30	0.24
AD	178	0.07	0.11	0.09
ID	214	0.18	0.28	0.22
FL	396	0.49	0.66	0.58
FW	396	0.39	0.56	0.44
DW	391	0.08	0.17	0.11
IND	229	0.18	0.56	0.34
ZB1	72	0.19	0.23	0.21
ZB2	72	0.10	0.12	0.11

Micrometric Formula 20-29/17-23/19-29/12-28

Discussion

Fenestella frutex McCoy (1844) is easily recognised by its rigid close meshwork, with straight branches of moderate width, the occurrence of a single row of quite closely spaced fairly large nodes along the median ridge of the obverse surface of branches, small rectangular or oblong fenestrules, with two or three apertures per fenestrule, at least one being situated on a dissepiment-branch junction.

Fenestella limbata Foerste (1887) is considered to be a junior homonym of *F. frutex* (Miller 1961, p. 233). Zoaria typically form planar fan-shaped expansions; branches are straight, rigid looking and of moderate width; nodes are quite closely spaced along the median ridge or carinae on the obverse surface of brances; fenestrules are small, rectangular or oblong having the same width as branches and there are usually two or three apertures per fenestrule. The micrometric formula is comparable in all respects (see Elias, 1937, Table 2).

Tavener-Smith (1973, p. 411) described *Fenestella frutex* in Asbian strata from Carrick Lough, Northern Ireland. He discussed the close structural resemblence to *Fenestella fenestratum* (Young and Young) 1874a and suggested that it is possible that the two species are conspecific. However, in the present study, syntype material of *F. fenestratum* has been examined, and this has shown that *F. fenestratum* is a junior synonym of *Fenestella bicellulata* Etheridge, Jun. (1873a) and not *F. frutex* as Tavener-Smith suggested.

Material

ABHR 3F	Cavity slide with 7 zoarial fragments. Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABP -118, -138, -144, -150, -151, -155, -159, -169, -175, -183, -184, -185, -186, -190, -194, -195.	Fifth Limestone (Asbian), Alston Group, Penruddock near Penrith, Cumbria.
ABP 300, -301, -305, -306, -308, -309.	Thin Sections. Horizon and locality as above.

ABR 7, -9, -11, -13	Redesedale Ironstone Shale (Asbian) Lower Limestone Group, Ridsdale, Northumberland.
HM D454-3	Carboniferous Limestone Shale, High Blantyre.
NMI F.6038	Labelled as holotype. Upper Limestone (Asbian?) Killymeal, Dungannon. The specimen was figured by McCoy (1844, Pl. 28, fig. 10) and Miller (1961, Pl. 25, fig. 1).
NMI.F.6041	Labelled as syntype. Upper Limestone (Asbian?), Killymeal, Dungannon. The specimen was referred to by Miller (1961, p. 232).
NH G.155. 63/2, -63/3, -63/5, -63/6, G.1555 63/1	Redesdale Ironstone Shale (Asbian), Lower Limestone Group, Ridsdale, Northumberland. J. Dunn Collection.

Stratigraphical Range

Asbian-Arnsbergian.

Occurrence

Fenestella frutex is very common in British Lower Carboniferous strata, and has quite a wide geographical distribution being recorded from the Midland Valley of Scotland, Northumberland, Cumbria, Yorkshire and Northern Ireland.

Fenestella multispinosa Ulrich, 1890

Fig. 40; Pl. 40, figs. a-b; Pl. 41, figs. a-b; Pl. 42, fig. a.

1890 Fenestella multispinosa Ulrich; p. 540, Pl. 50, figs. 3-3e.

1926 Fenestella multispinosa Ulrich; Nekhoroshev, p. 1245.

1926 Fenestella multispinosa Ulrich; Nikiforova, p. 178.

1933 Fenestella multispinosa Ulrich; Nikiforova, p. 16.

1942 Fenestella multispinosa Ulrich; Kaison, p. 93.

1942 Fenestrellina multispinosa (Ulrich); McFarlin, p. 444.

1944 Fenestella multispinosa Ulrich; Condra and Elias, p. 110.

1948 Fenestella multispinosa Ulrich; Nekhoroshev, p. 24.

1951 Fenestella multispinosa Ulrich; Shulga-Nesterenko, p. 83.

1962a Fenestella multispinosa Ulrich; Miller, p. 121, Pl. 23, fig. 2.

1973 Fenestella multispinosa Ulrich; Tavener-Smith, p. 416, Pl. 3, figs. 1-9.

Diagnosis

Fenestella with fairly open, planar fan-shaped zoaria. Branches are of moderate width, straight and parallel; obverse surfaces have a narrow median ridge bearing a single row of fairly closely spaced nodes; reverse surfaces are well rounded and finely pustulose. Dissepiments are quite thin, of moderate length, depressed on the obverse surface, less on reverse. Fenestrules are fairly small, rectangular to oval with well rounded extremeties and straight sides. Autozooecial apertures are of moderate size, circular with relatively thick complete peristomes, with usually three per fenestrule set about their own diameter apart.

Description

External

Zoaria typically form symmetrical reticulate, fairly open planar fan-shaped expansions, of moderate size, at least 6 cm in diameter.

Branches are of moderate width, straight or gently curving and parallel to one another. Obverse surfaces of branches have a narrow straight subangular median ridge bearing a single row of quite closely spaced nodes of moderate size. Branch sides are steeply inclined away from the median ridge. Reverse surfaces are fairly well rounded with irregularly distributed closely spaced pustules; all surfaces are finely granular. Prior to bifurcation branch width increases for up to three fenestrule lengths and may reach 0.52 mm.

Dissepiments are relatively thin, of moderate length, and are well depressed below the crest of branches on the obverse surface but only slightly depressed or flush on the reverse surface. They flare slightly or significantly towards dissepiment-branch junctions and become less depressed. The obverse surface of dissepiments may have a low narrow longitudinal ridge along their length, but dissepiments are usually well rounded on the reverse.

Fenestrules are quite small, rectangular to oblong, rarely oval, normally twice, but up to three times, as long as wide. They are distinctly wider than branches and have well rounded extremeties and straight sides, occasionally slightly undulatory.

Autozooecial apertures are of moderate size, circular with relatively thick complete upraised peristomes. They are fairly closely spaced about their own diameter apart, with normally three per fenestrule and are usually set flush on branch sides. Apertures rarely indent fenestrules, but they may do so when they have slightly elevated outer peristomal rims. These cause apertures to face away from fenestrules at a higher than normal angle and to indent fenestrule margins slightly. An incipient third row of apertures may develop for up to one fenestrule length prior to branch bifurcation.

Internal

Autozooecial chamber bases are hemi-hexagonal.

Dimensions (N = 37)

	NM	Mn	Mx	$\bar{X}$
BW	449	0.20	0.28	0.24
AD	338	0.08	0.10	0.09
ID	338	0.22	0.29	0.26
FL	465	0.55	0.701	0.65
FW	439	0.41	0.56	0.49
DW	429	0.08	0.16	0.13
IND	322	0.24	0.47	0.35

Micrometric Formula 18-23/15-22/20-25/10-21.

Discussion

In the Carboniferous bryozoan material examined in museum collections the taxon *Fenestella nodulosa* (Phillips) is abundant. However, (Miller, 1961) declared the taxon as *nomen dubium* as Phillips' type material was lost, and the taxon was incompletely described. Tavener-Smith (1965) revised *Fenestella nodulosa* and noted, that from Phillips original illustrations the taxon is referable to the genus *Minilya* Crockford.

The museum material examined in the present study has formerly been qualitatively examined and much of the material exposes the reverse surface only. Specimens have obviously been identified at F. nodulosa with no reference to Phillips original description and illustrations which clearly show the biserial arrangement of carinal nodes on the obverse surface (which is the diagnostic character of the genus Minilya). None of the material examined in museum collections and labelled as F. nodulosa is referable to Minilya owing to the uniserial arrangement of carinal nodes.

By comparison with other established species all the museum material labelled as F. nodulosa is conspecific with Fenestella multispinosa Ulrich 1890, on all aspects of skeletal morphology, and on the basis of the parameters measured. Tavener-Smith (1973, p. 417) gives a detailed account of the morphological variability of F. multispinosa and compares the systematic descriptions of several authors.

F. multispinosa is very common in British Lower Carboniferous strata, and although the colonial meshwork is similar to Fenestella frutex, it is slightly coarser, zooecial parameters are larger and carinal nodes are further apart.

Material

ABCL 2	10 zoarial fragments in a cavity slide. Calp shale - Upper Limestone (Asbian). Carrick Lough, Derrygonelly, Eire.
ABCL 17	1 specimen in a container. Horizon and locality as above.

ABHR 6, -19, -26, -30, -41	Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
BOM 25-09-182, -195 to 200, -203 to 207, -218, -224, -236, -240.	labelled as *Fenestella nodulosa*. Mountain Limestone, Halkyn (probably Brigantian), Near Mold, Clwyd, North Wales.
BMNH B.1773	Halkyn.
BMNH D.2372, -2374 to 2377, -2385 to 2392, -2419, -2425 to 2428, -2431, -2433, -2468.	labelled as *Fenestella nodulosa*. Carboniferous Limestone, Halkyn Mountain (probably Brigantian). G.W. Shrubsole collection.
HM D51/1	Labelled as *Fenestella nodulosa* Phillips Halkyn Mountain (probably Brigantian), Clwyd, North Wales. G.W. Shrubsole, Donor.
NH G155.68/3	Redesdale Ironstone Shale (Asbian). Lower Limestone Group, Ridsdale, Northumberland. J. Dunn Collection.

Stratigraphical Range

Asbian - Arnsbergian.

Occurrence

Fenestella multispinosa is very common in British Lower Carboniferous strata being recorded in the Midland Valley of Scotland, Yorkshire, North Wales and Northern Ireland. Elsewhere *F. multispinosa* has been recorded from the Carboniferous of the U.S.A and the Soviet Union.

Fenestella tuberculo-carinata Etheridge,Jun. 1873a

Figs. 41, 42; Pl. 43, figs. a-b; Pl. 44, figs. a-b; Pl. 45, fig. a; Pl. 46, figs. a-b; Pl. 47, figs. a-b.

1873a Fenestella tuberculo-carinata Etheridge,Jun. p.101.

1877 Fenestella arctica Salter, var. scotica, var. nov. Etheridge,Jun. p. 31, Pl. 2a, figs. 1, 2.

1881 Fenestella tuberculocarinata [sic] Etheridge; Vine, p. 336.

1882a Fenestella tuberculocarinata [sic] Etheridge; Young, p. 182

1885 Fenestella tuberculocarinata [sic] Etheridge, Vine, p. 76.

1961 Fenestella tuberculo-carinata Etheridge; Miller, p. 236, Pl. 27, fig. 2.

1969 Fenestella tuberculo-carinata Etheridge; Owen, p. 263.

Type

Miller (1961, p. 236) erected a neotype for Fenestella tuberculo-carinata Etheridge,Jun. because Etheridge, Jun.(1873a p.101) did not designate a holotype or figured any material and because his material is presumed lost. The neotype (GSE 89041-03) is one of nine very small zoarial fragments (about 2 x 3 mm) on a cavity slide, and Miller (1961, p. 237) interpreted the material as topotypes coming from Etheridges original collecting locality. The material is from the head of Mouse Water, Rottenburn, in the Wilsontown district, Lanarkshire, Scotland from the shales below the Hosie Limestone.

Emended Diagnosis

Fenestella with planar fan-shaped zoaria. Branches are relatively stout, straight or irregularly sinuous; on obverse surfaces there is a narrow rounded median carina on which a single row of very closely spaced nodes occurs, branch surfaces slope quite steeply away from the carina and reverse surfaces are well rounded, occasionally nodose.

Dissepiments are short, very stout slightly depressed on the obverse surface, flush on the reverse, and expanded considerably towards dissepiment-branch junctions. Fenestrules are quite small, oblong to elliptical, long and narrow. Autozooecial apertures are of moderate size, circular and with prominent thick complete peristomes, they are set about their own diameter apart low down on branch sides with three or four per fenestrule.

Description

External

Zoaria form close planar fan-shaped reticulate expansions up to 10 cm in diameter.

Branches are fairly robust, straight and subparallel or more commonly gently undulatory when dissepiments are alternately situated on opposite branch sides. The obverse surfaces of branches have a straight to gently sinuous narrow rounded median carina on which a single row of very closely spaced moderate sized nodes occurs. Branch sides slope quite steeply away from the carina. Reverse surfaces are usually well rounded and may bear a single row of small irregularly distributed nodes on the crests of branches. The regular gentle sinuosity of branches and the alternate disposition of dissepiments on opposite branch sides gives the meshwork an interlocking hexagonal appearance on the reverse surface of zoaria. All branch surfaces are fine granular. Prior to branch division branch width increases for up to two fenestrule lengths and may reach up to 0.55 mm.

Dissepiments are short, very robust about two thirds the width of branches and are slightly depressed below the crests of branches on the obverse surface but flush with branch crests on the reverse. They flare considerably towards dissepiment-branch junctions and on the obverse surface they commonly have a narrow low rounded ridge along their length and are well rounded on the reverse.

Fenestrules are quite small, oblong to elliptical, relatively long and narrow, between two and three times long as wide and fenestrule width is about the same as branch width. Fenestrule extremeties are very well rounded and lateral margins are straight to slightly undulatory due to the outer peristomal rims of apertures extending beyond normal branch margins into fenestrules.

Autozooecial apertures are of moderate size, circular with relatively thick prominent upraised complete peristomes. Apertures are set low down on branch sides, usually flush on the inclined branch sides and set slightly less than their own diameter apart with between 3 and 4 per fenestrule. Occasionally the outer peristomal rim may be slightly more elevated above the branch surface than the inner peristomal rim, resulting in apertures facing away from fenestrules at a higher angle than when apertures are flush on branch sides. A third row of apertures never develops prior to branch division, but an additional aperture is always symmetrically placed in the angle of bifurcation at the point of division.

Internal

Autozooecial chamber bases have a hemi-hexagonal shape and chambers develop a reniform shape in shallow tangential section.

Dimensions (N = 12)

	NM	Mn	Mx	$\bar{X}$
BW	133	0.29	0.32	0.30
AD	69	0.08	0.11	0.09
ID	69	0.22	0.25	0.23
FL	151	0.63	0.86	0.73
FW	151	0.50	0.64	0.57

	NM	Mn	Mx	X
DW	88	0.17	0.21	0.20
IND	87	0.19	0.21	0.20

Micrometric Formula: 17-21/12-16/20-25/23-30

Discussion

Fenestella tuberculo-carinata Etheridge, Jun. is a very distinctive species, easily recognised by its close relatively stout reticulate meshwork, the regular gentle sinuosity of branches with a very closely spaced single row of nodes on the median carina on obverse surfaces, short very robust dissepiments, quite small oblong elliptical fenestrules, and very prominent autozooecial apertures with three or four per fenestrule.

Etheridge, Jun. (1877, p. 31) described a variety of the taxon *Fenestella arctica*, var *scotica*, but his description was based on the appearance of the reverse surface, the obverse surface detail being unknown to him. However, the taxon, as Young (1882a, p. 182) suggested, appears to be conspecific with *F. tuberculo-carinata*. Etheridge noted the regular sinuosity of branches, and his figure of reverse surface detail (Pl. 2a, fig. 2) shows the typical interlocking hexagonal appearance of the sinuous branches and connecting dissepiments that characterise *F. tuberculo-carinata*.

Shrubsole (1879) placed both *F. arctica* var *scotica* and *F. tuberculo-carinata* as varieties of *F. plebeia* McCoy. However, Young's (1882a, pp. 182-188) detailed discussion of the two taxa showed that they are distinct species.

Material

HM D.14/1-4	Carboniferous Limestone shale. Lower Limestone Group, High Blantyre (Brigantian). J. Young Collection.
HM D.40/1-3	Carboniferous Limestone shale, Lower Limestone Group, Newfield, High Blantyre (Brigantian). J. Young Collection.
HM D.41	labelled as *F. tuberculocarinata*.
HM D.42	7 zoarial fragments on cavity slide. Blantyre Lime Quarry (Brigantian). J. Young Collection.
HM D.43	Carboniferous Limestone, Upper Limestone Group, Langside, Beith (Arnsbergian?). J. Young Collection.
HM D.44/1-2	Carboniferous, Lower Limestone Group, Roughwood, Beith (Brigantian). J. Young Collection.
HM D.45	Thin Section through 6 zoarial fragments. Lower Limestone Series, Laigh, Baidland, Dalry (Brigantian). J. Young Collection 1886.
HM D.46	Thin Section through 5 zoarial fragments. Lower Limestone Series, Laigh, Baidland, Dalry, (Brigantian). J. Young Collection 1886.
HM D.49	Thin Section through 2 zoarial fragments Carboniferous Limestone, Baidland, Dalry (Brigantian), Ayrshire. J. Young Collection 1891.
GSE 89041 R1-R5,L1-O4	Cavity slide with 9 zoarial fragments on. Shale below the Hosie Limestone, Lower Limestone Group (Brigantian) head of Mouse Water, Wilsontown, Scotland. One specimen - O3, was erected as Neotype by Miller (1961, p. 237) and was figured by him (Pl. 27, fig. 2).

Stratigraphical Range

Brigantian-(Arnsbergian?).

Occurrence

F. tuberculo-carinata is quite common in Brigantian strata in the Midland Valley of Scotland and is very rare elsewhere being described only by Vine (1881, 1885) in strata in North Yorkshire and Lancashire.

Fenestella plebeia McCoy, 1844

Figs. 43-45; Pl. 48, figs. a-d; Pl. 49, figs. a-d; Pl. 50, figs. a-b; Pl. 51, figs. a-b; Pl. 52, fig. a.

1844 *Fenestella plebeia* McCoy, p. 203, Pl. 29, fig. 3.
1844 *Fenestella ejuncida* McCoy, p. 201, Pl. 28, fig. 11.
1849 *Fenestella plebeia* McCoy; d'Orbigny, p. 152
1855 *Fenestella plebeia* McCoy; Sedgwick and McCoy, p. 114.
1879 *Fenestella plebeia* McCoy; Shrubsole, p. 278.
1881 *Fenestella plebeia* McCoy; Shrubsole, p. 179
1881 *Fenestella halkinensis* Shrubsole, p. 179
1881 *Fenestella plebeia* McCoy; Vine, p. 336.
1882a *Fenestella plebeia* McCoy; Young, p. 182
1883a *Fenestella plebia* [sic] McCoy; Vine, p. 164
1885 *Fenestella plebeia* McCoy; Vine, p. 75.
1887 *Fenestella plebeia* McCoy; Vine, p. 261
1890 *Fenestella plebeia* McCoy; Ulrich, p. 537.
1933 *Fenestella plebeja* [sic] McCoy; Nikiforova, p. 10.
1934 *Fenestella plebeja* [sic] McCoy; Prantl, p. 4.
1938 *Fenestella* aff. *plebeia* Mac Coy [sic]; Demanet, p. 48, Pl. 4, figs. 4-5.
1948 *Fenestella* aff. *plebeia* McCoy; Oakley, p. 89
1961 *Fenestella plebeia* McCoy; Miller, p. 225, Pl. 24, figs. 1-3.
1973 *Fenestella plebeia* McCoy; Tavener-Smith, p. 428, Pl. 7, figs. 1-7.

Type

As McCoy (1844, p. 203, Pl. 29, fig. 3) did not establish a holotype for *Fenestella plebeia*, Miller's reference (1961, p. 226) to McCoy's figures specimen as the holotype is not strictly correct. Consequently, a lectotype is formerly proposed here. This specimen (NMI F.6035) was figured in the upper of McCoy's two drawings of the taxon and is the only one present in the Griffith Collection of McCoy type material at the National Museum of Ireland, Dublin.

The proposed lectotype is a very poorly preserved large zoarial fragment (48 x 61 mm) embedded in a dark grey partly decalcified calcareous mudstone, and exposes the reverse surface. In most of the specimen the branches have weathered away, only moulds remaining. There are a few relics of internal structures and, in the extreme proximal area, the outline of the zooecial chamber bases remains.

Emended Diagnosis

Fenestella forming large planar foliaceous or conical expansions. Branches are quite robust, subparallel, straight or slightly sinuous; obverse surfaces have a narrow straight median ridge on which a single row of fairly closely spaced nodes occurs, from which branch sides slope steeply away; reverse surfaces are poor to well rounded. Dissepiments are relatively short, thick and well depressed on the obverse, less so on the reverse. Fenestrules are of moderate dimensions, rectangular to oblong. Autozooecial apertures are of moderate size, circular with complete peristomes, about their own diameter apart, set flush on branch sides with four or five per fenestrule.

Description

External

Zoaria form large reticulate planar fan shaped, foliaceous or conical expansions. Planar fan-shaped zoaria are most frequently developed and may be up to 25 cm in diameter. Low or high angle conical zoaria may occur. Low angled conical zoaria are typically horn-shaped and may be straight or gently curved, and autozooecial apertures may open on the inside or outside of the cone.

Branches are fairly robust, straight to slightly sinuous and are typically subparallel or parallel. Obverse surfaces of branches usually have a prominent narrow straight median ridge on which a single row of nodes occurs. Nodes are typically elliptical and there is considerable variation in their size and spacing, although they are usually fairly closely spaced. Rarely a narrow median carina may be developed. Branch sides are steeply inclined away from the median ridge. Reverse surfaces are poor to well rounded with irregularly arranged small round nodes or very large elliptical nodes situated above dissepiment-branch junctions. All surfaces are finely granular. Prior to bifurcation branches increase in width for up to three fenestrule lengths and may reach 0.68 mm.

Dissepiments are usually fairly short, thick and distinctly depressed below the crests of branches on the obverse surface, but almost flush on the reverse. They increase in width considerably towards the dissepiment-branch junction and become less depressed as they do so. Dissepiments may be poor or well rounded, and often have a narrow median ridge poorly developed on the obverse and usually more strongly developed on reverse surfaces.

Fenestrules have moderate dimensions and are typically rectangular or oblong, occasionally coffin-shaped and rarely elliptical. They are marginally to considerably wider than branches, and fenestrule extremeties are usually quite well rounded, lateral margins being straight, gently curved or rarely undulatory. When dissepiments are situated opposite the centres of adjacent fenestrules this may impart a low sinuosity to branches, resulting in coffin to elliptical-shaped fenestrules and shorter dissepiments than usual.

Autozooecial apertures are circular, of moderate size, with complete peristomes of variable prominence and thickness. There are usually four or five apertures per fenestrule, and they are closely spaced about their own diameter apart and set flush quite low down on the steeply inclined branch sides. Occasionally the outer peristomal lips may project slightly giving branch margins an undulatory appearance. Normally one aperture is situated on the dissepiment-branch junction and faces away from the fenestrule at a high angle.

Internal

Autozooecial chamber base shape varies from hemi-hexagonal to trapezoidal.

Dimensions (N = 45)

	NM	Mn	Nx	$\overline{X}$
BW	541	0.24	0.38	0.30
AD	314	0.08	0.15	0.11
ID	298	0.21	0.30	0.26
FL	567	0.83	1.41	1.02
FW	553	0.51	0.74	0.60
DW	537	0.09	0.24	0.16
IND	249	0.18	0.72	0.49
ZB1	28	0.24	0.27	0.26
ZB2	28	0.12	0.14	0.13

Micrometric Formula 14-20/8-14/17-35/7-32

Discussion

Fenestella plebeia McCoy (1844, p. 203) is the commonest fenestellid in British Lower Carboniferous strata, and is readily identifiable by its large zoaria, fairly stout straight branches, with quite closely spaced nodes along the median ridge or carina, short dissepiments, long and narrow fenestrules of moderate dimensions and the occurrence of four to five apertures per fenestrule.

In addition to describing F. plebeia, McCoy also described Fenestella ejuncida (ibid, p. 201, Pl. 28, fig. 11). In the present study all the available type material of F. ejuncida was examined. There is only one specimen in existence in the Griffith Collection of McCoy type material, (NMI F.6042) and this is McCoy's figured specimen. It is a well preserved zoarial fragment (28 x 16 mm) exposing the reverse surface, and is embedded in a medium grey/brown biosparrite with other bryozoan fragments.

The measurement of set parameters on the specimen reveals that it is referable to *F. plebeia*, and McCoy's original description of the taxon also suggests this. Consequently, as suggested by Miller (1961, p. 227), *F. ejuncida* is placed in synonymy with *F. plebeia*.

In the present study, syntypic material of *Fenestella halkinensis* Shrubsole (1881, p. 179) has been examined, and the taxon is here considered to be conspecific and is a junior synonym of *F. plebeia*.

Miller (1961, p. 226) redescribed *F. plebeia*, however he gave only the results of two parameters measured on the type, that of branch width and dissepiment width. This is quite inadequate for taxonomic purposes. His measurement of branch width is also slightly lower than the value obtained in the present study (0.12 to 0.24 mm compared to 0.22 to 0.28 mm).

Miller (ibid. pp. 227-228) also suggested the existence of a progressive increase in the number of carinal nodes in a unit distance from low Tournaisian horizons to the top of the Viséan. However, the present study has shown the existence of a considerable variation in nodal counts per unit distance in specimens at the same geological horizon, therefore such an evolutionary change is difficult to postulate.

Although Ulrich (1890, p. 537) commented on the similarities between *Fenestella rudis* Ulrich and *F. plebeia*, and Miller (1961, p. 228) thought the two might be conspecific, Tavener-Smith (1973, p. 430) showed, and the present study confirms, that the two taxa are not conspecific. *Fenestella plebeia* is a more robust species, branches and dissepiments are stouter, there are more nodes and fewer apertures per unit distance with more apertures per fenestrule. Tavener-Smith (1973, pp. 430-431) also compared *F. plebeia* with several other morphologically similar species.

Material

ABCL 5	3 cavity slides with 13 zoarial fragments. Calp Shale - Upper Limestone (Asbian), Carrick Lough, Derrygonelly, Northern Ireland.
ABCL 34	Cavity Slide with one zoarial fragment. Locality and horizon as above.
ABHR 6,-13,-42	Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABO 17, -18	Apron Reef Limestone, Bee Low Group (Asbian) Odin Fissure, near Castleton, Derbyshire.
ABP 4,-137,-145,-160,-161,-173.	Fifth Limestone (Asbian), Alston Group, Penruddock near Penrith, Cumbria.
ABMG 15-22	Hardraw Shales (Brigantian), Mill Gill, Askrigg, North Yorkshire.
BMNH B.62	labelled as *F. halkynensis* Shrubsole, Halkyn.
BMNH D.11612,-11617,-11636,-11659,-11675,-11684,-11690.	Carboniferous Limestone (Brigantian?), Halkyn Mountain, near Mold, Clwyd. F. Palin Collection.
BMNH D.2368 to 2371, -2457,-2458,-2461,-2538,-2540,-2544,-2545 to 2548, -2554,-2557,-2558,-2591	Carboniferous Limestone (Brigantian?), Halkyn Mountain, near Mold, Clwyd. G.W. Shrubsole Collection.
BMNH D.2394	labelled as *Fenestella halkynensis* Carboniferous Limestone, Halkyn. G.W. Shrubsole Collection.
BMNH D.10180 to D.10195,D.10199 to D.10222,-D.20263	Halkyn.
BMNH D.36429	Referred to by K.P. Oakley 1948. Lower Carboniferous, Upper Visean, Black Limestone (Brigantian), Halkyn Mountain, Flint (Clwyd).
ABA 15-18	Orton Group, Ashfell Sandstone (Arundian), Ashfell Edge Near Kirkby Stephen, Cumbria.

BOM GWS + O.12	Labelled as *Fenestella halkynensis* (Shrubsole), Carboniferous Limestone, Halkyn (Brigantian), N. Wales. Shrubsole Collection.
BOM 25-09-201, -210, -212 to 214, -217 to 222, -225 to 229, -231, -233 to 235, -237 to 240.	Carboniferous Limestone, Halkyn (Brigantian), Near Mold, N. Wales - G.R. Vine Collection.
HM. D.8	Labelled as *Fenestella subantigua* Carboniferous, Roughwood, Beith, J. Young Collection.
HM D.10/1-3	Labelled as *Fenestella plebeia*, Carboniferous, High Blantyre, J. Young Collection.
HM D12/1-2	Labelled as *Fenestella plebeia* McCoy, Carboniferous Limestone Shale, Newfield, High Blantyre, J. Young Collection.
HM D.454/1-2	Labelled as *Fenestella plebeia* McCoy, Carboniferous Limestone Shale, High Blantyre, J. Young Collection.
NMI F.6035	Labelled as holotype, Carboniferous slate, Killybrane, Killala. The specimen was figured by McCoy (1844, Pl. 29, fig. 3) and Miller (1961, Pl. 24, fig. 1).
NMI F.6042	Labelled as *Fenestella ejuncida* McCoy,Upper Limestone, Blacklion, Enniskillen, (Asbian). The specimen was figured by McCoy (1844, Pl. 28, fig. 11).
NMI. F.6079	Labelled as *Fenestella membranacea*, Lower Limestone, Kilcommock, Londford.
NMI F.6086	Labelled as *Fenestella membranacea*, Upper Limestone, Kildare.
NH G155.67/8	Redesdale Ironstone Shale (Asbian), Lower Limestone Group, Ridsdale, Northumberland.

Stratigraphical Range

Arundian-Arnsbergian

Occurrence

Fenestella plebeia is the commonest fenestrate bryozoan in British Lower Carboniferous Strata. It has a wide geographical distribution, being recorded throughout Ireland, Scotland, England and Wales, and is usually the dominant bryozoan species in bryozooiferous strata. *F. plebeia* is abundant in shallow water limestone reef facies where it is associated with a rich diverse fauna of algae, brachiopods, bryozoans, corals, crinoids, etc., and in deeper water muddy shelf environments where it occurs in association with more delicate bryozoan taxa such as *Penniretepora* and rhabdomesid species, and a reduced fauna of small brachiopods, gastropods and crinoids. Environmentally it appears to be a very tolerant species and may be found to occur alone, with a restricted fauna of a few brachiopods, in silty calcareous mudstones, or in environments characterised by an influx of some terriginous material.

Fenestella papillata (McCoy, 1844)

Pl. 53, figs. a-b; Pl. 54. fig. a.

1844 Polypora papillata McCoy, p. 206, Pl. 29, fig. 10.

1963 Fenestella papillata (McCoy), Miller, p. 170, Pl. 24, fig. 1.

Type

As McCoy (1844) did not erect a holotype for Polyora papillata, Miller's (1963) reference to McCoy's figured specimen as the holotype for the taxon is not strictly valid. Consequently a lectotype is proposed here for Fenestella papillata (McCoy). This specimen (NMI.F.607o) was figured by McCoy (Pl. 29, fig. 10) and Miller (Pl. 24, fig.1) and is the only specimen of the taxon in the Griffith collection of McCoy type material in the National Museum of Ireland, Dublin. The specimen is a reverse surface of a colony fragment, 20 x 20 mm, which has been partly ground down to reveal obverse surface detail, and the following taxonomic description is based solely on this specimen.

Description

External

The zoarium was probably a planar fan-shaped expansion.

Branches are robust and straight. The obverse surface of branches has a relatively narrow straight median ridge with a single row of very closely spaced small nodes. The reverse surfaces of branches are quite well rounded, with small closely spaced pustules arranged in quite widely spaced longitudinal rows. Prior to branch bifurcation branches may increase in width for up to two fenestrule lengths and may reach 0.75 mm.

Dissepiments are stout, fairly short, and are depressed below the crests of branches on the reverse surface. They flare considerably towards dissepiment-branch junctions and also become less depressed.

Fenestrules are of moderate size, relatively long and narrow, and are oblong or oval with well rounded extremeties and straight lateral margins, commonly indented slightly by the outer peristomal rims of apertures.

Autozooecial apertures are of moderate size, circular, with complete thin prominent peristomes, and are closely spaced set slightly more than their own diameter apart. Apertures are set close to the margins of branches, which may be slightly indented by the outer peristomal rims. Where branches divide, there is an aperture placed symmetrically in the angle of bifurcation.

Internal

Autozooecial chamber bases are hemi-hexagonal.

Dimensions (N = 1)

	NM	Mn	Mx	$\bar{X}$
BW	12	0.30	0.39	0.34
AD	12	0.10	0.12	0.11
ID	12	0.32	0.35	0.33
FL	12	1.12	1.40	1.27
FW	12	0.65	0.81	0.74
DW	12	0.17	0.27	0.20
IND	12	0.11	0.23	0.17

Micrometric Formula 13-14/8-9/15-17/28-30

Discussion

Although only a single specimen is available, it is certain that *Fenestella papillata* (McCoy) is a distinct species.

As Miller (1963, p. 170) stated, it is difficult to understand McCoy's (1844, p. 206) attribution of this taxon to the genus *Polypora*.

McCoy described the occurrence of three alternating rows of apertures on the smooth obverse surface of branches. However, his figured specimen (NMI.F.6070), exposing the reverse surface of a colony fragment, was examined by Miller who ground down part of the reverse surface to examine detail of the obverse surface. This revealed the occurrence of only two rows of apertures on branches separated by a narrow median ridge on which a single row of very closely spaced nodes occurs. It appears that the occurrence of autozooecial apertures close to the margins of branches, commonly indenting them, this being a similar feature to the preceding species he described (*Polypora marginata* McCoy, 1844, p. 206) prompted McCoy to place this taxon in the same genus. However, McCoy's description of the three alternating rows of apertures is puzzling, and there is no trace at all of three rows of apertures on the specimen.

Material

NMI.F.6070	labelled as holotype, Upper Limestone (Asbian), Blacklion, Enniskillen, County Fermanagh, Northern Ireland. The specimen was figured by McCoy (1844, Pl. 29, fig. 10) and Miller (1963, Pl. 24, fig. 1)

Stratigraphical Range

Asbian.

Fenestella morrisii McCoy, 1844

Pl. 55, fig. a.

1844 Fenestella morrisii McCoy, p. 212, Pl. 28, fig. 14.

1961 'Fenestella' morrisii McCoy; Miller, p. 238.

Type

The only specimen in the Griffith Collection of McCoy type material in the National Museum of Ireland, Dublin, is one (NMI F. 6034) figured by McCoy (1844, Pl. 28, fig. 14) in the upper of his two drawings of the taxon. As McCoy did not establish a holotype for Fenestella morrisii this specimen is here selected as lectotype. The following systematic description is based solely on this specimen which is a very poorly preserved colony fragment from the proximal portion of a high angle conical zoarium and exposes the reverse surface.

Diagnosis

Fenestella with a high angled conical zoarium. Branches are fairly straight, very robust. Dissepiments are quite short, and stout. Fenestrules are large, quadrate with straight sides and well rounded extremeties. Autozooecial apertures open onto the inside of the cone, and there are about six per fenestrule.

Description

External

The zoarium is the proximal area of a high angled cone (about 37 mm in diameter). Branches are fairly straight and very robust. Branch width is extremely variable due to closely spaced bifurcations in the proximal portion of the zoarium. The reverse surfaces of branches are quite well rounded and finely granular.

Dissepiments are fairly short and stout. Fenestrules are large quadrate with well rounded extremeties and straight lateral margins.

Autozooecial apertures are large, circular, alternately arranged in two longitudinal rows, moderately spaced with about six per fenestrule. A third row of apertures may develop immediately prior to branch divisions.

Internal

Autozooecial chamber bases are hemihexagonal.

Dimensions

	NM	Mn	Mx	$\overline{X}$
FL	7	1.10	2.00	1.80

Micrometric Formula 8-9/-/-/-

Discussion

Miller (1961, p. 238) declared 'Fenestella' morrisii McCoy a nomen dubium because of the bad state of preservation of the only existing specimen stating that nothing of its structure could be determined. However, examination of the specimen in the present study has shown that it is referable to Fenestella. Although very poorly preserved, examination of zooecial chamber bases revealed the occurrence of two alternately arranged longitudinal rows along branches with about six apertures per fenestrule.

The poor state of preservation of the specimen has allowed only a brief morphological analysis of the taxon and it is not possible to make a comparison with other species. However, Miller's suggestion that the species should be declared as a nomen dubium cannot be accepted because the specimen is clearly identifiable as a *Fenestella*.

Material

NMI F.6034	Labelled as holotype. Lower Limestone. Little Island (Holkerian? Asbian?) Cork. The specimen was figured by McCoy (1844, Pl. 28, fig. 14) and referred to by Miller (1961, p. 238).

Stratigraphical Range

Holkerian? Asbian?

Fenestella polyporata (Phillips, 1836)

Figs. 46-48; Pl. 56, figs. a-b; Pl. 57, figs. a-b; Pl. 58, figs. a-b; Pl. 59, figs. a-b.

1836 Retepora polyporata Phillips, p. 199, Pl. 1, figs. 19,20.

1844 Fenestella multiporata McCoy, p. 203, Pl. 28, fig. 9.

1844 Fenestella polyporata (Phillips); McCoy, p. 203

1879 Fenestella polyporata (Phillips); Shrubsole, p. 280.

1881 Fenestella polyporata (Phillips); Shrubsole, p. 185.

1926 Fenestella polyporata (Phillips); Nikiforova, p. 179.

1927 Fenestella aff. polyporata (Phillips); Nikiforova, p. 251.

1933 Fenestella polyporata (Phillips); Nikiforova, p. 23.

1938 Fenestella aff. polyporata (Phillips); Demanet, p. 44, Pl. 2 figs. 7, 11, Pl. 3, fig. 1.

1948 Fenestella c.f. polyporata (Phillips); Oakley, p. 88.

1951 Fenestella polyporata (Phillips): Shulga-Nesterenko, p. 59.

1956 Fenestella c.f. polyporata (Phillips); Nekhoroshev, p. 149.

1961 Fenestella polyporata (Phillips); Miller, p. 233, Pl. 26, figs. 3,4.

1973 Fenestella polyporata (Phillips); Tavener-Smith, p. 457, Pl. 16, figs. 4-8, Pl. 17, fig. 1.

Type

As Phillips (1836) did not erect a holotype for Fenestella polyporata and because his material is now presumed lost, Miller (1961) erected a neotype for the taxon. However, Miller's neotype is not valid because the specimen (NMI F.6041) figured by McCoy (1844, Pl. 28, fig. 9) as Fenestella multiporata came from Killymeal, Dungannon, Tyrone, Northern Ireland several miles from Florence Court where Phillips original material was collected. According to the International Code of Zoological Nomenclature Article 75C(5) a neotype is valid only when it is published with evidence that it came from as near as possible from the original locality. Therefore Miller's neotype of *F. polyporata* must be rejected. Unfortunately, in the limited time available for the present study it has not been possible to collect any topotype material from Phillips' locality at Florence Court in order to erect a neotype.

Diagnosis

Fenestella with large open planar fan-shaped zoaria. Branches are robust, gently regularly sinuous; obverse surfaces have a narrow rounded median carina or ridge on which small nodes in a single row commonly occur. Dissepiments are short, relatively thin, bar-like, well depressed on obverse surfaces and, usually with a longitudinal rib-like carina along their length, less depressed on reverse surfaces. Fenestrules are very large, rectangular, oblong or coffin-shaped with well rounded extremeties and straight sides. Autozooecial apertures are of moderate size, circular or reniform, about or slightly more than their diameter apart, set low down on branch sides with 6 or 7 per fenestrule.

Description

External

Zoaria form open planar fan-shaped reticulate expansions up to at least 10 cm in diameter.

Branches are very robust, straight and subparallel but are more commonly gently sinuous due to the alternate positions of widely spaced dissepiments on opposite branch sides. On the obverse surface of branches there is commonly a narrow low rounded straight to irregularly sinuous median carina or more usually a ridge on which a single row of nodes may occur. Nodes are typically small, oval-shaped and may be widely or closely spaced. Branch surfaces slope quite steeply away from the carina or ridge, and reverse surfaces are smooth and well-rounded. All surfaces are finely granular. Prior to branch bifurcation branch width increases for up to half a fenestrule length and may reach 0.80 mm.

Dissepiments are relatively thin, short and are typically bar-like expanding only in width close to dissepiment-branch junctions. On the obverse surface dissepiments are strongly depressed below the crests of branches and usually have a narrow rib-like carina developed along their length. The rib-like carina commonly continues onto the branch and may join up with the median carina of branches, and a small node-like development may mark their junction. Dissepiments are only slightly depressed on the reverse surface of branches and are well rounded.

Fenestrules are very large,rectangular, oblong, but are more commonly coffin-shaped, having their greatest width assymetrically midway along their length due-to the alternate positions of dissepiments resulting in the regular sinuosity of branches. Fenestrule extremeties are quite well rounded and lateral margins are straight to gently inwardly curving only occasionally slightly indented by the outer peristomal rims of apertures.

Autozooecial apertures are of moderate size, circular, oval or reniform with narrow low complete peristomes. They are set low down on branch sides between one and one and a half diameters apart, and although usually set flush with branch surfaces, their outer rims may be slightly elevated above branch surfaces. The outer rims of apertures also may extend beyond the normal lateral extremeties of branch margins and indent fenestrule margins slightly, and there are normally between 6 and 7 apertures per fenestrule. Secondary nanozooids occur.

Internal

Autozooecial chamber bases are hemi-hexagonal and closely interlock in two longitudinal rows. At the base of the short vestibular region of each autozooecium there is a thin plate-like superior hemiseptum.

Dimensions (N = 14)

	NM	Mn	Mx	X̄
BW	119	0.34	0.41	0.37
AD	65	0.09	0.13	0.11
ID	65	0.26	0.32	0.30
FL	116	1.65	2.39	2.10
FW	116	0.74	1.10	0.94
DW	117	0.19	0.26	0.22
IND	33	0.37	1.05	0.73
ZB1	15	0.30	0.36	0.31
ZB2	15	0.15	0.20	0.17

Micrometric Formula: 10-15/4-6/15-20/0-14

Discussion

Fenestella polyporata (Phillips, 1836) is readily distinguished by its large, open planar reticulate meshwork, with very robust gently sinuous branches, very large commonly coffin-shaped fenestrules, and the occurrence of between 6 and 8 apertures per fenestrule set about their own diameter apart.

There is no doubt that F. polyporata and Fenestella multiporata McCoy (1844, p. 203, Pl. 28, fig. 9) are conspecific. The two authors descriptions are quite comparable, both using the terms 'dissepiments thin, fenestrule large, irregular pores small', Phillips stating that they are numerous, while McCoy described the occurrence of between seven and eight apertures per fenestrule. McCoy (ibid) also redescribed *F. polyporata* and noted the occurrence of between 5 and 7 apertures per fenestrule. The large number of autozooecial apertures per fenestrule is shown in the published figures of both authors (Phillips, 1836, Pl. 1, figs. 19, 20; and McCoy 1844, Pl. 28 fig. 9). Consequently as Miller (1961, p. 234) stated *F. polyporata* and *F. multiporata* are conspecific, with the former name taking priority.

Miller (1961, p. 234) stated in respect of the two authors illustrations that the general appearance of the zoarium is distorted in both cases, with Phillips exaggerating the irregularity and McCoy the regularity of branch disposition. However, McCoy's figured specimen (NMI F.6041) examined in the present study, has shown that McCoy did not exaggerate the regularity of branches. The disposition of branches is uncharacteristic for the taxon in that branches are generally straight and parallel to one another not having the usual gentle sinuosity which Phillips does appear to have exaggerated in his illustration.

F. polyporata described from Carrick Lough by Tavener-Smith (1973, p. 457) is characterised by its unusually large meshwork dimensions (Fenestrule length ranging from 2.30 to 3.80 mm, averaging 3.067 mm) compared to any material examined in the present study. However, as Tavener-Smith stated (ibid, p. 177) measurements given by Nikiforova (1926, p. 177) and Shulga-Nesterenko (1951, p. 30-31) for the same taxon bridge this gap.

Material

ABHR 29,-30	Shales above the Main Limestones (Arnsbergian), Hurst, North Yorkshire.
ABMG 26 to 33	Hardraw Shales (Brigantian), Mill Gill, Askrigg, North Yorkshire.
ABO 11,-12,-14,-15	Apron reef Limestone, Bee Low Group (Asbian), Odin Fissure, near Castleton, Derbyshire.
BMNH D.2451	Halkyn Mountain (Brigantian?), C. Parkinson Collection 1884.
BMNH D.10241	Halkyn Mountain (Brigantian?), G. Shrubsole Collection.
BOM 172,-191,-192,-195	Carboniferous Limestone, Castleton, Derbyshire (Asbian?), G.R. Vine Collection.
BOM 225	Halkyn Mountain (Brigantian?), G.R. Vine Collection.
NH G.155.64/2,-G.155.67/3.	Redesdale Ironstone Shale (Asbian), Lower Limestone Group, near Ridsdale, Northumberland.
NMI F.6041	Labelled as type of *Fenestella multiporata* McCoy, Upper Limestone, Killymeal, Dungannon, (Asbian). The specimen was figured by McCoy (1844, Pl. 28, fig. 9) and Miller (1961, Pl. 26, figs. 3, 4)

Stratigraphical Range

Asbian - Arnsbergian.

Fenestella quadridecimalis McCoy, 1844

Pl. 60. figs. a-c.

1844 *Fenestella quadridecimalis* McCoy, p. 204, Pl. 28. fig.13.

1961 *Fenestella quadridecimalis* McCoy; Miller, p. 231, Pl. 26, fig. 2.

Type

As McCoy (1844) did not erect a holotype for the species, Miller (1961, p. 231) was incorrect in calling the specimen (NMI F.6036) figured by McCoy a (Pl. 28, fig. 13) holotype. However, as this specimen is the only one of the taxon present in the Griffith Collection of McCoy type material, it is consequently designated here as lectotype. The specimen is a large zooarial fragment (40 x 35 mm) exposing the reverse surface embedded in a medium brown/grey biosparite. Part of the zoarial surface is ground down and reveals obverse surface detail.

Emended diagnosis

Fenestella with large, lax, open planar fan shaped zoaria. Branches are very robust, gently sinuous; obverse surfaces have a low narrow median ridge on which a single row of very widely spaced nodes occur . Reverse surfaces are well rounded. Dissepiments are fairly short and well depressed. Fenestrules are very long and relatively narrow, oblong or elliptical. Autozooecial apertures are circular, of moderate size and closely spaced about their own diameter apart, with usually between eleven and fifteen per fenestrule.

Description

External

Zoaria form large, lax open reticulate, planar fan-shaped expansions.

Branches are quite robust and are gently sinuous. Obverse surfaces have a narrow, straight median ridge, or low, narrow well-rounded median carina on which a single row of very widely spaced nodes occurs. Branch sides are fairly gently inclined away from the median ridge or carina. Reverse surfaces are well-rounded, all surfaces are covered with very small closely spaced and irregularly distributed papillae.

Dissepiments are of variable length, but are usually fairly short, and are well depressed below obverse and reverse branch surfaces. They are relatively slender and poorly rounded, and flare quite close to dissepiment-branch junctions becoming less depressed as they do so.

Fenestrules are very large, long and narrow and of variable shape, but generally oblong to elliptical or coffin-shaped being widest at their midpoints. They have well rounded narrow extremeties, and straight or gently curved lateral margins.

Autozooecial apertures are circular, of moderate size, with complete low thick peristomes, set low down on branch sides and may protrude beyond branch margins slightly. Apertures are closely spaced, about their own diameter apart and there are usually between eleven and fifteen per fenestrule.

Internal

Zooecial chamber bases are hemi-hexagonal.

Dimensions (N = 2)

	NM	Mn	Mx	$\bar{X}$
BW	21	0.32	0.39	0.35
AD	24	0.10	0.12	0.11
ID	24	0.31	0.36	0.33
FL	15	3.54	4.13	3.73
FW	15	0.93	1.27	1.12
DW	15	0.16	0.31	0.22
IND	15	1.33	1.80	1.54

Micrometric formula 9-10/3-4/15-16/3

Discussion

Fenestella quadridecimalis McCoy is the largest species of Fenestella in British Lower Carboniferous strata, and is easily recognised by its open meshwork with very robust, slightly sinuous branches, extremely large fenestrule dimensions with very high numbers of autozooecial apertures per fenestrule, and very widely spaced carinal nodes.

McCoy's (1844, p. 204) description of the taxon although entirely qualitative is very good. However, the lower of his two drawings of the taxon (Pl. 28, fig. 13) showing the obverse surface details is not very accurate, and he has exaggerated the slenderness of the dissepiments considerably.

Miller (1961, p. 231) redescribed the taxon. His description was based solely on McCoy's figured specimen, here designated as lectotype. The specimen is a large zoarial fragment revealing the reverse surface and Miller ground down part of it to reveal details of the obverse surface. Although his description is accurate, the few measurement values he obtained on the parameters of Branch Width, and Dissepiment Width are considerably lower than those obtained for these parameters in the present study (Branch Width: 0.27 - 0.36 compared with 0.32 - 0.39; Dissepiment Width 0.14 - 0.20 compared with 0.16 - 0.31). It would appear from Miller's measurement values that he carried out his measurements at a considerably lower magnification than utilised in the present study. Such lower magnification could lead to a greater chance of error when using a graduated scale graticule.

Miller also gave the Micrometric Formula he obtained on the type specimens: 9-13/2½-3/21-22½/3. When compared with the micrometric formula obtained on the same specimen in the present study (9-10/3-4/15-16/3) the most striking difference between the two formula is the difference between the range of values in the number of apertures in a 5 mm line. A slight difference would be expected in the range of values, because Miller used the space count method, while in the present study the actual number method is used. The space count method generally leads to a slightly lower count value, and this is illustrated by comparison the the number of dissepiments in a 10 mm line in the two formula (2½-3 in Miller's formula compared to 3-4 obtained in the present study). However, Miller obtained a range of values for the number of apertures per unit distance 30% higher than the range of values obtained in the present study. In the present study, interapertural distance was measured (a parameter not measured by Miller), and the average value obtained corresponds to an average number of about 15 apertures in a 5 mm line. Miller compared F. quadridecimalis with three morphologically similar species, on the basis of the number of apertures per unit distance, and consequently this comparison cannot be validated. The present detailed quantitative and morphological analysis of F. quadridecimalis has allowed a more detailed comparison between some morphologically similar species.

Fenestella regalis Ulrich (1890, p. 538, Pl. 49, figs. 4, 4a) is obviously a closely related species. Zoaria form large open planar expansions, branches are strong, rather flexuous, dissepiments are relatively slender, fenestrules are extremely long, but there are only between 7 and 13 apertures per fenestrule considerably less on average than for *F. quadridecimalis*. Apertural dimensions are significantly larger than for *F. quadridecimalis*, averaging about 0.16 mm compared with 0.13 mm. Carinal nodes are very widely spaced, with about 6 in a 5 mm line compared to 3 for *F. quadridecimalis*. It is clear that the two species are closely related, however, it is not possible to discuss their relationship further without examination of material assigned to both species.

F. quadridecimalis is also morphologically similar to the Lower Permian taxon *Levifenestella unidecimalis* (Shulga-Nesterenko) 1936. This species is characterised by its large, lax planar meshwork, robust slightly sinuous branches, and extremely large fenestrule dimensions, with about 8 to 12 apertures per fenestrule and 15 in a 5 mm line. Carinal nodes are also very widely spaced.

Material

ABHR	Shales above the Main Limestone, (Arnsbergian), Hurst, North Yorkshire.
HM D4/1-2	labelled as *Fenestella quadridecimalis*? McCoy. Shales above the Gillfoot Limestone, Upper Limestone Group (Arnsbergian), Carluke, Rankin Collection.
NMI.F.6036	Labelled as holotype, Upper Limestone (Asbian), Blacklion, Enniskillen. The specimen was figured by McCoy (1844, Pl. 28, fig. 13) and Miller (1961, Pl. 26, fig. 2).

Stratigraphical Range

Asbian - Arnsbergian.

Occurrence

Fenestella quadridecimalis is a very rare species and is known from only a few localities in the British Isles from Eire, in Scotland and Northern England.

Subdivision of the Genus Fenestella

Fenestella is a very diverse genus and for many years workers have tried to seggregate the genus removing some groups of the species into new genera, e.g. Semicoscinium Prout (1859), Isotrypa Hall (1885), Loculipora Hall (1885), Hemitrypa Phillips (1841), Minilya Crockford (1944), Loculiporina Elias and Condra (1957) Levifenestella Miller (1961), Rhombofenestella Termier and Termier (1971), Rectifenestella Morozova (1974). Most genera have been based on developments of the carina, while recent workers have placed more emphasis on internal morphological detail.

The first attempt at a subdivision of Fenestella species into groups was made by Simpson (1895) who erected seven groups based on the character of the median carina. This subdivision was similar to Hall's (1885) separation of numerous subgenera or genera from Fenestella on the basis of the excessive development of the carina.

Elias (1937) attempted to group Upper Palaeozoic species on the different basis, of the number of autozooecial apertures per fenestrule and the number of rows of carinal nodes. He established four groups indicating the characteristic species of each, and expressed a belief in a close phylogenetic relationship between members of each group. However Elias paid no attention to the fact that the number of autozooecial apertures per fenestrule is extremely variable even in a single zoarium especially in taxa with larger fenestrule dimensions.

Russian palaeontologists were the first to show the importance of microstructure in a classification. The first workers to realise the different forms of zooecia shown in section for different taxa were Ulrich (1890) and Nekhoroshev (1932), the latter distinguishing within genus groups of species by the form of zooecia.

Trizna (1939) and Shulga-Nesterenko (1941) suggested a similar grouping for Permian species of *Fenestella* which they termed complexes and considered them to be phylogenetic rows. Shulga-Nesterenko (1949-1951) further arranged Upper Palaeozoic species of *Fenestella* and *Polypora* into ten phyletic branches termed lineages. Each group was characterised by different paths of evolution. In some lineages zooecial form or microstructure changed during phylogenesis, in others carinal structure changed but zooecial form remained unchanged. Her phylogenetic schemes are complex, subjective and similar species have been artificially separated into different phylogenetic branches.

Elias and Condra (1957) subdivided *Fenestella* into three sections and thirteen subgroups. The sections were based on the length of fenestrules and the number of apertures per fenestrule in which the subgroups were based on a random combination of characters such as zoarial growth form, development of carinal nodes and the structure of zooecial chambers. Their classification is an example of an artificial system based on the similarity of randomly selected characters.

Miller (1962a) recognised three groups of *Fenestella* species in both America and Britain based on British species end members.

	Britain		America
(1)	*Fenestella plebeia* (McCoy)	-	*Fenestella rudis* (Ulrich)
(2)	*Fenestella frutex* (McCoy)	-	*Fenestella limbata* (Hall)
(3)	*Fenestella bicellulata* (Etheridge, Jun.)	-	*Fenestella tenax* (Ulrich)

However, his groupings are artificial and end members for groups two and three are probably conspecific.

Termier and Termier (1971) distinguished six new genera, e.g.s: Rhombofenestella, Alternifenestella, Rugofenestella, basing each on separate phylogenetic branches established within the genus Fenestella by Shulga-Nesterenko and on the subgroups distinguished by Elias and Condra. However, none of their genera were formally diagnosed and no type species were indicated. Their classification is not valid.

Morozova (1974) revised the genus Fenestella and suggested a new diagnosis with only those species included in the genus which are similar to the type specimen. She established also ten new genera, e.g. Micrifenestella, Laxifenestella, Rectifenestella based on the following properties: branch and dissepiment width, zooecial chamber base shape, carinal structure, presence of diaphragms and hemisepta, and peculiar forms of polymorphism. She gave a diagnosis for each genus, establishing type species for each, and listed a number of species (Soviet species) under the generic headings. Although there is some obvious overlap in the morphology of her genera, it is evident Morozova's classification does appear to be the most realistic to date using a combination of external and internal morphological characters.

Popeko and Gorelova (1974) attempted a more objective systematic classification of Fenestella. They raised objections to classifications involving phylogeny and they based their classification on morphological properties that are stable within a colony or taxon. These properties are the number of rows of carinal nodes, zooecial chamber base shape, structure of zooecial apertures, and the microstructre of skeletal tissues (namely on the appearance of skeletal rods which they termed capillaries). Their 'classification of enumeration' was constructed on the basis of fifteen modifications of these four properties, and they established 120 'classes'. Although such a classification is of obvious practical value in the description of a taxon, it has no real value in the subdivision of *Fenestella* since it is possible to place all species ultimately in one group.

Obviously in a genus so diverse as *Fenestella* with over 2000 species any classification aimed at an objective subdivision of *Fenestella* would be useful. Although several classifications have been suggested none of these gain real value until all established species have been fully described in a standardised manner using external and internal morphological detail and supporting quantitative data. Only then can a subdivision of *Fenestella* be usefully achieved and phylogenetic lineages inferred.

Genus *Minilya* Crockford, 1944

Type species

Minilya duplaris Crockford, 1944

Diagnosis

As for *Fenestella*, with the exception that nodes on the midline of obverse branch surfaces are biserially arranged. Nodes are regularly disposed so that one corresponds with each autozooecial aperture.

Range

Carboniferous to Permian.

TAXONOMIC PROCEDURE

All the parameters measured as as decribed under the general taxonomic procedure for the Fenestillidae. Although in *Minilya* carinal nodes are biserially arranged the number of nodes in a 5 mm line is recorded in one row.

Minilya plummerae (Moore, 1929)

Fig. 49; Pl. 61, figs. a-b.

1929 Fenestella plummerae n.sp. Moore; p. 19, Pl. 2, figs. 8-10.

1951 Fenestella praerhomboidea Shulga-Nesterenko, p. 99.

1961 Fenestella ninae Viskova; p. 87.

1973 Minilya plummerae (Moore); Tavener-Smith; p. 466, Pl. 18, figs. 6-8, pl. 19, figs. 1-4.

Diagnosis

Minilya with delicate, fine textured, small fan-shaped zoaria. Branches are thin, straight, and subparallel; obverse surfaces have a narrow subangular median ridge carrying closely spaced biserially arranged carinal nodes; reverse surfaces are well rounded. Dissepiments are thin, fairly short, slightly depressed on obverse surfaces, and flare perceptibly towards dissepiment-branch junctions. Fenestrules are small, quadrate to elongate, with well rounded extremeties and strong median constrictions. Autozooecial apertures are small, widely spaced, circular and with thick complete peristomes; aptertural positions are stabilised, with one on each dissepiment-branch junction and the other midway between projecting well into fenestrules.

Description

External

Zoaria are delicate, small, fine textured reticulate meshworks and form planar fan-shaped expansions up to 3cm in diameter.

Branches are thin, straight, subparallel and curve gently distally. The obverse surface of branches have a narrow subangular median ridge on which closely spaced biserially arranged nodes occur. Nodes are small, ellipsoidal, and are regularly disposed with one situated near the distal extremity of each autozooecial aperture. As the nodes are closely spaced, nodal bases tend to run into one another giving a zig-zag often carinate appearance to the median ridge. From the median ridge branch sides slope steeply away, and reverse surfaces are well rounded. All surfaces are finely pustulose. Prior to bifurcation branch width may increase for up to two fenestrule lengths and may reach 0.3 mm in width.

Dissepiments are thin, of variable length but are usually fairly short. On obverse surfaces they are normally very slightly depressed, while on reverse surfaces they are only occasionally slightly depressed and are usually flush with branch crests. Dissepiments may be rounded, flattened, or have a narrow subangular median ridge along their length, and may flare slightly or markedly towards dissepiment-branch junctions.

Fenestrules are small, rectangular, quadrate occasionally more elongate, with well rounded extremeties and slightly undulatory to highly constricted lateral margins. They may develop a characteristic hour-glass shape when paired indentations are symmetrically opposed on the sides of many fenestrules, but usually assymetrical indentations give fenestrules a very irregular shape.

Autozooecial apertures are small, circular with thick upraised complete peristomes. They are widely spaced about two diameters apart, and their positions are normally stabilised with one on each dissepiment-branch junction and one midway between. In the latter case autozooecial apertures may be flush with branch sides and project only slightly beyond branch margins, or have extremely elevated outer margins causing them to project markedly into fenestrules. These apertures may be symmetrically opposed, but are usually assymetrically offset. An incipient third row of autozooecial apertures may develop immediately prior to branch bifurcation.

Dimensions (N = 5)

	NM	Mn	Mx	$\bar{X}$
BW	60	0.14	0.20	0.16
AD	42	0.05	0.07	0.07
ID	60	0.22	0.25	0.24
FL	60	0.46	0.48	0.47
FW	60	0.34	0.48	0.45
DW	60	0.08	0.11	0.10
IND	60	0.23	0.25	0.24

Micrometric Formula: 24-32/20-25/20-22/20-23

Discussion

This rare and delicate species is very similar to Fenestella ivanovi but is distinguished from it mainly by the biserial arrangement of carinal nodes, and the triangular shape of zooecial chamber bases.

Minilya plummerae (Moore) was originally assigned to Fenestella, however, Tavener-Smith (1973) noted that because of the biserial arrangement of carinal nodes the species must be placed in Minilya.

Tavener-Smith (1973) gives a detailed discussion and suggests possible synonyms of Minilya plummerae, and some of the material examined in the present study comes from the locality from which he described the species. All the material examined appears to be conspecific with Moore's Fenestella plummerae from the Pennsylvanian Graham Formation of Texas.

Material

ABCL:26	Container with four zoarial frgments. Calp Shale-Upper Limestone, Carrick Lough, Derrygonelly, Ireland (Asbian).
ABP:153	Fifth Limestone, Alston Group, near Penruddock Penrith (Asbian).

Stratigraphical Range

Asbian.

Occurrence

Minilya plummerae is very uncommon and has been recorded only from Asbian strata in Northern Ireland and Cumbria in Britain. Elsewhere, it has been recorded from the Lower Carboniferous of Texas, U.S.A. and the Donetz Basin, U.S.S.R.

Minilya nodulosa (Phillips, 1836)

Fig. 50; Pl.62, figs. a-b; Pl. 63, figs. a-c.

1836 Retepora nodulosa Phillips, p. 199, Pl. 1, figs. 32, 33

1965b Minilya nodulosa (Phillips); Tavener-Smith, p. 135, T.f. 1-2, Pl. 6, figs. 1-4.

1981 Minilya nodulosa (Phillips); Tavener-Smith, p. 566.

Type

Tavener-Smith (1965b) erected a neotype for the taxon. However, this was not valid since it was not from the original type locality. He therefore (1981) erected a new neotype (BMNH PD5339) collected from one of Phillips collecting localities.

Diagnosis

Minilya with quite close, compact, planar fan-shaped zoaria. Branches are relatively stout, straight; obverse surfaces have a well defined wide upraised median carina with fairly small closely spaced biserially arranged nodes; reverse surfaces are well rounded. Dissepiments are short of variable thickness. Fenestrules are quite small, rectangular to oblong, with well rounded extremeties and slight to strong lateral constrictions. Autozooecial apertures are circular, relatively small with complete peristomes, and moderately spaced; apertural positions are stabilised with one on each dissepiment-branch junction and one midway between which projects into fenestrules. An additional small node may be situated distal to apertures on the inclined branch sides.

Description

External

Zoaria form compact, close strong reticulate planar fan-shaped expansions several centimetres in diameter.

Branches are relatively stout, straight, and subparallel, and may curve gently distally. On the obverse surface of branches there is a relatively wide, well rounded, prominent upraised median carina on which closely spaced, fairly small elliptical nodes are biserially arranged. Nodes are regularly arranged, alternating in adjacent rows with one situated on the inside of each autozooecial aperture. Nodal bases tend to run into each other giving a zig-zag appearance to the crest of the median carina. Occasionally the alternate spacing of nodes may not be well developed and nodes may occur in closely spaced pairs. Branch sides are gently inclined away from the carina. A small round or ellipsoidal node is usually situated very close to the distal extremity of each autozooecial aperture. Reverse surfaces are well rounded, and all surfaces are texturally finely granular.

Dissepiments are relatively short, of variable thickness but usually quite thick. They are quite well depressed on the obverse surface, slightly less so on the reverse, and flare considerably towards dissepiment-branch junctions becoming less depressed as they do so. On the obverse surface dissepiments are flat to poorly rounded, occasionally with a poorly defined median ridge, while on the reverse they are usually well rounded.

Fenestrules are quite small, rectangular, quadrate to oblong, with well rounded extremeties and slightly or highly constricted lateral margins. Normally fenestrules are little wider than branches and may have a symmetrical hour-glass shape when paired indentations are opposed, but usually indentations are assymetrical and fenestrules have an irregular shape.

Autozooecial apertures are quite small and circular with complete peristomes of variable width and prominence. Apertures are moderately spaced, one to one and a half diameters apart and their positions are generally stabilised with one situated on each dissepiment-branch junction and one midway between. Rarely there may be three apertures per fenestrule, with one situated on a dissepiment-branch junction and two between, making fenestrules much larger than usual. Apertures situated midway along fenestrules are set low down on branch sides and may be flush on branch sides but normally project from branch margins and constrict fenestrules slightly or moderately.

Dimensions (N = 16)

	NM	Mn	Mx	$\bar{X}$
BW	132	0.24	0.40	0.34
AD	132	0.08	0.10	0.09
ID	132	0.27	0.34	0.31
FL	132	0.52	0.65	0.58
FW	132	0.49	0.53	0.53
DW	132	0.12	0.16	0.14
IND	132	0.27	0.34	0.31

Micrometric Formula: 16-21/15-21/17-21/17-21

Discussion

Retepora nodulosa Phillips referred to by subsequent authors (e.g. Shrubsole, 1979, 1881; Vine, 1885) as Fenestella nodulosa was declared a nomen dubium by Miller (1961) because the original type material was lost and the taxon was incompletely described.

Tavener-Smith (1965b) revised Retepora nodulosa and referred the species to Minilya on the basis of the biserial arrangement of carinal nodes on the obverse surface which Phillips clearly illustrated (1836, Pl. 1, figs. 32, 33). As the original type material of Phillips has been lost, Tavener-Smith erected a neotype (BMNH PD4495). However, Phillips material was collected from localities in Yorkshire and Tavener-Smith's neotype was collected from Carrick Lough in County Fermanagh, Northern Ireland. This was not valid, for according to International Code of Zoological Nomenclature Article 75c (5), a neotype is valid only when it is published with evidence that it came as nearly as practicaly possible from the original type locality. As a result, Tavener-Smith (1981) erected a new neotype (BMNH PD5339) which he collected from Greenhow Hill, North Yorkshire, one of Phillips collecting localities.

Minilya nodulosa is easily recognised by its close compact meshwork, small and irregularly constricted to hour glass shaped fenestrules, stable apertural positions and the common occurrence of an additional small node situated distally to each autozooecial aperture on branch sides.

Material

ABAF -1 to 3	Knipe Scar Limestone. (Asbian) Alston Group, Ashfell Road Cutting, Near Kirkby Stephen, Cumbria.

ABCL 18	Container with six zoarial fragments. Calp shale - Upper Limestone, (Asbian) Carrick Lough, Derrygonelly, Eire.
ABP 131,-135 a,b, -196	Fifth Limestone, (Asbian). Alston Group, Penruddock, Penrith, Cumbria.
BMNH PD5339	(Neotype) Duck Street Farm, Greenhow Hill, (Asbian).

Stratigraphical Range

Asbian.

Occurrence

Although uncommon in Asbian strata *Minilya nodulosa* has a fairly wide distribution, being recorded in Northern England and Northern Ireland.

Genus Ptiloporella Hall, 1885

Type species

Fenestrella (Ptiloporella) latiscrescens Hall, 1885

Diagnosis

Fenestellid with fan-shaped zoaria. Branches are of two types, with a few robust primary branches from which smaller secondary branches arise on one or both sides, diverging at acute angles. New primary branches may develop by bifurcation of a primary branch or by lateral growths from one. All branches are connected by dissepiments. Autozooecial apertures alternate in two rows on the obverse surface of branches, on either side of a median ridge or carina which may or may not carry nodes. Zooecial characters are usually graded between primary and secondary branches.

Range

Silurian to Carboniferous.

TAXONOMIC PROCEDURE

Due to the presence of two sizes of branches in the meshwork, two measurements of branch width are made; primary branch width (PBW) and secondary branch width (SBW). These are measured in the same manner as branch width described in the general taxonomic procedure for the Fenestellidae (p138).

Ptiloporella varicosa (McCoy, 1844)

Pl. 64, figs. a-b.

1844 Fenestella varicosa McCoy; p. 204, Pl. 28, fig. 8.

1961 Fenestella varicosa McCoy; Miller, p. 238.

1973 Ptiloporella varicosa (McCoy), Tavener-Smith, p. 473, Pl. 21, figs. 1-9.

Type

McCoy (1844) did not erect a holotype for the species, so specimen N.M.I. 6040 (Griffith Collection) which is labelled as the probable type, and was figured by McCoy (pl. 28, fig. 8) is here designated as lectotype for the species (not as holotype as Miller, 1961, p. 238 stated). The following systematic description is based solely on this specimen.

Description

External

The zoarium is a fan-shaped expansion. Two types of branches are present in the meshwork, primary and secondary. The reverse surfaces of all branches are well rounded and there is some evidence of fairly small, irregularly distributed elliptical nodes along branch crests.

Primary branches are quite robust, straight to gently sinuous. Most appear to originate in the proximal portion of the colony, and diverge gradually across the zoarium to develop a fan shape, and are quite irregularly arranged. New primary branches may arise by bifurcation or by lateral growth.

Secondary branches are of slender to moderate width, and develop as lateral offsets on either side of primary branches. They are irregularly distributed, diverge at low angles from primary branches, and curve distally to lie subparallel to primary branches. Secondary branches generally alternate on either side of primary branches and may give primary branches a slightly sinuous appearance. Apparently none of the secondary branches bifurcate.

Dissepiments are slender, of variable width, often relatively long and bar like. They are rounded, well depressed below the crest of branches, and flare only very close to dissepiment-branch junctions, becoming less depressed also.

Fenestrules are quite large, of variable shape and size, but are usually rectangular with well rounded extremeties. They may be very long and narrow, especially where several secondary branches occur between two primary branches.

Internal

Autozooecial chamber bases are hemihexagonal to trapezoidal, and there appears to be a considerable variation in size between primary and secondary branches.

Dimensions (N = 1)

	NM	MN	Mx	$\bar{X}$
P.BW	12	0.34	0.47	0.40
S.BW	12	0.20	0.25	0.23
FL	12	1.04	1.44	1.27
FW	12	0.53	0.82	0.75
DW	12	0.17	0.29	0.21

Micrometric formula 14-15/8-9/?/?

Discussion

Miller (1961) re-examined some of McCoy's type material in the Griffith Collection and referred Fenestella varicosa (McCoy, 1844) to the genus Ptiloporella.

Tavener-Smith (1973, p. 473) described Ptiloporella varicosa from the Visean of Carrick Lough, County Fermanagh and reference should be made to his data and systematic description to amplify the present description.

Material

NMI F.6040	(labelled as probable type) Upper Limestone, Blacklion. (Asbian) This specimen was figured by McCoy, 1844, pl. 28, fig. 8.

Stratigraphical Range

Asbian.

Genus Hemitrypa Phillips, 1841.

Type species

Hemitrypa oculata Phillips, 1841

Diagnosis

Like Fenestella but with a superstructure supported on carinal nodes, and consisting of a planar, perforate hexagonal interlocking lattice. One of the perforations of the lattice lies above each autozooecial aperture, and there are two rows of hexagons per branch.

Range

Devonian to Carboniferous.

THE SUPERSTRUCTURE

In Hemitrypa the zoarium consists of two distinct connected parallel meshworks. The main (lower) meshwork is identical with the fenestrate form of Fenestella. The upper meshwork, termed the superstructure, is supported by a uniserial row of large, regularly spaced carinal nodes which may be more properly regarded as pillars, that support the superstructure at a uniform distance above the main meshwork (Pl. 74, figs. a-d). The superstructure consists of a regular perforate hexagonal meshwork, which is continuous with the skeletal tissues of the main fenestrate meshwork below (Figs. 51,52), and covers the entire obverse surface of fan or cup-shaped zoaria, or the exterior surfaces of conical zoaria (e.g. Pl. 65, fig. a). The position of carinal nodes along branches corresponds to the positions of adjoining hexagonal mesh units (Fig.53). The importance of the spacing of carinal nodes is emphasised by the low within and between Colony Coefficients of variation recorded ranging between 2.14 - 2.95.

There are two lateral rows of interlocking hexagons between the midlines of adjacent branches (Fig.54). The junction between the hexagon rows above branches has a stouter construction than the unsupported junction between branches (i.e. above fenestrules) and provides the attachment points for the supporting ends of the nodes. Owing to this stouter construction the hexagonal arrangement is not so well defined above branches in comparison to the more delicate well defined, well faceted interlocking hexagons in a lateral line midway above the fenestrules (e.g. Fig.54; Pl. 69 , fig. b). The perforations of the hexagonal meshwork may be well faceted to rounded, and are usually of fairly constant size. Autozooecial apertures in the main meshwork are positioned directly below a perforation, usually to one side (Fig. 54).

In Hemitrypa hibernica McCoy (1844) there is a distinct manner in which carinal nodes of the main meshwork support the superstructure. There appears to be a delicate balance in the ratio of the number of carinal nodes to autozooecial apertures. The autozooecial aperture count ranges between 14 and 16 and the carinal node count ranges between 20 and 23 in a 5 mm line. The ratio of the number of carinal nodes to autozooecial apertures is 2:3. Two unsupported hexagonal sides occur between every two supported ones, and this appears to be the minimal number of supports necessary to keep the superstructure rigid.

However, Hemitrypa burulica Nikiforova (1927) has an almost identical autozooecial aperture and carinal node count in a 5 mm line (21-22 and 22 respectively) and has an aperture to node ratio of 1:1.

The between species variation in the ratio of autozooecial apertures to carinal nodes is possibly related to genetic and strong eco-phenotypic variation, with different species occupying different ecological niches.

Development of the superstructure

The perforate hexagonal mesh was probably formed by the symmetrical fusion of outgrowths from the pillars (Miller, 1962b).

The skeletal tissues of the superstructure are continuous with the skeletal tissues of the main meshwork (Figs. 51, 52 ; Pl. 77 , fig. a). Calcareous secretion must have taken place from an external epithelium continuous with the epithelium that is inferred to have covered the entire zoarial surface of the main meshwork (Tavener-Smith, 1969a). The primary granular skeleton that surrounds autozooecial chambers forms the narrow cores of pillars and is surrounded by thicker secondary laminated skeleton (Fig. 51 ; Pl. 77 , fig. a). In the proximal part of the pillar, the primary granular layer thins considerably, and forms a narrow core distally. Along the length of the pillar the secondary laminated skeleton also thins initially, but then thickens distally toward the superstructure and gives pillars a biconcave shape (Figs. 51 , 52 ; Pl. 75 , fig. b). The primary granular core thickens considerably prior to its division and development of the superstructure (Fig. 52 ; Pl. 75 , fig. b). At a constant level above the zoarial surface, the distal ends of pillars divide into three geometrically orientated bars (at 120° to each other) in the same plane as the meshwork (Figs. 51 ,52 ,53 ; Pl. 70, fig. a). The individual bars are composed of a central narrow primary granular rod bounded by the thicker secondary laminated skeleton (Figs. 51 ,52 ,53 ; Pl. 77 , fig. b). A narrow, thin portion of the primary granular core of the pillar may extend distally for a short distance above the point of division and the secondary laminated layer is typically thickened in this zone (e.g. Fig. 51 ; Pl. 76 fig. b).

At a constant unit distance away from the point of division, each bar bifurcates and the new bars are geometrically orientated to each other and the parent bar at angles of 120° (Fig. 53). The concurrent and equal development of bars from adjacent pillars on the same branch, and from pillars on adjacent branches enables the fusion of symmetrically disposed bars at half a unit distance after the bifurcation of new bars.

The fusion of these bars results in the development of the perforate hexagonal meshwork. The extreme regularity of this mode of growth is enhanced by the occurrence of perforations directly above autozooecial apertures, and by the very even size of hexagons (e.g. Figs. 53, 54).

Initially the perforations probably had quite well faceted extremeties, but with further secretion of the secondary laminated skeleton become rounded. There was probably also further secretion of the secondary laminated skeleton of the supporting pillars and the interlocking hexagonal units above the midline of branches to strengthen the superstructure.

Function of the Superstructure

The function of the superstructure relates to the presence of autozooecial apertures situated directly below the perforations.

Cole (1893) and Miller (1962b)envisaged an ascophoran cheilostome type of compensation sac in zooecial chambers which enabled zooidal tentacle crowns to extend beyond the hexagonal perforations of the superstructure . A compensation sac (ascus) is a flexible floored sac situated beneath the frontal shields of autozooids. It enclosed a water filled chamber, opening near the orifice and functioned as a hydrostatic system. The tentacle crown extrudes from the zooecium as a result of an equal volume of water introduced to the sac compensating for the displaced polypide.

In Hemitrypa there is no evidence of an ascophoran type of compensation sac in autozooecial chambers as suggested by Cole and Miller. Autozooecial chambers are too small to have incorporated a compensation sac of the size needed to extrude a polypide above the superstructure. It is unlikely that the tentacle crowns of polypides could have been extruded sufficiently to protrude above the superstructure. In living stenolaemate bryozoans lophophores are not known to extend farther than the bases of zooecial orifices.

It is probable that the extruded polypides functioned between the branch surface and superstructure, the latter affording some protection to the feeding zooids (Tavener-Smith, 1973, p. 478).

The hexagonal meshwork superstructure would certainly affect current flow over the surface of the colony and the primary function could well be as a current baffle altering the laminar flow of water through the colony. The eddy currents set up between the main meshwork and the superstructure probably facilitated the greater filtration of food particles by polypides. The presence of the superstructure possibly mutually increased the rigidity of the fenestrate mesh also.

TAXONOMIC PROCEDURE

The regularity in size of the individual hexagonal units comprising the superstructure is of considerable taxonomic value. In addition to the range of parameters measured on the main fenestrate meshwork below two measurements of superstructure length (SL) and width (SW) are recorded.

Superstructure length (SL): the length of a hexagon, parallel to the direction of zoarial growth measured between the centres of opposite ends of the hexagon.

Superstructure width (SW): the width of a hexagon, measured transverse to the direction of zoarial growth between the centres of opposite ends of the hexagon.

Hemitrypa hibernica McCoy, 1844.

Figs. 51-54; Pl. 65, figs. a-b; Pl. 66, figs. a-d; Pl. 67, figs. a-b; Pl. 68, figs. a-b; Pl. 69, figs. a-b; Pl. 70, figs. a-b; Pl. 71, figs. a- Pl. 72, figs. a-c; Pl. 73, figs. a-b; Pl. 74, figs. a-c; Pl. 75, figs. a- Pl. 76, figs. a-b; Pl. 77, fig. a.

1844 *Hemitrypa hibernica* McCoy; p. 205, Pl. 29, fig. 7.

1844 aff *Fenestella carinata* McCoy; p. 200, Pl. 28, fig. 12.

1893 *Hemitrypa hibernica* McCoy; Cole, p. 132, Pl. 8, figs. 1-5.

1927 non *Hemitrypa burulica* Nikiforova, p. 182.

1960 *Hemitrypa reticulata* n.sp. Burkle, p. 1091, Pl. 132, figs. 6-7.

1962b *Hemitrypa hibernica* McCoy; Miller, p. 313, 2 T.f., Pl. 15, figs. 1-4.

1973 *Hemitrypa hibernica* McCoy; Tavener-Smith, p. 475, Pl. 22, figs. 1-10.

1981 *Hemitrypa hibernica* McCoy; Morozova, p. 72, Pl. 18, fig. 1.

Type

McCoy (1844, p. 200) did not erect a holotype for *Hemitrypa hibernica*, and Miller's (1962b, p.313) reference to McCoy's figured specimen as being the holotype is not strictly valid. Consequently a lectotype is formally proposed here for the taxon: NMI F.6022. It was figured by McCoy (1844, Pl. 29, fig. 7) and Miller (1962b, Pl. 15, fig. 1).

Emended Diagnosis

Hemitrypa with quite close, fine textured, reticulate planar fan-shaped or conical zoaria. Branches are straight, stout, of moderate width and bifurcations are uncommon; obverse branch surfaces have a narrow straight median ridge on which a uniserial row of relatively large, quite close and regularly spaced nodes occur; reverse surfaces are quite well-rounded and nodose. Dissepiments are short, thick, typically biconcave, well depressed on the obverse surface, less so on the reverse. Fenestrules are fairly small, oblong to elliptical. Autozooecial apertures are relatively large, circular or oval with thin, often incomplete peristomes; they are closely spaced, set flush on branch sides with two or three per fenestrule. Ovicells are rare. The superstructure forms a delicate perforate hexagonal interlocking meshwork.

Description

External

Zoaria form reticulate, quite close, fine textured, fan-shaped, conical or rarely foliaceous expansions. Planar, fan-shaped and foliaceous expansions are of moderate size, up to 8 cm in diameter. Conical zoaria may be up to 17 cm in length and 5 cm in diameter and form low angle expansions, expanding distally, gradually. The obverse surface covered by the superstructure always occurs on the outer sides of conical expansions.

Branches are straight, of moderate width and are relatively stout. The obverse surfaces of branches have a narrow straight median ridge on which a uniserial row of relatively large, quite close and regularly spaced nodes occur. Nodes have ovoid very inflated bases, and narrow becoming rounded distally. They are long, and become wider and ovoid prior to their lateral trifurcation to form the superstructure. The height of the carinal nodes from the ridge to the superstructure ranges between 0.21 and 0.25 mm. Branch sides slope steeply away from the median ridge. The obverse surfaces of branches are finely granular. Reverse surfaces of branches are fairly well rounded, quite coarsely granular, commonly with a well defined single row of rounded, large closely spaced nodes. Prior to bifurcation, branch width increases for up to four fenestrule lengths and may reach 0.49 mm.

Dissepiments are short, thick and are well depressed below the crests of branches on the obverse surface. They are typically biconcave, thinnest in the middle and flare considerably becoming less depressed towards dissepiment-branch junctions, and are usually quite well rounded. On the reverse surface they are well rounded and are only slightly depressed below the crest of branches.

Fenestrules are fairly small, relatively long and narrow, and are approximately equal in width to branches. Fenestrules are rectangular, oblong or more commonly elliptical, with well rounded extremeties and straight or gently curved lateral margins.

Autozooecial apertures are relatively large, circular or oval, and with thin low complete peristomes. They are closely spaced, about or slightly less than their own diameter apart, and are set flush on branch sides and do not indent fenestrule margins. There are between two and three per fenestrule. Prior to branch bifurcation an incipient third row of apertures may develop for considerable distances, up to two fenestrule lengths prior to division. Ovicells are rare (see page 127).

The carinal nodes support the superstructure at a uniform distance above the zoarial surface. This is a delicate lattice-like expanse of interlocking hexagonal units, and two rows of hexagons correspond to a branch, and each perforation is situated above an autozooecial aperture. The junction between the hexagon rows above a branch has a stouter construction than that above fenestrules.

Internal

Autozooecial chamber bases are hemihexagonal, interlocking in two rows. In shallow tangential section, autozooecial chambers have a reniform shape.

The zooecial skeleton lining chambers is very thin and finely laminated. The primary granular skeleton is thin and the junctions between it and the inner zooecial and outer laminated skeletons are well defined. Between 8 and 12 skeletal ridges of the primary granular skeleton radiate from this zone. These ridges are fairly narrow and short, about four diameters apart, and are best developed on the reverse sides of chambers and become shorter and eventually disappear on the obverse side of chambers. Closely spaced narrow rods of the primary granular skeleton diverge from the ridges and curve in a proximal direction to the zoarial surface. The outer secondary laminated skeleton is thick, and laminae bend around the apices of the skeletal ridges, and maintain a broad oral flexure beyond the apices of the ridges close to the zoarial surface. Laminae are deflected orally around the narrow rods of primary granular material and form small pustules best developed on the reverse zoarial surface.

The superstructure is compound and continuous with the main meshwork below. The primary granular skeleton surrounding autozooecial chambers and forming the cores of carinal nodes is continuous into the bars of the superstructure and forms their cores. These cores are surrounded by thicker secondary laminated skeleton continuous with the outer secondary laminated skeleton of the main meshwork below.

Dimensions (N = 45)

	NM	Mn	Mx	$\bar{X}$
BW	323	0.22	0.31	0.26
AD	341	0.10	0.127	0.11
ID	339	0.21	0.28	0.22
FL	420	0.50	0.67	0.57
FW	420	0.40	0.55	0.45
DW	315	0.09	0.18	0.14
IND	372	0.31	0.52	0.37
SL	388	0.19	0.29	0.22
SW	325	0.22	0.33	0.25
ZB1	75	0.18	0.28	0.22
ZB2	75	0.11	0.16	0.13

Micrometric Formula 18-26/16-21/22-25/12-16

Discussion

Hemitrypa hibernica McCoy is the only species of *Hemitrypa* present in British Lower Carboniferous strata. It is distinguished from other fenestrate Bryozoa by the occurrence of a honeycomb-patterned superstructure attached to the main meshwork by the carinal nodes. Quite commonly the delicate superstructure has been destroyed leaving only the main meshwork intact. The large pillar-like carinal nodes may remain, and so render the taxon recognisable. However, usually these too have been removed and the taxon may then be identified by its' stout branches of moderate width with only rare bifurcations, the occurrence of ovicells, fairly small elliptical fenestrules, short stout dissepiments, and closely spaced relatively large autozooecial apertures set flush on branch sides with two or three per fenestrule.

McCoy (1844, p. 205) first described Hemitrypa hibernica and also described the form Fenestella carinata (ibid, p. 200). The only specimen in the Griffith Collection labelled as Fenestella carinata (NMI.F.6033) from the Carboniferous Shale of Enagh Tyrone is a grey-buff coloured biosparrite containing several fenestellid frond fragments. McCoy's two illustrations (Pl. 28, fig. 12) were drawn from two zoarial fragments on this specimen. In the upper of his two figures he illustrated a small fragment exposing the reverse surface of a colony. Much of the colony is only loosely attached to the limestone and temporary removal of this portion allowed examination of its obverse surface. This revealed the obverse surface to be covered by an interlocking hexagonal meshwork and the specimen is clearly referable to Hemitrypa hibernica.

Adjacent to this specimen is a larger fragment exposing the obverse surface, and was the fragment from which the second and larger of McCoy's two figures were made. The carinal nodes on the specimen are very large and prominent, and a small part of the specimen reveals the remnant of the hexagonal superstructure intact. This specimen is referable also to Hemitrypa hibernica.

Fenestella carinata is thus a synonym of Hemitrypa hibernica as Miller (1962b,p. 238) suggested.

H. hibernica is probably conspecific with Hemitrypa reticulata Burkle (1960, p. 1091) as suggested by Miller (1962b). They are comparable in all parameters measured. However, H. hibernica is probably not conspecific with Hemitrypa burulica Nikiforova (1927, p. 182) as tentatively suggested by Miller. The ratio of carinal nodes to autozooecial apertures is 1:1 and both nodes and apertures are significantly closer spaced than in H. hibernica.

An unusual feature observed on the material from Carrick Lough is the occurrence on the zoarium of arc-like zones of thickened dissepiments (see Tavener-Smith, 1973, p. 478, Pl. 22, fig. 2). These occur on the reverse surfaces of the meshwork, and the thickening may have occurred by pauses in the forward growth of the colony. Additionally, ovicells have been recorded only on the material from Carrick Lough.

Material

ABA 1	Top of the Ashfell Sandstone (Arundian), Fell Sandstone Group, Ashfell Edge, Nr. Kirkby Stephen, Cumbria.
ABA 2-17	16 zoarial fragments in a container. Horizon and locality as above.
ABA 201	Thin Section. Horizon and locality as above.
ABAF 5-11	Knipe Scar Limestone (Asbian), Alston Group. Ashfell Road Cutting, Nr Kirkby Stephen, Cumbria.
ABCL 12	Cavity slide with 12 zoarial fragments. Calp-Shale-Upper Limestone (Asbain), Carrick Lough, Derrygonelly, Northern Ireland.
ABCL 20	Cavity slide with 5 zoarial fragments. Horizon and locality as above.
ABO 2-6	Apron reef Limestone, Bee Low Group (Asbian), Odin Fissure, near Castleton, Derbyshire.
ABP 99	Container with 32 zoarial fragments. Fifth Limestone (Asbian), Alston Group, Penruddock near Penrith, Cumbria.
ABP 100-109, 112-115	Horizon and locality as above.
ABP 110-111	Acetate peels and remnants. Horizon and locality as above.

ABP 302-304	Thin Sections. Horizon and locality as above.
ABR 200,-201,-203	Thin Sections. Redesdale Ironstone (Asbian), Lower Limestone Group, Ridsdale, Northumberland.
ABRE 200-202,-204,-206,-209,-212,-213,-217,224-239,242-245,248-254.	Thin Sections. Seventh Limestone (Holkerian), Redmain, near Cockermouth, Cumbria.
BMNH PD.1033	Derbyshire. G.H. Morton Collection.
BMNH PD.1292	Carboniferous Limestone, Derbyshire. J.E. Lee Collection.
BMNH D.1686	Carboniferous Limestone, Oreton, Salop. Baugh Collection.
BMNH D.1690	Carboniferous Limestone, Ireland.
BMNH PD4055	Lower Carboniferous, Blue quarries, (Asbian), collected by T.G. Miller, 1961.
BMNH PD.4067 A,B,C	Lickar Limestone (Arnsbergian), Howick Haven, nr. Howick, Northumberland. Fergusson Collection.
BMNH D.29168-9	Carboniferous, Little Island, East of Cork (Arundian?-Holkerian?). J. Wright Collection.
BMNH D.33097	Bolland district, Yorkshire, Gilbertson Collection.
NMI.F.6022	Labelled as type. Lower Limestone (Arundian?-Holkerian?), Little Island, Cork. This specimen was figured by McCoy 1844, Pl. 29, fig. 7 and by Miller 1962b,Pl. 15, fig. 1.
NMI F.6065,F.6066	Two specimens on a card, labelled as probable second type for structure. Calp (Visean), Ballindrillick, Bundoran. Specimen F.6065 was figured by Miller, 1962b,Pl. 15, fig. 2.

NMI F.6033	labelled as 'Fenestella carinata' McCoy. Type? Carboniferous shale. Enagh, Tynan. This specimen was figured by McCoy 1844, Pl. 28, fig. 12.
NMI F.6080	Lower Limestone, Little Island, Cork.
NMI F.6081	Carboniferous Limestone, Little Island, Cork.

Stratigraphical Range

Arundian-Asbian.

Occurrence

Hemitrypa hibernica is very common in British Lower Carboniferous strata. It is typically most abundant in reef facies, and large conical zoaria occur in the Walsortian reef Limestones of Co. Limmerick, Eire. In the reef limestones of Carrick Lough and Derbyshire large planar, fan shaped or foliaceous zoaria occur.

Elsewhere Hemitrypa hibernica has a widespread distribution, being recorded in strata throughout the North of England and Ireland, and is typically found in shallow water facies, always in association with a rich Bryozoa fauna. It has not been recorded in Scottish or Welsh Lower Carboniferous strata.

Family Polyporidae Vine, 1883b

Type Genus

Polypora McCoy, 1844.

Diagnosis

Fenestrata with zoaria which are planar, foliaceous or conical reticulate expansions of branches connected by sterile dissepiments. Branches bear three or more rows of zooecia opening on one side of the zoarium; obverse surfaces are non-carinate, usually smooth or with low longitudinal ridges separating rows of apertures and may bear nodes. Reverse surfaces are smooth, longitudinal striate or pustulose.

Range

Ordovician to Permian.

TAXONOMIC PROCEDURE

The principal morphological characters used in the analysis of taxa within the family are the same as those for the Fenestellidae. Two additional characters are utilised.

External morphological characters

Zooecial parameters

Branch Width (BW): Measured as in the Fenestellidae.

Apertural Rows (AR): Recorded as in the Fenestellidae. In Polypora there are three or more rows of autozooecial apertures on the branches. The number is constant for a species and is of considerable taxonomic value. The number of apertural rows is recorded away from areas of branch bifurcation and the proximal part of a zoarium where the number of apertural rows is extremely variable due to closely spaced bifurcations. Prior to a branch bifurcation the number of apertural rows may increase from an average of 4 up to 6 or 7 with the increase in branch width. Immediately after a bifurcation the number of apertural rows may be reduced to 2 or 3, but increases again with the rapid increase in branch width.

Apertural Diameter (AD): Measured as in the Fenestellidae.

Interapertural Distance (ID): Measured as with the Fenestellidae.

Zoarial Parameters

Fenestrule Length (FL): Measured as with the Fenestellidae.

Fenestrule Width (FW): Measured as with the Fenestellidae.

Dissepiment Width (DW): Measured as with the Fenestellidae.

Internodal distance (IND): Measured as with the Fenestellidae.

Zooecial Apertures per Fenestrule (ZAF): Recorded as in the Fenestellidae.

Micrometric formula:

as with the Fenestellidae.

Internal morphological characters

Zooecial parameters

Zooecial Chamber Base Shape and Size: In the Polyporidae where three or more rows of zooecia occur zooecial chamber bases are not all the same shape and size. In the species of Polypora examined while lateral zooecial chambers have a typical hemihexagonal shape, the chamber bases of the median row or rows are typically rhombic and are of smaller size. In the present study measurements have been carried out separately on both types of zooecial chamber bases, in the same manner as they were measured in the Fenestellidae.

Genus *Polypora* McCoy, 1844

Type species

Polypora dendroides McCoy, 1844

Diagnosis

Polyporidae with zoaria forming large planar fan-shaped or conical reticulate expansions of branches connected by regularly spaced dissepiments. The obverse surfaces of branches bear three or more rows of autozooecial apertures; obverse surfaces are non-carinate, usually smooth or with ridges separating rows of apertures and may bear nodes. Reverse surfaces are usually smooth and finely granular. Secondary nanozooids occur.

Range

Silurian to Permian.

Polypora dendroides McCoy, 1844.

Pl. 78, figs. a-c; Pl. 79, figs. a-b; Pl. 80, figs. a-c; Pl. 81, figs. a-c; Pl. 82, figs. a-c; Pl. 83, fig. a.

1844 Polypora dendroides McCoy, p. 206, Pl. 29, fig. 9

1963 Polypora dendroides McCoy, Miller, p. 167, Pl. 23, figs. 1-3.

1973 Polypora dendroides McCoy, Tavener-Smith, p. 478, Pl. 23, figs. 1-7.

Type

As McCoy (1844, p. 206) did not erect a holotype for Polypora dendroides, Miller (1963, p. 167) established a lectotype for the taxon. The lectotype (NMI F.6073) was figured by McCoy (Pl. 29, fig. 9) and by Miller (Pl. 23, figs. 1-3) who revised the description of the taxon.

Emended Diagnosis

Polypora with large, open, robust, fan-shaped expansions. Branches are very robust, straight, sub-parallel and oval in cross-section. Obverse surfaces are smooth and well-rounded and commonly along the median line is a single row of large, widely spaced nodes. Reverse surfaces are well rounded. All surfaces are regularly pustulose. Dissepiments are relatively short, stout and depressed. Fenestrules are large, rectangular to oblong. Autozooecial apertures are large, oval, closely spaced, and apertural rims are ornamented by closely spaced pustules. There are usually four rows of apertures along a branch, arranged in quincunx, and there are between five or six apertures per fenestrule. Secondary nanozooids occur.

Description

External

Zoaria form large open robust reticulate fan-shaped expansions, at least 8 cm in length.

Branches are very stout, straight and sub-parallel, with an oval cross-section. The obverse surfaces of branches are well rounded, smooth and along the midline of branches a single row of widely spaced large rounded nodes may occur. The obverse surfaces of branches are flatter where branch width increases prior to bifurcation. Prior to branch division, branch width increases for up to two fenestrule lengths and may reach 1.6 mm in width. Reverse surfaces of branches are well rounded. The obverse surfaces of branches are pustulose, covered by quite widely spaced, regularly arranged pustules in gently sinuous rows between autozooecial apertures. Reverse surfaces are also finely pustulose, covered by pustules in closely spaced longitudinal rows.

Dissepiments are relatively short, stout (about, or more than, half the average branch width), and are quite considerably depressed below the crests of obverse branch surfaces, less so on the reverse. They are smooth with a circular, or more commonly oval, cross-section, and are thinnest in the middle and increase in width perceptibly towards dissepiment-branch junctions and become less depressed.

Fenestrules are large, but vary considerably in size, particularly in length. They are commonly rectangular or oblong, or occasionally oval, and have well rounded extremeties and straight or gently rounded lateral margins.

Autozooecial apertures are very large, and oval. Apertural rims carry fifteen or sixteen small round pustules which may slightly indent apertural margins. There are normally between four or five rows of apertures on the obverse of branches arranged in quincunx. Apertures are very closely spaced, in the same longitudinal row they are separated by between half and one diameter, diagonally adjacent apertures are extremely closely spaced less than half a diameter apart.

With the increase in branch width prior to branch bifurcation the number of apertural rows may increase up to seven, decreasing to three immediately after division. Secondary nanozooids occur.

Internal

Autozooecial chamber bases are acutely rhombic in the inner rows, while along branch margins outermost chamber bases are hemi-hexagonal. In shallow tangential section zooecial chambers become oval or pyriform.

The zooecial skeleton lining chambers is very thin and finely laminated. The primary granular skeleton is thin, but slightly thicker on the underside of zooecial chambers. The junction between the zooecial laminated skeleton and the primary granular skeleton is well defined. Closely spaced narrow and short ridges of the primary skeleton radiate out from this zone. Along these ridges narrow cylindrical rods of the primary granular skeleton diverge toward the zoarial surfaces at closely spaced intervals and diverge at oblique angles toward the zoarial surface in a proximal direction and may be gently curved.

The secondary laminated skeleton is of moderate thickness and the junction between it and the primary granular layer is well defined. Laminae curve around the apices of the primary granular ridges, and are deflected orally around the granular rods for short distances, forming pustules on the obverse and reverse zoarial surfaces.

Dimensions (N = 6)

	NM	Mn	Mx	$\bar{X}$
BW	75	0.61	0.78	0.67
AD	63	0.18	0.20	0.19
ID	75	0.33	0.38	0.36
FL	75	1.50	2.12	1.84
FW	75	1.11	1.42	1.21
DW	75	0.34	0.45	0.41
IND	75	0.78	1.15	0.97

Micrometric Formula: 6-10/5-7/14-15/4-7

Discussion

Polypora dendroides McCoy is recognised by its large robust open meshwork, straight stout branches, very robust fairly short dissepiments, large rectangular or oblong fenestrules, and the presence of very closely spaced large oval autozooecial apertures with ornamented pustulose rims, with usually four rows of apertures on branches.

McCoy (1844) figured two specimens of P. dendroides (Pl. 29, fig. 9). Although the lower of his two illustrations is referable to P. dendroides (the figured specimen NMI.F.6073 is the designated lectotype for the taxon), the upper figure is not conspecific with P. dendroides. This latter specimen (NMI.F.6072) is a reverse surface of a zoarium and is referable to Polypora verrucosa McCoy as Miller (1962, p. 168) suggested.

P. dendroides, described from Asbian strata of Carrick Lough (Tavener-Smith, 1973, p. 478) is probably conspecific with the type material of P. dendroides from Courceyan strata of Hookhead, County Wexford. The fact that all measured parameters are constantly slightly larger in the Carrick Lough material, and that nodes on the midline of the obverse surface of branches are only poorly developed may be accounted for by evolutionary and ecophenotypic variation.

Material

ABHH 1	Hookhead formation (Courceyan) Slade, Hookhead, County Wexford, Eire.
ABHH 12,-13,-20	Hookhead formation (Courceyan) Lighthouse, Hookhead, County Wexford, Eire.
NMI.F.6073	Lectotype. Carboniferous slate, Hookhead, Fethard. Figured by McCoy (1844, Pl. 29, fig. 9) and Miller (1963, Pl. 23, figs. 1-3). T.G. Miller (1962) prepared three thin sections from the lectotype, these are labelled F.6099 a-c. F. McKinney prepared 3 thin sections and six acetate peels from the lectotype, these are labelled F.6103 a-i.
NMI.F.6085	Carboniferous slate, Hookhead. (Courceyan).

Stratigraphical Range

Courceyan-Asbian.

Occurrence

Polypora dendroides has been described only from two localities, from Courceyan strata of Hookhead, County Wexford, Eire, and Asbian strata of Carrick Lough, County Fermanagh, Northern Ireland (see Tavener-Smith, 1973).

Polypora verrucosa McCoy, 1844

Pl. 84, figs. a-c; Pl. 85, figs. a-b; Pl. 86, figs. a-c; Pl. 87, figs. a-
Pl. 88, figs. a-b; Pl. 89, figs. a-c.

1844 *Fenestella crassa* McCoy, p. 201, Pl. 29, fig. 1.

1844 *Polypora verrucosa* McCoy, p. 206, Pl. 29, fig. 6.

1961 '*Fenestella*' *crassa* McCoy, Miller, p. 238.

1963 *Polypora* (?) *verrucosa* McCoy, Miller, p. 169, Pl. 24, fig. 2.

1973 *Polypora verrucosa* McCoy, Tavener-Smith, p. 480, Pl. 24, figs. 1-7.

Type

McCoy (1844) did not establish a holotype for *Polypora verrucosa*, thus Miller's (1963, p. 169) reference to the presence of a holotype is not strictly correct. Consequently a lectotype is formally selected here for the taxon. This specimen (NMI.F.6068) is McCoy's figured specimen (Pl. 29, fig. 6) and was also figured by Miller (Pl. 24, fig. 2) as the holotype.

Emended Diagnosis

Polypora with large planar fan-shaped (?) zoaria. Branches are straight, stout and subparallel, with a circular cross-section; obverse surfaces are well rounded and ornamented by fine, closely spaced sinuous ridges around apertures; reverse surfaces are well rounded. Dissepiments are short, bar-like and depressed. Fenestrules are very large-elongate, rectangular. Autozooecial apertures are of moderate size, circular, with complete upraised peristomes, arranged in quincunx, in 4 alternate longitudinal rows; lateral rows of apertures are set close to branch margins and indent fenestrules slightly; normally seven or eight per fenestrule.

Description

External

Zoaria form large, planar reticulate expansions, possibly fan-shaped, with an open rigid-looking meshwork.

Branches are robust, straight and subparallel and have a circular cross-section. The obverse surface of branches is well-rounded and ornamented by closely spaced, delicate, sinuous longitudinal ridges which curve around autozooecial apertures. Small nodes occasionally occur on the obverse surface of branches and are widely spaced and irregularly arranged, but are normally situated approximately along the midlines of branches. The reverse surface of branches is also well rounded and may be ornamented by closely spaced straight, fine longitudinal ridges.

Dissepiments are relatively short and bar-like. They are well depressed below the crests of branches on the obverse surface, less so on the reverse surface. Dissepiments increase only very slightly in width towards dissepiment-branch junctions, and also become less depressed.

Fenestrules are very large, and are elongate-rectangular, two or three times as long as wide. The lateral margins of fenestrules are straight and are regularly gently indented by protruding apertural margins.

Autozooecial apertures are quite large, circular or oval, with complete narrow upraised peristomes. They are arranged in quincunx, with four alternately arranged longitudinal rows occurring on branches, this number may increase to six before bifurcations and decreases to three immediately afterwards. Apertures in the same longitudinal row are quite widely spaced about two diameters apart, while apertures in the same transverse row are closely spaced about their own diameter apart.

The lateral rows of apertures are set close to branch margins and their outer rims indent fenestrule margins slightly, with usually between seven and eight per fenestrule.

Internal

The zooecial chamber base shape of the lateral rows of zooecia is hemi-hexagonal, while the shape of the central rows is an acute rhombic shape. The zooecial skeleton lining chambers is very thin and finely laminated, and the junction of this and the surrounding primary granular skeleton is well defined. The primary granular skeleton is well defined. The primary granular skeleton is thin, and between 12 and 16, short, narrow, and moderately spaced ridges of the granular skeleton radiate from this zone. The junction of the primary granular skeleton and the outer secondary laminated skeleton is very well defined.

The secondary laminated skeleton is quite thick and may occasionally be thicker on the obverse side of chambers rather than on the reverse side. Laminae curve around the apices of the ridges of primary granular skeleton, and gradually loose their curvature and become gently undulatory.

Dimensions (N = 5)

	NM	Mn	Mx	$\bar{X}$
BW	67	0.56	0.75	0.63
AD	69	0.12	0.13	0.125
ID	72	0.41	0.47	0.44
FL	52	3.50	4.22	3.93
FW	52	1.33	1.93	1.60
DW	68	0.18	0.40	0.25

Micrometric Formula: 6-9/3-5/11-14

Discussion

Polypora verrucosa McCoy (1844) is a very striking form, easily recognised by its rigid open meshwork of stout straight branches, very large, elongate rectangular fenestrules, connected by relatively thin bar-like dissepiments.

In addition to describing P. verrucosa, McCoy (1844, p. 206) also described the form Polypora dendroides. Specimen NMI.F.6072, figured by McCoy (1844, Pl. 29, fig. 9) as the upper of his two illustrations of P. dendroides, is referred to Polypora verrucosa as mentioned earlier (see page 235). The specimen is a small fragment showing the reverse surface of the proximal portion of a colony and is embedded in a pale grey biosparrite. Measurements of fenestrule dimenions and of the weathered zooecial chamber bases (revealed because of the weathering away of the surrounding skeletal tissues) are typical of Polypora verrucosa.

McCoy (1844, p. 201) also described Fenestella crassa. In the present study, examination of all available McCoy type material in the Griffith Collection at the National Museum of Ireland, Dublin, has revealed the existence of only one specimen of the taxon. This specimen (NMI.F.6039) was figured by McCoy (1844, Pl. 29, fig. 1), and is a large colony fragment, 48 x 38 mm showing the reverse surface embedded in a mottled grey biosparrite. Measurement of the external parameters, branch width, fenestrule length and width, and dissepiment width, show that the specimen is either a very large fenestellid or more likely a polyporid. In recent years thin sections and acetate peels have been prepared from the specimen by M.K. Elias and F.K. McKinney, and these have been examined in the present study. These have allowed the examination of internal morphological characters and the measurement of zooecial chamber base dimensions. Tangential sections have revealed the existence of four rows of zooecia along branches, thus the specimen is a polyporid, and measurements of zooecial chamber base dimensions correspond with *Polypora verrucosa*. The measurements of the external parameters also correspond to *P. verrucosa*. As a result of the present examination of all available type material, *Fenestella crassa* McCoy is here place in synonymy with *Polypora verrucosa* and not referred to as *Polypora crassa* as Miller (1961, p. 238) suggested.

Miller (1963, p. 166) emended the diagnosis of the genus *Polypora* citing as an essential character of the taxon the regularly spaced elevated nodes on the central line of the obverse surface of branches. As *Polypora verrucosa* does not agree with this diagnosis, Miller (1963, p. 169) only tentatively assigned the species to the genus *Polypora*. However, as Tavener-Smith (1973, p. 482) pointed out, not all species of *Polypora* have nodes, and their presence is not therefore diagnostic and such a requirement is rejected as unwarranted and over-restrictive.

Material

ABWB 1, 2	Middle Limestone (Brigantian), Middle Limestone Group, Morpeth Scar, Near West Burton, Wensleydale, North Yorkshire.
NMI.F.6039	Labelled as holotype of *Fenestella crassa* McCoy. Lower Limestone, Millicent, Clare, County Kildare. The specimen was figure by McCoy, 1844 (Pl. 29, fig. 1).
NMI.F.6068	Labelled as holotype of *Polypora verrucosa* McCoy. Upper Limestone, Blacklion, Enniskillen (Asbian). The specimen was figured by McCoy, 1844 (Pl. 29, fig. 6) and Miller, 1963 (Pl. 24, fig. 2).

NMI.F.6072	Labelled as ? type for form of *Polypora dendroides* McCoy. Carboniferous Limestone, Blacklion, (Asbian). The specimen was figured by McCoy, 1844 (Pl. 29, fig. 9b).
NMI.F.6082	Carboniferous Limestone, Kildare.
NMI.F.6104(2)	Two thin sections of *Fenestella crassa*, prepared by M.K. Elias.
NMI.F.6105	Three thin sections and five acetate peels of *Fenestella crassa*, prepared by F.K. McKinney.

Stratigraphical Range

Asbian - Brigantian.

Occurrence

Polypora verrucosa is uncommon in British Lower Carboniferous strata, and has been recorded from only a few localities in Eire and Northern Ireland, and in Wensleydale, North Yorkshire. It occurs in shallow marine facies, and reef limestones and is associated with a rich and diverse fauna of bryozoans, brachiopods and crinoids.

Polypora marginata McCoy, 1844

Pl. 90, figs. a-c.

1844 Polypora marginata McCoy, p. 206, Pl. 29, fig. 5

1963 Polypora marginata McCoy, Miller, p. 168, Pl. 24, fig. 3.

Type

As McCoy (1844, p. 206) did not erect a holotype for Polypora dendroides, Miller's (1963, p. 168) reference to McCoy's figured specimen (Pl.29, fig. 5) as the holotype is not strictly correct. Consequently a lectotype is formally proposed here for the taxon. This is specimen NMI.F.607o and is the one figured by McCoy and Miller (Pl.24, fig. 3) and is the only specimen of the taxon in the Griffith Collection.

The following systematic description is based solely on this specimen, which is the reverse surface of a small colony fragment, 25 x 11 mm ground away in part to reveal obverse surface detail.

Emended Diagnosis

Polypora with a large (?) planar zoarium. Branches are very robust, slightly sinuous with an elliptical cross-section. Dissepiments are stout and short. Fenestrules are large and rectangular or oblong with finely serrated lateral margins. Autozooecial apertures are of moderate size, circular, with five longtiduinal rows developed on branches and apertures are quite widely spaced in the same longitudinal row and the outer rows project slightly into fenestrules.

Description

External

The general appearance of the material available suggests that the zoarium was a large reticulate, fan-shaped expansion.

Branches are very robust, slightly sinuous and are elliptical in cross-section. Reverse surfaces of branches are smooth and finely granular. The specimen is a proximal portion of a colony, and branches bifurcate at closely spaced intervals, every two fenestrule lengths. Consequently branch width is very variable, and prior branch division, branch width may reach 1.8 mm.

Dissepiments are very stout, relatively short and are flush or occasionally slightly depressed below the crests of reverse branch surfaces. They increase in width slightly toward dissepiment-branch junctions.

Fenestrules are large, rectangular or oblong, with rounded extremeties and straight lateral margins, which are regularly finely serrated along their length.

Autozooecial apertures are of moderate size, circular, arranged in quincunx in five longitudinal rows on branches. In the same longitudinal row apertures are quite widely spaced about one and a half diameters apart, apertures diagonally adjacent are closely spaced, slightly more than half a diameter apart. The lateral rows of apertures are set close to branch margins and their outer margins indent fenestrules giving branches a slight but regular gently serrated outline.

Dimensions (N = 1)

	NM	Mn	Mx	$\bar{X}$
BW	12	0.70	0.83	0.78
AD	12	0.10	0.12	0.11
ID	12	0.27	0.38	0.31
FL	12	1.83	2.77	2.37
FW	12	1.13	1.87	1.58
DW	12	0.25	0.47	0.38

Micrometric Formula: 7-8/4-5/15-16/-

Discussion

Study of all known species of Carboniferous Polypora makes it clear that Polypora marginata is distinct although only one colony fragment of this species is known. More detailed analysis of it's morphology is not possible at present.

Material

NMI.F.6071	Upper Limestone (Brigantian), Killymeal, Dungannon, Northern Ireland. The specimen was figured by McCoy 1844 (Pl. 29, fig. 5) and Miller, 1963 (Pl. 24, fig. 3).

Stratigraphical Range

Brigantian.

Polypora sp.nov. A

Pl. 91, figs. a-b; Pl. 92, fig. a.

Type

Specimen HM D.356 is designated as holotype for the new species.

Diagnosis

Polypora with a large very high angle conical zoarium. Branches are straight, very robust; obverse surfaces are flat with a regularly arranged single row of very large nodes between each row of apertures. Dissepiments are short, stout, flush with the crests of branches on the obverse surface, and typically biconcave. Fenestrules are of moderate size, long and narrow, oval to elliptical. Apertures are very large, circular without peristomes, and are very closely spaced, arranged in quincunx, in three longitudinal rows on branches.

Description

External

The zoarium is a large, very high angle cone-shaped expansion (about 10 cm in diameter), with a very tight close reticulate meshwork. Autozooecial apertures open onto the interior surface (the upper surface) of the cone.

Branches are very robust and straight. The obverse surface of branches is flat, with sharply rounded lateral margins. Between each row of autozooecial apertures, there is a single row of very large nodes. The nodes are regularly arranged, with one situated centrally relative to adjacent apertures in adjacent transverse rows. There are normally two rows of nodes along branches and, because these nodes are large, adjacent nodal bases may not be defined and an upraised wall may develop around apertures in the middle longitudinal row.

Prior to bifurcation, branch width may increase for up to four fenestrule lengths and may reach 0.87 mm.

Dissepiments are short and very stout, being only slightly thinner than branches. The obverse surface of dissepiments is usually flush with the crest of branches, but may occasionally be slightly depressed. Dissepiments are well rounded, smooth, and have a well developed biconcave appearance as they increase in width markedly towards dissepiment-branch junctions.

Fenestrules are of moderate size, quadrate, oval or elliptical. They are typically long and narrow, up to three times long as wide, their width being commonly equal to or less than the width of branches and they have well rounded extremeties and gently curved or straight lateral margins.

Autozooecial apertures are very large, circular or oval without peristomes, and are arranged in quincunx; normally arranged in three alternate longitudinal rows. They are very closely spaced, set between half and one diameter apart in the same longitudinal row, with apertures in the same transverse row being considerably closer spaced. The lateral rows of apertures are set close to branch margins but never indent fenestrules at all, and there are usually between three and four apertures per fenestrule. Prior to branch bifurcation a fourth apertural row may develop for up to two fenestrule lengths (and a third row of nodes may develop). After branch division, the number immediately decreases to two (with only one row of nodes developed), soon increasing up to three as branch width increases.

Dimensions (N = 1)

	NM	Mn	Mx	$\bar{X}$
BW	14	0.47	0.80	0.62
AD	14	0.16	0.21	0.18
ID	14	0.29	0.36	0.32
FL	14	0.97	1.40	1.20
FW	14	0.80	1.08	0.97
DW	14	0.23	0.40	0.32
IND	14	0.24	0.47	0.34

Micrometric Formula 9-10/8-10/15-16/15-18

Discussion

Study of all known species of Carboniferous Polypora makes it clear that Polypora sp. nov. A is a distinct species although only one colony fragment is known.

Polypora sp. nov. A is easily identified by the occurrence of regularly arranged closely spaced nodes between autozooecial apertures, short stout dissepiments, long and narrow fenestrules of moderate size and the occurrence of three longitudinal rows of large round apertures on branches.

Material

HMD.356	labelled Carboniferous, Corrie Burn, Ex Dairon Collection. J. S. Nicholson Collection.

Stratigraphical Range

Brigantian.

CHAPTER VI

Family Acanthocladiidae Zittel, 1880

Type genus

Acanthocladia King, 1849

Diagnosis

Fenestrata with dichotomous, pinnate or fenestrate zoaria, with central stems from which numerous lateral branches diverge. Lateral branches are free or may be connected by dissepiments. Autozooecia open onto one face only and may or may not occur on dissepiments.

Range

Silurian to Permian.

Genus Diploporaria Nickles and Bassler, 1900

Type species

Diploporaria marginalis (Young and Young, 1875a)

Emended Diagnosis

Acanthocladiid with delicate pinnate zoaria. Branches are slender, straight or gently flexuous with a serrated outline; bifurcations and lateral offsets irregular and very widely spaced; obverse surfaces have a well defined median carina with or without nodes; reverse surfaces are well rounded; all surfaces are finely pustulose. Autozooecial apertures are small, circular with complete peristomes, and are set low down on branch sides in two alternate rows commonly with prominent elevated margins projecting from branch sides.

Range

Carboniferous to Permian

TAXONOMIC PROCEDURE

External Morphological Characters

Zooecial Parameters

Branch Width (BW): Measured as in the Fenestellidae. The width of the primary branch and of lateral branches is recorded away from localised increase in branch width which accompanies the development of lateral branches. There is no significant distal tapering of branches, so minima, maxima and average values may be recorded.

The Number of Apertural Rows (AR): Recorded as in the Fenestellidae. The number of apertural rows is constant along branches, with two rows separated by a median carina or ridge.

Autozooecial Apertural Diameter (AD): Measured as in the Fenestellidae.

Interapertural Distance (ID): Measured as in the Fenestellidae.

Zoarial Parameters

Internodal Distance (IND): Measured as in the Fenestellidae.

The Micrometric Formula

Only two components are used in *Diploporaria*, these are the number of autozooecial apertures and carinal nodes in a single row in 5 mms, and are recorded in the same manner as described for the Fenestellidae.

Internal Morphological Characters

Zooecial Parameters

Zooecial chamber base dimensions: Measured as in the Fenestellidae, with both ZCL and ZCW measured.

Diploporaria marginalis (Young and Young, 1875a)

Figs. 55, 56, Pl. 93, figs. a-f, Pl. 94, figs. a-e, Pl. 95, figs. a-b, Pl. 96, figs. a-b.

1875a Glauconome (Diplopora) marginalis (sp.nov); Young and Young, p. 326, Pl. 3, figs. 14-21.

1881 Glauconome marginalis Young and Young; Vine, p. 333.

1885 Diplopora marginalis (Young and Young); Vine, p. 83

1900 Diploporia marginalis (Young and Young); Nickles and Bassler, p. 233.

1975 Diploporia marginalis (Young and Young); Graham, p. 9, Pl. 4, figs. 6, 6a, b.

Type

As Young and Young (1875a) did not erect a holotype from their type material, Graham (1975, p. 9) chose a Lectotype for the species but did not cite a particular specimen. Consequently a new Lectotype (HM cavity slide D.122, specimen number 14) is proposed.

Emended Diagnosis

Diploporaria with very delicate, pinnate zoaria having a main-stem with widely spaced irregularly distributed bifurcations and lateral branches. Branches are very slender, straight or gently curving and strongly serrated; obverse surfaces are quite well rounded with a relatively wide median carina with a uniserial row of nodes; reverse surfaces are well rounded with longitudinal parallel pustulose ridges. Autozooecial apertures are small, circular, with complete relatively thick peristomes, and are situated low down on branch margins with laterally prominent elevated margins projecting well out of branch sides and giving the branches a pronounced serrated appearance.

Description

External

Zoaria form small (up to 2 cm in length) delicate pinnate expansions with a single mainstem from which infrequent widely spaced lateral branches and branch bifurcations develop.

Branches are very slender, with a mainstem from 0.2 to 0.4 mm in diameter, lateral branches being slightly thinner. Branches have a pronounced serrated outline and are straight to distally gently curving. Occasionally there may be a slight distal torsion of the branches through a low acute angle in an anticlockwise direction.

Obverse surfaces have a relatively wide low straight median carina on which a uniserial row of small to moderate sized round to oval nodes occur. Internodal distances vary significantly between zoaria and nodes may be fairly close or widely spaced, with between 8 to 22 recorded in a 5 mm line.

A narrow ridge occurs very close and parallel to each side of the carina, these ridges may be straight to slightly sinuous moving away from the carina where autozooecial apertures project from the outer margins of branches. On very delicate branches the ridges may be broken by the inner peristomal rims of autozooecial apertures. Obverse surfaces are quite well rounded, and branch sides are steeply inclined away from the carina. Reverse surfaces are well rounded with a series of quite coarsely pustulose longitudinal ridges separated by narrower troughs. All surfaces are finely pustulose.

Autozooecial apertures are small, circular and usually have complete relatively thick upraised peristomes and are situated marginally, low down on branch sides, relatively widely spaced, about one and a half diameters apart. Apertures have elevated outward projecting margins which are also laterally prominent projecting beyond branch margins and giving branches a very pronounced serrated outline. Apertures on opposite branch sides may face in the same direction or face away from each other at a low acute angle.

Internal

In deep tangential section autozooecial chamber bases have a rounded triangular to trapezoidal shape, and alternate in one interlocking row. In shallow tangential section they develop a characteristic reniform shape, with the vestibular region projecting out beyond branch margins at oblique angles. A very short thin plate-like superior hemiseptum is situated at the base of the vestibular region.

The zooecial skeleton lining chambers is extremely thin and very finely laminated. The primary granular layer is very thin and the junction with the outer secondary laminated skeletal layer is well defined. Skeletal ridges of the primary granular layer radiate out from this zone towards the zoarial surface. Individual ridges are very narrow, widely spaced, several diameters apart and are of variable length, but are usually short. There are between 14 and 16 skeletal ridges developed in a branch. The outer secondary laminated skeleton is thick and laminae bend around the skeletal ridges and maintain a broad oral flexure beyond the apices of the ridges out towards the zoarial surface. Near the zoarial surface, closely spaced, narrow, short and orally convex well rounded cones of laminae develop. Laminae are deflected orally for very short distances only and the cones form small pustules on the zoarial surface.

Dimensions (N = 36)

	NM	Mn	Mx	$\bar{X}$
BW	95	0.17	0.35	0.22
AD	183	0.05	0.07	0.06
ID	350	0.25	0.28	0.26
IND	143	0.24	0.64	0.47

Micrometric Formula 19-21/8-22

Discussion

Diploporaria marginalis (Young and Young) is a very distinct species recognised by its very small simple pinnate zoaria, very slender branches, and small widely spaced autozooecial apertures that project out beyond branch margins giving branches a serrated outline.

Young and Young in their original description of Glauconome (Diplopora) marginalis subgen.sp.nov.1875a described a secondary small orifice situated closely proximal to each autozooecial aperture, on the presence of which they erected a new subgeneric name Diplopora.

Young and Young stated that the narrow septum separating the two orifices is easily broken producing large pyriform apertures. In the present examination of Young and Young's type material, no such secondary orifices have been observed. Young and Young may have examined some weathered zoarial surfaces, which revealed the thin superior hemiseptum situated in the upper roof of the zooecial chamber at the base of the vestibular region. The secondary orifice is in fact the portion of the zooecial chamber weathered out proximal to the hemiseptum.

Ulrich (1890, p. 351) also realised Young and Young's misinterpretations, and he considered that the result of attrition combined with a paucity of calcareous secretion by the zooids explains the development of a secondary pore. The thin septum which Young and Young said separated the two orifices Ulrich also stated was nothing more than the superior hemiseptum.

Ulrich (1890, p. 637, Pl. 62, figs. 11-11c) described the form Diplopora biserialis from the Lower Coal Measures of Seville, Illinois which he regarded as closely allied to D. marginalis. Branches are more robust in D. biserialis but with the same serrated outline. Reverse surfaces are striated. The median carina carries no nodes and has no defined ridges on each side unlike D. marginalis. Autozooecial apertures on D. biserialis are subcircular opening obliquely outwards with elevated peristomes, and are a lot larger than those of D. marginalis averaging 0.1 mm in diameter. There are about 20 autozooecial apertures in a 5 mm line for both species. It is difficult to establish a definite relationship between the two species without access to material of both but D. marginalis and D. biserialis appear not to be closely related.

Graham (1975, p. 9, Pl. 4, figs. 6, 6a, 6b) in his revision of Scottish acanthocladiid Bryozoa redescribed D. marginalis. However, he stated that the average branch diameter of the type specimens was 0.4 mm, but present measurements on all the available type material produced a range of values between 0.2 mm and 0.4 mm. No other statistically useful measurements or meristic data is provided in Graham's redescription.

Material

ABMG 11	Hardraw shales, Mill Gill, Askrigg, (Brigantian).
BMNH PD1063-74	Cavity slide with 11 zoarial fragments. Hairmyres, (Brigantian), East Kilbride. G.R. Vine Collection.
BMNH D.50	Carboniferous shales, Belston Burn, Lanarkshire. (Brigantian?) G.R. Vine Collection.
BOM 25-09-202	Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.
GAGM 01-53 vt	Cavity slide with 26 zoarial fragments. (Syntypes) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride. F.K. McKinney prepared 6 thin sections and 3 acetate peels from specimens on the card; labelled 01-53 vt specimens 1 to 6.
GAGM 01-53 vu	Cavity slide with 22 zoarial fragments. (Syntypes) Lower Limestone series (Brigantian), Boghead, near Hamilton. F.K. McKinney prepared 2 thin sections and 4 acetate peels from specimens on the card; labelled 01-53 vu specimens 1 and 2.
GAGM 01-53 vw	Cavity slide with 6 zoarial fragments. (Syntypes) Lower Limestone series (Brigantian), Boghead, near Hamilton.
HM D121	Cavity slide with 10 zoarial fragments. (Syntypes), Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.

HM D122	Cavity slide with 25 zoarial fragments. (Syntypes) Hosie Limestone, Lower Limestone Group, East Kilbride. One specimen was figured by Graham (1975, **Pl.** 4, figs. 6, 6a, 6b).
HM D61	Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.

Stratigraphical Range

Brigantian.

Occurrence

Diploporaria marginalis is common in the Brigantian strata of the Midland Valley of Scotland, uncommon in the North of England and has not been recorded outside these areas.

Genus *Penniretepora* D'Orbigny, 1849

Type species

Penniretepora pluma (Phillips, 1836)

Concept of the Genus

This is historically and morphologically confused, arising primarily from the superficial resemblance to *Glauconome*. Olaloye (1974) gives a detailed accurate account of the generic concept of *Penniretepora* D'Orbigny from its establishment to its presently accepted form. She erected a neotype for the genus, since Phillips (1836) original specimens have been lost, and constructed an emended diagnosis for the genus. This diagnosis, though accurate, lacks continuity and in the present revision, including a study of type material of British Carboniferous *Penniretepora* an emended diagnosis is proposed.

Emended Diagnosis

Acanthocladiid with pinnate or commonly bipinnate zoaria with a straight to sinuous mainstem from which two rows of regularly spaced lateral branches diverge at acute angles in the same plane. Obverse surfaces have a central median ridge or carina, with or without a uniserial row of nodes; lateral branches flanking the mainstem are normally slightly offset, most are relatively short without secondary diverging lateral branches, others which are widely spaced are much longer with their own closely spaced very short laterally diverging branches; lateral branches are not connected by dissepiments. Branch surfaces are granular or pustulose, reverse surfaces are commonly striated pustulose or occasionally nodose. Autozooecial apertures are arranged in two alternate rows on obverse surfaces and their positions are stabilised in a species. Zoarial and zooecial dimensions in branches of decreasing order are graded throughout colonies.

Branch status

The mainstem is the stoutest and longest branch with the largest parameters and is the branch from which all others diverge. Two rows of lateral branches diverge from the mainstem at regularly spaced intervals at acute angles in the same plane. They are normally paired, usually with one flank set slightly higher on a branch side than the opposite series. Lateral branches are not connected by dissepiments. Two types of lateral branches diverge from the mainstem.

2:1 primary branches are slightly thinner, and with slightly smaller parameters than the mainstem. They are usually widely spaced, relatively long and may be irregularly or regularly developed along the mainstem, and have laterally diverging branches flanking both sides along their length (e.g. Pl.108, fig. b).

1:2 minor branches are relatively short and are significantly thinner than the mainstem, with smaller measured parameters. They are close and regularly spaced along the mainstem with no diverging lateral branches of their own (e.g. Pl. 108, fig. b).

2:2 minor branches are the shortest, thinnest and are usually the most delicate in a colony with the smallest parameters and are the lateral offsets of 2:1 primary branches (e.g. Pl. 108, fig. b). Very rarely these branches may have extremely short, thin lateral branches of their own (e.g. Pl. 108, fig. b). 2:2 minor branches are not immediately developed along diverging 2:1 lateral branches due to adjacent closely spaced 1:2 lateral branches on both sides. 2:2 lateral branches only develop fully beyond the distal extremeties of adjacent 1:2 lateral branches. (If they were immediately developed along 1:2 lateral branches, branches would overlap each other and could result in some fusion of branches).

Colony form

The terms bipinnate and tripinnate are used here to describe the increasing complexity of zoarial form beyond simple pinnate expansions.

Pinnate zoaria are diagnosed as possessing only 1:2 minor lateral branches diverging from the mainstem (Fig57a). In bipinnate zoaria very widely spaced 2:1 primary branches are developed along the mainstem (Fig. 57b). Tripinnate zoaria are very rare, and are diagnosed as those in which some 2:2 minor lateral branches that diverge from the 2:1 primary branches have small lateral branches of their own (Fig. 57c).

TAXONOMIC PROCEDURE

In the present study, the taxonomic procedure outlined by Tavener-Smith (1973) for fenestrates, which was emended by Olaloye (1974) for the genus Penniretepora has largely been followed.

Because zoarial and zooecial parameters are graded in branches of decreasing order, in the taxonomic analysis of Penniretepora species the selected parameters should be measured on all orders of branches to allow the complete morphological limits of a species to be determined. However, colonies are normally found in a fragmented state with only part of the mainstem and the proximal areas of lateral branches preserved. As a result in the present study the complete range of parameters were measured on the mainstem only, with additional measurements of branch width made on 2:1 and 1:2 lateral branches. These are sufficient to allow the systematic analysis of a taxon, and discrimination between taxa (see Fig. 58).

External Morphological Characters

Zooecial Parameters

Branch Width (BW): The mainstem (MS) is measured transverse to its growth axis, away from the base of lateral branches where there may be localised increase in width accompanying the development of lateral branches. The mainstem tapers distally gradually and only minima and maxima are recorded.

The width of 2:1 and 1:2 lateral branches is recorded close to the junction of the mainstem where they are widest, but away from their points of origin. Only the maximum values are recorded as lateral branches taper distally.

Number of Apertural rows (AR): The number of apertural rows is constant, with two rows situated on all branches separated by a median carina or ridge.

Autozooecial Apertural Diameter (AD): Measured as in the Fenestellidae.

Interapertural Distance (ID): Measured as in the Fenestellidae.

Zoarial Parameters

Lateral Branch Spacing (LBS): Measured between the centres of adjacent lateral branches, close to their points or origin parallel to the growth axis of the mainstem.

Number of Apertures between adjacent Lateral Branches (ALB): In a taxon the number of autozooecial apertures between adjacent lateral branches is constant. For example, in Penniretepora flexicarinata (Young and Young) one aperture is situated on each mainstem-lateral branch junction and one midway between. In Penniretepora elegans (Young and Young) one aperture is situated on each mainstem-lateral branch junction and two between. This parameter is thus of great taxonomic value.

Internodal distance (IND): Measured as in the Fenestellidae.

Micrometric formula

The basic formula is emended for the purposes of identifying the meshwork variability in species of Penniretepora. As the mainstem is usually the largest colony fragment, the individual parameters of the formula will be made with reference to the mainstem. The following parameters are used:

LB10: The number or range in the number of lateral branches in one row diverging from the mainstem, parallel to the growth axis of the mainstem for a distance of 10 mm.

A5: The number or range in the number of autozooecial apertures in one row along the mainstem parallel to its growth axis for a distance of 5 mm.

N5: The number or range in the number of carinal nodes in one row along the mainstem parallel to its growth axis for a distance of 5 mm.

Internal Morphological Characters

Zooecial parameters

Zooecial chamber base dimensions: In the species of Penniretepora examined in the present study autozooecial chamber bases tend to be curved in contrast to Fenestella where chamber bases are flat. Consequently while it is possible to measure chamber base dimensions in Fenestella it is not possible in Penniretepora.

Penniretepora stellipora (Young and Young, 1874a)

Fig. 59 ,60 ; Pl. 97, figs. a-c.

1874a *Glauconome stellipora* (sp.nov.) Young and Young, p. 682, Pl. 40, figs. 5-8.

1875a *Glauconome (Acanthopora) stellipora* (sub. gen.nov.) Young and Young, p. 327-328, Pl. 4, figs. 25, 26.

1881 *Glauconome stellipora* Young and Young; Vine, p. 333, Pl. 16, fig. 1.

1975 non *Penniretepora pluma* (Phillips); Graham, p. 6.

1975 non *Penniretepora flexicarinata* (Young and Young,; Graham, p. 6.

Type

Young and Young (1874a) did not erect a holotype for the species, consequently a Lectotype (HM cavity slide D.128, specimen number 17), is proposed here from their syntypic material.

Emended Diagnosis

Penniretepora with small delicate, pinnate, rarely bipinnate zoaria. The mainstem is thin, straight with very thin coplanar widely spaced lateral branches, diverging at high angles with opposite flanks slightly offset. On obverse surfaces there is a low straight to gently sinuous relatively narrow median carina from which branch sides slope steeply away; reverse surfaces are flat and finely pustulose. Autozooecial apertures are small, circular with incomplete thick upraised peristomes each with a narrow proximal rimule and are quite closely spaced, one set above each lateral branch junction and one midway between on the mainstem and primary lateral branches.

Description

External

Zoaria form small delicate pinnate rarely bipinnate expansions with all branches straight and coplanar. The mainstem is very thin, straight with a sub-triangular cross-section. Lateral branches are widely spaced, just over two diameters apart, and diverge at high angles between 60° and 80°.

Lateral branches of opposing flanks are paired, but one flank is set slightly higher (½ to 1 branch diameter) on a branch than the opposite series. Diverging branch bases are well defined with only minor flaring of the parent branch prior to divergence of a lateral branch. 2:1 primary branches are widely spaced, and are distinguished from the mainstem by their slightly smaller parameters and more rounded cross-sections. 1:2 minor lateral branches are thin, short with well rounded cross-sections. 2:2 minor branches are very short, thin, and are quite widely spaced, slightly less than two diameters apart.

On the obverse surface of branches there is a low, relatively narrow median carina, which may be straight or gently sinuous. On thinner branches the carina may be very sinuous due to the closeness of the two alternating rows of autozooecial apertures. The carina may be finely granular or pustulose, when very narrow and sinuous the carina may be ornamented by a single row of closely spaced pustules. Branch sides slope steeply away from the carina. Reverse surfaces are flat with sharply rounded lateral margins and are covered with closely spaced quite fine pustules, while obverse surfaces may be granular or finely pustulose.

Autozooecial apertures are small, circular with thick, incomplete upraised peristomes and the proximal border of each peristome is completely dissected by a narrow rimule. The inner rims of peristomes are denticulated giving apertures a stellate appearance, and eight small spines may protrude well into the aperture from around the inner rim of the peristome. The peristomal rims may be ornamented by a row of pustules, which when large enough give apertures a petalloid appearance.

Autozooecial apertures are quite closely spaced on the mainstem from one to one and a half total diameters apart, slightly closer spaced on 2:1 lateral branches, their positions are stabilised with one situated on each diverging lateral branch junction and one midway between. These latter ones are situated close to branch margins, with upraised outer peristomes and may project slightly beyond branch margins. The upraised outer peristomes may result in both alternate rows of autozooecial apertures facing the same direction away from the obverse branch surface. This is also the case for the more closely spaced autozooecial apertures on minor lateral branches. Ovicells occur (see pp. 127-128).

Dimensions (N = 29)

	NM	Mn	Mx	$\bar{X}$
MS;BW	58	0.24	0.27	-
2:1;BW	8	0.21	0.27	-
1:2;BW	181	0.15	0.20	0.17
AD	290	0.05	0.06	0.06
ID	280	0.25	0.30	0.27
LBS	182	0.49	0.65	0.54

Micrometric Formula: 19-21/29-21/-

Discussion

Penniretepora stellipora (Young and Young, 1874a) is the most delicate species of British Carboniferous Penniretepora. It is characterised by its small, usually pinnate zoaria, very slender mainstem, narrow straight, smooth and rounded median carina, and the presence of a rimule dissecting the peristomes of each autozooecial aperture at their proximal extremeties.

Young and Young (1875a, p. 327) suggested as a new subgeneric name 'Acanthopora' for their Glauconome stellipora, based on the species highly denticulate autozooecial apertures. The name was soon abandoned as other species exhibited denticulate autozooecial apertures though often less well developed. Young and Young (ibid.) also described the presence of a second small orifice situated very close to the proximal extremity of the primary orifice separated from it by a very narrow wall. However, no secondary orifice has been observed in the type material examined, it is possible Young and Young were trying to describe the rimule which sometimes is not very well defined, and may be partly overgrown, or more pronounced due to weathering.

Graham (1975, pp. 6-7) incorrectly identified P. stellipora as well as Penniretepora flexicarinata to be conspecific with Penniretepora pluma, McCoy. However, the present revision has shown that all three species have statistically significant different measured parameters and morphological features and should be maintained as separate species.

Material

ABHR A1	Cavity slide with seven zoarial fragments. Shale above the Main Limestone, (Arnsbergian) Hurst, N. Yorkshire.
BMNH D50	Carboniferous shales, Belston Burn (Brigantian?) Lanarkshire, G.R. Vine Collection.
BMNH PD1206-12	Cavity slide with seven zoarial fragments, three of which are referable to P. stellipora. Hairmyres, (Brigantian?), G.R. Vine Collection.
GAGM 01-53 vq	Cavity slide with 19 zoarial fragments. (Syntypes) Lower Limestone Group (Brigantian), Capelrig, East Kilbride. F.K. McKinney prepared one thin section and one acetate peel from specimens on the slide.
GAGM 01-53 vr	Cavity slide with 35 zoarial fragments, of which only 4 are P. stellipora. (Syntypes). Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride.
GAGM 01-53 vs	Cavity slide with 19 zoarial fragments (Syntypes). Upper Limestone Group (E2 Arnsbergian), Gare near Carluke. One specimen was figured by Young and Young (1874a, Pl. 40, fig. 6). F.K McKinney prepared one thin section and one acetate peel from specimens on the card. One specimen from the card is on a stub.

HM D128 Cavity slide with 23 zoarial fragments, of which only 7 are *P. stellipora* (Syntypes). Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.

Stratigraphical Range

Brigantian-Arnsbergian.

Occurrence

P. stellipora is common in Brigantian to Arnsbergian strata in the Lower Carboniferous of the Midland Valley of Scotland, but elsewhere has been recorded only in Arnsbergian strata in the North of England.

Penniretepora spinosa (Young and Young 1874a)

Fig. 61 ; Pl. 98, figs. a-h, Pl. 99, figs. a-d.

1874a Glauconome stellipora var spinosa sp. nov. Young and Young, p. 682, Pl. 40, figs. 9, 10.

1875a Glauconome (Acanthopora) stellipora var spinosa (sub.gen.nov.) Young and Young, p. 328.

1881 Glauconome stellipora var spinosa Young and Young; Vine, p. 334, Pl. 16, fig. 2.

1885 Acanthopora stellipora var spinosa (Young and Young); Vine, p. 84.

1975 non Penniretepora recticarinata? (Young); Graham, 1975; p. 5, Pl. 2, figs. 3, 4.

Type

As Young and Young (1874a) did not erect a holotype for the species a lectotype (HM. cavity slide D.128, specimen number 7) is proposed here from their syntypic material.

Emended Diagnosis

Penniretepora with small, delicate pinnate rarely bipinnate zoaria. Branches are straight and coplanar. The mainstem is very slender and has widely spaced, very thin lateral branches diverging at high angles, with opposing series slightly offset. Branches have a subrounded cross-section; on obverse surfaces there is a low, relatively narrow median carina with a uniserial row of closely spaced nodes; branches slope steeply away from the carina; reverse surfaces are quite well rounded with widely spaced coarse pustules arranged in parallel longitudinal rows. Autozooecial apertures are small, circular, with complete relatively thick upraised peristomes, whose inner rims are normally highly denticulated; apertures are widely spaced, one set on each lateral branch junction and one midway between on the mainstem and primary lateral branches. Ovicells occur.

Description

External

Zoaria are delicate, small pinnate rarely bipinnate expansions with all branches straight and coplanar. The mainstem is thin, with a subrounded cross-section. Lateral branches diverge at regularly spaced intervals from the mainstem at high angles between 60° and 80° and are widely spaced, set between two and three diameters apart. Lateral branches are arranged in opposing pairs, with one flank set slightly higher (½ to 1 branch diameter) than the opposite series.

Diverging branches have well defined bases with no defined flaring of the parent branch prior to divergence. 2:1 primary branches are slightly thinner than the mainstem, and have well rounded cross-sections, and slightly smaller parameters. 1:2 branches are thin, relatively short with a well rounded cross-section. 2:2 minor branches are very thin, short and are quite widely spaced about two diameters apart.

On obverse surfaces of branches there is a well defined low, relatively narrow median carina, which may be straight or slightly sinuous. A single row of quite small, very closely spaced round nodes occurs on the carina. The nodes are fairly regularly spaced, one normally situated on the inside of each autozooecial aperture. A very narrow pustulose ridge closely flanks each side of the carina. The ridges may be straight to slightly sinuous, parallel to the carina, and are often broken by the peristomal rims of apertures.

Branch sides slope steeply away from the carina. Reverse surfaces are quite well rounded. Obverse surfaces are finely granular, while reverse surfaces are covered by quite widely spaced, coarse rounded pustules arranged in single, widely spaced, normally well defined parallel longitudinal rows.

Autozooecial apertures are small, circular, with relatively thick upraised complete peristomes. The inner rims of peristomes are highly denticulated with eight small spines protruding well into the aperture from the inner rim giving apertures a stellate appearance. Apertures are fairly widely spaced on the mainstem, set about two total diameters apart, and are slightly closer spaced on 2:1 lateral branches. Their positions are stabilised with one situated on each lateral branch junction and one midway between. These latter ones are situated close to branch margins, with upraised outer margins which extend outwards from branch surfaces and may project beyond branch margins slightly. This results in both alternate rows of autozooecial apertures facing the same direction away from the obverse surface of branches. This is also true for the more closely spaced autozooecial apertures on minor lateral branches, but as these branches are much thinner the apertures project beyond branch margins alot more.

Internal

In deep tangential section the autozooecial chamber bases have a well rounded trapezoidal shape,alternating in one row. The zooecial skeleton lining autozooecial chambers is extremely thin and finely laminated. The primary granular skeleton is thin, and the junctions between it and the inner zooecial and outer secondary laminated layers are well defined. Widely spaced, very narrow skeletal ridges radiate from the primary granular layer. These ridges are long, extending through most of the outer secondary laminated zone. The outer secondary laminated skeleton is relatively thick and laminae are continuous and bend around the apices of the skeletal ridges. Near the zoarial surface, short narrow, orally convex nests of skeletal laminae are developed and form the pustules most prominent on the reverse surface of branches.

Dimensions (N = 32)

	NM	Mn	Mx	$\bar{X}$
MS;BW	64	0.25	0.33	-
2:1;BW	4	0.26	0.30	-
1:2;BW	201	0.16	0.20	0.18
AD	320	0.05	0.06	0.06
ID	313	0.28	0.33	0.31
LBS	245	0.58	0.66	0.62
IND	346	0.15	0.17	0.16

Micrometric formula: 17-19/17-18/33-38.

Discussion

Glauconome stellipora was established by Young and Young in 1874a to describe a very delicate small distinctive species. In the same paper a variety Glauconome stellipora var spinosa was established on the presence of closely spaced nodes on the median carina, the species s.s. lacking any evidence of such nodes. Although the variety showed other slight zoarial and zooecial modifications which the authors outlined, they considered these to be insufficient to distinguish two species on the material examined.

In the present revision of type species of British Carboniferous Penniretepora, it has proved possible to distinguish P. stellipora (Young and Young) and Penniretepora stellipora var spinosa (Young and Young) as two distinct species.

On obverse surfaces P. stellipora has no nodes on the median carina while P. stellipora var spinosa always has regularly closely spaced carinal nodes. In the specimens examined the number ranged from 33 to 38 over a 5 mm unit distance. P. stellipora var spinosa has a well defined narrow pustulose ridge set close and parallel to the median carina on both sides, these are absent or extremely poorly defined in P. stellipora s.s. In cross-section, branches in P. stellipora are subtriangular, reverse surfaces are relatively flat and covered with fine rounded pustules, whereas in P. stellipora var spinosa branches are more rounded, reverse surfaces are quite well rounded with widely spaced coarse round pustules in parallel widely spaced normally well defined uniserial rows.

In P. stellipora peristomes are dissected by a narrow proximal rimule, but are always complete in P. stellipora var spinosa.

Significant differences are obtained on statistical data for the two forms. P. stellipora var spinosa has consistently slightly lower meristic counts for the number of autozooecial apertures in 5 mm. Measured interapertural distances are significantly higher in P. stellipora var spinosa.

Consequently it is proposed to raise the varietal name to species level. The name P. stellipora is retained for the other distinct species.

Graham (1975, p. 5) incorrectly states that P. stellipora var spinosa is conspecific with Penniretepora recticarinata (Young and Young, 1880). In fact, they are two different species, with significantly different measured parameters and general morphological features. *P. recticarinata* is a much more robust species with much larger measured parameters.

Material

ABHR A4	Cavity slide with five zoarial fragments. Shales above the Main Limestone (Arnsbergian) Hurst, N. Yorkshire.
BMNH PD1206-12	Cavity slide with seven zoarial fragments, four of which are referable to *P. spinosa*, Hairmyres (Brigantian?). G.R. Vine Collection.
GAGM 01-53 vr	Cavity slide with 35 zoarial fragments, of which 31 are *P. spinosa* (syntypes). Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride. Two specimens were figured by Graham (1975, Pl. 2, figs. 3, 4). F.K. McKinney prepared two thin sections and five acetate peels from specimens on the slide. These are labelled 01-53 vr specimen 1 and 2. Another specimen from the slide is fixed onto a stub.
HM D128	Cavity slide with 23 zoarial fragments of which 14 are *P. spinosa*. (Syntypes). Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.

Stratigraphical Range

Brigantian - Arnsbergian.

Occurrence

As for *P. stellipora*.

Penniretepora sp. nov. A

Fig.62 , Pl. 100, figs. a-b.

Type

Specimen HM D62/1 is designated as holotype for the species, and HM D62/2 is a paratype.

Diagnosis

Penniretepora with slender pinnate zoaria. The mainstem is straight or gently flexuous, from which moderately spaced, coplanar, thin lateral branches diverge at high angles, with opposite flanks slightly offset. On the mainstem obverse surfaces are well rounded, with feint gently sinuous longitudinal ridges, while on lateral branches a quite well defined median ridge may be developed. Reverse surfaces are well rounded with closely spaced longitudinal rows of pustules on. Autozooecial apertures are quite small, circular with relatively thick complete peristomes, and are widely spaced, set close to branch margins with one above each lateral branch junction and one midway between on the mainstem.

Description

External

Zoaria form slender pinnate expansions. The mainstem is slender, straight or gently flexuous with a sub-rounded cross-section. Lateral branches are moderately spaced, set about two diameters apart and diverge at high angles between 60° and 70° from the mainstem. They are paired on opposite sides but are normally offset slightly (usually by about one branch diameter) with one flank set slightly higher than the other. Lateral branch bases are quite well defined, with only minor flaring of the mainstem accompanying their development. 1:2 minor lateral branches are straight or gently sinuous, narrow and may attain lengths of at least 1.5 mm. The obverse surface of the mainstem is well rounded with feint, very narrow gently sinuous longitudinal ridges along their length, while on lateral branches a quite well defined median ridge may be developed.

Autozooecial apertures are quite small, circular with relatively thick raised complete peristomes. On the mainstem apertural positions are stabilised with one set above each lateral branch junction and one midway between. The latter are set close to branch margins, and their raised outer rims may indent branch margins slightly. On the mainstem apertures are widely spaced nearly two diameters apart, while on 1:2 minor lateral branches they are slightly closer together (about one to one and a half diameters apart), and may indent branch margins slightly.

Internal

Zooecial chamber bases on 1:2 lateral branches are rounded triangular to trapezoidal, and alternate in one interlocking row.

Dimensions (N = 2)

	NM	Mn	Mx	$\bar{X}$
MS;BW	2	0.34	0.35	-
1:2;BW	18	0.20	0.21	0.20
AD	14	0.08	0.09	0.09
ID	12	0.33	0.42	0.38
LBS	28	0.58	0.82	0.74

Micrometric Formula 14/14/-

Discussion

Penniretepora sp.nov. A is statistically and morphologically distinct from all known British Lower Carboniferous species of Penniretepora. Comparison with other described species of Penniretepora from abroad also supports this.

P. sp.nov. A is characterised by the well rounded, smooth obverse surface of the mainstem, and widely spaced, small circular autozooecial apertures set low down on branches, with thick complete peristomes.

Material

HM D62, 1-2.	Shale above the second Kingshaw Limestone. (Arnsbergian), Carluke.

Stratigraphical Range

Arnsbergian.

Penniretepora sp.nov. B

Fig.63 , Pl. 101, figs.a-d.

Type

Specimen ABHR/A5-1 is designated as holotype for the species, and specimens ABHR/A5-2 to 5 are paratypes.

Diagnosis

Penniretepora with small pinnate zoaria. The mainstem is slender, straight with quite closely spaced lateral branches, diverging at high angles, one flank set slightly higher on a branch than the opposite series. Obverse surfaces have a well defined, straight median carina of moderate width, on which a single row of quite widely spaced nodes is situated; branch surfaces are flat away from the carina; reverse surfaces are quite flat; all surfaces are finely pustulose. Autozooecial apertures are small, circular to oval, with incomplete collar to lunaria-like peristomes, and are widely spaced on the mainstem with one on each lateral branch junction and one midway between. Ovicells occur.

Description

External

Zoaria are small pinnate expansions. The mainstem is slender, straight, and has an oval cross-section. Lateral branches diverge from the mainstem at high angles between 55° and 70° and are quite closely spaced, set slightly less than two diameters apart. Lateral branches of opposite flanks are paired, but are slightly offset (½ to 1 branch widths distance) on opposite sides. Lateral branch bases are well defined with only slight flaring of the mainstem accompanying their development. 1:2 minor lateral branches are thin, straight or gently flexed and are quite long.

On obverse surfaces of branches there is a low very well defined median carina of moderate width, which is usually straight with vertical sides and a flat top on which a single row of quite widely spaced small oval nodes occur. Away from the carina branch surfaces are flat or inclined at a very low angle. Reverse surfaces are flat to poorly rounded, and are covered by wide parallel low longitudinal rows separated by narrow troughs. All surfaces are finely pustulose.

Autozooecial apertures are small, circular to oval, with very prominent incomplete peristomes, developed as upraised high collars, even helmet-like around lateral and distal margins of apertures, and may partially occlude apertures. Apertures are widely spaced, between two and two and a half diameters apart and are set quite close to branch margins. On the mainstem apertural positions are stabilised, with one situated on each lateral branch junction and one midway between. In these later ones, the outer rims of apertures protrude beyond branch margins slightly giving branch margins a gentle undulatory appearance. Ovicells occur (see pp. 127-128).

Dimensions (N = 3)

	NM	Mn	Mx	$\bar{X}$
MS;BW	10	0.31	0.36	-
2:1;BW	1	0.32	-	-
1:2;BW	10	0.25	0.27	-
AD	21	0.07	0.09	0.08
ID	18	0.36	0.40	0.38
LBS	11	0.71	0.80	0.77
IND	10	0.60	0.78	0.69

Micrometric Formula: 13-14/13/7-8

Discussion

Penniretepora sp.nov. B is statistically and morphologically different from all other known British and other Lower Carboniferous species of *Penniretepora*. It is characterised by the presence of a well defined low flat median carina with a single row of widely spaced nodes, and small widely spaced autozooecial apertures with incomplete collar to lunaria-like peristomes.

Material

ABHR A5	Cavity slide with five zoarial fragments. Shales above the Main Limestone, (Arnsbergian) Hurst, N. Yorkshire.

Stratigraphical Range

Arnsbergian.

Penniretepora flexicarinata (Young and Young, 1875a)

Figs. 64 , 65 , 66 , 67 ; Pl. 102, figs. a-d; Pl. 103, figs. a-d.

1875a	Glauconome flexicarinata (sp.nov.) Young and Young, p. 239, Pl. 2, figs. 1-7.
1880	Glauconome recticarinata (sp. nov.) Young, p. 257.
1885	Pinnatopora recticarinata (Young); Vine, p. 79.
1974	non Penniretepora c.f. flexicarinata (Young and Young); Olaloye, p. 496, Pl. 19, figs. 1-9.

Type

A Lectotype (HM cavity slide D121 specimen number 8) is proposed from Young and Young's syntypic material, because the authors did not establish a holotype for the taxon.

Emended Diagnosis

Penniretepora with medium sized bipinnate zoaria. Branches are straight and coplanar. Lateral branches are quite closely spaced diverging at high angles, with opposite series slightly offset. On obverse surfaces there is a relatively wide tripartite median carina composed of three pustulose gently sinuous and closely spaced ridges, the middle one is more prominent than those flanking it, and may carry a uniserial row of widely spaced large round nodes; reverse surfaces are flat and covered by closely spaced narrow parallel pustulose ridges. Autozooecial apertures are relatively large, oval, with thick low pustulose peristomes, and are closely spaced, one being situated on each dissepiment branch junction and one midway between on the mainstem and primary lateral branches. Secondary nanozooids occur.

Description

External

Zoaria are medium sized, bipinnate expansions with straight and coplanar branches. The mainstem is of variable width, slender to robust and with a well rounded to oval cross-section. Lateral branches are quite closely spaced, one to one and a half diameters apart and diverge at high angles between 55° and 70° from the mainstem with some minor flaring of the mainstem accompanying their development.

Lateral branches are paired, not directly opposed, but are displaced (½ to 1 branch widths distance apart) on opposite sides of branches. 2:1 lateral branches are widely spaced and slightly thinner than the mainstem. 1:2 and 2:2 minor lateral branches are quite short, thin with more rounded cross-sections.

On obverse surfaces there is a relatively wide tripartite median carina, composed of three pustulose ridges. The median portion is wider and most prominent and forms the main part of the carina and is usually gently sinuous. Narrower ridges on either side comprise the lateral components of the carina and inpart form the inner peristomal lips of apertures. An additional ridge may run along branch margins on both sides and may in-part form the outer peristomal lips of apertures. All ridges are pustulose, the lateral ones may not be defined as ridges, but a uniserial row of pustules is still normally present. On narrower branches the carina is straighter. A uniserial row of relatively widely spaced large rounded nodes may be present or absent on the median ridge of the carina.

Obverse surfaces are gently inclined away from the carina. Reverse surfaces are flat and are covered by closely spaced narrow, parallel longitudinal pustulose ridges.

Autozooecial apertures are fairly large, round, oval to pyriform and are quite closely spaced from less than one to one and a half diameters apart, alternating on both sides of the wide median carina. On the mainstem and primary lateral branches apertural positions are stabilised with one aperture set on each diverging lateral branch junction and one midway between, these later ones may project slightly beyond branch margins giving branches a feint undulatory outline. The two alternate rows are inclined at a low angle away from each other. Apertures have relatively wide pustulose peristomes, when the pustules are well developed they give peristomes a beaded appearance. The outer peristomal rim may be considerably raised.

On minor lateral branches autozooecial apertures are smaller, more rounded and closer spaced. Secondary nanozooids occur.

Dimensions (N = 38)

	NM	Mn	Mx	$\overline{X}$
MS;BW	76	0.32	0.53	-
2:1;BW	10	0.24	0.46	-
1:2;BW	283	0.18	0.28	0.25
AD	325	0.10	0.15	0.13
ID	410	0.35	0.49	0.41
LBS	312	0.68	0.91	0.81
IND	184	0.30	0.77	0.55

Micrometric Formula: 10-13/10-13/0-16

Discussion

Penniretepora flexicarinata (Young and Young, 1875a)is very distinct and is characterised by its gently sinuous tripartite pustulose median carina, flat reverse surfaces covered by narrow parallel longitudinal pustulose ridges, and quite large oval autozooecial apertures with thick pustulose peristomes with one situated on each lateral branch junction and one midway between on the mainstem and primary lateral branches.

Young and Young (1880, pp. 257-259) erected the species Glauconome recticarinata, and in their discussion stated that it may be a variety of G. flexicarinata Young and Young (1875a)but separated the two species on the distinctive strong, straight median carina characteristic of the former.

In the present study, type material of both species has been examined and it is obvious that the two forms are conspecific. Both species have very similar overall zoarial and zooecial morphologies, with similar branch diameters, lateral branch spacing, apertural diameters and interapertural spacing. The only apparent difference between the two forms outlined by Young and Young (1880, p. 258), that of the distinctive median carina of G. recticarinata is not a sufficient distinguishing character to separate the two species, and there is considerable overlap in the morphology of the median carinas of both species.

Examination of the type material labelled as G. recticarinata shows that the central ridge of the tripartite carina is usually well defined, narrow, quite straight and often composed of a single row of very closely spaced small to large rounded pustules which may abut against each other. Occasionally, a uniserial row of quite widely spaced nodes may occur on the central ridge. In the type material of G. flexicarinata the central ridge of the tripartite carina is of variable form, and may or may not carry a single row of very closely spaced small pustules, and occasionally may be fairly straight. It is thus concluded, on the basis of the overall zoarial and zooecial morphologies, and on the similar and overlapping measured parameters between the type materials of G. flexicarinata and G. recticarinata that they are conspecific. The name Penniretepora flexicarinata (Young and Young) takes priority as it was erected earlier.

Penniretepora bellula Ulrich (1890, p. 619, Pl. 66, figs. 8-8b) is closely allied with P. flexicarinata. Both have tripartite median carinae, though it is not so well defined in P. bellula, and carry a single row of widely spaced nodes. The number of autozooecial apertures on P. bellula averages 12 in a 5 mm line, and between 11 and 13 in P. flexicarinata. The number of lateral branches is very similar on both species, Ulrich recorded 5 in a 5 mm line while there are between 10 to 12 in a 10 mm line on P. flexicarinata. Autozooecial apertures are slightly smaller in P. bellula, about 0.1 mm in diameter, with well developed peristomes. Interapertural distances from Ulrich's illustrations appear to be very similar. Both have longitudinal rows of closely spaced pustules on their reverse surfaces, the reverse surface of P. bellula is more rounded than P. flexicarinata.

Penniretepora ardmorensis Elias (1957, p. 423, Pl. 48, figs. 13-16) is also closely allied to P. flexicarinata. It is very difficult to compare descriptions, as Elias gave only one meristic count, even that was incorrectly written, i.e. the number of zooecial apertures ranging from 14 to 15 per 1 mm, the actual figure should read 14 to 15 in 5 mm. He described the species as having no carina but possessing a set of three parallel, serrate lines or striae, the midline being stronger than the other two, the lateral lines being gently undulatory, "these striae meanders gently and regularly between the two rows of apertures, which are disposed in alternate manner."

One aperture is situated on each lateral branch junction and one midway between. Zooecial chamber bases are triangular to trapezoidal. From the above description it is obvious that P. ardmorensis and P. flexicarinata are closely allied. Their exact relationship is difficult to ascertain without access to material of both species, and the comparison of standardised data is necessary.

P. c.f. flexicarinata (Olaloye, 1974, p. 496, Pl. 19, fig. 1-9) is closely related but is probably not conspecific with P. flexicarinata as Olaloye postulated. Many of Olaloye's observations are incorrect because she did not examine any type material of P. flexicarinata, but relied solely on Young and Young's original qualitative description and illustrations.

There are some basic morphological similarities, the presence of a tripartite median carina with its widely spaced nodes and very similar interapertural dimensions. However, there are several important differences. The spacing of lateral branches is significantly higher in Olaloye's material. There is a very large discrepancy in the size of autozooecial apertures; apertural diameters in Olaloye's material are almost twice the size of those measured on type material of P. flexicarinata, although interapertural distances are only slightly different.

Olaloye does point out certain discrepancies between the type material of P. flexicarinata from the Lower Carboniferous of Scotland and her material from Carrick Lough, Ireland. She recorded an average angle of divergence of lateral branches from the mainstem of 86° on her Carrick Lough material, correctly stating that Young and Young recorded a value of 40° on their type material. However, examination of this type material shows that the angle of divergence of lateral branches ranges between 50° and 75°.

Olaloye compared Young and Young's meristic counts over unit distances for the number of lateral branches and autozooecial apertures. Olaloye did not realise that Young and Young used the actual number method while she used the space count method, and her conclusions drawn up from a comparison of meristic counts of her and Young and Young's material are in error. As a result of lower values obtained on her material, through the use of the space count method, she concludes that zooecial chambers in Young and Young's type material are much smaller than in her material. However, a comparison of values of interapertural distance calculated on the type material, and of Olaloye's material shows that interapertural distances are only marginally different, indicating similar autozooecial chamber sizes.

Olaloye also points out that differences in zoarial size and apertural spacing between her material and the type material may be accounted for by the development of the later specimens in an unfavourable environment. However, although autozooecial apertures are much larger, and have very narrow interveining lateral walls in Olaloye's material, interapertural distances are very similar. Olaloye has reached an incorrect conclusion, because she did not examine any type material of P. flexicarinata. Furthermore equatable results on measured parameters have been obtained on specimens of P. flexicarinata from different localities at similar horizons to the type material precluding any idea that the type specimens had developed in an unfavourable environment. Although closely related, P. c.f. flexicarinata is not actually conspecific with P. flexicarinata. Graham (1975, p. 6) in an examination of type material of P. flexicarinata considered it and P. stellipora (Young and Young, 1874) to be conspecific with Penniretepora pluma (Phillips, 1836). He did not examine any specimens of Penniretepora pluma and only figured Phillips original illustrations (1836, Pl. 1, figs. 13-16). There are several important morphological differences between P. pluma and P. flexicarinata. P. pluma has rather more slender zoaria than P. flexicarinata. The median carina is straight and rib-like, with a single row of nodes, which are more closely spaced and regularly developed in P. pluma. The spacing of lateral branches is also shorter and there are always two autozooecial apertures between adjacent lateral branches instead of one as in P. flexicarinata. Apertures are very closely spaced in P. pluma, significantly closer than in P. flexicarinata, and apertures always have incomplete eccentric arcuate peristomes, thickest at their distal extremeties, thinning laterally. (For a detailed emended diagnosis and description of P. pluma see Olaloye, 1974, p. 486).

Graham's assignment of P. flexicarinata as a junior synonym of P. pluma is in error and lacks reference to detailed standardised measurement parameters or meristic counts over set distances, omitting also some morphological details.

P. stellipora is a very delicate species, with much smaller measured parameters and extremely different morphological features and is not conspecific with P. flexicarinata or P. pluma. The present work shows that Grahams conclusions cannot be substantiated and P. stellipora, P. flexicarinata and P. pluma are thus ranked as three distinct species.

Material

ABHR A3	Cavity slide with five zoarial fragments. Shales above the Main Limestone, (Arnsbergian), Hurst, N. Yorkshire.

ABHR 10, 29, -35, -38.	Shales above the Main Limestone, (Arnsbergian) Hurst, N. Yorkshire.
ABR 4, -12, -16	Redesdale Ironstone shale, Lower Limestone Group (Asbian), Ridsdale, Northumberland.
ABMG 1, -2	Hardraw shales, (Brigantian) Mill Gill, Askrigg, N. Yorkshire.
BMNH D50	Carboniferous Shales, Belston Burn (Brigantian?), Lanarkshire. G.R. Vine Collection.
BMNH D88	Carboniferous shales, Boghead (Brigantian?) Lanarkshire, Scotland.
BMNH D164	Lower Carboniferous Shale, Redesdale (Asbian?). G.R. Vine Collection.
BMNH D2381	Halkyn, (Brigantian), Clwyd, North Wales. G.R. Vine Collection.
BMNH B1777	Carboniferous Limestone, Halkyn, (Brigantian?). N. Wales.
GAGM 01-53 vb	Cavity slide with 14 zoarial fragments. (Syntypes of _G._ _recticarinata_ Y and Y 1880) Lower Limestone Group, (Brigantian), Capelrig, East Kilbride. One specimen was figured by Graham (1975, Pl. 1, fig. 5, 5a).
GAGM OL-53 vz	Cavity slide with 9 zoarial fragments. (Syntypes) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.
GAGM 01-53 vz*	Cavity slide with 9 zoarial fragments. (Syntypes) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.

HM D120	Cavity slide with 27 zoarial fragments (syntypes) Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride.
HM D121	Cavity slide with 16 zoarial fragments. (Syntypes) Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride. One specimen was figured by Graham (1975, Pl. 2, fig. 6).
HM D128	Cavity slide with 23 zoarial fragments, labelled as *G. stellipora*, one of which is *P. flexicarinata* (syntypes) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.
HM D455	Lower Limestone Group (Brigantian), Dykehead Pit, High Blantyre. Labelled as unfigured holotype. Graham (1975) designated this specimen as the Lectotype for *P. recticarinata* (Young and Young, 1880), and was figured by him (Pl. 1, figs. 6a, 6b).

Stratigraphical Range

Asbian - Arnsbergian

Occurrence

P. flexicarinata is a common species, and is widely distributed in Lower Carboniferous strata of Scotland, Northern England and North Wales.

Penniretepora pulcherrima (McCoy , 1844)

Figs. 68 , 69, 70, 71; Pl. 104, figs. a-b; Pl. 105, figs. a-c; Pl. 106, figs. a-e.

1844 Glauconome pulcherrima (sp.nov.) McCoy, p. 1-9, Pl. 29, fig. 4.

1875a Glauconome retroflexa (sp.nov.) Young and Young, p. 330-331, Pl. 2, figs. 8-10, pl. 3, figs. 11-13.

1881 Glauconome retroflexa Young and Young; Vine, p. 335.

1885 Pinnatopora retroflexa (Young and Young); Vine p. 80.

1938 Pinnatopora c.f. pulcherrima (McCoy); Demanet, p. 48, pl. 4, figs. 6, 7.

1975 Penniretepora pulcherrima (McCoy); Graham, p. 8, Pl. 3, figs. 1-4, 7.

Type

Only one specimen of P. pulcherrima (McCoy , 1844) is present in the Griffith collection of McCoy type Carboniferous fossils in the National Museum of Ireland, Dublin. This is McCoy's figured specimen (Pl. 28, fig. 4) which is a quite poorly preserved large zoarial fragment in a pale grey biomicritic matrix showing the reverse surface. This specimen (NMI F.6023) was designated by Graham (1975, p. 8) as Lectotype.

Emended Diagnosis

Penniretepora with medium sized, robust pinnate or bipinnate zoaria. The mainstem is robust, straight or slightly flexuous, with a subrounded cross-section. Lateral branches are closely spaced, retroflexed, paired, with one flank set slightly higher on a branch than the opposite series; minor laterals are extremely short. On obverse surfaces of the mainstem and primary lateral branches there is a wide, straight, upraised median carina, with a uniserial row of closely spaced nodes; reverse surfaces are well rounded, with one or more rows of closely spaced nodes; all surfaces are quite coarsely pustulose. Autozooecial apertures are large, acutely elliptical, closely spaced and abut the base of the carina, with their wide outer rims projecting slightly beyond branch margins; one aperture is situated on each diverging lateral branch junction and one midway between on the mainstem and primary laterals.

Description

External

Zoaria are medium sized, robust pinnate occasionally bipinnate expansions. The mainstem is straight or occasionally gently flexuous, robust, with a subrounded cross-section. Laterals branches diverge at closely spaced intervals along the mainstem at high angles between 60° and 80°. Diverging branch bases are well defined with only slight flaring accompanying their development. Lateral branches retroflex at an acute angle immediately away from the obverse surface of the mainstem. 1:2 and 2:2 minor lateral branches are relatively wide where they join the mainstem or primary lateral branch but rapidly decrease in width distally and are very short. Minor lateral branches have a subrounded cross-section. All lateral branches are paired, they are not directly opposed but are offset half to one branch diameter on opposite sides of a branch.

On obverse surfaces of the mainstem and 2:1 lateral branches there is a well defined, wide upraised straight median carina with occasional slightly sinuous lateral margins due to autozooecial apertures abutting its base. A single row of closely spaced small round nodes is situated on the median carina. On minor lateral branches the carina is absent and is replaced by a narrow sinuous subangular median ridge. Reverse surfaces are well rounded. All branch surfaces are covered by closely spaced relatively coarse pustules which, on the reverse surface, may be aligned in closely spaced parallel longitudinal rows. One or two, poor to well defined longitudinal rows of small round nodes occur on the crests of reverse surfaces.

On the mainstem autozooecial apertures are very large, acutely elliptical and are two to three times long as wide and without peristomes.

The inner lateral margins of autozooecial apertures abut the base of the median carina and are not as curved as their outer lateral margins. On the mainstem apertures are closely spaced, less than their own diameter apart, slightly closer and smaller on 2:1 primary lateral branches, and their positions are stabilised with one on each diverging lateral branch junction and one midway between. The two rows alternate on either side of the carina and face in the same direction or slightly away at a low angle from each other. The outer margins of apertures situated between lateral branch junctions are typically inflated and may project beyond branch margins slightly.

On 2:1, 1:2 and 2:2 lateral branches, immediately prior to branches being retroflexed, apertures are significantly smaller, circular and extremely closely spaced. On 2:1 lateral branches normal apertural shape and spacing resumes after branches have retroflexed. However, as 1:2 and 2:2 minor lateral branches are extremely short and decrease in width rapidly, apertural diameters decrease towards the branch extremeties, they are extremely closely spaced with very thin zooecial walls separating them and never develop normal apertural shape and spacing. Secondary nanozooids occur.

Internal

In deep tangential section autozooecial chamber bases have a rounded triangular shape and become oval to elliptical in shallow tangential section.

Dimensions (N = 43)

	NM	Mn	Mx	$\bar{X}$
MS;BW	86	0.34	0.49	-
2:1;BW	8	0.31	0.36	-
1:2;BW	384	0.22	0.34	-
AD	313	0.16	0.20	0.18
ID	418	0.35	0.42	0.39
LBS	341	0.71	0.84	0.77
IND	512	0.17	0.21	0.19

Micrometric Formula: 12-14/12-14/24-30

Discussion

Penniretepora pulcherrima (McCoy) is readily identified by its robust mainstem, retroflexed lateral branches, wide prominent median carina with a single row of very closely spaced nodes, and very large elliptical autozooecial apertures, one situated above each lateral branch junction and one midway between on the mainstem and primary lateral branches.

The form Glauconome retroflexa Young and Young (1875a,p. 330), from the lower Carboniferous of Scotland, is conspecific with Glauconome pulcherrima McCoy, but as McCoy's description is earlier, the name *P. pulcherrima* takes priority (see Graham, 1975, p. 8)

Olaloye (1974) did not realise that *P. pulcherrima* (McCoy) and *P. retroflexa* (Young and Young) are conspecific and incorrectly compared *P. pulcherrima* to *P. normalis* sp.nov. Olaloye (p.492 , Pl. 18, figs. 1-7) and *P. retroflexa* to *P. rotunda* sp. nov, Olaloye (p.502, Pl. 2 In her comparisons she outlined basic differences between the species but many of her observations are incorrect, because she did not examine any type material of *P. pulcherrima* or *P. retroflexa* but relied solely on the author's original descriptions and illustrations. The detailed examination of the type specimen of *P. pulcherrima* and type material of its junior synonym *P. retroflexa*, has allowed a comparison to be made with *P. normalis* and *P. rotunda*.

While agreeing with Olaloye that *P. pulcherrima* and *P. normalis* are distinct species, they are however possibly related. Both species have similar interapertural distances, lateral branch spacing and a relatively wide median carina on the mainstem. However, carinal nodes which are very closely spaced on *P. pulcherrima* are irregular and widely spaced in *P. normalis*. Autozooecial apertures are much smaller in *P. normalis*. Reverse branch surfaces are well rounded on *P. pulcherrima*, but are flat in the former. Both species have very short lateral branches, however they are usually coplanar in *P. normalis* and are larger and always retroflexed in *P. pulcherrima*.

Olaloye compared *P. retroflexa* (Young and Young) with *P. rotunda*. She states that the angle of divergence of lateral branches in *P. retroflexa* is about 40°, the figure Young and Young stated in their original description of the species (1875a,p. 331). However, examination of type material of *P. retroflexa* has shown that the actual angle of divergence of lateral branches ranges between 70° and 85°. Also autozooecial apertures do not have prominent peristomes on their outer margins, as Olaloye stated, but only the outer branch margins are inflated beyond apertures.

There are many significant differences between P. pulcherrima and P. rotunda. The latter has a poorly defined median carina, on which nodes are widely and irregularly spaced. Autozooecial apertures are circular, where-as in P. pulcherrima they are acutely elliptical and much larger. In P. rotunda the spacing of lateral branches is significantly greater than in P. pulcherrima. It is concluded that P. pulcherrima and P. rotunda are distinct species.

Material

ABHR A4	Cavity slide with 15 zoarial fragments. Shales above the Main Limestone, (Arnsbergian) Hurst, North Yorkshire.
ABMG 9	Hardraw shales, (Brigantian), Mill Gill, Askrigg, N. Yorkshire.
BMNH -	Yoredales, Little Urswich, near Ulverstone.
BMNH B208	Carboniferous Limestone, Fair, Carluke (Upper Limestone Group,(Arnsbergian). D.R. Rankine Collection.
BMNH D88	Carboniferous Shales, Boghead (Brigantian?) Lanarkshire, Scotland. G.R. Vine Collection.
BMNH D229	Yoredales, Little Urswick, (Brigantian?), N. Lancashire. G.R. Vine Collection.
BMNH PD 1145-9	Cavity slide with four zoarial fragments. Upper Limestone shales (Arnsbergian) Gair, Argyllshire.
GAGM 01-53 us	(Syntype of Glauconome retroflexa Young and Young 1875) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.

GAGM 01-53 ut	Cavity slide with 15 zoarial fragments. (Syntypes of *Glauconome retroflexa* Young and Young,1875a) Hosie Limestone, Lower Limestone Group, (Brigantian), Hairmyres, East Kilbride.
GAGM 01-53 uu	(Syntype of *Glauconome retroflexa* Young and Young 1875a)Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.
GAGM 01-53 vz	(Syntype of *Glauconome retroflexa* Young and Young,1875a) Hosie Limestone, Lower Limestone Group (Brigantian), Hiarmyres, East Kilbride.
HM D125	Cavity slide with 18 zoarial fragments. (Syntypes of *Glauconome retroflexa* Young and Young, 1875a) Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride. One of the specimens was figured by Graham (1975, Pl. 3, figs. 1, 1a).
HM D126	Cavity slide with 27 zoarial fragments. (Syntypes of *Glauconome retroflexa* Young and Young, 1875a) Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride.
HM D127	Cavity slide with 8 zoarial fragments. (Syntypes of *Glauconome retroflexa* Young and Young, 1875a) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.
NMI F.6023	Upper Limestone (Asbian), Blacklion, Enniskillen. This specimen was figured by McCoy (1844, Pl. 28, fig. 4); and Graham (1975, Pl. 3, fig. 2, pl. 4, fig. 2).

Stratigraphical Range

Asbian - Arnsbergian.

Occurrence

P. pulcherrima is a very common and widely distributed species, being most abundant in Brigantian strata of the Midland Valley of Scotland and the Yoredales of Northern England, and occurring also in the Visean Limestones of North Wales and Ireland.

P. pulcherrima has also been recorded from the Dinantian of Belgium.

Penniretepora robusta (Young and Young, 1878)

Pl. 107, figs. a-c.

1878 Glauconome robusta (n.sp) Young and Young, p. 354, Pl. 2,
figs. 4, 7, 8, 9, 10.

1885 Pinnatopora robusta (Young and Young); Vine p. 80.

1975 non Penniretepora pulcherrima (Young and Young) Graham, p. 8.

Type

As Young and Young (1880) did not erect a holotype for G. robusta a Lectotype (HM.D54,-2) is proposed here from their syntypic material.

Diagnosis

Penniretepora with large robust, pinnate zoaria. The mainstem is very robust, straight with closely spaced lateral branches diverging at high angles. Lateral branches are relatively short, thick and retroflexed, with one flank set slightly higher on a branch than the opposite series. On the obverse surface of the mainstem there is a wide prominent median carina with a single row of widely spaced nodes. Reverse surfaces are well rounded, with one or more rows of closely spaced nodes. All surfaces are coarsely pustulose. Autozooecial apertures are large, elliptical and closely spaced, one set on each lateral branch junction and one midway between.

Description

External

Zoaria form large robust pinnate expansions up to at least 20 mm in length. The mainstem is very stout, straight and has a subrounded cross-section. Lateral branches are closely spaced diverging from the mainstem at high angles between 70° and 80°, with branches on opposite flanks paired, but slightly offset by about a half branch width distance. Lateral branches are retroflexed at an acute angle away from the obverse surface of the mainstem and are relatively short. Lateral branch bases are quite poorly defined with slight to considerable flaring of the mainstem accompanying their development.

On the obverse surface of the mainstem there is a very wide upraised straight median carina with a well rounded crest and steeply inclined sides. A single row of widely spaced large rounded nodes is situated on the median carina. On lateral branches the carina is poorly defined and is replaced by a rounded straight median ridge on which nodes are slightly more closely spaced. Lateral branches are well rounded.

All surfaces are quite coarsely pustulose. Reverse surfaces are very well rounded, and the pustules may be aligned in closely spaced parallel longitudinal rows. One or two poor to quite well defined longitudinal rows of small rounded nodes occur on the crests of the reverse surfaces of branches.

Autozooecial apertures are very large, oval to acute ellipses, two to three times long as wide, and without peristomes. On the mainstem they are situated on the relatively flat branch surface at the base of the carina well away from branch-margins, and are closely spaced, about three quarters of a diameter apart. Their positions are stabilised on the mainstem, with one situated on each diverging lateral branch junction and one midway between. On lateral branches they are set flush on the inclined branch sides away from carina or ridge and are extremely closely spaced, slightly smaller and more oval in appearance.

Dimensions (N = 5)

	NM	MN	Mx	$\bar{X}$
MS; BW	10	0.51	0.88	-
2:1; BW	3	0.55	0.67	-
1:2; BW	51	0.35	0.41	0.38
AD	22	0.19	0.21	0.20
ID	20	0.36	0.41	0.39
LBS	50	0.90	1.05	0.96
IND	25	0.75	0.93	0.83

Micrometric Formula 10-12/10-12/6-8

Discussion

Young and Young (1878 p. 354) erected a new species Glauconome robusta which they stated was closely allied to their Glauconome retroflexa (1875a,p. 330) (here placed in synonomy with Penniretepora pulcherrima (McCoy)), but was distinguished from it by its stouter branches, wider spaced carinal nodes, and more numerous autozooecial apertures in proportion to the number of lateral branches.

Graham (1975, p. 8) considered P. pulcherrima (McCoy) and P. robusta (Young and Young) to be conspecific, stating that the only difference between the two forms was the comparatively thicker branches of P. robusta. However the present examination of the type specimen of P. pulcherrima (and type material of P. retroflexa) and type material of P. robusta has shown that P. robusta is a distinct species.

While there are some similarities between the species, such as similar apertural shapes, dimensions and interapertural distances, there are many important significant differences.

Branches are more stouter in *P. robusta* ranging from 0.51 to 0.89 mm in width compared with 0.36 to 0.49 mm for *P. pulcherrima*. Lateral branch spacing is significantly greater in *P. robusta* averaging 0.94 mm compared to 0.77 mm for *P. pulcherrima*. Carinal nodes are further apart in *P. robusta* ranging between 6 and 7 in a 5mm line along the mainstem compared to between 24 and 30 in a 5 mm line in *P. pulcherrima*. In *P. pulcherrima* as 1:2 minor lateral branches are extremely short, and decrease in width very rapidly from their points of origin, autozooecial apertures never reach normal dimensions and spacing. However, in *P. robusta* 1:2 minor lateral branches are considerably longer and apertures retain normal dimensions and spacing although these parameters are reduced. It is concluded that *P. robusta* is a distinct species.

Material

GAGM 01-53 VN	Upper Limestone Group (E2 Arnsbergian), Gillfoot near Carluke. Figured by Graham (1975, pl. 3, fig. 7)
HM D54	1 to 4, Shale above Gillfoot Limestones (E2 Arnsbergian), Carluke.
ABMG 11	Hardraw shales (Brigantian), Mill Gill, Askrigg, N. Yorkshire.

Stratigraphical Range

Brigantian-Arnsbergian.

Penniretepora elegans (Young and Young, 1875a)

Figs. 72, 73, 74; Pl. 108, figs. a-d; Pl. 109, figs. a-f;
Pl. 110, figs. a-b; Pl. 111, figs. a-b.

1875a Glauconome elegans (sp.nov.) Young and Young, p. 328, Pl.4, figs. 27-32.

1881 Glauconome elegans Young and Young; Vine, p. 334 Pl. 16, fig. 4.

1885 Pinnatorpora elegans? (Young and Young); Vine, p. 81.

1975 Penniretepora elegans (Young and Young); Graham, p. 4, Pl. 1, Figs. 1-4, pl. 4, fig. 5.

Type

As Young and Young(1875a) did not erect a holotype for P. elegans Graham (1975) designated a lectotype (GAGM cavity slide 01-53 WD, specimen number 6) which was figured by him (Pl. 1, figs. 3, 3a).

Emended Diagnosis

Penniretepora with large bipinnate zoaria. The mainstem is straight or gently sinuous of moderate width and has a sub-oval cross-section. Lateral branches are coplanar, quite widely spaced and diverge at high angles with opposite flanks slightly offset. On the obverse surface there is a very low, poorly defined wide median carina on which there is a single row of widely spaced, small round nodes; obverse surfaces are poorly rounded; reverse surfaces are flat; all are finely pustulose. Autozooecial apertures are quite small circular with thin, low peristomes, and are widely spaced with one situated on each lateral branch junction and two between on the mainstem and primary lateral branches. Secondary nanozooids occur.

Description

External

Zoaria form medium to large normally bipinnate rarely tripinnate expansions. Branches are straight or gently sinuous and are coplanar. The mainstem is of variable width, quite slender to robust and has a sub-rounded to oval cross-section, and may be very long, up to 50 mm in length. Lateral branches are widely spaced, set between one and a half and two diameters apart and diverge from the mainstem at high angles between 50° and 75°. Lateral branch bases are quite well, to poorly defined and considerable flaring of the mainstem may accompany their development. Lateral branches are paired, usually one flank is set slightly higher on a branch (½ to one branch width distance) than the opposite series. Occasionally, lateral branches may alternate at equidistant intervals on opposite branch margins, this leads to the mainstem being gently flexuous. 2:1 minor lateral branches are very widely spaced, up to 18 mms apart, with slightly smaller parameters relative to the mainstem and may be very long, up to 30 mm in length. 1:2 minor lateral branches are quite thin, of variable length, commonly quite long and with oval cross-sections.

On the obverse surface of branches, there is usually no carina, but occasionally a very poorly defined low broad median carina may be developed. On minor lateral branches the midline may be more ridge-like. Branch sides slope away from the carina or ridge at a low angle. Along the midline of branches there is a single row of widely spaced small round nodes. Reverse surfaces are flat to poorly rounded and all surfaces are finely pustulose. On obverse branch surfaces there are closely spaced parallel longitudinal rows of very small pustules, while on reverse surfaces the same pattern occurs but pustules tend to be slightly coarser.

Autozooecial apertures are fairly small, circular to oval with complete low, thin, peristomes, arranged in two alternate rows set close to branch margins. On the mainstem they are widely spaced about two diameters apart, slightly closer on 2:1 lateral branches, and their positions are stabilised with one situated on each lateral branch junction and two between.

The latter may have upraised, slightly inflated outer margins which may protrude slightly beyond branch margins. The two rows may face the same direction or are inclined at a low angle from each other. Secondary nanozooids occur.

Dimensions (N = 41)

	NM	Mn	Mx	$\bar{X}$
MS;BW	82	0.35	0.53	-
2:1;BW	15	0.34	0.49	0.44
1:2;BW	425	0.26	0.32	0.29
AD	480	0.07	0.12	0.09
ID	482	0.30	0.36	0.33
LBS	353	0.84	1.06	0.96
IND	231	0.40	0.93	0.79

Micrometric Formula: 10-12/15-17/6-12

Discussion

Penniretepora elegans (Young and Young) is a very distinctive species. The absence of a proper median carina, broad ill-defined latera branch bases, and the positions of autozooecial apertures, one at each lateral branch junction and two between, make this species readily identifiable.

Graham (1975, pp. 4-5) indicated that Young and Young (1875a, p. 328-329) incorrectly described some minor zooecial and zoarial features in their original definition of the species. Young and Young stated that zooecial apertures and lateral branches are generally inclined towards the zoarial surface. Graham stated that the lateral margins of zooecial apertures are more elevated than the inner margins. However, from Young and Young's original description it is obvious that they were trying to describe the more elevated outer margins of zooecial apertures.

Young and Young were incorrect in describing lateral branches as being turned towards the obverse surface, that is protoflexed. In the present revision, lateral branches are found to be usually coplanar with the mainstem. Young and Young also stated that the angle of divergence of lateral branches is 35°. However, Graham (1975, p. 5) obtained values between 50° and 70° which are confirmed in the present revision. One of Young and Young's figured specimens shows an angle of divergence of 40°, but, as Graham pointed out, this is atypical of the species.

Material

BMNH B.1777	Halkyn, (Brigantian?) Clwyd, N. Wales.
BMNH D.55	Capelrig, (Brigantian?) East Kilbride, Lanarkshire. G.R. Vine Collection.
BMNH D.88	Carboniferous shales Boghead (Brigantian?), Lanarkshire, Scotland. G.R. Vine Collection.
BMNH D.230	Yoredales, (Brigantian?), Gleaston Castle. G.R. Vine Collection.

BMNH D.231	Hurst, N. Yorkshire. G.R. Vine Collection.
BMNH D2318-19	Carboniferous Limestone, Halkyn, (Brigantian?) Clwyd, N. Wales. G.R. Vine Collection.
BMNH D.2383	Halkyn, (Brigantian?). G. Shrubsole Collection.
BMNH D.2384	Halkyn, (Brigantian?). G. Shrubsole Collection.
GAGM 01-53 wc	(Syntype) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.
GAGM 01-53 wd	Cavity slide with 6 zoarial fragments (syntypes) Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride. One specimen was figured by Graham (1975, Pl. 1, figs. 3, 3a) and was designated as Lectotype.
GAGM 01-53 wf	(Syntype) Lower Limestone Group (Brigantian), Dykehead Pit, High Blantyre. Specimen was figured by Graham (1975, Pl. 1, fig. 4).
GAGM 01-53 wg	(Syntype) Lower Limestone Group (Brigantian), Dykehead Pit, High Blantyre.
GAGM 01-53 wi	(Syntype) Lower Limestone Group (Brigantian), Dykehead Pit, High Blantyre.
GAGM 01-53 wj	(Syntype) Lower Limestone Group (Brigantian), Dykehead Pit, High Blantyre.
HM D.123	Cavity slide with 26 zoarial fragments (syntypes) Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride. Two specimens were figured by Graham (1975, Pl. 1, figs. 1, 1a, 2, 2a).
HM D.124	Cavity slide with 9 zoarial fragments (syntypes). Lower Limestone Group (Brigantian), Capelrig, East Kilbride.

HM D.125	Cavity slide with 12 zoarial fragments, (syntypes) Hosie Limestone, Lower Limestone Group (Brigantian) Hairmyres, East Kilbride.
HM D.13	Locality unknown.

Stratigraphical Range

Brigantian - ?Arnsbergian.

Occurrence

P. elegans is very common in Brigantian strata of the Midland Valley of Scotland, and is uncommon elsewhere, but has a fairly wide distribution, being recorded from the Brigantian strata of Yorkshire and North Wales.

Penniretepora laxa (Young and Young, 1875a)

Figs. 75, 76; Pl. 112, figs. a-f; Pl. 113, figs. a-c.

1875a Glauconome laxa (sp.nov.) Young and Young, p. 331, Pl. 4, figs. 33, 34.

1877 Glauconome elegantula (sp.nov.) Etheridge,Jun. p. 35, Pl 2a, figs. 3-6.

1975 Penniretepora laxa (Young and Young); Graham, p. 8, Pl. 2, figs. 9, 9a, 10, 10a, Pl. 6, figs. 1, 2.

Type

As Young and Young (1875a, p. 331) did not erect a holotype for Glauconome laxa, Graham (1975) in his revision of the taxon chose a lectotype from their type material. Although he figured two specimens (Pl. 2, figs. 9, 9a, 10, 10a) he did not indicate which was to be designated lectotype. He stated (p.8) that the lectotype was GAGM 01-53 vk, which is in fact a cavity slide with twelve zoarial fragments, two of which were figured by him.

In a letter to Dr. Campbell of the Institute of Geological Sciences, Edinburgh, dated 7.7.75, Graham indicated his preference for the specimen he figured as Pl. 2, figs. 9, 9a to be designated lectotype. This preference is followed here.

Emended Diagnosis

Penniretepora with medium sized pinnate or bipinnate zoaria. The mainstem is quite slender and gently flexuous; lateral branches are widely spaced alternately situated on opposite branch sides and diverge at high angles; obverse surfaces have a wide upraised median carina with a single row of widely spaced nodes; reverse surfaces are well rounded; all surfaces are finely pustulose. Autozooecial apertures are large, oval, closely spaced; on the mainstem and primary lateral branches one is situated on each lateral branch junction and two between.

Description

External

Zoaria are medium sized pinnate occasionally bipinnate expansions. The mainstem is slender and has a subrounded cross-section. It may be straight, but is normally gently sinuous. The stem, being gently curved from side to side has convexities corresponding to the position of alternate equidistant lateral branches. Only very slight flaring of the mainstem accompanies the development of lateral branches. 1:2 minor lateral branches are widely spaced, averaging three diameters apart, and are relatively thin, short and although usually coplanar, may be slightly retroflexed at a low acute angle. They diverge at high angles between 55° and 70° and may be paired and slightly offset, but usually alternate at equal intervals on opposite branch sides. 2:1 primary lateral branches are only very occasionally developed in zoaria.

On the obverse surface of branches there is a well defined relatively wide prominent, well rounded median carina, which may be straight or gently sinuous, with occasionally slightly indented lateral margins caused by the inner lips of autozooecial apertures abutting its base. Carina margins often appear rather bulbous and may slightly overhang the inner margins of autozooecial apertures. Although the carina is well rounded and steep sided on the mainstem on minor lateral branches it is more ridge like. On the carina there is a single row of very widely spaced moderately sized nodes. Away from the carina branch sides are steeply inclined. Reverse surfaces are well rounded. All surfaces are quite finely pustulose.

Autozooecial apertures are large and oval. The inner margins of apertures occasionally abut onto and slightly indent the base of the carina.

Apertures are closely spaced, about their own diameter apart, and on the mainstem and 2:1 primary lateral branches their positions are stabilised, one situated on each lateral junction and two between. On 1:2 minor lateral branches apertures are smaller and closer spaced. Peristomes are absent, but those apertures situated between lateral branch junctions, and on 1:2 minor lateral branches may be bound by slightly inflated outer margins which may marginally project beyond branch margins.

<u>Dimensions</u> (N = 21)

	NM	Mn	Mx	$\bar{X}$
MS;BW	42	0.37	0.48	-
2:1;BW	3	0.34	0.38	-
1:2;BW	148	0.26	0.30	-
AD	218	0.14	0.16	0.15
ID	234	0.36	0.42	0.38
BLS	135	1.03	1.27	1.15
IND	58	0.92	1.36	1.12

Micrometric Formula: 8-9/12-14/4-5

Discussion

Penniretepora laxa (Young and Young, 1875a)is readily distinguished from other species by its slender zoarial form; its widely spaced lateral branches alternately situated on opposite branch sides causing a regular alternate flexure of the mainstem, and the positions of the large oval autozooecial apertures which occur one at each lateral branch junction and two between.

The present study has shown that P. laxa is conspecific with Glauconome elegantula Etheridge Jun (1877, p. 35, Pl. 2a, figs. 3-6) as Graham (1975) had suggested. As P. laxa was described earlier this name takes priority.

Olaloye, 1974 compared P. laxa with a new species he erected, Penniretepora cucullea (p. 493-496, Pl. 20, figs. 1-5). He outlined some basic differences between the two species, but he did not examine type material of P. laxa, his conclusions being drawn from Young and Young's original qualitative description and illustrations only. Olaloye's precise scheme of measurement and descriptions of P. cucullea and the present revision of P. laxa allows a more detailed comparison of the two species.

Both have quite slender mainstems, and well defined median carinae. Apertural positions are the same, one aperture being situated on each lateral branch junction and two between each junction. Branches are straight in P. cucullea but in P. laxa they tend to be sinuous. In P. cucullea carinal nodes are much closer and regularly spaced. The spacing of lateral branches is significantly closer in P. cucullea averaging 0.73 mm compared to 1.1 mm in P. laxa.

Autozooecial apertures are oval to elliptical in P. laxa and much larger than in P. cucullea where they are circular. In the latter they also have peristomes which are lacking in P. laxa, which only possess inflated outer rims.

Olaloye compared Young and Young's meristic counts over set distance for the number of lateral branches and autozooecial apertures to results obtained on his species. He did not realise that Young and Young counted the actual number of autozooecial apertures and lateral branches over the unit distance while he used the space count method, thus his conclusions drawn from this comparison are invalid. On his Carrick Lough material, Olaloye recorded 10 autozooecial apertures and 4 lateral branches in a 6 mm line, compared to Young and Young's respective values of 18 and 6. (On type specimens of P. laxa, values of between 12-14 autozooecial apertures in a 5 mm line and 8-9 lateral branches in a 10 mm line are recorded here).

Olaloye was incorrect in stating that zooecial chamber bases are smaller in P. laxa than P. cucullea. Examination of type specimens of P. laxa shows interapertural distances to be slightly larger than for P. cucullea. As interapertural distances are a direct consequence of zooecial base dimensions it follows that zooecial chamber dimensions are larger in P. laxa. The two species are obviously very different, and if Olaloye had examined type material of P. laxa he would have been able to reach more accurate conclusions.

Material

ABMG 8	Hardraw Shales (Brigantian) Mill Gill, Askrigg, N. Yorkshire.
GAGM 01-53 CLJ	Cavity slide with 24 zoarial fragments. (Syntypes) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride. Two specimens were figured by Young and Young (1875a, Pl. 4, figs. 33, 34).
GAGM 01-53 VK	Cavity slide with 12 zoarial fragments. (Syntypes) Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride. Two specimens were figured by Graham, (1975, Pl. 2, figs. 9, 9a, 10, 10a).
GSE 2096	Labelled as *Glauconome elegantula* Etheridge. Lower Limestone Group (Brigantian), Harelaw Quarry, Longniddry. The specimen was figured by Etheridge (1877, Pl. 2a, figs. 5, 6) and Graham (1975, Pl. 6, fig. 2).
GSE 2109	Labelled as *Glauconome elegantula* Etheridge. Horizon and locality as above. The specimen was figured by Etheridge (1877, Pl. 2a, figs. 3, 4) and Graham (1975, Pl. 6, fig. 1).
HM D131	Cavity slide with 16 zoarial fragments (Syntypes). Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, East Kilbride.

Stratigraphical Range

Brigantian.

Occurrence

P. laxa is very common in Brigantian strata of the Midland Valley of Scotland, and its presence in the Hardraw Shales, Mill Gill in North Yorkshire is the first record of the species outside Scotland.

Penniretepora grandis (McCoy, 1844)

Fig. 77; Pl. 114, figs. a-c.

1844 Glauconome grandis McCoy, p. 199, Pl. 28, fig. 3.

Type

McCoy (1844, p. 199, Pl. 28, fig. 3) did not erect a holotype for the species and as his figured specimen (NMI F.6024) is the only obverse surface of the species available, this is here designated as lectotype.

Emended Diagnosis

Penniretepora with large pinnate zoaria. Branches are straight and coplanar; the mainstem is robust; lateral branches are quite closely spaced with opposite series slightly offset, and diverge from the mainstem at fairly high angles; the obverse surface of the mainstem is poorly rounded with a low straight narrow median carina; on lateral branches the carina is sinuous and branch sides slope steeply away; reverse surfaces are flat to quite well rounded. Autozooecial apertures are fairly large, circular with complete thick peristomes, set low down on branch sides and commonly slightly indent the margins of lateral branches; apertures are closely spaced, with one set on each lateral branch junction and three between on the mainstem.

Description

External

Zoaria form large pinnate expansions. The mainstem is straight, robust with regularly arranged lateral branches diverging from it at high angles between 55° and 65° at quite closely spaced intervals.

Lateral branches are paired on opposite branch sides, but are slightly offset with one flank set slightly higher (about one branch diameter) on the mainstem than the opposite series, and some slight flaring of the mainstem accompanies their development.

The mainstem has a suboval cross-section. The obverse surface of the mainstem is poorly rounded, and has a weakly defined low, very narrow, straight median carina, from which branch sides slope gently away. The reverse surface of the mainstem is quite flat. 1:2 minor lateral branches are coplanar, slender and usually straight, although some slight gently flexed branches may occur. Lateral branches are quite long, up to at least 4.7 mm in length. On the obverse surface of minor lateral branches the narrow low median carina is gently sinuous and branch sides slope steeply away from it. Reverse surfaces of the lateral branches are more rounded, giving lateral branches a subrounded cross-section. Reverse surfaces are covered in very fine pustules arranged in narrow closely spaced longitudinal rows.

Autozooecial apertures are fairly large and are circular with quite prominent thick complete peristomes. They are closely spaced, set slightly more than one total diameter apart on the mainstem, and are closer together on lateral branches. Apertures are set flush and quite low down as branch sides, and although they do not indent the lateral margins of the mainstem their outer peristomal rims commonly indent the margins of slender 1:2 lateral branches. On the mainstem apertural positions are stabilised with one situated above each lateral branch junction and three between.

Dimensions (N = 3)

	NM	Mn	Mx	$\bar{X}$
MS;BW	2	0.60	-	-
1:2;BW	19	0.39	0.48	0.40
AD	12	0.10	0.15	0.13
ID	14	0.32	0.41	0.37
LBS	28	1.19	1.39	1.31

Micrometric Formula: 8/14/-

Discussion

Penniretepora grandis (McCoy) is a very large distinct species, characterised by its very robust mainstem and relatively widely spaced lateral branches. Apertural positions are diagnostic, with one situated above each lateral branch junction and three between. It is an extremely rare species, and only three specimens present in the Griffith Collection are known.

Graham (1975) considered P. grandis to be conspecific with Penniretepora pluma (Phillips), Penniretepora stellipora (Young and Young), Penniretepora flexicarinata (Young and Young) and Penniretepora aspera (Young and Young). However, the present study has shown that Graham's conclusions cannot be substantiated. They are all different species with significantly different measured parameters and general morphological features.

Material

NMI F.6024	Meelick Chapel, Clare. (Asbian) This specimen was figured by McCoy (1844, Pl. 28, fig. 3), and by Graham (1975, Pl. 4, fig. 4).
NMI F.6087, 1-2	Carboniferous Limestone, Kildare.

Stratigraphical Range

Asbian

Genus *Ptylopora* McCoy, 1844

Type species

Ptylopora pluma McCoy, 1844

Diagnosis

Acanthocladiid with fan or funnel-shaped zoaria with a strong straight central mainstem from which two rows of regularly spaced lateral branches diverge. Lateral branches are connected by regularly spaced dissepiments. Obverse surfaces have a strong central median carina, with or without nodes. Autozooecial apertures are arranged alternately in two longitudinal rows on the mainstem and lateral branches. Zoarial and zooecial parameters are graded between the mainstem and lateral branches.

Range

Devonian - Permian.

TAXONOMIC PROCEDURE

There is a significant difference in the calculated values of measured parameters on the robust mainstem and more slender lateral branches, with values constantly higher on the midrib. Consequently two separate sets of measured parameters are given, one for the mainstem and one for lateral branches.

External Morphological Characters

Zooecial Parameters

Branch Width (BW): The width of the mainstem (MS;BW) is measured transverse to its growth axis away from any localised increase in width which may accompany the development of lateral branches. As the mainstem tapers distally care must be taken in using its width for comparative purposes.

Lateral branches are noticeably thinner than the mainstem, and lateral branch width is measured away from their points of origin with the mainstem and away from dissepiments or occasional areas of branch bifurcation.

The number of Apertural Rows (AR): Recorded as in the Fenestellidae. The number of apertural rows is constant, with two rows situated on the mainstem and lateral branches on either side of a median carina or ridge.

Autozooecial apertural diameter (AD): Measured as in the Fenestellidae.

Interapertural distance (ID): Measured as in the Fenestellidae.

Zoarial Parameters

Lateral Branch Spacing (LBS): Measured between the centres of adjacent lateral branches, close the their points of origin with the mainstem, and parallel to the growth axis of the mainstem.

Fenestrule Length (FL): Measured as in the Fenestellidae.

Fenestrule Width (FW): Measured as in the Fenestellidae.

Dissepiment Width (DW): Measured as in the Fenestellidae.

Internodal Distance (IND): Measured as in the Fenestellidae.

Zooecial Apertures Per Fenestrule (ZAF): Recorded as in the Fenestellidae.

The Micrometric Formula

This is expressed as for the Fenestellidae but the general definitions of the individual parameters differ. There are significant differences in the size of zooecia and in the spacing of nodes on the mainstem compared with lateral branches. As a result, there are two entries in the micrometric formula to express this variation in the number of autozooecial apertures and nodes in a 5 mm line. The formula takes on an extended form as follows :

$$B10//D10//A5^1/A5^2/N5^1/N5^2$$

B10: The number, or range in the number of lateral branches transverse to the growth axis of lateral branches in a 10 mm line.

D10: The number, or range in the number of dissepiments in a single row parallel to the growth axis of lateral branches in a 10 mm line.

A5: The number, or range in the number of autozooecial apertures in a single row on the mainstem parallel to its growth axis in a 5 mm line.

$A5^2$: The number, or range in the number of autozooecial apertures in a single row on lateral branches parallel to their growth axis in a 5 mm line.

$N5^1$: The number, or range in the number of carinal nodes in a single row on the mainstem parallel to its growth axis in a 5 mm line.

$N5^2$: The number, or range in the number of carinal nodes in a single row on lateral branches parallel to their growth axis in a 5 mm line.

Internal Morphological Characters

Zooecial Parameters

Zooecial chamber base dimensions: Measured as in the Fenestellidae. Since zooecial dimensions between the mainstem and lateral branches are graded, zooecial chamber bases are measured both on the mainstem and lateral branches.

Ptylopora pluma McCoy, 1844

Pl. 115, figs. a-c; Pl. 116, figs. a-c; Pl. 117, figs. a-f, Pl. 118, figs. a-b; Pl. 119, figs. a-b; Pl. 120, figs. a-b; Pl. 121, figs. a-c; Pl. 122, figs. a-b; Pl. 123, fig. a.

1844 Ptylopora pluma McCoy, p. 200, Pl. 28, fig. 6.

1844 Ptylopora flustriformis (Phillips), McCoy, p. 200.

1883a Ptylopora phillipsi (sp.nov.) Vine, p. 167.

1973 Ptylopora pluma McCoy parva, sub sp. nov. Tavener-Smith, p. 483, Pl. 25, figs. 1-10.

Type

As McCoy (1844, p. 200) did not establish a holotype for Ptylopora pluma Tavener-Smith's (1973, p. 486) reference to McCoy's figured specimen as the holotype is not strictly correct. Consequently a lectotype is formally proposed here; this specimen (NMI F.6046) was figured by McCoy (1844, Pl. 28, fig. 6).

Emended Diagnosis

Ptylopora with fan or funnel-shaped zoaria. The mainstem is of variable thickness, usually very robust and tapers distally; lateral branches are of moderate width, straight and rarely bifurcate. On the obverse surface of the mainstem there is a prominent relatively wide median carina, lateral branches are more ridge-like, all with closely spaced single rows of nodes; reverse surfaces are well rounded. Dissepiments are short, stout and depressed. Fenestrules are of moderate size, oval to quadrate. Autozooecial apertures are quite large, circular and fairly closely spaced. Zooecial chamber bases are hemihexagonal.

Description

External

Zoaria are penniform, and develop a broad planar fan-shape, slightly foliaceous fan-shape, or low angle funnel-shape. Fan-shaped zoaria are of variable size, but may be large, up to 10 cm in length, and develop a very broad planar form up to 12 cm in width, and is the most common zoarial form developed. Zoaria may also be slightly foliaceous, with lateral branches typically retroflexed. Funnel-shaped zoaria are very rare, and form fairly small, very low angle, narrow, distally expanding funnels, up to 4 cm in length. Lateral branches diverge and retroflex away from the mainstem at a constant angle. Branches curve around, and opposite flanks converge at an acute angle, and fuse in a straight line directly opposite to the mainstem. Occasional bifurcation of branches leads to the development of a low angle distally expanding funnel shape up to 1.7 cm in diameter.

The mainstem is extremely robust, of variable width (0.56 to 2.7 mm in width) and usually straight only occasionally developing a slight distal curve. On the obverse surface of the mainstem there is a very prominent wide, well-rounded raised median carina bearing a single row of quite closely spaced, fairly small oval nodes. The crest of the median carina may be ornamented by very closely spaced, well defined longitudinal rows of papillae. Branch sides slope gently away from the median carina, and are covered with closely spaced and irregularly arranged papillae. Reverse surfaces of the mainstem are well rounded, smooth, finely granular or with longitudinal striae.

Lateral branches diverge from the mainstem at very low angles between 25° and 45°, and the junction between the mainstem is very poorly defined. Lateral branches are of slender to moderate width, straight and rarely bifurcate. Obverse branch surfaces slope steeply away from a narrow median carina, or more usually a narrow median ridge which may be straight or slightly sinuous. Nodes are small and closely spaced on the carina. There is no direct continuation of the median carina of the mainstem to lateral branches, and the crests of the carina or ridge on lateral branches is significantly depressed relative to the mainstem. Reverse surfaces are well rounded and are also very depressed relative to the mainstem.

Dissepiments are short and stout, well depressed below the crests of branches on the obverse, less so on the reverse surface. On obverse surfaces they are poorly rounded and often have a central ridge along their length, but are well rounded on the reverse. Dissepiments flare considerably towards branches and become less depressed. Laterally adjacent dissepiments tend to be situated the same distance away from the mainstem with their ends roughly in opposition, so that they form a more or less continuous dissepimental zone. There are a series of these zones on either side of the mainstem and roughly parallel to it.

Fenestrules are moderately large, long and narrow, oblong to oval, with well rounded extremeties and straight or slightly indented lateral margins.

Autozooecial apertures are quite large, circular and with or without peristomes. On the mainstem they are set flush on the relatively gently inclined branch sides at the base of the median carina, and are quite closely spaced set slightly more than one diameter apart. On lateral branches autozooecial apertures are set flush on the steeply inclined branch sides. They are closely spaced, about their own diameter apart on lateral branches with between three and four per fenestrule. Secondary nanozooids occur.

Internal

Zooecial chamber bases are hemihexagonal, and there is a gradation in dimensions between those on the midrib and those on lateral branches. Zooecial chamber bases on the mainstem and lateral branches are situated at the same level. The first two chambers on lateral branches away from the mainstem have a rounded triangular shape.

The zooecial laminated skeletal layer lining chambers is very thin and finely laminated. The primary granular layer is also very thin and the junction with the outer secondary laminated skeletal layer is well defined, ridges of the primary granular layer are short of moderate width and spacing and with well rounded apices. The secondary laminated layer is extremely thick on the mainstem. Laminae are continuous around the rods of primary granular material and the laminated skeleton is arranged in extremely closed spaced narrow zones of orally flexed nests, radiating out towards the zoarial surface. They appear to originate from the apices of the primary granular ridges, and many bifurcate along their length, and additional nests may develop at different levels within the later. They form chevron-like structures, that extend onto the zoarial surface as small pustules or papillae.

Lateral branches have the same overall structure, and the outer secondary laminated layer is markedly thinner than on the mainstem.

Dimensions (N = 28)

	NM	Mn	Mx	$\bar{X}$
Primary Branch				
MS;BW	54	0.56	2.80	-
AD	266	0.14	0.18	0.16
ID	392	0.28	0.34	0.31
IND	249	0.24	0.52	0.32

	NM	Mn	Mx	$\bar{X}$
ZB1	48	0.29	0.36	0.32
ZB2	48	0.20	0.23	0.22
Secondary Branches				
BW	420	0.27	0.43	0.34
AD	363	0.11	0.19	0.15
ID	442	0.27	0.32	0.29
FL	336	0.80	1.30	1.06
FW	336	0.48	0.83	0.65
DW	267	0.16	0.31	0.22
IND	365	0.23	0.43	0.31
ZB1	54	0.26	0.31	0.29
ZB2	54	0.17	0.20	0.19

Micrometric Formula: 15-21/9-12/15-16/9-20/15-18/12-21

Discussion

Ptylopora pluma McCoy is the only species of Ptylopora in British Lower Carboniferous strata, and is readily distinguished by its penniform zoaria, having a robust straight mainstem from which two sets of lateral branches diverge in the same plane, and are connected by dissepiments.

The mainstem is very robust, and occasionally is the only part of the zoarium preserved together with the proximal areas of the slender lateral branches. Sometimes zoarial fragments consisting of only lateral branches have been found. The measurement of set parameters, and their morphological appearance has enabled the taxonomic position of such fragments to be identified. The fairly robust, straight lateral branches, which only rarely bifurcate, short stout dissepiments, narrow oval fenestrules of moderate size, very large closely spaced autozooecial apertures, and the distinct nature of the secondary laminated skeleton make the species readily identifiable.

McCoy (1844, p. 200) in addition to describing Ptylopora pluma also described Ptylopora flustriformis (Phillips). Phillips (1836, p. 198) did not properly describe the form Retepora flustriformis, but from his illustrations of the taxon (Pl. 1, figs. 11, 12) it appears to be a fenestellid, thus McCoy's reference to it in the genus Ptylopora is a curious one. Examination of McCoy's type material in the Griffith Collection at the National Museum of Ireland in Dublin of Ptylopora flustriformis, has shown that this type material is conspecific with Ptylopora pluma. The two specimens examined (attached to the same card and labelled NMI.F.6089) have relatively large overall measured parameters for the taxon.

A specimen labelled as Ptylopora macropora (NMI.F.6088) was also examined in McCoy's type material, however this taxon was never described by him. The specimen is a fairly large zoarial fragment 42 x 10 mm, revealing the obverse surface. There are two series of branches obliquely inclined to one another at a low angle, that fuse distally in a straight line. It is possible that the specimen is a zoarial fragment of a large funnel shaped colony of Ptylopora. In such colonies the lateral branches are strongly retroflexed away from the mainstem, at a high angle, and curve around, and opposite flanks coverge at an acute angle in a straight line directly opposite to the mainstem. It is this latter area of the colony that appears to be preserved in this case. The morphology and the measured parameters are those of Ptylopora pluma.

Vine (1883a, p. 167) described the form Ptylopora phillipsi. He established the new species on the basis of its conical zoaria, differing from the planar fan-shaped zoaria of P. pluma. However, the present study has shown, by examination of some of Vine's syntypic material of *P. phillipsi* and all available type and comparative material of *P. pluma*, that the two species are conspecific. All the measured parameters are comparable and the unusual funnel-shaped zoaria of Vine's material is not a sufficient distinguishing character. Indeed, many species of Fenestrate Bryozoa show considerable variation in their morphological appearance. Thus *P. phillipsi* is considered a junior synonym of *P. pluma*.

Tavener-Smith (1973, p. 483) established a new subspecies *Ptylopora pluma parva*. He based his new subspecies on a comparison of all his material from Carrick Lough (Asbian) with only the holotype of *P. pluma* from Hookhead (Courceyan). For a more sound comparison he should also have examined the syntypic material in the Griffith Collection of the McCoy type material. In the present study all the type material of *P. pluma* has been examined and additional topotype and other comparative material has also been examined. This has shown that *P. pluma parva* is morphological comparable in all respects with *P. pluma*, thus the subspecies name *parva*, is untenable.

Material

ABHH. 2,-3,-4,-5,-6,-8,-10,-11,-14,-15,-16,-17,-18,-19,-21,-22.	
	Hookhead Formation (Courceyan), Lighthouse, Hookhead, County Wexford, Eire.
ABMG 3	Hardraw Shales (Brigantian). Mill Gill, Askrigg, N. Yorkshire.
ABO 16	Apron Reef Limestone, Bee Low Group (Asbian), Odin Fissure, near Castleton, Derbyshire.

BOM 25-09-175, 1 to 3	Castleton, Derbyshire.
BMNH B.184	Carboniferous Limestone.
BMNH D.2533	Halkyn.
BMNH D.29188	Hookhead (Courceyan), J. Wright Collection.
BMNH PD.1637	Hookpoint, Carboniferous Limestone (Courceyan) G.H. Morton Collection.
HM D.207	Labelled as *Fenestella*, Carboniferous Limestone, Hencliff.
NMI F.6046	Labelled as holotype. Carboniferous slate, (Courceyan), Hookhead. The specimen was figured by McCoy 1844 (Pl. 28, fig. 6).
NMI.F.6069	2 specimens, labelled as topotypes (by F.K. McKinney). Carboniferous slate, (Courceyan), Hookhead.
NMI.F.6088	labelled as *Ptylopora macropora*, Carboniferous slate, Poulscadden.
NMI F.6089	2 specimens labelled as *Ptylopora flustriformis* Carboniferous slate, Kildare.
NMI F.6095	2 specimens labelled as *Ptylopora macropora*. Carboniferous slate.
NMI F.6102 A to I	3 thin sections and 6 acetate peels, prepared by F.K. McKinney from the larger block of topotypes (F.6069).

Stratigraphical Range

Courceyan - Brigantian.

Occurrence

Ptylopora pluma is uncommon in British Lower Carboniferous strata, and is most commonly found in reef facies, and shallow marine limestones where it is associated with an abundant fauna of brachiopods, bryozoans, crinoids and corals.

The Double-Walled Concept as a Model for Fenestrate Growth

All available evidence suggests that fenestrates were double-walled bryozoans. The main reasons for this are discussed below and are based on personal observations and the works of Tavener-Smith (1969a)and Gautier (1973) who applied the double-walled growth concept to fenestrates.

(a) There are important parallels between the skeletal characteristics in the recent double-walled cyclostome *Hornera* and fenestrates (see Tavener-Smith, 1969a). The basic arrangement of wall components in *Hornera* is essentially comparable and suggests the former existence of an external membraneous colonial investment in fenestrates, a feature occurring in *Hornera*.

In fenestrates an external inner hypostegal epithelium was probably responsible for secreting most of the calcareous skeleton (the primary granular layer and surrounding secondary laminated layer) with its internal equivalent (with which it was continuous) the zooidal epithelium lining zooecial chambers and secreting the laminated lining to chambers. An external coelomic space was probably situated above the secreting epithelium and beneath the outer eustegal epithelium that secreted the cuticular cover of the entire colony, and allowed the transfer of nutrients across the colony. This would have been the only means of nutrient interchange between zooids as mural pores in interzooecial walls that are an additional means of communication in *Hornera* and in most cyclostomes are absent in fenestrates.

(b) Skeletal structures such as dissepiments, carinal nodes, and spinose outgrowths have no internal communication with autozooecial chambers and were formed independently of them. They are all composed of cores of primary granular skeleton surrounded by secondary laminated tissues. Secretion of these structures must have taken place entirely from an external secreting epithelium. It is also quite possible that in many taxa where the carinal nodes form short spine-like outgrowths that these aided the stability of the external epithelial tissues that surrounded branches.

(c) Colonial holdfasts and supporting structures in the proximal areas of colonies are typically heavily calcified by massive localised deposition of secondary laminated tissues. Their development can only be reasonably explained in terms of massive calcite secretion from an external epithelium.

Discussion of the Coefficients of Variation of Selected Parameters measured on Taxa within the Order Fenestrata

(See Table 2)

External Morphological Characters

Zooecial Parameters

Branch Width (BW): Although branch width is a zooecial character and gives an indication of the relative width of autozooecial chambers within colony CV's are slightly higher than expected ranging from 3.56 to 16.54 ($\bar{X}$ 8.23), and between colony CV's are only slightly lower ranging from 3.43 to 15.58 ($\bar{X}$ 7.42). These average values are higher than expected because the dimension incorporates a variable component produced by secondary growth of the outer laminated skeleton. Although the outer laminated skeleton does gradually increase in thickness throughout colony life, and branches in proximal areas are additionally thickened because they form the support for the entire colony, there was probably considerable variation in laminae secretion due to micro-environment factors causing localised increase in branch width within the framework. Considerable localised additions to branch width may be produced by mineral replacement during preservation. Such factors help to explain the only marginal differences between the within and between colony CV's. Overall, CV's are quite low and branch width is a useful parameter for taxonomic purposes.

Apertural Diameter (AD): The aperture is the opening of the auto-zooecial chamber, through which the polypide extruded, and such a genetically controlled character would be expected to be of fairly constant size in a taxon. However, there is a tendency for apertures to become constricted by secondary accretion, most attributable to post mortem mineralisation. Consequently, within colony CV's are higher than expected, ranging from 3.56 to 12.46 ($\bar{X}$ 8.15). Between

	BW			AD			ID			BS			FL			FW			DW			IND			ZB1			ZB2		
	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T
Fenestella bicellulata	8.99	7.18	6.71	10.75	13.80	15.58	5.23	6.94	8.53	-	-	-	4.86	11.33	11.40	7.12	7.72	6.81	5.66	15.90	17.46	8.41	12.77	7.71	5.31	4.85	4.85	6.30	3.14	3.81
F. ivanovi	8.00	7.24	8.53	6.51	6.45	10.26	4.31	5.50	6.21	-	-	-	10.41	6.47	12.69	8.52	7.67	9.06	14.50	13.89	15.84	18.52	15.84	25.05	-	-	-	-	-	-
F. frutex	11.54	8.43	9.84	12.40	11.02	13.64	8.54	5.77	13.51	-	-	-	9.84	6.27	8.35	9.38	8.23	9.51	25.34	14.49	23.75	19.57	13.95	41.20	5.83	3.31	3.75	5.65	2.15	2.98
F. multispinosa	10.83	11.25	14.51	7.45	5.36	9.83	5.21	4.24	7.31	-	-	-	6.58	5.52	7.84	8.14	6.99	10.51	19.51	18.51	23.54	10.53	8.76	19.31	-	-	-	-	-	-
F. tuberculo-carinata	9.51	-	6.23	8.51	-	11.09	6.41	-	6.55	-	-	-	8.51	-	10.24	9.13	-	7.25	17.65	-	5.10	9.63	-	5.95	-	-	-	-	-	-
F. plebeia	10.84	5.14	11.95	12.89	10.81	17.10	9.10	7.18	9.55	-	-	-	15.65	12.01	14.89	8.34	7.76	9.66	23.65	10.04	21.45	10.15	21.90	35.24	8.51	6.85	9.63	6.51	5.43	8.54
F. papillata	9.32	-	-	4.18	-	-	2.84	-	-	-	-	-	6.60	-	-	5.89	-	-	11.91	-	-	24.21	-	-	-	-	-	-	-	-
F. polyporata	6.77	3.43	8.16	7.80	12.22	14.73	3.96	3.22	8.02	-	-	-	6.15	7.34	11.31	11.76	10.77	12.88	11.23	11.59	12.18	28.80	38.41	54.32	5.31	-	-	5.45	-	-
F. quadridecimalis	5.25	-	-	4.65	-	-	6.66	-	-	-	-	-	4.98	-	-	11.70	-	-	19.20	-	-	12.05	-	-	-	-	-	-	-	-
Minilya plummerae	8.91	3.91	5.84	3.56	2.50	3.84	5.31	2.50	4.64	-	-	-	5.32	3.30	5.41	6.31	5.20	6.85	8.90	5.89	8.91	10.31	5.90	9.40	-	-	-	-	-	-
M. nodulosa	11.64	8.47	10.50	3.97	1.00	4.64	7.25	5.57	8.91	-	-	-	7.64	6.22	8.90	10.85	7.25	13.51	23.45	21.46	25.32	10.65	5.77	9.55	-	-	-	-	-	-
Ptiloporella varicosa	9.84	-	-	-	-	-	-	-	-	-	-	-	8.20	-	-	10.43	-	-	16.36	-	-	10.96	-	-	-	-	-	-	-	-
Hemitrypa hibernica	14.40	5.92	11.12	12.31	6.25	7.63	8.10	3.69	12.07	-	-	-	11.98	7.15	8.09	11.60	4.71	12.94	25.31	10.18	14.70	14.54	4.56	15.76	8.25	3.75	12.91	11.45	4.14	18.71
Polypora dendroides	9.44	9.43	12.54	7.39	4.82	10.92	10.93	5.14	5.92	-	-	-	9.97	11.51	12.54	12.01	10.88	10.54	17.21	12.99	17.84	16.88	15.11	17.85	-	-	-	-	-	-
P. verrucosa	4.65	-	11.15	9.75	-	1.69	5.65	-	6.86	-	-	-	20.98	-	6.56	11.60	-	16.11	17.20	-	34.44	-	-	-	-	-	-	-	-	-
P. marginata	5.72	-	-	8.51	-	-	9.50	-	-	-	-	-	12.40	-	-	14.40	-	-	19.48	-	-	-	-	-	-	-	-	-	-	-
P. sp. nov. A	9.54	-	-	8.40	-	-	7.65	-	-	-	-	-	7.51	-	-	10.01	-	-	15.31	-	-	8.42	-	-	-	-	-	-	-	-
Diploporaria marginalis	16.54	15.58	19.74	7.92	5.90	6.06	4.37	4.37	4.73	-	-	-	-	-	-	-	-	-	-	-	-	31.91	31.92	30.23	-	-	-	-	-	-
Penniretepora stellipora	3.84	6.45	7.50	9.45	5.56	8.30	4.68	3.98	7.81	4.91	4.52	7.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. spinosa	3.90	7.75	6.89	5.14	5.29	4.73	5.98	2.75	4.60	3.07	4.85	4.44	-	-	-	-	-	-	-	-	-	9.90	3.28	4.71	-	-	-	-	-	-
P. sp. nov. A	3.56	-	-	6.51	-	-	5.21	-	-	4.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. sp. nov. B	6.85	4.53	-	6.84	5.93	-	8.56	4.17	-	5.85	4.42	-	-	-	-	-	-	-	-	-	-	16.54	12.99	-	-	-	-	-	-	-
P. flexicarinata	6.30	7.81	11.20	7.72	5.90	6.20	7.88	5.94	5.90	3.83	6.55	7.20	-	-	-	-	-	-	-	-	-	10.41	11.20	14.80	-	-	-	-	-	-
P. pulcherrima	4.66	5.81	5.89	8.83	6.56	6.56	6.93	4.72	4.77	4.31	4.42	4.75	-	-	-	-	-	-	-	-	-	11.43	6.94	6.69	-	-	-	-	-	-
P. robusta	5.84	6.90	6.95	4.59	5.48	5.90	5.68	5.31	4.88	6.50	7.61	8.41	-	-	-	-	-	-	-	-	-	12.68	11.61	10.95	-	-	-	-	-	-
P. elegans	7.16	8.44	10.10	12.46	8.43	13.00	6.57	4.97	7.48	5.28	3.92	4.89	-	-	-	-	-	-	-	-	-	12.21	20.92	19.04	-	-	-	-	-	-
P. laxa	7.45	8.30	9.30	9.58	4.72	4.79	3.20	5.82	5.19	3.13	4.91	5.89	-	-	-	-	-	-	-	-	-	9.31	13.72	15.35	-	-	-	-	-	-
P. grandis	8.99	-	-	11.23	-	-	8.58	-	-	8.99	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptylopora pluma	8.39	6.54	13.42	8.90	6.41	20.20	5.20	3.21	4.40	-	-	-	7.52	4.35	15.67	9.31	4.20	16.02	15.30	11.21	26.93	12.64	9.78	30.09	4.90	3.21	4.05	5.10	3.85	5.10
$\bar{X}$	8.23	7.42	9.91	8.15	6.72	9.37	6.41	4.75	7.04	4.99	5.15	6.14	9.17	7.41	10.30	9.80	7.40	10.90	17.06	13.29	19.03	14.04	13.96	19.64	6.35	4.39	7.04	6.74	3.74	7.83

colony CV's are slightly lower, ranging from 1.00 to 13.80 ($\bar{X}$ 6.72) and are due to the balancing out of the causes of within colony variation. Overall, CV's are quite low and apertural diameter is a quite valuable parameter for taxonomic purposes.

Interapertural Distance (ID): Autozooecial chamber shape and size is genetically controlled, and colonies consist of a number of such asexually budded clones. As interapertural distance is the external equivalent of autozooecial chamber length, in fenestellids and polyporids, this parameter is thus of high taxonomic value. Within colony CV's are slightly higher than expected, ranging from 2.84 to 10.93 ($\bar{X}$ 6.41), and between colony CV's are lower, ranging from 2.5 to 7.18 ($\bar{X}$ 4.75).

The higher values of within colony CV's are attributable to slight genetic variation and microenvironmental factors causing variations in chamber length, such variation is evened out when a number of colonies in a population are examined.

Lateral Branch Spacing (LBS): Lateral branch spacing in the genus Penniretepora is genetically controlled, and lateral branches diverge from a primary branch at constant intervals in a taxon. This interval is related to the number and positioning of autozooecial chambers, for example lateral branches in a taxon may diverge at constant intervals with every alternate autozooecium. Lateral branches are always offset on opposite branch sides in taxa due to the alternate interlocking nature of autozooecial chambers in one or two rows.

The constancy of lateral branch spacing is reflected in the low within colony CV's, ranging between 3.07 and 8.99 ($\bar{X}$ 4.99), and between colony CV's, ranging between 3.92 and 7.61 ($\bar{X}$ 5.15), and this parameter is of high taxonomic value in the genus Penniretepora.

Zoarial Parameters

Fenestrule dimensions (FL,FW): are a useful measure of the coarseness of the reticulate meshwork occurring in most fenestrates. Additionally Fenestrule length and Fenestrule Width are the least variable of the zoarial parameters and are of considerable taxonomic value. For Fenestrule length within colony CV's range from 4.86 to 15.65 ($\bar{X}$ 9.17) and between colony CV's range from 3.30 to 12.01 ($\bar{X}$ 7.41), and for fenestrule width colony CV's range from 5.89 to 14.40 ($\bar{X}$ 9.80) and between colony CV's range from 4.20 to 10.88 ($\bar{X}$ 7.40).

The lower average between colony CV's are due to the fact that any microenvironmental variation which such zoarial characters may be subject to is balanced out when a number of colonies comprising a population are examined. The within and between colony CV's for Fenestrule Width tend to be higher with increasing dimensions, as these larger species display a more lax mode of growth showing a greater sinuosity of branches.

Dissepiment Width (DW): Dissepiment Width is extremely variable and is only of limited taxonomic value but has a comparative value.

Dissepiments like branches are extremely susceptable to secondary mineralisation of the outer laminated skeleton. Additional to a proximal thickening they may be locally thickened due to microenvironmental factors. For example there is a common increase in dissepiment width at colony extremeties where the flow regime was obviously different to that of the mid area of a reticulate colony. Such an increase in width in this region and within the mid area of the colony framework possibly aided the rigidity of the reticulate meshwork.

Due to these factors values of CV are relatively high, within colony CV's range between 5.66 to 25.31 ($\bar{X}$ 17.06) and between colony CV's range from 5.89 to 21.46 ($\bar{X}$ 13.29). The considerably higher within colony CV's are due to such factors as outlined above, the affects of which are evened out when a number of colonies within a population are examined.

Internodal Distance (ID): This is the most irregularly distributed of zoarial components and their taxonomic value is usually low. CV's are relatively high, within colony CV's range between 8.41 and 31.91 ($\bar{X}$ 14.04) and between colony CV's range between 3.28 and 38.41 ($\bar{X}$ 13.96). In many taxa there is as much variation displayed between colonies within a population as within colonies, as the only very slight difference between the average value of within colony CV's and between colony CV's show. This shows that in most taxa the taxonomic value of internodal distance is low.

However, in some taxa, e.g. in the species of Minilya and Hemitrypa examined nodes are regularly arranged and internodal distance is of considerable taxonomic value. In these taxa although within colony CV's are moderate, the between colony CV's are very low.

Internal Morphological Characters

Zooecial Parameters

Autozooecial Chamber Dimensions (ZBD1, ZBD2): Chamber shape and size is genetically controlled and colonies consist of a number of asexually budded clones. In the Fenestellidae and Polyporidae autozooecial chambers tend to be box-like, and measurement of basal chamber dimensions is possible. The two parameters of basal chamber length and width are of high taxonomic value because chambers are genetically controlled asexually produced clones, and CV's are very low. Within colony CV's for the two parameters range from 5.11 to 11.50 ($\bar{X}$ 6.54) and between colony CV's range from 2.15 to 6.85 ($\bar{X}$ 4.06). The higher within colony CV's are due to genetic and microenvironmental variations whose affects are evened out when a number of colonies in a population are examined.

For all the parameters measured, CV's for the total number of colonies examined in a taxon is higher than the within and between colony CV's. This is due to the fact that such CV's are the result of all aspects of variation outlined previously, in individual colonies, between colonies in a population coupled with additional environmental and possible evolutionary causes.

In the systematic description of fenestrate taxa it is probably necessary to retain all of the parameters used in the present study despite the obvious variation in their usefulness. The value of some parameters for taxonomic purposes is obvious, but others, such as Dissepiment Width or Internodal Distance, do have a comparative value and should be retained. Indeed as previously discussed, nodes may be very regularly distributed in some genera and are then of considerable taxonomic value. In any case it is necessary to examine the entire morphological variability of a taxon. In the systematic description of taxa it is of course necessary to utilise details of internal skeletal microstructure as well as the morphological parameters used for biometric analyses.

CHAPTER VIII

ORDER TREPOSTOMATA Ulrich, 1882

Diagnosis

Stenolaemata with adnate or erect ramose cylindrical rarely bifoliate zoaria. Autozooecia are tubular, budded on a thin basal lamina in adnate forms; in erect ramose forms autozooecia are budded throughout the endozone generally in curved distally arched zones, and are of variable length. Zooecia bend toward the exozone at increasing angles, usually bending more abruptly in the base of the exozone to become orientated at high angles often perpendicular to the zoarial surface. Autozooecial walls are compound, with no defined median primary granular layer, but entirely composed of skeletal laminae; in the endozone laminae are orientated parallel to the length of zooecial walls, in the exozone laminae are orally convex and may or may not be continuous between adjacent autozooecia. Endozone walls are very thin and either thicken gradually or abruptly with the development of the exozone wall. Exozone walls are normally quite thin, but of variable thickness and may have straight sides and be of uniform thickness throughout, or they may be club-shaped, undulatory or moniliform. In the endozone autozooecia have a well faceted rectangular to polygonal cross-section and may become rounded in the exozone region. Basal diaphragms are very common, hemiphragms, cystiphragms and ring septa are uncommon. Autozooecial apertures are of variable shape and size, commonly large and circular, very closely spaced, and are equally developed around erect ramose zoaria. Mesozooecia and exilazooecia are common, occurring as scattered individuals or forming maculae and monticules. Stylets are abundant and structurally diverse.

Range

Ordovician to Permian (? Triassic)

Discussion

When the Bryozoa were first recognised by Thompson (1830, as "Polyzoa") and Ehrenberg (1831, as "Bryozoa") members of the Trepostomata were assigned to the corals because their massive zoaria contrasted sharply with those of many living Bryozoa. In the later part of the nineteenth century, considerable controversy arose concerning the zoological affinities of the trepostomes. Confusion arose because of poorly defined concepts of the taxonomic groups called the favositids, monticuliporoids, stenoporoids, chaetitids and trepostomes. Depending upon the particular prejudices of workers at the time these groups contained bryozoans and corals in varying proportion and genera were identified as bryozoans or corals on entirely erroneous grounds.

Nicholson (1876, 1879) using thin sections, recognised the main aspects of internal skeletal structure used in the present classification of the trepostomes or monticuliporoids as they were then called. However, he believed the group to have strong affinities with the corals, as did Waagen and Wentzel (1886, p. 855) and Vine (1883b, p. 182).

Ulrich (1882) agreed with Nicholson on the interpretation of many of the groups internal structures, but believed the group to be bryozoans by comparison with Post Palaeozoic cyclostome bryozoans and consequently erected the suborder Trepostomata (1882, p. 151).

Cumings (1912) helped to clarify the phyletic position of the Trepostomata, and showed that they were similar to the Cryptostomata in their early stages of colony development, radically differing from typical tabulate corals.

Ulrich (1886, 1889, 1890) subdivided the Trepostomata into the familial classification recognised today. He used the same examination technique as Nicholson and described zooecial wall structure on their appearance in tangential section. He noted the amalgamate or discrete appearance of walls between adjacent zooecial tubes depended on the presence or absence of a dark line marking the tube boundaries. This dark line was termed the primordial wall by Nicholson (1881, p. 37) and the primative wall by Ulrich (1890, p.310).

Ulrich and Bassler (1904) in their revision of Palaeozoic Trepostomata recognised two divisions of the order on the basis of the nature of zooecial boundaries exhibited in Tangential thin sections (1904, p. 15).

(a) Amalgamata - in which, "the boundaries of adjacent zooecia are obscured by more or less complete amalgamation of their walls".

(b) Integrata - in which, "the boundaries of adjacent zooecia are strongly defined by a well marked divisional line".

Dissatisfaction was expressed by workers with this classification. Lee (1912) and Cumings and Galloway (1915) noted that a species could display both amalgamate and integrate appearances in tangential sections. Cumings and Galloway examined material in tangential and longitudinal thin sections at higher magnifications than previously employed and recognised that the presence or absence of a divisional line was dependent on the steepness of pitch of laminae which, in turn was dependent on whether the growing edge of the wall was thin or wide and was variable within a species or even a single specimen. They concluded that the dark divisional line was exhibited in thin walls with laminae having a steep pitch and bending over sharply. In wider walls laminae are gently orally flexed and the pitch is less with no evident divisional line. They inferred that the zooecial wall was a single unit secreted as one. However, Cumings and Galloway, like Nicholson (1888), Ulrich and Bassler (1904), misunderstood the concept of the different appearances of skeletal laminae in tangential sections and interpreted the central hyaline portion where laminae are orientated parallel to the plane of section, as a primary central secreted unit. The secondary laminated zone of these authors is simply those areas where laminae are cut at high angles to the plane of section adjacent to zooecial cavities in tangential section. Boardman and Cheetham (1969, p. 212) reiterated Cumings and Galloway's (1915) opinion that the appearance of zooecial boundaries may be a function of the angle at which laminae intersect the zooecial boundary.

The subdivision of the Trepostomata into two suborders based on the amalgamate or integrate appearance in tangential section has proved not internally consistent even in a completely phenetic classification (Boardman and Cheetham, 1969, p. 213).

Boardman (1960, p.29) pointed out however, that although zooecial wall appearance is highly variable in some genera, one aspect may be constant. He tentatively arranged the genera he studied into supergenic categories, based on the character of the lamina as they approach the zooecial boundary. Boardman and Cheetham (1969, p. 213) noted that the nature of zooecial boundaries does have potential importance in future classifications because several inferred evolutionary stocks, such as halloporoids in the Ordovician and Silurian, show a progression through time from well marked broken zooecial boundaries to completely merging zooecial boundaries.

Obviously as many taxonomic characters as possible should be utilised in a classification, however as relatively few trepostome genera have been critically studied, the overall evaluation of family characters is impossible. In the present study the currently recognised familial classification of trepostomes has been followed and six taxa within the families Stenoporidae and Dyscritellidae have been examined.

SIGNIFICANT ASPECTS OF TREPOSTOME SKELETAL MORPHOLOGY

Budding and zoarial growth in Erect Ramose forms

In erect, ramose zoaria, autozooecia are initiated throughout the endozone, normally in groups in gently arched distal curves with new zooecia intercalated in a band between opposite bases of the exozone region. New autozooecia arise interzooecially, by bifurcation of the zooecial walls which separate zooecia proximal to the new zooecium. Initially they are pointed and variation in the angle of divergence of newly developed zooecial walls may produce a narrow, sharply pointed, deep cup (lower angle of divergence), or a broader more rounded cup (higher angle of divergence).

Constant branch diameter is maintained during the intercalation of new zooecia by the outer half of all zooids in a generation bending progressively away from the central axial line of the branch into the exozone. The axial half of the generation that remains in the endozone extends distally, until the next growth phase when these too bend outwards. By this means the number of autozooecia is kept constant per unit area along a branch and thus the branch diameter remains the same (Boardman and Cheetham, 1969, p. 216). Autozooecia in the endozone bend towards the exozone at a constantly increasing angle, bending more abruptly in the base of the endozone to become orientated at high angles or perpendicular to the zoarial surface.

Newly developed autozooecia have a well faceted triangular to quadrate cross-section, and develop a typically hexagonal or polygonal cross-section when mature. In the exozone region autozooecial cavities are of variable shape; where exozone interzooecial walls are of uniform width, club-like (i.e. generally expanding distally with a well rounded tapering distal portion) tube walls are usually well-rounded, where they are moniliform (i.e. walls with bilaterally symmetrical thickenings separated by thin walled portions) the narrow walled portions are often quite well faceted, while thick walled portions are usually well rounded.

Secondary Overgrowths

Some of the erect ramose colonies of the taxa examined in the present study have secondary overgrowths of the colony formed externally (distal) to an earlier formed exozone region of the parent colony.

Each overgrowth consists of a layer of zooecia with similar characters to those of zooecia of the earlier formed portion of the colony. The overgrowths examined in the present study originate from distally located zooecia on the parent zoarium. An overgrowth extends proximally from a point of increased exozone wall thickness (see Pl.124, fig. a). The sudden increase in exozone wall thickness at this point probably originated at the growth tip, and its development was possibly related to degeneration-regeneration cycles with the cessation of growth and failure of more proximal zooids to regenerate or some exogenous factors causing the continued growth of exozone walls distally above this zone.

The overgrowths observed originate at the proximal extremity of this zone and new zooecia are developed interzooecially; initially the zooecia of the overgrowth are recumbent, and the recumbent portion of successive zooecia coalesce into a thin sheet-like basal lamina which fits into and over the irregularities of the outer zoarial surface below (e.g. into autozooecial apertures and over stylets). New zooecia develop in a proximal direction, and are initially recumbent orientated in an opposite direction to those of the parent branch below, and bend sharply through 90° to become perpendicular to the zoarial surface (see Pl.124 , fig b, Pl.125, fig. a).

The endozone region of the overgrowth zooecia is very short and commonly may not be developed at all (Pl.125, fig. a). Exozone walls have the normal morphology and structures (e.g. diaphragms) as those developed in the subjacent parent branch. The position of zooecia of the secondary overgrowth commonly show no relation to the zooecia of the underlying exozone region of the parent branch. Overgrowths end by the basal lamina simply abutting against a more proximally located zooecium.

Autozooecial Wall Structure

In the endozone, interzooecial walls are very thin, composed of skeletal laminae orientated parallel to the direction of growth (e.g. Pl.164,fig. b). Although interzooecial walls are compound and were secreted by adjacent zooidal epithelia, with laminae grown edgewise parallel to the length of the wall, no plane of discontinuity occurs along the median line of interzooecial walls as no median primary granular layer is present. With the development of the exozone region, walls thicken and skeletal laminae become orally convex and may or may not be continuous across centres of bilateral symmetry (e.g. Pl.164, fig. b).

As discussed previously (p. 343) the higher taxonomic subordinal classification of the Trepostomata has been based on the nature of skeletal laminae at zooecial boundaries in tangential section. Although this bipartite subordinal classification has proven to be internally inconsistent, the appearance of skeletal laminae in the exozone wall may have considerable potential in future classifications (Boardman, 1960, p. 29).

In the present study of some stenoporid trepostome taxa and in the one dyscritellid examined skeletal laminae are continuous across zooecial boundaries in the exozone wall. Skeletal laminae are sharply inclined and diverge orally from the edge of one intrazooecial space toward the central part of the exozone wall where laminae bend through an arc of 120°, becoming steeply inclined again to converge aborally toward the next intrazooecial space.

Exozone walls are of variable morphology and may be of uniform width along their length, club-like, or moniliform. The morphology of exozone walls is fairly constant in a taxon and is of strong taxonomic value. The steepness of pitch of laminae is dependent on the thickness of the wall. In exozone walls of uniform thickness this is fairly constant, while in moniliform walls the steepness of pitch is variable. The nature of skeletal laminae in exozone walls will be discussed prior to the systematic description of the several tabuliporids examined, and within the systematic descriptions of the single species of Stenodiscus and Dyscritella examined.

Autozooecial apertures and Interapertural walls

Autozooecial apertures are of variable size, circular, oval or often irregularly shaped, and very closely spaced. In erect ramose forms they are equally developed around the zoarial surface, no specific gemmation type is usually evident for, besides new autozooecia being budded in well defined zones in the endozone, zooecia may develop also between these zones. The intercalation of the latter and the common development of exilazooecia in the exozone affects the arrangement of autozooecial apertures on the zoarial surface (e.g. Pl.131 , fig. 3).

Interapertural walls are of very variable width in a zoarium due to the irregular arrangement of the closely spaced autozooecial apertures and the common occurrence of exilazooecia. In the stenoporid trepostomes examined in the present study they are very narrow, well-rounded to subangular, while in Dyscritella they are wider and flat (e.g. Pl. 131, fig. c ; Pl. 161, fig. a).

Stylets

In the Trepostomata stylets are abundant, and are structurally diverse with types A, B and C occurring. In the stenoporid trepostomes examined in the present study, type A and C stylets occur very regularly arranged around autozooecial apertures. Type A stylets are situated at interzooecial angles and type C stylets are closely spaced in uniserial rows between (e.g. Pl.133, fig. b).

TAXONOMIC PROCEDURE

The taxonomic procedure followed in the present study of some trepostome taxa is that outlined by Cuffey (1967, p. 29). He described twenty-two morphological characters used in the systematic description of the stenoporid trepostome Tabulipora Carbonaria. However, in the present study only those characters have been used which display the lowest values of coefficients of variation and are of evident taxonomic value in the particular taxa examined.

Measurement of the parameters was carried out using the external zoarial surface, thin sections and acetate peels prepared in specific orientations. The preparation of sections in specific orientations (shallow tangential, longitudinal and transverse) is extremely important in the identification of trepostome taxa. In the stenoporid trepostome taxa examined it is often not possible to distinguish between species solely on gross external morphological characters. The preparation of longitudinal sections is by far the most important in the identification of trepostomes. It reveals particularly characters of great taxonomic value such as the form of the exozone walls, and the type and abundance of any interzooecial structures.

As with rhabdomesid cryptostomes examined in the present study the measurement of apertural diameters and interapertural distances were made on the external zoarial surface.

Figure 78 illustrates the parameters measured for biometric purposes.

External Morphological Characters

Zooecial Parameters

(Z1): The number or range in the number of complete autozooecial apertures in one square millimetre.

(Z2): The number or range in the number of complete autozooecial apertures in a two millimetre line.

Autozooecial Apertural Diameter (AD): Apertural shape is quite variable in a single zoarium, commonly ranging from circular to oval, well-rounded to subangular. As a result only one measurement of autozooeical apertural diameter is recorded. This is measured across the maximum diameter of the aperture.

Interapertural Wall thickness (IWT): Because autozooecial apertures are irregularly arranged on the zoarial surface, only one measurement of interapertural wall thickness is recorded. This is measured as the minimum interapertural wall thickness between two adjacent autozooecial apertures.

Exilazooecia apertural diameter (ED): The shape of exilazooecia is extremely variable, and exilazooecia apertural diameter is measured across the maximum diameter of the aperture.

Zoarial Parameters

(ZD): The average diameter of a branch measured transverse to its growth direction.

Internal Morphological Characters

Zooecial Parameters

(MTZ): The maximum thickness of an adnate zoarium measured from the base of the basal lamina to the zoarial surface.

(RZ): The number or range in the number of ring septa in a mature autozooecial tube.

(BZ): The number or range in the number of basal diaphragms in a mature autozooecial tube.

The axial ratio (AXR): recorded as with rhabdomesid cryptostomes (see page 66).

Family Stenoporidae Waagen and Wentzel, 1886

Type Genus

Stenopora Lonsdale, 1844

Diagnosis

Trepostomata with adnate, or erect ramose cylindrical, rarely bifoliate dichotomous zoaria. Interzooecial walls are very thin in the endozone, exozone walls are of variable thickness, and may be of uniform width along their length, undulatory, club-shaped or moniliform. In the exozone walls laminae are usually continuous across centres of bilateral symmetry. Basal diaphragms are very common, ring septa and hemiphragms are uncommon. Autozooecial apertures are large, well rounded to subangular and very closely spaced. Mesozooecia and exiliazooecia are very common, both as scattered individuals and as maculae and monticules. Stylets are abundant and structurally diverse, usually type A stylets situated at interzooecial angles and type C stylets closely spaced between.

Range

Ordovician to Permian.

Genus Tabulipora Young, 1883a

Type species

Tabulipora urii (Fleming, 1828)

Diagnosis

Stenoporidae with erect ramose cylindrical irregularly dichotomous zoaria, rarely adnate. Endozone interzooecial walls are very thin, exozone walls are of variable thickness, rarely of uniform width along their length, normally moniliform. Skeletal laminae are continuous between adjacent autozooecia in the exozone. Ring septa are always developed, and are regularly disposed in the exozone; basal diaphragms and hemiphragms are rare. Autozooecial apertures are large, circular to subangular and very closely spaced. Exilazooecia are very common, as scattered individuals and often occurring in clusters as maculae and monticules, which may be regularly arranged. Stylets are abundant with large type A stylets situated at interzooecial angles, and small type C stylets commonly arranged in closely spaced uniserial rows along interzooecial walls.

Range

Carboniferous to Permian.

SIGNIFICANT ASPECTS OF THE SKELETAL MORPHOLOGY OF TABULIPORA

Zooecial Boundaries

The following discussion is based on the taxa examined in the present study and on all available taxonomic descriptions of Tabulipora species (e.g. Cuffey, 1967).

In the endozone, interzooecial walls are very thin and are composed of skeletal laminae orientated parallel to the direction of growth.

With the development of the exozone region, walls thicken and skeletal laminae become orally convex, and are continuous between adjacent autozooecial tubes. Skeletal laminae are sharply inclined and diverge orally from the edge of one intra-zooecial space towards the central part of the wall, becoming steeply inclined again to converge aborally toward the next intra-zooecial space. In Tabulipora exozone walls are normally characterised by the regular development of monilae. These are bilaterally symmetrical thickenings, and are separated by thin walled segments, giving exozone walls the appearance of a string of beads (e.g. Pl.135, fig. b).

In thin walled portions, laminae have a very steep pitch and curve very abruptly, never being parallel to the zoarial surface for even a short distance.

As a result, tangential sections intersect the wall laminae at high angles displaying the laminated nature throughout its entire thickness (Pl.126, fig. a). A very narrow zone of hyaline, or granular dark coloured zone may be present along the median line of the wall, and is produced by the laminae turning over in a very narrow zone so that they are orientated parallel to the plane of section (Pl.126, fig. a).

In longitudinal and transverse sections, in narrow walled portions, a dark narrow, and straight, or gently flexuous to irregularly sinuous zone is visible down the median line of an interzooecial wall, (Pl.126, fig. b). The dark line is an area where skeletal laminae bend over sharply and appear to be more clustered. Skeletal laminae continue across this zone without interruption. However, occasionally there are some slight irregularities such as an abrupt local increase in the degree of convexity of skeletal laminae. The median line is well defined in thinner walls as laminae have a steep pitch and never curve enough to become parallel to the zoarial surface for even a short distance.

Where walls thicken with the development of monilae the pitch of the laminae is less, and they turn gently over a wider area so that the line is not evident (Pl.127, fig. a). At the anterior end of monilae the line re-appears with the quite sudden increase in the pitch of the laminae and the development of a narrow walled portion (Pl.127, fig. b). In walls of equal thickness the median line may be intermittently present in long segments (e.g. Pl. 152, fig. a).

In thicker portions laminae bend over more gently so that the plane of the tangential section cuts skeletal laminae orientated parallel to the plane of laminae over a wide area. The plane of thin section lies within very few laminae and the laminated nature of laminae will not be apparent over a much wider area. The result is a very wide hyaline portion, some laminae which actually do cut the plane of section appear diffuse and vaguely contour-like. Skeletal laminae only intersect the plane of transverse thin section at high angles close to the intra-zooecial space (e.g. Pl.133, fig. a).

Zoarial Growth in Erect Ramose Colonies of Tabulipora

The nature of zooecial walls in Tabulipora is very distinctive and provides an excellent record of zoarial growth. The tabuliporian zoarium has two distinct regions, the endozone and exozone. Endozone walls are very thin, but may be periodically thickened along traces of abandoned growth tips. Exozone walls are normally slightly thicker and are characterised by the regular development of monilae separated by thinner walled segments.

In the exozone region, monilae are inter-zooecially aligned forming layers parallel to the zoarial surface (the growth surface) (e.g. Pl.135, fig. b). The similarity of shape and size of monilae in a layer suggests that these layers are zoarial growth increments (Gautier, 1970, p. 11). These monilae are the continuation of thickened endozone layers interpreted as abandoned growth tips present in the endozone region. Here the short, thick-walled monilae-like segments may extend across the endozone in distally convex arched zones into exozone walls where they lie parallel to the zoarial surface.

A single growth increment consists of a posterior thin walled portion and an anterior thickened portion - the monila. In any single growth increment, in the central endozone the length of the wall was much longer than in the corresponding exozone wall phase. The length of the wall in one increment decreases towards the exozone wall, continuing into the exozone proximally where short exozone wall phases of successive increments may merge (see Fig. 79).

Cuffey (1967, p. 68) and Gautier (1970, p. 11) postulated that in an individual growth increment in a colony, the narrow walled endozone grew more rapidly than the corresponding thicker walled exozone phase. In the thin walled portion of endozone walls the growth of laminae is characterised by an edgewise enlargement of laminae parallel to the direction of growth.

In the exozone lateral equivalent of a long endozone growth increment, a very short unit was deposited (Fig.79). In some species the posterior thin walled portion may dominate in individual growth increments, in others successive monilae may be continuous with one another. Normally the relative lengths of thin and thick walled portions are variable between successive increments (e.g. Pl.152, fig. b).

In the exozone region, and in thick walled growth tip remnants, laminae were secreted in a plane transverse to the growth direction, and are convexly arched and continuous between adjacent zooecia. In a single growth increment in the posterior thin walled portion laminae are steeply pitched and arch over abruptly. In contrast, in the anterior thick walled portion (and in the thick walled growth tip remnants in the endozone region) laminae are more rounded, have a lower pitch, and are gently orally flexed. Exozone wall growth was achieved by the successive addition of some laminae orally and by the edgewise enlargement of others (Boardman and Cheetham 1969, p. 208; Armstrong, 1970, pp. 585-588).

Although Cuffey (1967) and Gautier (1970) did not take account of the difference in the mode of laminae deposition between the posterior thin walled portions of a growth increment in the endozone and exozone regions, it is apparent that the rate of growth of this thin walled portion decreased toward the exozone region in which direction they became shorter. The decrease in the growth rate into the exozone is supported by the fact that proximally in the exozone successive growth increments can merge together (e.g. Pl. 135, fig. b). Exozone wall deposition was associated with the maximum stage of astogenetic development of zooids in a colony, zooecia having reached their maximum length and dimensions.

With the development of the anterior thick walled portion, formed at the growth tip and down the sides of the zoarium in the exozone region, there was an increase in the area of laminae deposition, a reduction in the rate of growth and polypide development.

A typical zoarial growth cycle in an erect ramose colony would have proceeded as follows:

New zooecia were added to those already in the endozone. With the intercalation of new autozooecia other laterally located older zooecia bend progressively away from the central axial line of the branches as they developed, eventually becoming perpendicular to the zoarial surface. Rapid lateral extension of endozone walls occurred, and walls were directly connected to the thick walled remants of the previous cycle thus forming a continuous tube. The rate of lateral extension is slower toward the exozone region and produced a short thin walled phase in the exozone.

Next, the rate of growth slowed down over the entire growing surface, laminae was secreted over a wider area, as a thick walled exozone portion was formed at the growth tip and down the sides of the zoarium and mature polypides developed. The thick walled phase in any one increment tends to be of fairly constant thickness along the length of the zoarial wall, away from the growing tip for considerable distances proximally, where successive thick walled phases may merge.

With the development of the mature polypide, basal diaphragms may have developed posterior to the living chamber and ring septa were later formed distal to the living chambers. Ring septa are commonly positioned on the inner sides of monilae or in the intervening thin walled intervals but their position may vary.

This phase of growth was followed by resorption of skeletal material adjacent to the polypide. Resorption was necessary in order to develop normal endozone thin walled growth of a branch (Boardman, 1960, p. 18). In the central endozone region, the short thick walled growth tip was often mostly resorbed, while in exozone portions resorption was not so marked. Resorption removed the distal most lengths of thick walled phases over the zoarium.

In the central endozone, the remnants of previous growth tips may not be well preserved since resorption removed most of their length, and, as a result most of their zooecial structures such as diaphragms or ring septa. The rate and amount of resorption was variable in successive growth increments.

The period of resorption was followed by the renewed rapid extension of endozone walls and a thin walled phase in exozone portions. Renewed growth was very marked in exozone walls where a thin walled phase was deposited directly on the anterior surface of a thick walled monila (e.g. Pl. 128, fig. a). In endozone walls, where the growth tip has been only partially resorbed the same kind of feature is produced. However, when the growth tip is completely resorbed the wall laminae of the preceding thin walled phase are continuous with laminae of the new thin walled phase .

The mode of growth indicates that overall zoarial growth was cyclic, with the lateral and vertical development of successive individual growth increments traceable along considerable lengths of the colony.

Proximally the width of the exozone and number of diaphragms increases progressively towards the colony base indicating that the distal growth of zooids in exozones continued roughly proportional to time. The axial ratio of exozone wall thickness to zoarium thickness was not constant throughout the colony, as suggested by Lee (1912, p. 143), but was dependent on the gradual proximal addition of deposits in the exozone.

The few studies on cyclic growth (Borg, 1933; Gautier, 1970) suggest that there were more episodes of cyclic growth in an endozone region than in adjacent exozone regions proximally. Growth increments defined in an endozone wall may merge proximally in the exozone wall phase. The variation in cyclic correlation between zooids over the entire colony was probably due to the cessation of skeletal growth or to the death of more proximal zooids, as more proximal parts reached a stage of maximum ontogenetic development (Boardman, 1960, p. 39, fig. 14; Cuffey, 1967, p. 67). Any later renewed growth possibly relates to more favourable microenvironmental conditions. As Boardman (1971, p. 22) suggested, attempts to correlate zoarial growth cycles have significance only in distal portions of ramose colonies which were growing when the colony died.

A study by Malecki (1968) on some Permian species of Tabulipora indicated a near one to one correlation between abandoned growth tips in the endozone and layers of monilae in the exozone with attached ring septa. In many species there may be one ring septum to several monilae. This suggests that variation in cyclic correlation between zooecial and overall colony growth was very complex and due to several factors.

Borg (1933, p. 298-305, T.fig. 10) described cyclic growth in modern cyclostomes and suggested that it was annular. In any one increment spring represented a period of renewed growth culminating in the development of a mature polypide, and resorption occurred during the autumn and winter periods. Borg recognised different growth rates in endozone and exozone walls, short thin exozone wall phases being the lateral equivalents of longer thin walled endozone phases, and representing a period of slower growth. However, most studies have shown that there are more endozone increments recognised than exozone increments in a zoarium.

Cuffey (1967, p. 70) also argued that cyclicity was of an annular or seasonal nature. He compared the growth rates of the Permian species Tabulipora carbonaria to the living anascan cheilostome Bugula and showed that at the distal growing tips of branches the possible life spans of individual zooecia were of the right order of magnitude for periods of slow thick walled growth to be of an annular or seasonal nature.

Gautier (1970, p. 13) postulated that cyclic zoarial growth was associated with the degeneration and regeneration of soft parts. The slowing of growth rates and extension of branches may have occurred simultaneously with the regeneration of a polypide in the exozone. He also mentioned that the cyclic slowing of branch extension may have been a response to environmental influences. If the development of ring septa was necessary for the operation of the polypides it is quite possible that the rarity of ring septa compared to monilae might suggest that soft parts did not always regenerate at those times.

The large variation in Tabulipora species in the correlation of the number of endozone growth segments and exozone growth segments, and in the ratio of monilae to ring septa, suggests that there is a complex interaction of several factors such as overall zoarial growth, zooid development and environmental influences affecting cyclic growth.

Diaphragms

In Tabulipora there are three types of diaphragm which cross autozooecial cavities normal, or at high angles, to zooecial walls.

(a) Perforate Diaphragms

1. Ring septa, which are transverse partitions with a median foramen.

(b) Imperforate Diaphragms

1. Basal diaphragms
2. Ring septa with the foramen sealed.

All diaphragms are composed of skeletal laminae which are extensions of zooecial wall laminae.

(a) Perforate Diaphragms

1. Ring Septa

These have previously been termed perforate diaphragms, or ring diaphragms. Gautier (1970, p. 5) proposed the term ring septum. Tabulipora is characterised by the development of ring septa in the upper endozone and throughout exozone regions and they may also occur in endozone thick walled growth tip remnants. They are irregularly developed in upper endozones, very regularly spaced in exozone regions (e.g. Pl.136, fig. a) and their appearance is associated with the development of mature polypides.

Ring septa in the upper endozone are quite widely and irregularly spaced, a septum is usually thin and foramena may be fairly wide (e.g. Pl.137, fig. b). In this region zooecial walls are thin and were secreted at a faster rate than exozone walls.

In exozone regions, ring septa are close, very regularly spaced and much thicker, with smaller formena (e.g. Pl.137, fig. b). In exozone regions walls are regularly moniliform, associated with the degeneration and regeneration of polypides, and develop very slowly through each growth phase. Ring septa are commonly associated with the thick walled phases in exozone walls, i.e. with the generation of polypides and are commonly developed at similar levels in adjacent autozooecia (e.g. Pl.137, fig. a).

Microstructural evidence and the relationship of wall laminae shows that ring septa were secreted close to autozooecial apertures. The regularity and association with exozone thick walled phases, the similarity in shape, size and positions of the foramina suggest that the septa formed the anterior walls of living chambers and that the foramina served as openings through which moveable soft parts were extruded (Gautier, 1970, p. 10; Boardman, 1971, p. 20).

The septa could have afforded some protection for the living polypide, or for the zooecial cavity in the degenerated state. Ring septa were secreted unequally from both surfaces (Gautier, 1970, p. 9).

Gautier (1970,pp. 7, 8) considered the growth of a ring septum. This development occurred with the concurrent deposition of laminae adding to the thickness of the zooecial wall. Just below the autozooecial aperture a small infold of laminae developed and extended part of the way around the zooecial cavity (Fig.80a). Skeletal laminae are continuous with wall laminae on anterior and posterior sides of the infolds (Fig.81a). With the lengthening of zooecial walls this fold was made wider and slightly longer by continued laminae deposition around it (Fig.80b). This phase was followed by the dominant deposition of laminae in a horizontal plane or slightly oblique to the anterior surface (Fig. 81b). Proximally, laminae are still partly continuous with the wall laminae, but not so distally (Fig.81b). The horizontal or low angle deposition of laminae makes up most of the thickening of the septum. Within the septum, quite close to the posterior surface, laminae bend over abruptly and terminate obliquely at the posterior septum wall, and are not continuous with the wall laminae at all (Fig.81b, Pl.128, fig. a). Gautier (1970, p. 7) described some cases where laminae in the posterior zone extend proximally parallel to the zoarial surface back toward the zooecial wall where they lap posteriorly onto the zooecial wall, but are not continuous with the wall laminae.

In cases where laminae bend over tightly, a dark line may be apparent along the length of this zone (Pl. 128, fig. b). This line, as Gautier suggested, is synonymous with the line present in narrow zooecial walls at the zooecial boundary where laminae bend over very abruptly in a narrow zone. The rims around foramena are usually thickened and curved posterioly, the deflection of the rim is usually continuous around the foramen, but its form may vary (Fig. 80c, Pl. 129 Fig. a). The posterior thickening is developed by the oblique deposition of laminae at an increased angle away from the anterior surface (Fig. 81c) . Skeletal laminae in this zone bend away from both surfaces of the septum at low oblique angles. In addition the anterior portion of the rim is often thickened, by the addition of laminae onto anterior surfaces (Fig. 81d; Pl. 129, fig. b). Skeletal laminae in this zone adjacent to the rim are not usually continuous with wall laminae (Fig. 81d).

The thickening of the septum ridge developed only after the foramen reached its optimum size. The shape of the foramen is variable but is normally oval or reniform, and often has an eccentric position (e.g. Pl.133 fig. a, Pl.147, fig. c).

In some species, the proximal side of the septum may be constantly thicker than the distal side, (e.g. Pl.138, fig. b).

(b) Imperforate Diaphragms

1. Basal Diaphragms.

True basal diaphragms are quite rare in Tabulipora. Gautier (1970, p. 10) showed that in some cases basal diaphragm position was dependent on the position of ring septa. As they formed the posterior walls of living chambers ring septa being the anterior walls, their respective positions indicate living chamber size. Their rarity does not preclude the former presence of non-calcified diaphragms, but there is no direct indication of living chamber length.

2. Ring Septa with the Foramen Sealed

The second type of imperforate diaphragms occasionally developed, occur as a result of ring septa which had their foramena closed by the secretion of an additional lamina plate. These also formed living chamber floors.

Tabulipora urii (Fleming, 1828)

Pl. 130, figs.a-c; Pl.131, figs.a-c; Pl.132, figs.a-c; Pl. 133, figs.a-c; Pl.134, figs.a-b; Pl.135; figs.a-c; Pl.136, figs.a-c; Pl.137, figs.a-b; Pl.138, figs.a-b.

1828 Cellepora urii Fleming, p.533.

1883a Tabulipora urii (Fleming), Young, p. 154.

1883b Tabulipora urii (Fleming), Young, p. 264.

1883 Tabulipora urii Young, Nicholson, p. 295.

1912 Tabulipora scotica sp.nov. Lee. p. 162, Pl. 14, fig. 4A-4D, Pl. 15, figs. 12, 13, 17, 18.

1953 Tabulipora scotica Lee, Bassler, p. G105, Fig. 70, la-b.

1969 Tabulipora scotica Owen, p. 262, Pl. 22, figs. D.E.

1970 Tabulipora urii (Fleming), Gautier, p. 19, Pl. 7-8, fig. 1.

1973 Tabulipora scotica? Lee, Owen, p. 302.

Type

Gautier (1970) redescribed Tabulipora urii (Fleming) and erected a lectotype (HM D.787) and number of paralectotypes for the taxon.

Emended Diagnosis

Tabulipora with fairly robust erect ramose irregularly cylindrical dichotomous zoaria. Autozooecia are developed throughout an endozone region of moderate width. Endozone walls are very thin, exozone walls are developed quite abruptly and are quite thin either with long segments of equal width or with slender elliptical, oval monilae separated by short thin walled portions. Ring Septa are common, usually with five or six per autozooecium, developed in the upper endozone and exozone region, and are more numerous than monilae. Autozooecial apertures are large, round to oval, very closed spaced. Exilazooecia are common, as scattered individuals, rarely in clusters forming maculae. Stylets are abundant, with type A stylets situated at interapertural angles and type C stylets in closely spaced uniserial rows between.

Description

External

Zoaria are fairly robust, erect ramose with cylindrical irregularly dividing branches ranging from 2 to 6 mm in diameter.

Autozooecial apertures are quite large, circular to oval, very closely spaced, and separated by thin interapertural walls of variable thickness which are subangular to well rounded. On adnate zoaria autozooecial apertures are more oval with their longest axes parallel to the direction of growth.

Exilazooecia are very common, as scattered individuals over the zoarial surface and usually occur in small clusters of two's and three's between autozooecial apertures. They are small, but of variable size, and are normally circular to oval, and tend to be more elongate on adnate zoaria. On some zoaria there are areas of variable size where exilazooecia are more commonly developed, but maculae are very rarely developed, and then are only poorly defined.

Relatively large type A stylets (0.04 to 0.09 mm in diameter) are usualy situated at interapertural angles with few developed along interapertural wall lengths and up to six may occur around an autozooecial aperture.

Very small rounded type C stylets (0.007 to 0.012 mm in diameter) are situated in quite well defined uniserial rows along the interapertural walls between type A stylets. They may be sporadically distributed and may be absent along small sections of interapertural walls, but are normally closely spaced in a uniserial row with up to twenty present around an autozooecial aperture. Where interapertural walls are thicker, and also at interzooecial angles, they may be more numerous, and in the latter case some clustering may occur and individual rows may not be defined.

Internal

Autozooecia are developed throughout an endozone region of moderate width. In erect ramose forms autozooecia bend toward the exozone at a low constantly increasing angle, increasing more rapidly near the top of the endozone and into the basal exozone region where they become orientated at high angles nearly perpendicular to the zoarial surface along most of their length.

In the endozone interzooecial walls are very thin, they may thicken slightly near the base of the exozone region, or the exozone wall may develop quite abruptly. Exozone walls vary from thin to moderately thick, with monilae developed along their length, but occasionally interzooecial walls may be of uniform thickness in long segments. Monilae are oval to elliptical, usually quite thin, occasionally very poorly defined and separated by fairly short, thin walled portions. There are usually four, but may be up to six, monilae may be present along the length of an exozone wall and monilae of similar size are normally interzooecially aligned.

Ring septa are developed in upper endozone and exozone regions. One or two ring septa may be irregularly developed in the upper endozone, here they are normally very thin, short and quite widely spaced. In exozone regions they are regularly developed, generally slightly less than one diameter apart and of variable form, and may be interzooecially aligned. The foramena are oval to reniform and usually have an eccentric position. The proximal sides of ring septa are generally slightly thicker than distal sides, and opposite sides may be offset. There are between four and nine (average 6) per autozooecium, and they are slightly more numerous than monilae.

Type A and type C stylets are developed. The large type A stylets are usually situated at interzooecial angles, but some occur also along interzooecial walls, and they originate in the lower to middle exozone wall. Stylets do not decrease in diameter in the thinner portions of an exozone wall between monilae and they often protrude into zooecial tubes. If they originate in the lower part of the exozone wall the narrow, well defined axial cores which may be gently curved following the angle of divergence of interzooecial walls, but usually they are straight and orientated perpendicular to the zoarial surface.

Type C stylets are very small, and are situated along the mid-lines of interzooecial walls in closely spaced single rows, and originate in the top portion of the exozone wall.

Dimensions (N = 44)

	NM	Mn	Mx	$\bar{X}$
Z1	61	10.00	13.00	11.36
Z2	61	6.00	7.00	6.7
AD	233	0.22	0.27	0.27
IWT	233	0.05	0.09	0.06
ED	189	0.07	0.10	0.09
ZD	18	2.60	5.10	3.63
RZ	214	2	9	5
ET	63	0.45	1.75	0.89
AR	23	0.27	0.65	0.51

Discussion

Tabulipora urii (Fleming, 1828) is the type species of *Tabulipora* Young (1883a. Ure (1793, p. 328, pl. 20, figs. 1-2) figured a fossil which he called *Millepore* describing its zoarial form, zoarial surface appearance and noting its abundance in Kilbride and the West of Scotland. Fleming (1828) cited Ure's figure with his description of his new species *Cellepora urii* (p. 533). Young (1883a) proposed the subgeneric name *Tabulipora* for species having perforate diaphragms (here termed ring septa) and erected *Cellepora urii* as the type species by monotypy.

Lee (1912) revised *Tabulipora*, described several new species, abandoned the name *T. urii* and designated a new type species *Tabulipora scotica* (p. 150) for the genus. As he explained, he did not retain the specific name *urii* for the type species (Lee used the name *urei*, which was possibly a mis-spelling or an intentional alteration stemming from other mis-spellings by Young, 1888, 1893) for two reasons.

> "The first is that Young did not really propose it as a new specific name, but assumed his materials to be conspecific with Fleming's *Cellepora urei* and as Fleming's type, i.e. Ure's '*Millepore*' is lost, the retention of the name would imply specific identity, and this cannot be proved. The other reason is that Young's materials include several species, and as he gave no figures it is impossible to select one as the type with the specific name proposed by Young."

However, as Gautier (1970, p. 4) stated, since *T. urii* is the type species by monotypy, Lee's choice of *T. scotica* is invalid. Gautier, as part of a study on the interprative morphology and taxonomy of the Genus Tabulipora located Ure's collection in the Hunterian Museum, Glasgow and redescribed the type species, T. urii. He selected a lectotype for the species as Ure's figured specimen was lost. Tabulipora scotica Lee is thus nomen dubium and a junior synonym of T. urii.

It is easily distinguished from other British Lower Carboniferous species of Tabulipora by its endozone region of moderate width, fairly thin exozone walls of variable morphology composed of relatively small elliptical monilae thickened in long portions, by the occurrence of 5 or 6 ring septa per autozooecium, and by its poorly developed maculae.

Tabulipora scotica Lee described by Owen (1969, p. 262, pl. 22, figs. D, E) from the Hurlet Limestone (Asbian) at Hessilhead and Trearne, near Glasgow is probably conspecific with T. urii (Fleming). However, autozooecial apertures are considerably smaller than those measured on the type material.

Tabulipora scotica Lee described by Owen (1973, p. 302) from Asbian strata near Tullaghoge, County Tyrone, Ireland, is probably not conspecific with T. urii. Unfortunately, Owen's description is rather brief and he gives no information on the number of ring septa per autozooecium. However, the markedly beaded appearance of exozone walls he mentions is generally not characteristic of T. urii.

Material

HAGM 01-53 bxs	Thin section with several zoarial fragments on. Originally labelled Ure's Millepore - Tabulipora urii, Fleming. Hillhead quarry (Brigantian?), Beith. John Young Collection 1884. Re-labelled as cotype of Tabulipora scotica by Lee (1912). One fragment was figured by him, pl. 15, fig. 13.

HM. D300	One specimen in a container. Lower Limestone series, Lower Carboniferous. Trearne (Brigantian) Beith, J. Young Collection. Referred to by Gautier, 1970, p. 19.
HM.D301	Seven specimens and two thin sections (prepared by J. Ross, 1961). Top or second Hosie Limestone Lower Limestone series (Brigantian), Lower Carboniferous. Capelrig quarry, East Kilbride. J. Young collection. Referred to by Gautier, 1970, p. 19.
HM.D304	One thin section. Lower Limestone series (Brigantian), Hillhead quarry, Beith. J. Young Collection 1891. Referred to by Gautier, 1970, p. 19.
HM.D305	1 thin section. Lower Limestone series (Brigantian), Hillhead quarry, Beith. J. Young collection 1884. Referred to by Gautier, 1970, p. 19.
HM.D306	1 thin section. Lower Carboniferous Limestone (Brigantian) Boghead quarry near Hamilton. J. Young Collection 1882. Referred to by Gautier, 1970, p. 19.
HM.D307	1 thin section. Lower Limestone series (Brigantian), Howood quarry near Paisley. J. Young Collection 1887. Referred to by Gautier, 1970, p. 19.
HM.D785	One specimen in container. Lower Limestone Group (Brigantian?), Lower Carboniferous. East Kilbride. D. Ure Collection. Paralectotype of Gautier 1970, p. 19.

HM.D786	One specimen in container. Lower Limestone Group (Brigantian?), Lower Carboniferous, East Kilbride. D. Ure Collection. Paralectotype of Gautier, 1970, p. 19.
HM.D787	3 thin sections, 5 acetate peels and 27 assorted duplicate peels. Lower Limestone Group (Brigantian) Lower Carboniferous, East Kilbride. D. Ure Collection. Lectotype of Gautier 1970, p. 19, and figured by him; Pl. 7, figs. 1-1e, Pl. 8, figs 1-1e.
HM.D900	One thin section in container. Lower Limestone Group (Brigantian) Lower Carboniferous, East Kilbride. D. Ure Collection. Paralectotype of Gautier 1970, p. 19, and figured by him; Pl. 8, fig. 2.
HM.D901	One thin section in container. Lower Limestone Group (Brigantian), Lower Carboniferous, East Kilbride. D. Ure Collection. Paralectotype of Gautier, 1970, p. 19.
HM.D902	One thin section in container. Lower Limestone Group (Brigantian), Lower Carboniferous. East Kilbride. D. Ure Collection. Paralectotype of Gautier, 1970, p. 19.
HM.D903	11 transverse serial peels and 1 remnant. Lower Limestone Group, (Brigantian), Lower Carboniferous. East Kilbride. D. Ure Collection. Paralectotype of Gautier, 1970, p. 19.

HM.D904	9 transverse serial peels and 1 remnant. Lower Limestone Group (Brigantian) Lower Carboniferous, East Kilbride. D. Ure Collection. Paralectotypes of Gautier 1970, p. 19.
HM.D905	9 transverse serial peels and 1 remnant. Lower Limestone Group (Brigantian), Lower Carboniferous. East Kilbride. D. Ure Collection. Paralectotypes of Guatier, 1970, p. 19.
HM.D906	9 tangential serial peels and 1 remnant. Lower Limestone Group (Brigantian), Lower Carboniferous. East Kilbride. D. Ure Collection. Paralectotypes of Gautier 1970, p. 19.
HM.D907	60 zoarial fragments in a container. Lower Limestone Group (Brigantian), Lower Carboniferous, East Kilbride. D. Ure Collection. Paralectotypes of Gautier, 1970, p. 19.

Stratigraphical Range

Asbian?-Brigantian.

Occurrence

Tabulipora urii is very common in Brigantian strata of the Lower Limestone series in the Midland Valley of Scotland, but has rarely been recorded elsewhere.

Tabulipora howsii (Nicholson, 1881)

Pl.139, figs.a-b; Pl.140, figs.a-c; Pl. 141, figs.a-c; Pl. 142, figs.a-c; Pl.143, figs.a-c; Pl. 144, figs.a-c; Pl. 145, figs.a-b; Pl. 146, figs,a-b.

1881 Stenopora howsii Nicholson, p. 83, fig. 12

1883 Stenopora howsii Nicholson, p. 12, Pl. 10, fig. 1.

1912 Tabulipora howsei (Nicholson). Lee, p. 166, Pl. 14, figs. 9A-C, pl. 15, figs. 22-24.

Type

Lee (1912) did not erect a holotype for Tabulipora howsii, consequently a lectotype is here selected. The proposed lectotype (GAGM 01-53 bxw) is on a thin section through nine zoarial fragments of which five are referable to T. howsii. The proposed lectotype was figured by Lee (Pl. 15, fig. 11).

Emended Diagnosis

Tabulipora with robust, erect ramose cylindrical dichotomous zoaria, rarely adnate. In erect, ramose forms, autozooecia are budded throughout a relatively narrow endozone region; endozone walls are very thin, exozone walls are thin and moniliform, with monilae commonly separated by short thin walled portions. Ring septa are regularly disposed in exozone portions with between eight and twelve per autozooecium, and are less numerous than monilae. Autozooecial apertures are large, circular, well rounded to subangular and are very closely spaced. Exilazooecia are very common, occurring as scattered individuals and as clusters in monticules and maculae which are usually regularly arranged. Stylets are abundant with type A stylets situated at interzooecial angles and closely spaced type C stylets between them along the narrow interzooecial walls.

Description

External

Adnate zoaria are rare and may be up to 1.7 mm thick. Erect ramose zoaria are very robust, branches are subcylindrical to cylindrical (7 to 22 mm in diameter) and divide irregularly.

Autozooecial apertures are very large, circular to oval, subangular or rectangular to well rounded and very closely spaced with narrow subangular to well rounded interapertural walls.

Exilazooecia are very common, small, often irregularly shaped but commonly oval to circular, occurring as scattered individuals over the colony surface and as clusters in monticules and maculae. Individual exilazooecia may be rare to very common and often two or three may occur together. Clusters of exilazooecia occur, and maculae and monticules up to 2mm in diameter are commonly developed and regularly arranged. The clusters may be flush with the zoarial surface, but more commonly form low domes above the general colony surface.

Clusters vary from being circular to more commonly elongate and well defined, to irregularly shaped with sinuous linear tracts of exilazooecia. The distance between clusters is very regular, and the average distance apart in a colony is proportional to its branch diameter, with clusters farther apart in more robust colonies (from 4 to 7 mm apart). Exilazooecia comprising maculae and monticules are of variable diameter and some may be up to 0.15 mm in diameter. Occasionally, a small autozooecial aperture may be situated within the clusters of exilazooecia. The clusters of exilazooecia are surrounded by several irregularly defined rows of extremely large autozooecia, which decrease in size away from the exilazooecia clusters and grade into autozooecial apertures of normal dimensions.

Stylets are abundant, with type A and type C stylets developed. Type A stylets are relatively large (0.04 to 0.10 mm in diameter) and are situated at interapertural angles around autozooecial apertures, ranging from 3 to 7 in number around them. Type C stylets are very small (0.009 to 0.015 mm in diameter) and are closely spaced in single rows on the midlines of interapertural walls between large type A stylets and between exilazooecia on maculae and monticules. Usually between ten and eighteen occur around autozooecial apertures of normal dimensions, and up to 30 occur around the very large autozooecial apertures adjacent to clusters of exilazooecia.

Internal

In erect ramose colonies autozooecia are developed throughout a relatively narrow endozone region. Autozooecia bend towards the exozone region, and only become orientated perpendicular to the zoarial surface very close to it. The wide exozone region is thus characterised by its gentle curvature.

In the endozone interzooecial walls are very thin, exozone walls are developed gradually with some minor thickening of endozone walls occurring near the top of the endozone region. Exozone walls are thin, and are typically moniliform along their entire length. Individual monilae are small, but of variable size, and generally have a very slender oval or elliptical appearance. Successive monilae may be continuous with one another, but often a short, thin walled portion is developed. Monilae are arranged in interzooecial layers and monilae of a similar size occur at the same level in a layer.

Monilae are more numerous than the number of ring septa and there are between fourteen and twenty-four (up to thirty) along the length of an exozone wall. Ring septa are irregularly developed in autozooecia in the upper endozone region and are regularly developed and closely spaced (about one diameter apart) along the length of the exozone region. There are normally between eight and twelve (up to twenty-two) ring septa along an autozoöecium. The foramena are oval, reniform to circular and usually have an eccentric position. The thickness of a ring septum varies, and may be thicker on the proximal side, and the distal extremeties of ring septa abutting the foramen shows considerable variation in morphology.

Basal diaphragms are very rare, but occasionally the foramen may be sealed by a secondary layer of skeletal laminae.

The large type A stylets originate in the lower exozone region. The axial cores are narrow, and are quite well defined; in the lower parts of the exozone wall they may be gently curved following the angle of divergence of interzooecial walls.

Type C stylets are very short and narrow, and are very closely spaced usually in well defined closely spaced single rows. They originate in the upper portion of the exozone wall. Very rarely some poorly developed lens shaped small granular cores may be present.

Dimensions (N = 38)

	NM	Mn	Mx	$\bar{X}$
Z1	58	9	14	19
Z2	69	6	8	7
AD	238	0.27	0.32	0.29
IWT	227	0.05	0.07	0.06
ZD	28	7	22	-
MTZ	-	-	1.7	-
RD	115	7	22	12
ET	39	2.29	5.35	3.76
AXR	12	0.32	0.52	0.36

Discussion

Tabulipora howsii is distinguished from other British Carboniferous Trepostomata by its very robust, erect ramose zoaria; quite thin pronounced beadlike moniliform exozone walls, with many small, closely spaced monilae, and the high number of ring septa in autozooecia.

Initially, Nicholson (1881) gave only a very brief description of Stenopora howsii (p. 83) but later (1883) expanded on his original description and gave a very detailed account of the morphology of the taxon. In the endozone region ('axial region' of Nicholson) all autozooecial diaphragms are perforate. That is they are true ring septa and Nicholson's reference to imperforate diaphragms was incorrect and arose from an effect of the plane of section(i.e. the plane of section may cut through a ring septum beyond the central foramen, giving the appearance of an imperforate diaphragm). Nicholson himself noted that this could be the case in the exozone region (peripheral region of Nicholson).

Nicholson (p. 289) also described a variety, Stenopora howsii var arctica, from the Carboniferous of the Feilden Isthmus, Arctic. However, from Nicholson's description, the two species do not appear to be conspecific; the variety has fewer and more widely spaced ring septae, significantly thicker exozone walls and smaller autozooecial chambers.

Tabulipora americana (Ulrich, 1890, pl. 74, fig. 1-1a) is closely allied to T. howsii. As with T. howsii, erect ramose zoaria are very robust (25-40 mm in diameter), ring septa are numerous and closely spaced (about their own diameter apart), and exozone walls are fairly thin, with abundant small oval monilae whose number exceeds that of ring septa . However, without examination of material referred to T. americana it is not possible to resolve their systematic position further.

Lee (1912) redescribed Stenopora howsii and referred it to the genus Tabulipora. However, he unintentionally incorrectly mis-spelt the species name howsii as howsei. He described the hollow and solid mode of growth of erect ramose colonies, noting the common occurrence in the same colony fragment (p. 163). The hollow endozone region of some erect ramose zoaria is probably due to the chemical dissolution of the very thin zooecial walls that characterise this region. As most are infilled with sediment, this suggests that chemical dissolution occurred early during diagenesis. Lee was probably the first worker to recognise the existence of distinct types of stylets (he used the term 'acanthopore'). He recognised large deep-seated stylets situated at interzooecial angles and small, closely spaced ones between.

Material

ABR 116	Redesdale Ironstone shale (Asbian), Lower Limestone Group, Ridsdale, Northumberland.
GAGM 01-53 bxw	Thin section of 9 zoarial fragments, of which 5 are referable to T. howsii, Lower Carboniferous Limestone, Trearne, Beith (Asbian?). Originally labelled as Ure's Millepore (Monticulipora) Tabulipora urii Fleming. John Young Collection. Re-labelled as Tabulipora sp.nov. Lee (1912). One fragment was figured by him, Pl. 15, fig. 11.

NH 435, G155.83	Card with 10 zoarial fragments. Acetate peels have been prepared from specimens 83/1, -83/7, -83/9. Redesdale Ironstone shale (Asbian), Lower Limestone Group, Ridsdale, Northumberland, J. Dunn Collection.
NH 438, G155.86	Card with 7 zoarial fragments. Acetate peels have been prepared from specimens 86/3, -86/5, -86/6, -86/7. Horizon and locality as above. J. Dunn Collection.
NH 439, G155.87	Card with six zoarial fragments. Acetate peels have been prepared from specimens, 87/4, -87/5, -87/6. Horizon and locality as above. J. Dunn Collection.

Stratigraphical Range

Asbian.

Occurrence

Although *Tabulipora howsii* is uncommon in Asbian strata, it has a fairly wide geographical distribution, and has been recorded from strata in the Midland Valley of Scotland, Northern England, the Isle of Man and Northern Ireland.

Tabulipora minima Lee, 1912

Pl.147, figs.a-e; Pl.148, figs.a-b; Pl. 149, figs.a-b; Pl. 150, figs.a-c.

1912 Tabulipora minima sp.nov. Lee, p. 164, Pl. 15, fig. 21.

Type

Lee (1912) did not erect a holotype for the species, consequently a lectotype is proposed here. The proposed lectotype is a longitudinal section through a zoarial fragment, one of twenty-five fragments on a thin section (GAGM 01-53 BYC), and was figured by Lee, Pl. 15, fig. 21.

Emended Diagnosis

Tabulipora with slender, erect ramose cylindrical irregularly dichotomous zoaria. Autozooecia are developed throughout a relatively wide endozone region. Endozone walls are very thin, exozone walls are quite thin, bulb-like to poorly developed moniliform. Ring septa are common with two or three per autozooecium. Autozooecial apertures are quite large, circular to subangular and very closely spaced. Exilazooecia are common, as scattered individuals, rarely in small clusters. Stylets are abundant with type A stylets situated at interzooecial angles and small type C stylets closely spaced between.

Description

External

Zoaria are slender, erect ramose with subcylindrical irregularly divided branches ranging from 1 to 2.6 mm in diameter.

Autozooecial apertures are large, circular to irregularly polygonal, very closely spaced with interapertural walls being relatively narrow, usually quite well rounded, or subangular.

Exilazooecia are irregularly distributed, rare or even absent in some zoaria, while being common in others with several occurring together. Maculae are never developed. Exilazooecia are very small, well rounded to irregularly polygonal.

Types A and C stylets occur. Type A stylets are moderately large (0.03 to 0.09 mm in diameter) and may attain a height of 0.12 mm above the zoarial surface. They are situated at interapertural junctions, and between 3 and 8 occur around an autozooecial aperture. Within rare clusters of exilazooecia these stylets have a smaller than average size.

Type C stylets are very small, and occur in both very irregular and regularly defined closely spaced single rows or occasionally in irregularly defined multiple rows along the midline of interapertural walls between type A stylets. The number in a row around an autozooecial aperture commonly exceeds twenty. On very narrow subangular interapertural walls, some stylets occur on the sides of the narrow ridges, and may project inwards toward the aperture.

Internal

Autozooecia develop throughout a wide endozone region. Autozooecia bend toward the exozone at a low, but gradually increasing angle. Towards the top of the endozone autozooecia bend more rapidly into the exozone, or there may be an abrupt increase in the angle of divergence of them at the base of the exozone, and they become orientated at high angles occasionally perpendicular to the zoarial surface.

Interzooecial walls are very thin in the endozone and thicken gradually or quite abruptly to form the exozone wall. There is considerable variation in the morphology of exozone walls; they may be thin with one or two poorly developed monilae present along their length, or more often they may develop a prominent narrow to relatively wide bulb shape, of moderate width, and are commonly orientated at a high oblique angle to the zoarial surface. Occasionally exozone walls may be of uniform width along their length.

Ring septa are developed in the upper endozone and exozone regions, with normally two or three (up to four) per autozooecium, and are set slightly less than one diameter apart. The foramen usually has an eccentric position, and the proximal sides of ring septa are usually significantly thicker and longer than distal margins.

Exilazooecia are very narrow tubes and their development is restricted to the middle and upper exozone wall. Their proximal extremeties may be rounded or pointed and they commonly widen towards the zoarial surface.

Type A stylets have a well defined relatively narrow axial core up to 0.02 mm in diameter. Most originate in the lower exozone region, but some appear to develop in the uppermost endozone region.

Type C stylets develop in the uppermost exozone wall and are narrow and short.

Dimensions (N = 37)

	NM	Mn	Mx	$\bar{X}$
Z1	48	12.00	15.00	13.50
Z2	48	5.00	7.00	6.10
AD	191	0.25	0.32	0.29
IWT	191	0.04	0.08	0.06
ED	145	0.05	0.14	0.07
ZD	16	1.01	1.85	1.48
RZ	184	1	4	3
TE	23	0.006	0.376	0.217
AXR	15	0.55	0.87	0.73

Discussion

Tabulipora minima is characterised by its slender zoaria, narrow exozone region with bulb-like or poorly moniliform interzooecial exozone walls, and low numbers of ring septa with only two or three per autozooecium.

Lee's (1912) original description of the species is adequate, however the row of minute 'black dots' he refers to along interzooecial walls in shallow tangential sections are in fact, very small, closely spaced type C stylets.

Material

ABHR 1T	Cavity slide with twenty zoarial fragments. Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABHR 259 to 269	Thin sections. Horizon and locality as above.

GAGM 01-53 BXP, BYB, BYC	Three thin sections with seventy-eight zoarial fragments. Lower Limestone Series (Brigantian), Howood Quarry, Renfrewshire. Labelled as Ure's *Millepore* *Tabulipora* *urii* Fleming. John Young Collection, 1886. Relabelled as Cotypes of *Tabulipora* *minima* Lee (1912). One fragment was figured by him from slide 01-53 BYC, pl. 15, fig. 21.

Stratigraphical Range

Brigantian - Arnsbergian.

Occurrence

T. *minima* is rare in the Lower Limestone Series of Scotland and elsewhere has only been recorded from the shales above the Main Limestone, Hurst, North Yorkshire.

Tabulipora youngi Lee, 1912

Pl.151, figs.a-b; Pl.152, fig.a.

1912 Tabulipora youngi sp.nov. Lee, p. 164, Plate 15, figs. 19, 20.

Type

Lee (1912) did not erect a holotype for Tabulipora youngi, consequently a lectotype is proposed here for the species. The lectotype (GAGM. 01-53 bxr) is a thin section with several zoarial fragments, all derived from the same colony and showing longitudinal sections only. All the fragments are designated as lectotype for the species because they are derived from the same colony.

Emended Diagnosis

Tabulipora with fairly robust, erect ramose zoaria. Autozooecia are developed throughout a fairly narrow endozone region. Endozone walls are very thin, exozone walls are abruptly developed, of moderate thickness and of uniform width along their length. Ring septa are common, developed in the upper endozone and exozone region, with five or six per autozooecium, set slightly more than one diameter apart.

Description

Internal

Zoaria are fairly robust, with cylindrical branches ranging from 2 to 6 mm in diameter.

Autozooecia are developed throughout a fairly narrow endozone region. Autozooecia bend towards the exozone at a low gradually increasing angle, at the top of the endozone there is a fairly abrupt increase in the angle of divergence and zooecia diverge at a high angle, perpendicular to the zoarial surface throughout the length of the exozone wall.

In the endozone region interzooecial walls are very thin, exozone walls develop quite abruptly and are of moderate thickness, and of uniform width along their length approximately equal to that of autozooecia.

Ring septa are developed in the upper endozone and throughout the exozone region in autozooecia. There are between five and six per autozooecium and they are spaced more than one diameter apart, and may be interzooecially aligned. The foramena usually have an eccentric position and proximal sides of ring septa are usually thicker and better developed than distal sides.

Type A stylets occur and originate in the lower to middle exozone region.

<u>Dimensions</u> (N = 5)

	NM	Mn	Mx	$\bar{X}$
Z2	7	-	10	-
IWT	-	-	-	-
ZD	5	5.10	5.30	-
RD	46	5	6	-
ET	15	1.17	1.37	1.27
AXR	5	0.50	0.52	0.51

Discussion

Tabulipora youngi Lee is easily distinguished from other species of British Lower Carboniferous *Tabulipora* by its comparatively small, quite closely spaced autozooecial apertures, and its interzooecial walls which are of moderate and uniform width.

Material

GAGM 01-53 bxr	Thin section with 6 zoarial fragments. Lower Limestone Series (Brigantian), Hillhead quarry, Beith. Originally labelled as *Tabulipora Urii* Fleming. John Young Collection, 1884. Relabelled *Tabulipora youngi* Lee (1912); one fragment was figured by him Pl. 15, fig. 19.

Stratigraphical Range

Brigantian.

Occurrence

Tabulipora youngi is a very rare species and has been recorded only from the Lower Limestone Group of the Midland Valley of Scotland.

Genus Stenodiscus Crockford, 1945

Type species

Stenodiscus moniliformis Crockford, 1945.

Diagnosis

Stenoporid with zoaria erect ramose cylindrical irregularly dividing or rarely adnate. Endozone interzooecial walls are very thin, exozone walls are of variable width, normally quite thin and of uniform width, occasionally poorly moniliform. Skeletal laminae are continuous between adjacent autozooecia in the exozone. Basal diaphragms are common. Autozooecial apertures are large, circular to subangular and very closely spaced. Exilazooecia are common, as scattered individuals, and often occur in clusters as maculae. Stylets are abundant with large type A stylets situated at interzooecial angles, and small type C stylets commonly arranged in closely spaced uniserial rows along interzooecial walls.

Range

Carboniferous to Permian.

Stenodiscus tumida (Phillips, 1836)

Pl.153, figs.a-b; Pl.154, figs.a-b; Pl.155, figs.a-b; Pl. 156, figs.a-c; Pl.157, figs.a-b; Pl.158, figs.a-b; Pl.159, figs.a-b;

1836 Calamopora tumida Phillips, p. 200; Pl. 1, figs. 49-57.

1844 Favosites tumida (Phillips) McCoy, p. 193

1881 Monticulipora tumida (Phillips); Nicholson, p. 120, Pl.13, fig. 1.

1883 Monticulipora ? tumida (Phillips); Nicholson, p. 29; Fig. 3, a.b.

1884 Monticulipora tumida (Phillips); Vine, p. 381.

1912 Stenopora redesdalensis sp. nov. Lee, p. 153; Pl. 14, figs. 5a-5d; Pl. 15, figs. 1, 2.

Type

Phillips original type material of Calamopora tumida is now presumed lost and although two of his several listed collecting localities have been visited during the present study (Greenhow Hill and Brough) no material referable to the taxon has been found. Consequently it has not been possible to erect a neotype for Calamopora tumida Phillips.

Diagnosis

Stenodiscus with erect ramose zoaria of cylindrical, irregularly dividing branches or rarely adnate. Autozooecia are developed throughout a wide endozone region; endozone walls are very thin, exozone walls are of moderate thickness of uniform width, bulb-like, occasionally poorly moniliform. Basal diaphragms are quite common. Autozooecial apertures are large, circular to oval, very closely spaced. Exilazooecia are common, as scattered individuals or occurring rarely in clusters as maculae. Stylets are abundant, with large type A stylets situated at interzooecial angles and closely spaced small type C stylets between.

Description

External

Zoaria are robust, erect ramose, with cylindrical branches (2.7 to 7.7 mm in diameter) irregularly dividing. Rarely zoaria form thin adnate sheets.

Autozooecial apertures are large, closely spaced, circular to oval. Interapertural walls are usually well rounded, when subangular, the positioning of stylets along the midline of walls superimposes a pentagonal to hexagonal shape too autozooecial apertures.

Exilazooecia are common, they are small, circular to oval or irregularly shaped, usually occurring as scattered individuals, but are also often arranged in clusters as maculae. These are relatively small, irregularly developed on a zoarium, and may be circular to elongate and up to 2mm in diameter. Interapertural walls are commonly thicker between clusters of exilazooecia.

Quite large type A stylets (0.03 to 0.07 mm in diameter) are situated at interapertural angles and range in number from four to eight around autozooecial apertures. Closely spaced small type C stylets (0.005 to 0.015 mm in diameter) occur in single well defined rows between the large type A stylets, and range in number from eight to seventeen around autozooecial apertures.

Internal

Autozooecia are developed throughout a wide endozone. Autozooecia in the endozone bend toward the exozone at a constantly increasing angle, bending more abruptly at the top of the endozone becomeing orientated at high angles or perpendicular to the zoarial surface.

In the endozone interzooecial walls are very thin, exozone walls are quite abruptly developed and of quite narrow to moderate and uniform width throughout their length. They are commonly slightly undulatory but never truly moniliform.

In the endozone interzooecial walls are composed of skeletal laminae orientated parallel to the direction of growth. With the development of exozone regions skeletal laminae become orally convex and are continuous between adjacent autozooecia. As interzooecial walls are usually of equal width or club-shaped skeletal laminae bend over fairly gently between adjacent intrazooecial spaces. A median dark narrow, straight or irregularly sinuous zone is usually only visible in proximal portions of an exozone wall, where they are initially thinner and laminae bend over more sharply, but may also be developed intermittently along the length of an exozone wall.

Basal diaphragms are common, and are developed in the uppermost endozone and throughout the exozone in autozooecia. Normally two or three occur per autozooecium set slightly more than one diameter apart.

Exilazooecia are short, narrow cavities, originating in the middle and upper exozone wall. Their proximal extremeties are subangular to well rounded and they commonly expand gradually to the zoarial surface.

Type A stylets usually originate in the lower exozone wall, although some may develop in the upper endozone. The axial cores are quite narrow, up to 0.015 mm in diamter, and some may narrow abaxially. In the lower parts of the exozone wall they may be gently curved following the angle of divergence of interzooecial walls.

Type C stylets are short and narrow, closely spaced and developed in the middle and upper portions of the exozone wall. Some may have very poorly defined, very short cores.

Intrastylets are present in exozone walls. They are short, extremely narrow, and are composed of irregularly bifurcating nests of skeletal laminae and develop throughout the exozone. They may be orientated perpendicular or at oblique angles to the zoarial surface.

Dimensions (N = 24)

	Mn	Mx	$\bar{X}$
Z1	8.50	12.00	10.56
Z2	5.00	7.00	6.06
AD	0.25	0.32	0.29
IWT	0.04	0.09	0.07
ED	0.03	0.14	-
ZD	2.69	7.67	4.56
BZ	1	8	2
TE	0.41	1.52	0.80
AXR	0.48	0.86	0.65

Discussion

Stenodiscus tumida (Phillips) is recognised by its large fairly robust, erect ramose cylindrical irregularly dichotomising zoaria with large oval autozooecial apertures, bulb-like to commonly undulatory (poorly moniliform) exozone walls, with between two and three basal diaphragms per autozooecium.

Phillips (1836, p. 200) described the form Calamopora tumida. His description was very brief, his illustrations were of poor quality, and he only examined external morphological details.

It appears, as discussed by Nicholson (1883, p. 294) and Vine (1884, p. 378), that Phillips included at least two different forms under the name Calamopora tumida. One form figured by him (Pl. 1, figs. 49-51) is almost certainly the form described here as Stenodiscus tumida. The other figured by him (Pl. 1, figs. 52, 56, 57) appears to be referable to the genus Tabulipora; his figures 56 and 57 certainly show the occurrence of ring septa close to autozooecial apertures.

McCoy 1844 (p. 193) placed the taxon within the coralline genus Favosites and noted that because of the irregular form of zoaria different species and even genera may have been confounded under the one name. Nicholson (1881, p. 120) fully redescribed the taxon utilising internal morphological detail and placed it within the genus Monticulipora. Ulrich (1884) placed the taxon within the genus Batostomella.

Lee (1912) in his revision of British Carboniferous Trepostomata redescribed the taxon and placed it in the genus Stenopora. Additionally, he altered the species name to redesdalensis. However, such a change is considered to be untenable using present zoological nomenclature and consequently in the present study the original species name is used.

The present study has enable a re-assessment of the taxons generic position, and accordingly it is placed in the genus Stenodiscus (Crockford, 1944). The two genera Stenopora and Stenodiscus are morphologically similar, but Stenodiscus is distinguished by the occurrence of basal diaphragms, which are absent in the former. Stenodiscus paucitabulatus Wilson (1961, p. 98, Pl. 2, figs. 1, 2) is probably conspecific with S. tumida Phillips. Their external appearance is comparable, both have slightly moniliform or undulatory exozone interzooecial walls, axial ratios are very similar (0.6:1:0 in *S. paucitabulatus* compared with 0.65:1:0 in *S. tumida*) and both are crossed by between 2 to 3 basal diaphragms.

Material

ABR 1-15	Individual colony fragments in containers, from which acetate peels ABR 100 to 115 have been prepared. Lower Limestone Group, Redesdale Ironstone shale, (Asbian), Ridsdale, Northumberland.
ABR 27,-28,-33,-34,-38 to 41,-44,-47,-50.	Horizon and locality as above.
ABR 57	300 colony fragments in two containers. Horizon and locality as above.
ABR 200-209	Thin sections, horizon and locality as above.
AUGD 10642a	One specimen on a cavity slide. Horizon and locality as above. Nicholson Collection.
AUGD 10642b, 10642c, 10642d.	Thin sections, labelled *Monticulipora tumida*. Horizon and locality as above. Nicholson Collection.
AUGD 10135	468 specimens in a container with nearly all referable to *Stenodiscus tumida*, labelled as *Monticulipora tumida* (+ var *miliaria*). Locality and horizon as above. Nicholson Collection.
HM D.10	Multiple thin section of seven specimens labelled as *Monticulipora Heterotrypa tumida* Phillips. Locality and horizon as above. Young Collection.

HM D.17	Thin section labelled as <u>Monticulipora</u> <u>Heteropora</u> <u>tumida</u> Phillips, var <u>miliaria</u>. Locality and horizon as above. J. Young Collection 1883.
NM 430,G155.78	Card with 14 zoarial fragements of which one is referable to <u>S.</u> <u>tumida</u>. Horizon and locality as above. J. Dunn Collection.
NH 431,G155.79	Card with 9 zoarial fragments of which two are referable to <u>S.</u> <u>tumida</u>. An acetate peel was prepared from specimen 79/1. Horizon and locality as above. J. Dunn Collection.
NH 432,G155.80	Card with 15 zoarial fragments. Horizon and locality as above. J. Dunn Collection.
NH 433,G.155.81	Card with 17 zoarial fragemtns. An acetate peel was prepared from specimen 81/1. Horizon and locality as above. J. Dunn Collection.
NH 434,G155.82	Card with 20 zoarial fragments. Horizon and locality as above. J. Dunn Collection.

<u>Stratigraphical Range</u>

Asbian.

Family Dyscritellidae Dunaeva and Morozova, 1968

Type Genus

Dyscritella Girty, 1911

Diagnosis

Trepostomata with erect ramose cylindrical, dichotomous, rarely adnate zoaria. Interzooeical walls are very thin in the endozone but of variable thickness in the exozone and usually of uniform width. In the exozone, skeletal laminae are continuous between adjacent autozooecia. Basal diaphragms are common. Autozooecial apertures are of variable size, circular to oval, quite closely spaced. Exilazooecia are abundant, covering the interapertural walls between autozooecia, with maculae quite commonly developed. Stylets are abundant and structurally diverse.

Range

Carboniferous to Permian.

Genus Dyscritella Girty, 1911

Type species

Dyscritella robusta Girty, 1911

Diagnosis

Dyscritellidae with zoaria erect ramose cylindrical dichotomous, or rarely adnate. Interzooecial walls are very thin in the endozone, exozone walls are normally quite thin and of uniform width. In the exozone skeletal laminae are continuous between adjacent autozooecia. Basal diaphragms are uncommon. Autozooecial apertures are usually relatively small, circular to oval, quite closely spaced. Exilazooecia are abundant, covering interzooecial walls between autozooecial apertures, with maculae quite commonly developed. Sytlets are abundant and structurally diverse.

Range

Carboniferous.

Dyscritella miliaria (Nicholson, 1881)

Pl.160, figs.a-d; Pl.161,figs.a-c; Pl. 162, figs.a-b;
Pl.163, figs.a-b; Pl.164, figs.a-b.

1881 *Monticulipora tumida* var *miliaria* Nicholson, p. 123, Pl. 3, fig. 2.

1912 *Dyscritella miliaria* (Nicholson), Lee, p. 178, Pl. 16, figs. 9,10.

Type

In the present study only some of Nicholson's syntypic material from the collections of Aberdeen University Geology Department have been examined, and consequently it is not possible at present to erect a lectotype. Most of the material examined in the present study is topotype material coming from Nicholson's original collecting locality at Ridsdale, Northumberland in the Redesdale Ironstone Shale.

Emended Diagnosis

Dyscritella with fairly robust, erect ramose, cylindrical irregularly dividing zoaria, rarely occurring as thin adnate sheets. In erect ramose forms autozooecia are developed throughout an endozone region of moderate diameter. Endozone walls are very thin, exozone walls are quite thin, club-like or of uniform width between autozooecia. Basal diaphragms are quite common. Autozooecial apertures are of moderate size, circular to oval and quite closely spaced. Exilazooecia are abundant between autozooecia and maculae are commonly developed. Stylets are abundant with types B and C stylets developed.

Description

External

Erect ramose zoaria are fairly robust with cylindrical branches (3 to 7 mm in diameter) which divide irregularly. Adnate zoaria are rare and occur as thin sheets up to 1 mm thick.

Autozooecial apertures are of moderate size, circular to oval and are quite closely spaced. Occasionally apertures have complete low thin rounded rims. Interapertural wall dimensions are highly variable with autzooecia generally slightly less than their own diameter apart. Interapertural walls are flat and normally covered with exilazooecia.

Exilazooecia occur as very small irregularly shaped, closely spaced structures and are very abundant. They may be subangular to well-rounded, and commonly range from 0.05 mm to 0.08 mm in diameter. Normally a single 'row' is developed between autozooecia and very small clusters of several exilazooecia occur at interapertural angles. However, there is considerable variation in the development of exilazooecia within and between zoaria. In some, exilazooecia occur only occasionally in small clusters at interapertural angles, while in other zoaria they cover the entire surface of interapertural walls, being more elongate and present in a single row where interapertural walls are narrower, and are only absent where interapertural walls are too narrow.

Maculae are commonly developed on zoaria. They are composed entirely of very closely spaced exilazooecia which may be of a larger than average size than those occurring between autozooecia. Generally maculae are of irregular shape, normally elongate, occasionally circular, with a maximum diameter of 1.3 mm. They are absent in some zoaria, but frequent and regularly developed in others.

Stylets are abundant with types B and C stylets developed. Type B stylets are of moderate size (0.025 to 0.6 mm in diameter), and are situated close to the rims of autozooecial apertures at interapertural angles and range from three to seven in number around an aperture. They are only occasionally developed between exilazooecia.

Type C stylets are small (0.006 to 0.02 mm in diameter), very numerous and are closely spaced between the larger type B stylets around the rims of autozooecial apertures and between exilazooecia, and range in number from five to twelve around an autozooecial aperture.

Internal

Autozooecia are developed throughout an endozone region of variable diameter. Autozooecia bend towards the exozone at low but constantly increasing angles, near the top of the endozone there is a rapid increase in the angle of divergence and autozooecia become orientated at high angles, often perpendicular to the zoarial surface.

Endozone interzooecial walls are very thin, exozone walls develop quite abruptly, accompanying the rapid increase in the angle of divergence of autozooecial tubes, and are quite thin, club-like, or more usually of uniform width. Occasionally interzooecial walls may be somewhat undulatory.

In the endozone interzooecial walls are composed of skeletal laminae orientated parallel to the direction of growth. With the development of the exozone wall skeletal laminae become orally convex and are continuous between adjacent autozooecia. As exozone walls are usually of uniform width, skeletal laminae bend over fairly gently between adjacent intrazooecial spaces. A median dark, narrow, straight or irregularly sinuous zone is usually only visible in proximal portions of an exozone wall where they are initially thin and laminae bend over more abruptly, but may be intermittently developed along the length of an exozone wall.

Basal diaphragms are quite commonly developed normally in the upper endozone region, but occasionally also in the exozone region. Normally one or two (up to four) occur and are spaced at slightly more than one diameter apart. Some interzooecial alignment of diaphragms is evident.

Exilazooecia occur as narrow tubes of variable width, quite closely spaced and their development is restricted to the exozone wall in which they may originate at different levels. The proximal extremeties of exilazooecia are subangular to rounded, their sides are slightly undulatory and they generally widen towards the zoarial surface. Where exozone walls are relatively wide, the closely spaced exilazooecia give the exozone wall a digitate appearance.

Type B stylets and type C stylets occur. Type B stylets originate quite low down in exozone walls and have poorly to well defined narrow axial cores across which skeletal laminae are continuous. Type C stylets originate in the upper portion of the exozone wall. Intrastylets are present as irregularly developed very narrow short abaxially convex nests of skeletal laminae in the exozone wall, and do not extend towards the zoarial surface.

Dimensions (N = 18)

	Mn	Mx	$\bar{X}$
Z1	17.00	26.00	19.00
Z2	8.00	10.00	9.00
AD	0.13	0.21	0.18
IWT	0.04	0.10	0.70
ED	0.04	0.07	0.06
ZD	2.39	7.27	4.03
BZ	0	5	-
ET	0.40	1.87	0.76
AXR	0.46	0.46	0.65

Discussion

Dyscritella miliaria (Nicholson) is easily recognised by its very slender erect ramose zoaria with relatively small oval to circular autozooecial apertures, the abundance of very small exilazooecial apertures which usually cover interapertural walls between autozooecia, the common occurrence of maculae and of basal diaphragms in autozooecial tubes.

Nicholson (1881, p. 123) erected a new variety of *Monticulipora tumida*. The variety (var *miliaria*) was distinguished from the species s.s. by its smaller autozooecial apertures and the abundance of exilazooecia (he used the term 'mesopores').

Lee (1912, p. 178) redescribed the taxon altering its genetic position and placing it within the newly erected genus *Dyscritella* Girty 1911, and elevated the varietal name to species level. Girty's original generic definition stated that both autozooecia and exilazooecia lacked diaphragms (he used the term tabulae). However, Lee (1912) described two British forms (including *Dyscritella miliaria*) which possessed diaphragms (Lee also used the term tabulae) and he correctly proposed a modification of the original generic diagnosis.

Material

ABP 95	5 specimens in a container. Alston Group, Fifth Limestone (Asbian), Penruddock nr. Penrith, Cumberland.
ABR 117,-118	Two specimens in containers. Lower Limestone Group, Redesdale Ironstone Shale (Asbian), Ridsdale, Northumberland. Acetate peels have been prepared from the specimens.
ABR 230,-231	Thin sections. Locality and horizon as above.
AUGD 10135.	468 specimens in a container labelled as *Monticulipora tumida* (+ var *miliaria*) of which only several specimens are referable to *Dyscritella miliaria*. Locality and horizon as above. Nicholson Collection.
HM D.11	Five specimens in a cavity slide. Labelled as *Monticulipora Heterotrypa miliaria*. Whichhope Burn near Plashetts (Asbian), Northumberland. J. Rhodes Donor 1883.
HM D.16	Multiple thin section of 6 specimens, labelled as *Monticulipora Heterotrypa* var *tumida* Nicholson. Locality and horizon as above. J. Young Collection 1883.

HM D.20	Multiple thin section of 19 fragments. Labelled as *Moniculipora Heterotrypa miliaria* Nicholson. Carboniferous Limestone series, Wickope, Cumberland (Asbian), J. Young Collection 1880.
HM D.21	Multiple thin section of three specimens. Labelled as *Monticulipora Heterotrypa miliaria* Nicholson. Carboniferous Limestone, Wickhope Burn, near Plashetts, Northumberland. J. Rhodes Donor.
HM D.22	(Multiple thin section of 20+ specimens. Labelled as (Monticulipora) *Heterotrypa miliaria* Nicholson. Lower Limestone series, Kirklanholme, E. Kilbride, (Brigantian?). J. Young Collection 1890.
NH 430,G155.78	Card with 14 zoarial fragments of which 13 are referable to *D. miliaria*. An acetate peel has been prepared from 78/4. Redesdale Ironstone Shale (Asbian), Ridsdale, Northumberland. J. Dunn Collection.
NH 431,G155.79	Card with 9 zoarial fragments of which 7 are referable to *D. miliaria*. Acetate peels have been prepared from 79/2,-79/5,-79/7,-79/9. Locality and horizon as above. J. Dunn Collection.

Stratigraphical Range

Asbian (- Brigantian?).

Occurrence

Dyscritella miliaria is uncommon in British Lower Carboniferous strata, being recorded in Asbian strata from Northumberland, Cumberland and the Midland Valley of Scotland.

The Double-Walled Concept of Growth Applied to trepostomes

All available evidence suggests that trepostomes were double-walled bryozoans. The main reasons for this are discussed below and are based solely on the material examined in the present study.

(a) The essentially equal extent of distal growth of neighbouring autozooecia in erect ramose forms suggests the existence of an orally situated colony wide depositing epithelium controlling growth.

(b) The laminar microstructure of exozone interzooecial walls which are orally flexed toward the zoarial surface suggests that calcareous deposition took place on the outermost surfaces of zoaria by an orally situated depositing epithelium.

(c) The continuity of skeletal laminae across inferred zooecial boundaries suggests the existence of a colony-wide depositing epithelium.

(d) Basal diaphragms in autozooecial chambers were secreted by epithelial tissues situated on their oral sides because the diaphragms are orally flexed at their junctions with vertical interzooeical walls and continuous with laminae lining interzooecial walls distal to them. Basal diaphragms were evidently deposited by an epithelium lining autozooecial chambers which was continuous with an externally situated epithelium.

(e) In some of the stenoporid trepostome taxa examined exozone interzooeical walls are characterised by the regular development of monilae. These bilaterally symmetrical thickenings are separated by thin-walled portions giving exozone interzooecial walls a bead-like appearance. Monilae are typically interzooecially aligned forming layers parallel to the growth surface (the zoarial surface), and the similarity of shape and size of monilae in any layer suggests that these layers are zoarial growth increments. Individual increments (consisting of a proximal thin walled portion and a monila) may extend from the growth tip down the sides of a zoarium considerable distances before merging with previously formed increments. This suggests the existence of at least semi-colony wide control of growth by an orally situated secreting epithelium.

(f) Moniliform exozone interzooecial walls are possibly related to regeneration-degeneration cycles of soft parts, with monilae representing periods of polypide regeneration and function while thin walled portions represent stages of polypide degeneration. The typical interzooecial alignment of monilae suggests at least semi-colony wide control of growth by an orally situated secreting epithelium.

(g) Ring septa are developed in autozooecial tubes in the species of Tabulipora examined in the present study. In exozone regions ring septa are close and very regularly spaced. They are commonly associated with monilae and consequently they often occur at similar levels in adjacent zooecial tubes. This suggests at least semi-colony wide control of growth by an orally situated secreting epithelium.

(h) In all the stenoporid trepostome taxa examined stylets are regularly arranged, situated at interapertural angles, and small type C stylets are closely spaced between often in uniserial rows along interapertural walls. Following the functional interpretation of stylets (Chapter 3, pp.46-52) it appears that type A stylets acted as loci of attachment for such epithelial tissues that probably covered the entire surface of the zoarium, while the small type C stylets acted as stablisers for the epithelial tissues.

Applying the double-walled model of growth in recent hornerid and lichenoporid cyclostomes the above lines of evidence suggest than an externally situated colony wide inner hypostegal epithelium and its internal equivalent the zooidal epithelium (with which it was continuous), secreted all the calcareous skeleton. In trepostomes interzooecial walls are non-porous and an externally situated hypostegal coelomic space was probably responsible for nutrient interchange between autozooecia across the colony. External to the coelomic cavity an outer eustegal epithelium was responsible for secreting only the cuticular cover of the colony including the terminal vestibular membranes of zooids.

Discussion of the Coefficients of Variation of selected parameters measured on taxa within the Order Trepostomata (see Table 3)

The calculated CV's in the present study are based on the measurement of parameters undertaken on small colony fragments. Although erect ramose trepostomes are composed of large irregularly dichotomising cylindrical branches, complete colonies are very rare as they are easily fragmented post mortem.

As a consequence of measuring parameters on small colony fragments it should be noted that the CV's of some of the parameters are not a true expression of the within, and between colony morphological variation displayed by a taxon (as was also the case for the rhabdomesids). Because zoaria form irregularly dichotomising cylinders with branches of variable diamter, for parameters such as zoarial diameter and exozone thickness within colony CV's (in table 3) of these parameters should be significantly higher than those stated. The within colony CV's are based on small branch fragments where zoarial diameter, and exozone thickness are fairly constant. The between colony CV's for these parameters reflect only the difference in zoarial diameter and exozone thickness between branch fragments. The examination of a number of complete colonies involving the measurement of these parameters would obviously significantly alter the values of within and between colony CV's. This would probably result in the within colony CV's for these parameters being elevated and values of between colony CV's lowered.

However, all other parameters do not show any significant variation in their values whether a fragment or a more complete colony is examined. Consequently for these parameters, the CV's stated in table 3 are considered to be a true expression of the within and between colony morphological variation.

	Z1			Z2			AD			IWT			ED			MZAD			ET			AXR		
	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T
Tabulipora urii	15.50	10.37	10.51	11.50	5.60	7.31	15.30	9.61	11.51	21.45	17.51	17.40	29.58	14.93	14.85	9.51	31.05	39.50	8.50	48.51	40.34	8.61	19.51	18.95
Tabulipora howsii	14.35	11.16	-	13.31	7.05	-	18.60	5.60	-	26.48	12.58	-	23.60	18.81	-	13.38	38.35	-	8.35	31.94	-	8.10	10.08	-
Tabulipora minima	12.31	3.41	-	19.60	7.30	-	14.85	7.63	-	23.81	18.00	-	27.75	17.30	-	8.95	19.65	-	5.32	51.05	-	5.30	15.97	-
Stenodiscus tumida	12.60	5.96	-	14.50	7.30	-	21.23	9.20	-	25.31	18.57	-	27.60	18.30	-	9.32	22.75	-	9.41	39.48	-	5.81	32.23	-
Dyscritella miliaria	15.48	4.10	5.30	12.34	3.48	6.39	9.52	5.23	8.68	36.30	16.51	18.98	13.30	10.51	13.80	7.54	32.88	33.21	5.31	60.63	38.31	3.21	25.02	26.30
$\bar{X}$	14.05	7.40	7.90	14.25	6.55	6.85	15.92	7.45	10.10	26.67	16.63	18.23	24.00	15.97	14.32	9.74	28.94	36.35	7.38	46.32	39.32	6.21	20.56	22.62

External Morphological Characters

Zooecial Parameters

Number of Autozooecial Apertures in 1 mm^2, and in a 2 mm line.

Within colony CV's are fairly high for the two parameters, ranging from 11.50 to 19.60 and are significantly higher, about twice as large as those between colony CV's. Within colony CV's are fairly high because, unlike rhabdomesids, there is no regularity in the disposition of autozooecial apertures on the zoarial surface. The irregularity is explained by the fact that in addition to new autozooecia being budded in well defined gently arched groups new ones are developed between these groups. Their intercalation and the common development of exilazooecia in the exozone effects the arrangement of autozooecial apertures on the zoarial surface. Other exogenous factors such as microenvironment may significantly contribute to the high within colony CV's.

Between colony CV's are significantly lower, ranging between 4.0 to 11.16, and reflect the balancing out of this within colony variation when a number of colonies in a population are examined.

Autozooecial Apertural Diameter (AD): Only one parameter of apertural diameter was measured in trepostomes due to the irregularity in the shape of autozoocial apertures.

Within colony CV's are quite high, ranging between 9.52 and 21.33 ($\bar{X}$ 15.92). These high values are explained by the irregular budding of autozooecia and by the common development of exilazooecia in the exozone. The common intercalation of new autozooecia between well defined gently arched groups of new autozooeica and the occurrence of exilazooecia affects the arrangement, hence the shape and size of autozooeical apertures. Exogenous factors such as microenvironment may help also to account for the fairly high CV's.

Between colony CV's are significantly lower, ranging between 5.23 and 9.61 ($\bar{X}$ 7.45) and reflect the balancing out of such within colony variation when a number of colonies in a population are examined.

Interapertural Wall thickness (IWT): Within colony CV's are very high ranging between 21.45 and 36.30 ($\bar{X}$ 26.67), and are explained by the high irregularity in the spatial arrangement of autozooecial apertures, and the high variability in autozooecial apertural dimensions.

Although between colony CV's are significantly lower they are still fairly high ($\bar{X}$ 16.63) showing the high morphological variation which exists between colonies in a population.

Exilazooecia Diameter (ED): Within colony CV's are very high ranging from 13.30 to 29.58 ($\bar{X}$ 24.00). These values reflect the degree of variation which exists commonly in their development. In stenoporid trepostomes exilazooecia develop commonly at various levels in the exozone wall, and usually they increase in diameter toward the zoarial surface. Consequently, as they develop at various levels in the exozone wall in a colony, there is a large variation in their apertural dimensions and this is reflected in the high within colony CV's for this parameter. Factors such as variability in the spacing of autozooecia also influences exilazooecia diameter.

In Dyscritella miliaria within colony CV's are significantly lower than average, because exilazooecia are regularly developed in this taxon. They are commonly so numerous on interapertural walls as to isolate autozooecial apertures, and they are very closely spaced. Generally they are developed at a similar level in the exozone of a zoarium, and this is reflected in the significantly lower CV's than for other taxa.

Between colony CV's are significantly lower than within colony CV's ranging between 10.51 and 18.81 ($\bar{X}$ 15.97) and this reflects the balancing out of the within colony variation when a number of colonies in a population are examined.

Zoarial Diameter (ZD): As discussed in the introduction to this section the calculated CV's of this parameter do not reflect the true degree of morphological variability within and between colonies. The low within colony CV's reflects only the fairly high genetic control of growth with branches maintaining a fairly constant diameter. Constant branch diameter is maintained during the intercalation of new zooecia by the outer half of all zooids in a generation bending progressively away from the central axial line of the branch into the exozone. Constant branch diameter is maintained despite the irregular development of new autozooecia between successive growth phases.

Internal Morphological Characters

Zooecial Parameters

Exozone Thickness (ET): As with zoarial diameter the calculated CV's of this parameter do not reflect the true degree of morphological variation within and between colonies. However, the low within colony CV's stated in table 3, ranging from 5.31 to 9.41 ($\bar{X}$ 7.38), do reflect the high genetic control over zoarial growth with the change from endozone to exozone growth occurring at fairly constant diameters in a branch.

Axial Ratio (AXR): Within colony CV's are low, ranging from 3.21 to 8.10 ($\bar{X}$ 6.21), and reflects a high genetic control over zoarial growth, with the change from endozone to exozone growth occurring at constant diameters in a branch. There appears to be no significant variation in the axial ratio in a colony.

Between colony CV's are significantly higher and range between 10.08 to 32.24 ($\bar{X}$ 20.56) and reflect the high degree of genetic variation in the mode of development of autozooecia between colonies in a population.

The morphological parameters utilised in the present study of some trepostomatous Bryozoa show the existence of considerable morphological variability occurring in even a single colony of a taxon. Such variability is readily accounted for by the mode of development of autozooecia in a colony. However, the measurement of such parameters is necessary since it is by their measurement that such variability can be quantitatively expressed.

It should be noted that the sole measurement of externally based morphological parameters is not sufficiently useful to differentiate taxa. Indeed in the stenoporid trepostomes examined in the present study it is not possible to differentiate species on external appearance alone, and study of orientated sections revealing internal morphological characters is essential. It is with these sections that characters such as exozone wall appearance, occurrence of diaphragms, and ring septa may be described qualitatively thus allowing the differentiation of species.

CHAPTER VIII

ORDER CYSTOPORATA Astrova, 1964

Diagnosis

Stenolaemata with adnate or erect ramose bifoliate rarely fenestrate zoaria. Autozooecia are tubular, of variable length and may be budded on or above a basal lamina in adnate forms, or from a median wall in bifoliate and fenestrate zoaria. Autozooecia are initially recumbent and become erect when mature. Autozooecial walls may be entirely compound, or partly bound by a simple interior wall. Cystiphragms and basal diaphragms are common. Autozooecia may be isolate, separated by extra-zooidal vesicular tissues and stereom, or with compound interzooecial walls occasionally with communication pores. Autozooecial apertures are large, circular, oval to pyriform often with lunaria at their proximal extremeties. Exilazooecia and intra-autozooecial polymorphs are common, basal polymorphic zooecia and gonozooecia are rare. Monticules are common.

Range

Ordovician - Permian.

Discussion

Astrova (1964) established the Order Cystoporata to include those families within the Cyclostomata and Trepostomata which she considered to have phylogenetic affinities close to some primitive Gymnolaemates, and which display several unique morphological characters, and some other characters found in few other tubular bryozoans. There are two suborders, the Ceramoporoidea (range -

Ordovician to Lower Devonian) and the Fistuliporoidea (range - Silurian to Permian).

SIGNIFICANT ASPECTS OF CYSTOPORATE SKELETAL MORPHOLOGY

(a) The often isolate nature of zooecia in the suborder Fistuliporoidea, which may be separated by large amounts of extrazooidal skeletal material termed vesicular tissue.

(b) New autozooecia within the suborder Fistuliporoidea may be budded on or above a basal lamina, and may develop directly on extrazooidal vesicular tissues.

(c) While most double walled tubular bryozoans have compound interior zooecial walls, in many fistuliporids part of an autozooid may be bound by a simple interior wall. This may not occur in other double walled Bryozoa.

(d) The Ceramoporidae probably had two means of interzooidal communication: between zooids via the coelomic fluid in the hypostegal coelom, as in other double walled bryozoans, and secondly between zooids via communication pores in zooecial walls. This latter type is extremely rare among Palaeozoic tubular Bryozoa.

(e) Most cystoporates have a lunarium developed at the proximal extremeties of autozooecia and projecting above the general zoarial surface and above the peristomes of autozooecia. Lunaria consist of thicker and often microstructurally distinct deposit developed throughout the exozonal region of autozooecia.

(f) Members of the suborder Fistuliporoidea are characterised by the occurrence of large amounts of vesicular tissue, which is usually structurally simple, and abuttress between isolated or partly isolated zooecia.

(g) Polymorphic zooecia are common in cystoporates. In the ceramoporids exilazooecia are usually developed, but basal zooidal polymorphs may also occur. Additionally, the presence of funnel cystiphragms, flask shaped chambers in the Fistuliporoidea and Ceramoporoidea, suggests that intra-autozooecial polymorphism was widespread. Some fistuliporids also possessed gonozooecia.

In the present study some taxa within the Fistuliporoidea have been systematically studied.

SUBORDER FISTULIPOROIDEA Astrova, 1964

Diagnosis

Cystoporata with adnate, or erect ramose bifoliate rarely fenestrate zoaria. Autozooecia may be budded on or above a basal lamina in adnate forms, or from a median wall in bifoliate and fenestrate forms. Autozooecia are initially recumbent, soon becoming erect and diverge to the zoarial surface at high angles. Autozooecia are commonly isolate, and are separated by extra-zooidal vesicular tissues and stereom. Vesicular tissues are structurally simple, rarely compound. Autozooecial apertures are large, circular, oval to pyriform, often with a lunarium. The lunarium is usually compound, and is developed throughout most of the length of the zooecium and may or may not be microstructurally continuous with lateral and distal zooecial walls. Basal diaphragms and cystiphragms are common. Intra-autozooecial polymorphic zooecia are common, gonozooecia are rare. Communication pores are absent. Monticules are common.

Range

Silurian to Permian.

Discussion

When Astrova (1964) erected the suborder Fistuliporoidea, only taxa within the trepostome family Constellariidae and the cyclostome familty Fistuliporidae were placed in it. Utgaard (1973) increased the number of families within the suborder, which now includes the Actinotrypidae, Anolotichiidae, Botrylloporidae, Constellariidae, Fistuliporidae, Goniocladiidae, Hexagonellidae, Sulcoreteporidae and Rhinoporidae.

In the present study some taxa within the families Fistuliporidae, Goniocladiidae and Sulcoreteporidae have been systematically examined.

SIGNIFICANT ASPECTS OF FISTULIPOROID SKELETAL MORPHOLOGY

The following discussion is based principally on the definitive work on the Cystoporata by Utgaard (1973) and on the five taxa examined in the present study.

Budding

In many fistuliporoids new autozooecia are normally partly or totally isolated at the basal layer (e.g.Fig.82;Pl.172,fig.a) or median wall by extrazooidal vesicular tissues (e.g. Pl.182, fig. b). Especially in the Fistuliporidae new autozooecia may develop not only at a budding edge on the basal lamina, but also above the basal lamina on older zooecial walls or directly on vesicular tissues in the exozone or anywhere on the free surface of the colony (see Fig. 82). New autozooecia are initially recumbent, conical, expanding distally and are hemispherical in cross-section. The proximal recumbent portion is short and zooecia soon become erect, reach their maximum dimensions and commonly have a cylindrical cross-section (see Figs.82,83). Autozooecia which develop above a basal lamina or median wall commonly have only an extremely poorly developed recumbent portion.

Extrazooidal Vesicular tissues and Stereom

Fistuliporoids are characterised by large amounts of extrazooidal skeletal material termed vesicular tissues and stereom which served as a buttress between isolated or partly isolated autozooecia (fig.82; e.g. Pl.169, fig. a).

Vesicles are commonly hemispherical to box-like, and are bounded by calcified walls and a roof. Vesicle walls and roof are deposited as one curved plate and are typically thin walled. In most fistuliporoids, and in all the taxa examined vesicular tissues consist of two layers: a thin dark grey inner granular primary layer on which lies a thicker, pale grey secondary granular-prismatic layer. Individual curved plates are stacked on one another and on the upper layer of adjacent vesicles (Fig. 84; e.g. Pl.165,figs.a,b). In most fistuliporoids, vesicles are thin walled throughout the thickness of the zoarium. In adnate fistuliporids, in the basal region of a zoarium, where autozooecia budded on the basal lamina are recumbent, vesicles form low rounded, hemispherical units, irregularly arranged and of a larger than average size. Distally where these autozooecia are erect vesicles form inverted cup-like, rectangular to box shaped units, and are more regularly arranged in vertical stacks (see Fig. 84).

In many fistuliporoid families, zoaria are ramose, erect, bifoliate rarely anastomosing and autozooecia are budded on a median wall. In the endozone, where autozooecia are recumbent, vesicles are typically thin walled, however in the exozone region, where autozooecia become erect, vesicles become thick walled, and commonly vesicular cavities become partly or entirely infilled by dense calcareous tissue termed stereom (e.g. pl. 182 fig. b).

The nature of vesicular tissues and stereom suggests that they were deposited as single curved plates, from an epithelium on the outside of vesicles, and contained no viable soft parts and were not zooecia.

Lunaria

Lunaria are commonly developed in fistuliporoids. They are located at the proximal extremity of each autozooecial aperture, and project above the general zoarial surface and above the peristome of the aperture (e.g. pl.173, fig. b). Lunaria may vary from small, slight and collar-like, or large and helmet-like features arched over the top of the autozooecial aperture. The lunarium is commonly developed early in zooecial ontogeny, and is a distinct skeletal structure, usually significantly thicker than lateral and distal zooecial walls (see Fig. 83, Pl. 174, fig. b).

In most fistuliporoids, and in the taxa examined which have granular and granular-prismatic wall microstructure, the microstructure of the lunarial deposits is broadly similar to that of the rest of the skeleton. The lunarium is compound, composed of a thin dark grey granular layer bound on both sides by thicker, lighter pale grey granular-prismatic layers and is commonly thicker towards the zoarial surface (Fig. 83).

Autozooecial Wall Composition

While most double walled tubular bryozoans have compound zooecial walls, in many fistuliporoids part of the autozooid may be bound by a simple interior wall. This is well illustrated in the taxa examined in the present study. The proximal lunarial wall is always compound and may or may not be microstructurally continuous with lateral and distal walls which are of variable composition. This variation occurs between zooecia within the same zoarium. In some autozooecia lateral and distal walls are compound, and are microstructurally continuous with the thicker proximal lunarial wall, (e.g. Figs. 85,86, Pl. 174, fig. a). In other autozooecia they are composed of the superimposed vertical stacks of vesicular tissues, abut abruptly against the apices of the proximal lunarial wall and are structurally simple (e.g. Figs. 85, 86). In this situation the outer secondary thicker pale grey granular-prismatic layer lines the autozooecium, and lateral and distal walls may be quite undulatory (Figs. 85, 89 ; pl.171 fig. b).

In cases where both the proximal lunarial and lateral and distal walls of an autozooecium are compound, walls were formed by a simple infolding of the inner (hypostegal) epithelium. This resulted in the common development of a low peristome-like rim around the apertures on lateral and distal walls away from the proximal lunarium (Fig. 85).

Where lateral and distal walls are simple, no peristome is formed. When the proximal lunarial wall is formed from an infolding of the inner hypostegal epithelium at lateral and distal walls, the inner zooidal epithelium simply curved up and out to continue as the inner hypostegal epithelium (Fig. 85).

Basal Diaphragms

Basal diaphragms are very commonly developed in fistuliporoids in the mature region of autozooecial tubes, and consist of a thin, light grey granular-prismatic layer, and abut against the light grey granular-prismatic layer of zooecial walls (e.g. Pl.170, fig. c). Their development is thought to coincide with regeneration and degeneration cycles of polypides in autozooecia and the oral extension of autozooecial walls (see Chapter 2, pp.26-27).

Interzooecial Communications

In fistuliporoids, there was no means of interzooecial communication such as interconnecting 'communication pores', and communication was only possible through the hypostegal coelom above the zoarial surface.

Monticules

Monticules are commonly developed in the Fistuliporoidea. In the adnate fistuliporids especially, they were extremely common and are very regularly arranged in individual colonies. They form low rounded elevations above the general level of the zoarial surface, and consist of a small central area, round to oval, devoid of autozooecial apertures, with only vesicles of a larger than average size occurring. On the sloping surfaces away from the crests autozooecial apertures are irregularly to radially arranged around the monticular centre with the lunarium on the side of the aperture nearest the monticular centre. Autozooecia situated on monticule slopes have slightly larger diameters, and apertures are spaced slightly further apart than on the normal zoarial surface (e.g. pl.167, fig. b). The possible function of monticules with reference to the fistuliporids has already been discussed (see Chapter 3, p.34).

Polymorphic zooecia

Fistuliporoids usually have only normal feeding autozooecia and some larger monticular autozooecia. The larger monticular autozooecia are comparable in all respects with intermonticular zooecia. As a result, Utgaard (1973, p. 342) suggested that large monticular zooecia housed slightly larger feeding autozooids and were not reproductive or brooding structures.

Intra-autozooecial polymorphism is quite common in fistuliporoids. Normal autozooecial chambers may have a modified shape produced by funnel cystiphragms forming flask shaped chambers.

Funnel cystiphragms were possibly secreted by retracted or newly proliferated zooidal epithelia. The flask shaped chambers appear to have contained modified polypides and were not formed by normal autozooids but can alternate with portions of normal autozooecial tube and commonly occur at similar levels in adjacent autozooecia. (Utgaard, 1973, p. 339). The function of such modified polymorphic autozooecia is uncertain, but a reproductive function seems feasible. Boardman (1971, p. 25-26) who suggested the term intra-autozooecial polymorphism, postulated that they could be male reproductive zooids.

Some fistuliporoids developed zooecia with a normal autozooid aboral portion and an expanded hemispherical oral portion which may cover adjacent extrazooidal vesicular tissues. On the zoarial surface they form typically low round hemispherical blisters, each with a small circular terminal and marginal pore, commonly occurring at the same level in a colony and very few in number compared to normal autozooecia. Their structure, size, shape and number suggest they had a reproductive function, involved with the production of eggs and brooding of embyos. Their similarity with gonozooecia in some recent cyclostomes prompted Utgaard (1973, p. 342) to use the term gonozooecia for these structures. Gonozooecia and flask shaped chambers have not as yet been observed occurring together.

Family Fistuliporidae Ulrich, 1882

Type genus

Fistulipora McCoy, 1850

Diagnosis

Fistuliporoidea with adnate, rarely erect ramose zoaria. Autozooecia, budded on a basal lamina along a growing edge, but may also bud above the basal lamina directly on other autozooecia or on vesicular tissues, over the whole colony surface. Vesiclar tissues are structurally simple and thin walled. Autozooecial apertures large, circular to pyriform commonly with a lunarium. The lunarium is compound, and is developed throughout most of the length of the zooecium, and may be microstructurally continuous with compound thin lateral and distal zooecial walls, or is distinct with lateral and distal zooecial walls structurally simple composed of superimposed stacks of vesicular tissue. Basal diaphragms and cystiphragms are common. Intra-zooecial polymorphs quite common. Monticules are common and regularly arranged.

Range

Silurian - Permian.

TAXONOMIC PROCEDURE

The parameters measured in the present morphological study of some fistuliporids has been derived largely from the scheme developed by Warner and Cuffey (1973). Their comprehensive scheme involved the quantification of twenty-four individual parameters. However, in the present study, only the characters in Warner and Cuffey's scheme which exhibited the lowest levels of morphological variability and were of obvious taxonomic value have been utilised. Some of the abbreviations used for the parameters measured in the present study differ from those used by Warner and Cuffey.

The measurement of these parameters was carried out in the standard manner using the zoarial surface, thin sections and acetate peels prepared in specific orientations: shallow tangential, longitudinal and transverse (see Fig. 87).

No measurements were made in monticular regions, near possible ancestrulae, in obliquely orientated sections or in diagenetically altered zooecia and zoaria.

External Morphological Characters

Zoarial Parameters

Intermonticular Distance (MS): Measured as the distance between the centres of adjacent monticules.

Morphological Characters measured in Tangential Section

Zooecial Parameters

(Z1): The number, or range in the number of complete autozooecial apertures in a one square millimetre area.

(Z2): The number, or range in the number of autozooecial apertures along a two millimetre line parallel to the zoarial growth direction.

Longitudinal Autozooecial Apertural Diameter (LAD): Measured parallel to the proximal-distal axes of the zooecium, between the inner surface of the dark wall layer of the lunarium and the zooecial wall opposite the lunarium.

Transverse Autozooecial Aperture Diameter (TAD): Measured transverse to the proximal-distal axis of the zooecium, between the inner surfaces of the dark wall layer, of opposite lateral walls of a zooecium at the widest expanse of the aperture.

Longitudinal Interapertural Distance (LID): Measured as the minimum distance between the proximal limit of a lunarium and the exterior surface of the dark wall layer of the nearest zooecium toward which the lunarium is orientated.

Transverse Interapertural Distance (TID): Measured as the minimum distance between the exterior surface of the dark wall layer of a zooecium and the nearest zooecium lateral to it.

Lunarium Depth (LD): The depth of the lunarial cavity measured as the maximum transverse distance from a line connecting the ends of the lunarium to the apex of the inner lunarial surface.

Lunarium Thickness (LT): The maximum thickness of the lunarium, measured between the proximal and distal surfaces of the lunarium.

Lunarium Width (LW): The maximum width of the lunarium, measured between parallel tangents to the outer surfaces of the lunarial ends.

Zoarial Parameters

(V1): The number of vesicles in a one-millimetre line, between autozooecia parallel to the growth direction.

Morphological characters measured in Longitudinal and Transverse Section

Zooecial Parameters

(DZ): The number, or range in the number of basal diaphragms in a mature zooecial tube.

Zoarial Parameters

(V2) (not recorded by Warner and Cuffey): The number, or range in the number of vesicles in a one millimetre line parallel to the growth direction of autozooecia.

(MTZ): The maximum thickness of the zoarium in transverse/ longitudinal section.

Genus Fistulipora McCoy, 1850

Type species

Fistulipora incrustans (Phillips, 1836)

Diagnosis

Fistuliporidae with thin adnate sheet-like zoaria, rarely erect ramose. Autozooecia budded on or above a basal lamina over the entire free colony surface. Basal diaphragms are common. Vesicles are small, thin walled and structurally simple. Autozooecial apertures large, circular to pyriform with indistinct to moderately developed lunaria. Lunaria compound, microstructurally continuous or discontinuous with lateral and distal zooecial walls. Polymorphic zooecia absent. Monticules are common and regularly spaced.

Range

Silurian - Permian

Fistulipora incrustans (Phillips, 1836)

Figs. 88, 89; Pl. 166, figs. a-c; Pl. 167, figs. a-c; Pl. 168, figs. a-c; Pl. 169, figs. a-c; Pl. 170, figs. a-c; Pl. 171, figs. a-c; Pl.171, figs.a

1836 *Callamopora incrustans* (sp.nov.), Phillips, p. 200, Pl. 1 Figs. 63, 64.

1844 *Berenicea megastoma* McCoy, p. 195, Pl. 26, fig. 13.

1850 *Fistulipora minor* (n.g.) McCoy, pl. 130, figs. A.b.

1855 *Fistulipora minor* McCoy: McCoy, p. 79, Pl. 3B, figs. 12, 12b.

1879 *Fistulipora minor* McCoy: Nicholson, p. 306, figs. 39a, b.

1880 *Ceramopora megastoma* (McCoy). Vine, p. 359, Pl. 13.

1882b *Fistulipora minor* McCoy. Young, p. 427

1885 *Fistulipora incrustans* (Phillips). Nicholson and Foord, p. 500, figs. 3A-E.

1888 *Fistulipora minor* McCoy. Etheridge,Jun. p.212.

1888 *Diastopora megastoma* (McCoy). Etheridge,Jun. p. 246.

1888 *Fistulipora incrustans* (Phillips). Etheridge,Jun. p. 447.

1888 *Ceramopora megastoma* (McCoy). Etheridge,Jun. p. 457.

1888 *Fistulipora incrustans* (Phillips). Young, p. 237.

1890 *Fistulipora incrustans* (Phillips). Ulrich, p. 382, p. 474.

1929 non *Fistulipora incrustans* (n.sp) Moore, p. 3, Pl. 1, figs. 1a, b.

1953 *Fistulipora* aff. *incrustans* (Phillips). Nekhoroshev, p. 46, Pl. 1, fig. 1.

1953 *Fistulipora minor* McCoy. Bassler, p. G83, figs. 48, 1a-c.

1966 *Fistulipora incrustans* (Phillips). Owen, p. 138, Pl. 8, figs. A,B.

1969 *Fistulipora minor* McCoy. Owen, p. 258, Pl. 21, figs. C.D.

1969 *Fistulipora incrustans* (Phillips). Owen, p. 258, Pl. 21, figs. A-D, Pl. 22, fig. A.

1973 *Fistulipora incrustans* (Phillips). Owen, p. 298.

1973 *Fistulipora incrustans* Moore. Warner and Cuffey, p. 8, Pl. 1, figs. 1-7.

Type

Although Phillips (1836) did not erect a holotype for *Callamopora incrustans*, Owen (1969, p. 258) referred to Phillips figured specimen (Phillips, 1836, Pl. 1, figs. 63,64) as the holotype. Since this is not strictly correct a lectotype is formally proposed here for the taxon. The lectotype is represented by three thin sections (BMNH.R.29096, R.29097, R.29098) cut from Phillips figured specimen.

Emended Diagnosis

Fistulipora with thin adnate unilaminar sheet-like zoaria. Autozooecial apertures are large, circular, rarely pyriform with small low collar-like lunaria. Basal diaphragms are common. Vesicles are small hemispherical to box-like. Monticules are common and regularly arranged.

Description

External/Tangential

Zoaria form thin or thick encrusting unilaminar sheets commonly between 1 to 3 mm in thickness, but ranging from 0.7 mm to 9.5 mm.

Autozooecial apertures are large, circular, oval, rarely pyriform. They are quite closely spaced, arranged in straight to curved, often alternating parallel rows with proximal-distal axes subparallel in large mature zoaria. Lunaria are thin to moderately thick, normally crescent shaped, not very long, and cover about one third of the circumference of autozooecial apertures, and form low collar-like, rarely hood-like structures, reaching a maximum height of 0.07 mm above the zoarial surface. Lunarial walls are normally steeply inclined, with straight, rounded or pointed crests. The interior walls at the distal extremeties of lunaria may occasionally protrude into an aperture.

Vesicles are quite small, of variable size, commonly rectangular to polygonal and are thin walled and normally quite well faceted.

Monticules are common and regularly arranged in large colonies. The crestal area varies from round to oval and may be up to 2.4 mm in diameter, and consists of vesicles of a larger than average size.

Internal

The basal lamina is very thin (usually 0.015 mm to 0.025 mm, but may be up to 0.04 mm) and is normally well defined. Autozooecia may be budded on or above a basal lamina, not only at a budding edge but over the entire surface of the colony. Initially conical and recumbent zooecia rapidly become erect, increasing dimensions distally, and reaching maximum dimensions two thirds along their length, and diverge to the zoarial surface at very high angles of 80° to 85°.

Basal diaphragms are commonly developed, usually with one or two, but up to a maximum of seven in thick colonies. Diaphragms are normally irregularly spaced, usually slightly more than one diameter apart, and are usually horizontal, but may also be inclined at a low angle. They occur only in the erect mature portions of zooecial tubes, and are about 0.02 mm thick.

The lunarium is compound and is developed early in zooecial ontogeny and usually increases in thickness slightly toward the zoarial surface. The proximal lunarial wall may be microstructurally continuous with thin lateral and distal zooecial walls, or is distinct with lateral and distal walls composed of superimposed stacked vesicular tissues. Where the entire zooecial wall is compound and microstructurally continuous, the proximal lunarial wall thins gradually and passes into the thinner lateral and distal walls. However, where lateral and distal walls are simple, the proximal lunarial wall terminates abruptly against the thin simple wall.

Often in this situation the distal apices of the proximal lunarial wall in shallow tangential section may curve and protude into the zooecia. The amount of protusion decreases aborally. Simple lateral and distal zooecial walls may often be gently undulatory due to the curvature of individual stacked vesicles.

Vesicles are quite small, hemispherical, inverted, cup-shaped to box-like, occurring in irregular to regularly arranged vertical stacks. In the endozone vesicles are larger than average (up to 0.30mm in diameter), more rounded and generally irregularly arranged. In the exozone they are smaller (up to 0.18mm in diameter), inverted cup-like and regularly arranged in vertical stacks.

<u>Dimensions</u> (N = 42)

	NM	Mn	Mx	$\bar{X}$
MS	75	4.26	7.1	6.1
Z1	178	5.00	7.00	6.12
Z2	178	4.00	5.00	4.50
LAD	448	0.31	0.34	0.32
TAD	448	0.29	0.33	0.31
LID	448	0.07	0.14	0.09
TID	448	0.08	0.17	0.10
LD	448	0.06	0.11	0.07
LT	448	0.06	0.10	0.08
LW	448	0.20	0.30	0.23
V1	153	7.0	11.0	8.97
DZ	133	0	6.0	-
V2	25	8.0	11.0	-
MTZ	24	0.95	9.50	-

Discussion

Fistulipora incrustans (Phillips, 1836) is the only species of *Fistulipora* in British Lower Carboniferous strata. It is easily recognised by its large circular autozooecial apertures, poorly developed low collar-like lunaria, common occurrence of basal diaphragms and regularly arranged monticules.

F. incrustans most commonly encrusts crinoid ossicles but also encrusts, algae, ramose trepostomes, fenestrate Bryozoa, and occasionally brachiopod shells and spines.

F. incrustans is conspecific with *Fistulipora minor* McCoy, (1850) (see Nicholson and Foord, 1885, pl. 502; Young, 1888, p. 258; Owen 1969, p. 258) and as *F. incrustans* was described first this name takes priority. Owen examined the 'holotype' of *Callamopora incrustans* Phillips (thin sections:BMNH.R.29096, R.29097, R.29098) and a paratype of *F. minor* McCoy (Sedgwick Museum, Cambridge, E.5373) and considered the two species to be conspecific. Owen's plate 21, figs. A, B, C, D, shows this to be the case.

Berenicea megastoma McCoy (1844, p. 195), called *Diastopora megastoma* by Morris (1854) and later renamed as *Ceramopora megastoma* by Vine (1884, p. 359) is conspecific with *F. incrustans*. As Young (1882b,p. 429) noted, the overall zoarial form of *C. megastoma* (McCoy) described as a parasitic spot-like crust, with cells radiating from a centre, the inclined nature of cells to the zoarial surface, and occurrence of lunaria at their proximal extremeties, is obviously the earliest stage of colony development of *F. minor* (here placed in synonomy with *F. incrustans*). Young also noted that with further growth the cells become erect, and the encrustation becomes larger and thicker and develops the form of *F. minor* McCoy.

Fistulipora incrustans Moore (1929) is not conspecific with *F. incrustans* (Phillips, 1836), apertural diameters are much larger in the former species. As *F. incrustans* (Phillips) was described earlier this usage of the species name takes priority and Moore's usage is invalid as the name was already preoccupied. However, *F. incrustans* Moore (Warner and Cuffey, 1973) is conspecific with *F. incrustans* (Phillips).

Fistulipora excelens Ulrich (1884) is probably conspecific with *F. incrustans*. The meristic data and measurements recorded on *F. incrustans* compare in all respects with *F. excelens* redescribed by Perry and Horowitz (1963, p. 20).

Material

ABA 18	20 zoarial fragments in a container. Top of the Ashfell Sandstone (Arundian) Oreton Group, Ashfell Edge, near Kirkby Stephen, Cumbria.
ABAF 12,-13,-14	Knipe Scar Limestone (Asbian), Alston Group, Ashfell Edge, near Kirkby Stephen, Cumbria.
ABCL 23	19 zoarial fragments in a container. Calp shale-Upper Limestone (Asbian), Carrick Lough, Derrygonelly, Northern Ireland.
ABHR 123	Acetate peel and remnant. Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABHH 2, -7,-16	Hookhead formation (Courceyan), Lighthouse, Hookhead, County Wexford, Eire.
ABP 250-256	Acetate peels and remnants. Fifth Limestone (Asbian), Alston Group, Penruddock, near Penrith, Cumbria.
ABP 257	114 Colony Fragments in a container. Locality and horizon as above.

ABR 38,1-3	Redesdale Ironstone Shale (Asbian), Lower Limestone Group, near Ridsdale, Northumberland.
ABRE 204,-217,-224,-225,-227,-229,-233,-236,-237,-238,-240,-243,-244,-249,-251,-253,-254. Thin Sections.	Seventh Limestone (Holkerian), Redmain, near Cockermouth, Cumbria.
ABWB 200, 202,-204,-206,-210,-212,-221,-223,-225,-226,-235,-237,-246,-248,-248,250,-253,-254,-258,-261,-263,-266,-267,-268,-269,-270,-278,-284,-295,-305,-306,-308,-315. Thin Sections	Middle Limestone (Brigantian), Middle Limestone Group, Morpeth Scar, Near West Burton, Wensleydale, North Yorkshire.
BMNH DD.367	Brownber Pebble Bed (Arundian), Ravenstondale, J.S. Turner Collection.
BMNH.PD.373b	Friars Point, (Courceyan), Barry, Glamorgan, South Wales. A.V. Morgan Collection.
BMNH.PD.933	Gayton Boring, Carboniferous Limestone, Northants. G.R. Vine Collection.
BMNH.PD.1001	Bron-y-garth, Upper Grey LImestone (Brigantian) Near Chirk, Clwyd, North Wales, Morton Collection.
BMNH.PD.4035	Dockra Limestone (Brigantian). Lower Limestone Series, Trearne, Near Beith, North Ayrshire. G. Rae Collection.
BMNH.PD.4057	Carboniferous Limestone, Mid-Section of Friars Point, (Courceyan), Barry, Glamorgan, South Wales. A.V. Morgan Collection.
BMNH.PD.5473	Scandal Beck Limestone (Chadian), Rigg End Farm, Ravenstondale, Cumbria.

BMNH.R.109	Carboniferous LImestone, Bolland, South-West Yorkshire. W. Geilbertson Collection.
BMNH.R.29096, R.29097,R.2908	Thin Sections cut from the 'Holotype'. Carboniferous Limestone, Bolland, South-West Yorkshire. J. Phillips Collection. The holotype was figured by Phillips (1836, Pl. 1, figs. 63, 64).
GAGM 01-53 aej	Labelled as *Diastopora megastoma* McCoy. Lower Limestone, Carboniferous, Corrieburn, Campsie, Young Collection + two thin sections of the specimen.
GAGM 01-53 cc	Labelled as *Fistulipora minor* McCoy, Lower Limestone, Carboniferous, Hillhead Quarry, (Brigantian) Beith, Young Collection.
HM.D12	Thin Section, labelled as *Fistulipora* (*F.Minor* McCoy) *incrustans*, Roscobie near Dunfermline, Carboniferous Limestone Series. Mr. J. Bennie Donor 1881.
HM.D15	Redesdale (Asbian?), Northumberland, Carboniferous, J. Young Collection, 1883.
NH 436,G155.84	Card with 7 zoarial fragments, Acetate peels were prepared from specimen 84/7. Redesdale Ironstone Shale (Asbian), Lower Limestone Group, Ridsdale, Northumberland, J. Dunn Collection.
NH 437,G155.85	Card with 7 zoarial fragments. Acetate peels have been prepared from specimens 85/5,-85/6,--85/7. Horizon and locality as above. J. Dunn Collection.

NH 438,G155,86	Card with 7 zoarial fragments. Acetate peels have been prepared from specimens 86/3,-86/5,-86/6,-86/7 Horizon and locality as above. J. Dunn Collection.
NH 439,G155.87	Card with 6 zoarial fragments, one of which is *Fistulipora incrustans*. Horizon and locality as above. J. Dunn Collection.

Stratigraphical Range

Courceyan to upper Permian.

Occurrence

Fistulipora incrustans is a very common species, with a very wide geographical distribution, and long stratigraphical range. In the present study, it has been found to occur in Lower Carboniferous strata of the Midland Valley of Scotland, Cumbria, Northumberland, Yoredale facies of Yorkshire, Reef Limestones of North Derbyshire, and the limestones of North and South Wales, Northern Ireland and Eire.

Elsewhere, *F. incrustans* has been recorded from the Lower Carboniferous of Russia, and in upper Palaeozoic strata of North America.

F. incrustans is common in shallow water facies, especially in reef limestones, where it may be locally abundant enough to be an important component of the reef framework e.g. Derbyshire reef complex. It is associated with a rich and diverse bryozoan fauna, and a high faunal diversity of corals, crinoids, brachiopods etc.

Genus Eridopora Ulrich, 1882

Type species

Eridopora macrostoma Ulrich, 1882

Diagnosis

Fistuliporidae with thin adnate sheetlike zoaria. Autozooecia are budded on or above a basal lamina, over the whole surface of the colony. Basal diaphragms are uncommon. Vesicles are quite small, thin walled and structurally simple. Autozooecial apertures are large, rounded triangular to pyriform with prominent to helmet-like lunaria. Monticules are uncommon and irregularly arranged.

Range

Devonian-Permian.

Eridopora c.f. *beilensis*

Fig. 90; Pl. 173, figs. a-b; Pl. 174, figs. a-c; Pl. 175, fig. a.

1962 *Eridopora beilensis* n.sp. Perkins and Perry, p. 12, pl. 3, fig. 1-4.

Diagnosis

Eridopora with thin adnate unilaminar sheet-like zoaria. Autozooecial apertures large, rounded triangular to pyriform quite closely spaced and with prominent hooded to helmet-like lunaria. Vesicles are quite small, hemispherical to box-like. Monticules are uncommon and irregularly arranged.

Description

External/Tangential

Zoaria form thin encrusting sheet-like unilaminar colonies (1 to 2 mm thick).

Autozooecial apertures are large, rounded triangular to pyriform, widest at their distal extremeties, quite closely spaced, and are arranged in approximately curved alternate parallel rows with their proximal-distal axes sub-parallel in large mature zoaria. Lunaria are relatively thick, crescent shaped, or very long and extending almost the entire length of the sides of autozooecial apertures. They are prominent hooded to helmet-like and may reach a height of 0.20 mm above the zoarial surface. The lunarial walls may be gradually or steeply inclined above the zoarial surface and their crests may be straight, rounded or pointed and may be slightly thickened. The interior walls at the distal extremeties of lunaria may occasionally protrude into an autozooecial aperture.

Monticules are uncommon, and irregularly arranged, and consist of a round central area up to 1.0 mm in diameter around which autozooecial apertures are radially arranged. Within the crestal area vesicles are of a larger than average size. On the normal zoarial surface vesicles are quite small, rectangular to polygonal, rounded to well faceted and thin walled. Vesicle walls may commonly continue onto the lower slopes of the outer walls of lunaria.

Internal

The basal lamina is very thin. Autozooecia may develop on the basal lamina along a budding edge, but may be budded above the basal lamina directly on vesicular tissues, on older autozooecia over the entire surface of the colony. Zooecia are intially recumbent and conical, rapidly become erect, diverging at very high angles to the zoarial surface (between 75^{o} to 85^{o}) and reach maximum dimensions close to the zoarial surface.

Lunaria are compound and are developed early in zooecial ontogeny, and usually increasing in thickness towards the zoarial surface. The proximal lunarial wall may or may not be microstructurally continuous with the much thinner lateral and distal zooecial walls. Where the entire zooecial wall is compound the thick proximal lunarial wall gradually thins laterally and may run along the entire extent of the lateral wall. Where lateral and distal walls are simple, the proximal lunarial wall terminates against the thin simple wall abruptly, and is a relatively thick crescent shape. Lateral and distal walls are composed of superimposed stacked vesicular tissues and may be quite undulatory due to the curvature of individual stacked vesicles.

Vesicles are small, hemispherical to inverted cup-like, thin walled and while larger than average, (up to 0.26 mm in diameter) hemispherical and irregularly arranged in the endozone, in contrast they are smaller (up to 0.11 mm in diameter) inverse cup-shaped to rectangular and regularly arranged in vertical stacks in the exozone.

Dimensions (N = 6)

	NM	Mn	Mx	$\bar{X}$
Z1	10	6.00	7.00	6.50
Z2	10	4.00	5.00	4.50
LAD	67	0.31	0.33	0.32
TAD	67	0.27	0.31	0.39
LID	65	0.06	0.14	0.10
TID	65	0.11	0.21	0.15
LD	67	0.14	0.22	0.18
LT	67	0.06	0.09	0.08
LW	67	0.21	0.29	0.26
V1	10	7	11	9
V2	4	11	18	14
MTZ	3	0.77	2.00	-

Discussion

Eridopora c.f. beilensis Perkins and Perry is superficially similar to Fistulipora incrustans (Phillips) but is distinguished from it by the pyriform shape of autozooecial apertures, significantly thicker and prominent hoodlike lunaria, the irregular occurrence of monticules and the small size of vesicles.

E. c.f. *beilensis* from the shales above the Main Limestone (Arnsbergian), Hurst, No. Yorkshire, is comparable in most respects to *E. beilinesis* described by Perkins and Perry from the Lecompton Limestone (Westphalian), Kansas, except that apertural dimensions are slightly smaller.

Material

ABHR 46	Container with six zoarial fragments. Shales above the Main Limestone (Arnsbergian), Hurst, North Yorkshire.
ABHR 100-102	Acetate peels and remnants. Horizon and locality as above.
ABHR 250, -252, -254, -255	Thin sections. Horizon and locality as above.

Stratigraphical Range

Arnsbergian.

Eridopora macrostoma Ulrich, 1882

Figs. 91, 92; Pl. 176, figs. a-b; Pl. 177, figs. a-c; Pl. 178, figs. a-b.

1882 Eridopora macrostoma (nov. gen. sp.nov.) Ulrich, p. 137, Pl. 6, figs. 2, 2a.

1884 Eridopora macrostoma Ulrich; Ulrich, Pl. 3, fig. 8.

1895 Eridopora macrostoma Ulrich; Simpson, p. 561, fig. 128.

1953 Eridopora macrostoma Ulrich; Bassler, p. G85, fig. 50, 3a-c.

1963 Eridopora macrostoma Ulrich; Perry and Horowitz, p. 24, figs. 1-2.

Diagnosis

Eridopora with thin adnate unilaminar sheet-like zoaria. Autozooecial apertures are very large, rounded triangular to pyriform with prominent helmet-like lunaria, and very closely spaced. Basal diaphragms are uncommon. Vesicles are quite small, hemispherical to box-like. Monticules are very uncommon and irregularly arranged.

Description

External/Tangential

Zoaria form thin encrusting sheet-like unilaminar colonies 1 mm to 3 mm thick.

Autozooecial apertures are very large, rounded triangular to pyriform with their maximum width at their distal extremeties, and are closely spaced, arranged in straight to curved alternating sub-parallel to parallel rows. They are often so closely spaced that the broadly rounded distal wall of an aperture is in contact with the narrow proximal apex of the lunarium of a distally adjacent aperture. Such spacing may occur over an entire zoarial surface. Lunaria are thick and may be relatively short crescent shaped, but are more commonly very long and running the entire length of the lateral margins of apertures. Lunaria are very prominent, hooded to helmet-like and may reach heights of 0.60 mm above the zoarial surface. Their outer walls may gradually curve upwards or be very steeply inclined with their distal extremeties above the aperture, being straight rounded, or pointed and commonly thicker compared to the side walls.

Vesicles are quite small, rectangular to polygonal, rounded to well faceted and thin walled. Vesicle walls may develop on the lower slopes of the outer walls of lunaria, and where autozooecial apertures are very close together, vesicles may be very small and irregularly developed between zooecia.

Monticules are very uncommon, irregularly arranged in large colonies. The crestal area is round or oval, up to 1.0 mm in diameter, and consists of vesicles of a larger than average size.

Internal

The basal lamina is very thin (0.02 mm to 0.03 mm thick) and is well defined. Autozooecia can develop on the basal lamina at the budding edge, but also above the basal lamina directly on vesicular tissues, or older autozooecia over the entire surface of the colony. Initially conical and recumbent, autozooecia rapidly become erect, increasing in diameter distally and reach maximum dimensions close to the zoarial surface. Autozooecia diverge to the zoarial surface at high angles (75° to 85°).

Basal diaphragms occasionally occur in autozooecial tubes with up to two present in any one zooecium. They are slightly more than one diameter apart and are usually horizontal.

Lunaria are compound, and are developed early in autozooecial ontogeny, increasing in thickness, often quite markedly, toward the zoarial surface. The lunarial proximal wall may be microstructurally continuous with thinner lateral and distal zooecial walls or is distinct with lateral and distal walls composed of superimposed stacked vesicular tissues. Where the entire zooecial wall is compound the thick proximal lunarial wall may be a fairly short crescent shape, or, more commonly gradually thins laterally and may extend the entire length of the lateral wall. Where lateral and distal walls are simple, the proximal lunarial wall terminates abruptly against a thin simple wall. In this situation, curvature of individual stacked vesicles forming the simple wall causes lateral and distal walls to become quite undulatory.

Vesicles are quite small, hemispherical to inverse, cup-like, rarely rectangular. In the endozone region, they are larger than average (up to 0.45 mm in diameter), hemispherical and irregularly arranged. In the exozone they are smaller (up to 0.20 mm in diameter), inverse cup-shaped and more regularly arranged in vertical stacks. Where zooecia are extremely closely spaced, vesicles become very irregular in shape and size, and are very narrow.

Dimensions (N = 19)

	NM	Mn	Mx	$\bar{X}$
Z1	59	4	7	4.73
Z2	52	3	5	4.10
LAD	285	0.37	0.45	0.41
TAD	185	0.33	0.45	0.39
LID	183	0.05	0.14	0.09
TID	183	0.09	0.20	0.12
LD	185	0.19	0.32	0.24
LT	185	0.07	0.11	0.09
LW	185	0.29	0.34	0.32
V1	15	9	14	10.5
DZ	16	0	2	–
V2	10	14	–	10.5
MTZ	5	1	3	–

Discussion

Eridopora macrostoma is a very distinct fistuliporid, characterised by its extremely large very closely spaced pyriform autozooecial apertures and prominent hood to helmet-like lunaria.

The material examined in the present study is conspecific with *E. macrostoma* described by Ulrich (1882, p. 137) and by Perry and Horowitz (1963, p. 24). Perry and Horowitz's detailed description is supported by quantitative data, including measurements recorded on the Holotype (United States National Museum, specimen 43228). The material examined in the present study corresponds in all respects to the data given by them.

Material

ABAF 100, -101	Two acetate peels and remnants. Top of the Ashfell Sandstone (Arundian) Ashfell Edge, Near Kirkby Stephen, Cumbria.
ABAF 214, -215	Two thin sections. Horizon and locality as above.
ABHR 6	Shales above the Main Limestone (Arnsbergian). Hurst, North Yorkshire.
ABHR 45, 1-2	Container with twelve zoarial fragments. Horizon and locality as above.
ABHR 110 to 122	Thirteen acetate peels and remnants. Horizon and locality as above.
ABHR 251, -253, -256, -257	Thin Sections. Horizon and locality as above.

Stratigraphical Range

Arundian to Arnsbergian.

Occurrence

Eridopora macrostoma has only been recorded from two localities in Britain, from Arundian strata at Ashfell Edge, Cumbria, and in Arnsbergian strata from the shales above the Main Limestone, Hurst, North Yorkshire.

Elsewhere E. macrostoma has been recorded from the Lower Carboniferous (Middle Chester) of Indiana and Kentucky.

FAMILY Goniocladiidae Nikiforova, 1938

Type Genus

Goniocladia Etheridge, Jun. 1876.

Diagnosis

Fistuliporoidea with erect ramose zoaria, with slender elliptical, oval or pyriform bifoliate branches, forming reticulate expansions of anastomosing short angular branch units, or pinnate expansions of straight branches. Branches are bissected by a straight compound median wall from both sides of which autozooecia are developed; the median wall commonly projects as a ridge on the frontal surface of branches, and as a carina on the well rounded non-porferous surface of branches.

Autozooecia are budded in well defined longitudinal rows; initially recumbent they rapidly become erect and orientated at high oblique angles to the zoarial surface and all grow towards the frontal surface. The proximal lunarial wall is compound, while lateral and distal walls are composed of stereom. Autozooecia in the same longitudinal row are commonly in contact when recumbent, but become isolate when mature. Basal diaphragms are common. Vesicles are structurally simple, bilamellar, thin walled and forming irregularly stacked hemispherical units close to the median wall where autozooecia are recumbent, but soon becoming completely infilled with stereom.

Autozooecial apertures are of variable size, circular, oval or pyriform occasionally with poorly developed collar-like lunaria at their proximal extremeties.

Range

Carboniferous to Permian.

Genus Goniodadia Etheridge, 1876

Type species

Carinella cellulifera Etheridge, Jun. 1873a

Diagnosis

Goniodadiidae with zoaria forming reticulate expansions of anastomosing angular pyriform bifoliate branches. Fenestrules are large and polygonal. Branches are bissected by a straight compound median wall from both sides of which autozooecia are developed; the median wall usually projects as a ridge on the frontal surface of branches, and as a carina on the well rounded non-poriferous surface of branches.

Autozooecia are budded in well defined longitudinal rows, initially recumbent and are commonly in contact; they rapidly become erect, isolate and orientated at high oblique angles to the zoarial surface, all growing toward the frontal surface. The proximal lunarial wall is compound, while lateral and distal walls are structurally distinct and are composed of thick walled stereom. Basal diaphragms are common. Vesicles are thin walled, and form hemispherical units close to the median wall where autozooecia are recumbent, but soon become infilled with stereom.

Autozooecial apertures are large, circular, oval or pyriform, commonly with low collar-like lunaria. There is a gradation in the distance between apertures in adjacent longitudinal rows, with the distance between apertures in a row decreasing towards the frontal ridge of branches.

Range

Carboniferous to Permian.

TAXONOMIC PROCEDURE

(see Fig. 93)

External Morphological Characters

Zooecial Parameters

Branch Width (BW1); is measured across a branch transverse to its growth axis, across the longest dimension of a branch between the median ridge of the poriferous surface and the midline of the non-poriferous surface.

Branch Width (BW2); is measured across a branch transverse to its axis, and its longest dimension, where a branch is at its widest.

Z1: Recorded as for the Fistuliporidae.

Z2: Recorded as for the Fistuliporidae.

Longitudinal Autozooecial Apertural Diameter (LAD); measured parallel to the proximal-distal axes of the aperture between the inner surfaces of apertural margins.

Transverse Autozooecial Apertural Diameter (TAD); measured transverse to the proximal-distal axes of the aperture between the inner surfaces of apertural margins at the widest expanse of the aperture.

Interapertural Distance (ID); measured between the midpoints of adjacent apertures in the same longitudinal row.

Zoarial Parameters

Fenestrule Length (FL); measured parallel to the growth axis, between the midpoints of successive anastomoses of branches.

Fenestrule Width (FW); measured transverse to the growth axis, between the midpoints of adjacent branches where fenestrules are widest.

Goniocladia cellulifera (Etheridge, Jun. 1873a)

Pl. 179, figs. a-b; Pl. 180, figs. a-c; Pl. 181, figs. a-d; Pl. 182, figs. a-c; Pl. 183, figs. a-d; Pl. 184, fig. a: Pl. 185, figs. a-b.

1873a Carinella cellulifera gen.et.sp.nov. Etheridge, Jun. p. 28, Pl. 15, figs. 1-3.

1873b Carinella cellulifera Etheridge, Jun: Etheridge, Jun. p. 101.

1876 Goniocladia cellulifera (Etheridge, Jun.); Etheridge, Jun. p. 522.

1887 Goniocladia cellulifera (Etheridge, Jun.); Young, p. 461.

1888 Goniocladia cellulifera (Etheridge, Jun.); Vine, p. 77, Pl. 4, figs. 14-16.

1889 Goniocladia cellulifera (Etheridge, Jun.); var. robusta, Vine, p. 78, Pl. 4, fig. 17.

1953 Goniocladia cellulifera (Etheridge, Jun.); Bassler, p. G.89, Fig. 54, fig. 1.

Type

Etheridge (Jun.)'s type material of Carinella cellulifera is now believed lost and consequently a neotype is required. However, although in the present study a considerable amount of topotype material has been examined its small and fragmentary nature does not justify selection of a neotype. Shortage of time for the present study precluded further search for suitable type material.

Emended Diagnosis

Goniocladia with large planar reticulate zoaria. Branches are slender, with an elongate pyriform cross-section, and anastomose at closely spaced intervals. The median ridge of the poriferous surface of branches is angular, and the non poriferous surface is well rounded and carinate. Fenestrules are very large, pentagonal to polygonal. Autozooecial apertures are large, oval, pyriform to keyhole-shaped and are arranged in 3 to 7 longitudinal rows on each side of the apex. Low collar-like lunaria are usually developed.

Description

External

Zoaria form large planar reticulate expansions up to at least 5 cm in diameter. Branches are bifoliate, with a very narrow elongate pyriform cross-section, and anastomose at closely spaced intervals with angles of bifurcation between 30° and 70°. Branch bifurcations are distinctly angular, and branches re-unite so as to form very large, quite well faceted pentagonal, hexagonal or polygonal fenestrules. The median ridge of the poriferous surface of branches is very narrow, angular with opposite branch surfaces diverging at a very low angle. The adjoining non-poriferous surface is fairly narrow and comparatively well rounded and has a very narrow low, but well defined median carina. This carina is situated in a plane directly opposite to the median ridge of the poriferous surface, and both follow exactly the prominent angular bifurcations of branches. Branch surfaces are coarsely granular, and the non-poriferous surface occasionally may be longitudinally striate.

On the poriferous surface, there are between three and seven longitudinal rows of autozooecial apertures, with apertures in adjacent rows being slightly offset. The zoarial surface immediately around apertures is commonly slightly elevated. Autozooecial apertures are large, oval to pyriform and normally with collar-like lunaria at their proximal extremeties and all apertures are orientated toward the angular median ridge of branches. Lunaria may be very prominent and are always best developed in the first longitudinal row of apertures beyond the non-poriferous surface, and become less well developed to usually absent in successive rows towards the angular median ridge of branches. Lunaria are normally crescent shaped but may extend along the entire length of the lateral margins of apertures. The distal extremeties of crescent-shaped lunaria commonly project into the apertures giving them a 'keyhole' shape.

There is a gradation is the distance between apertures in adjacent longitudinal rows towards the median ridge of branches. At the thinnest part of branches, adjacent to the ridge apertures are very closely spaced less than their own diameter apart. This increases with successive longitudinal rows to about almost two diameters apart in the last row of apertures adjacent to the non-poriferous surface and at the point where branches are thickest.

Internal

Autozooecia are budded in well defined longitudinal rows on both sides of a compound median wall, composed of a central dark grey granular layer bounded by lighter thicker granular-prismatic layers. Autozooecia are budded transverse to the growth direction of branches towards the median ridge of the frontal surfaces of branches.

Initially recumbent, they soon become erect and diverge toward the zoarial surface at high oblique angles. Due to the elongate narrow pyriform cross-section of branches, and their tapering towards the median ridge from the non-poriferous surface, autozooecia are significantly better developed where branches are thickest at a point just beyond the non-poriferous surface. Here autozooecia are longest, and they have long erect portions diverging towards the zoarial surface at high angles between 50° and 70°. However, towards the median ridge they become shorter, and at the ridge they are not long enough to become erect, and open onto the zoarial surface at low angles between 10-20°.

The proximal lunarial wall is thin, compound, and usually extends around most of the diameter of the autozooecium, and gradually thickens towards the zoarial surface. The small distal portion of the wall which is not compound is structurally simple, and is composed of a wall of stereom. The proximal lunarial wall terminates quite abruptly against this simple distal wall, and the distal apices of the proximal lunarial wall, in shallow tangential sections, may curve inwardly into autozooecia.

In the same longitudinal row the recumbent portions of adjacent autozooecia are in contact and the compound wall is shared between them.

Vesicles are developed only on and close to the median wall where autozooecia are recumbent. Here, their bilamellar composition is well defined and they are thin walled forming quite small well rounded hemispherical units irregularly stacked on one another. When autozooecia become erect, the vesicles abruptly become thick walled, completely infilled with stereom, and only occasional localised curved portions of the lower dark granular skeleton are defined.

<u>Dimensions</u> (N = 19)

	Mn	Mx	$\bar{X}$
BW1	1.03	2.15	1.41
BW2	0.38	0.55	0.46
AD1	0.16	0.18	0.17
AD2	0.15	0.18	0.16
FL	4.80	6.50	5.65
FW	2.47	3.20	2.92

The following parameters measured in the present study showed the existence of a gradation in the distance between apertures in adjacent longitudinal rows towards the median ridge of branches.

For the Parameter Interapertural Distance nine colonies from one locality were selected for measurement to show the precise quantitative nature of the gradation in the distance between apertures in adjacent longitudinal rows towards the median ridge of branches (see Fig. 94).

→ Median Ridge

(Row Number) =	1	2	3	4	5
Z1	4	4+	4+/-5	5	5+/-6
Z2	9				12

Interapertural Distance (ID)

→ Median Ridge

	Row	1	2	3	4	5
Colony:	1	0.67	0.56	0.42	0.40	0.39
	2	0.60	0.52	0.43	0.42	0.40
	3	0.60	0.54	0.40	0.39	0.38
	4	0.61	0.53	0.41	0.39	0.38
	5	0.60	0.54	0.43	0.41	0.39
	6	0.65	0.53	0.41	0.40	0.36
	7	0.67	0.53	0.43	0.39	0.38
	8	0.65	0.56	0.42	0.38	0.35
	9	0.63	0.53	0.43	0.38	0.35
	$\bar{X}$	0.63	0.54	0.42	0.39	0.37

Discussion

Goniocladia cellulifera Etheridge, Jun. is the only species of *Goniocladia* in British Carboniferous strata and is readily distinguished by its bifoliate branches which are pyriform in cross-section and anastomose to form a reticulate meshwork, and the occurrence of between 3 and 7 rows of autozooecial apertures on both sides of branches, which have low collar like lunaria.

Etheridge, Jun. (1873a, p. 28) erected the new genus *Carinella* and named the new species *C. cellulifera* as its only species. He drew a comparison between *Fenestella* and *Polypora* stating that the new genus was a connecting link between the two. This reasoning was based on the fact that *Carinella* was carinate like *Fenestella* and has numerous rows of apertures like *Polypora*.

In a later article, Etheridge, Jun (1876, p.522) renamed the genus. He realised the name *Carinella* was already pre-occupied by a Nemertidian Annelid, and proposed the name *Goniocladia* naming *G. cellulifera* as the only species.

Vine (1889, p. 78) established a new variety of *Goniocladia cellulifera* - var *robusta*. This variety he stated differed from the species s.s. in its more compressed, robust branches and greater distances between apertures. No material answering this brief description has been examined in the present study and it is not possible to validate Vine's findings because his material is probably lost.

Material

ABCL 40	Cavity slide with 8 zoarial fragments. Calp Shale - Upper Limestone (Asbian), Carrick Lough, Co. Fermanagh.
ABCL 41	Container with 40+ zoarial fragments. Locality and horizon as above.
ABHB 1	Shales above the 3 Yard Limestone (Brigantian) Hudeshope Beck, Middleton in Teesdale.
ABHR 1G	Cavity slide with 30 zoarial fragments. Shales above the Main Limestone (Arnsbergian), Hurst, N. Yorkshire.
ABWB	267, 268, 271, 275, 287, 309, 312, 324, 333, 336. Thin sections. Middle Limestone Group (Brigantian) Morpeth Scar Limestone, West Burton, Wensleydale, N. Yorkshire.
BMNH D.85	Topotype material. Gair (Brigantian), Argyllshire, Scotland. G.R. Vine Collection.
BMNH D.2405	Halkyn Mountain, Clwyd, G. Shrubsole Collection.
BMNH D.32637	Topotype material. Cavity slide with 10 zoarial fragments. Carluke (Brigantian), Scotland. Shrubsole Collection. 12 thin sections and 14 cavity slides have been prepared from material formerly on the slides.
BMNH PD675-80	Topotype material. Gair, Dumfrieshire, Scotland. G.R. Vine Collection.
HM D.119	Topotype material. Cavity slide with 14 zoarial fragments, labelled *Cystodictya* *(Carinella)* *cellulifera*, Etheridge. Gair, near Carluke (Brigantian). J. Young Collection.

YM 1983/657 F Leyburn, Lancs. Reed Collection.

Stratigraphical Range

Asbian - Arnsbergian.

Occurrence

Goniocladia cellulifera is quite common in British Lower Carboniferous strata and has a fairly wide geographical distribution being recorderd from the Midland Valley of Scotland, Cumbria, North Yorkshire, Lancashire and Northern Ireland.

FAMILY Sulcoreteporidae Bassler, 1935

Type Genus

Sulcoretepora D'Orbigny, 1849.

Diagnosis

Fistuliporoidea with erect ramose zoaira forming pinnate expansions with branches bifoliate, oval or elliptical in shape; branches are bisected by a straight or undulatory compound median wall from one or both sides of which autozooecia are developed. Autozooecia are arranged in well defined longitudinal rows, typically they have long recumbent portions before curving orally towards the zoarial surface at high oblique angles; when developed from both sides of the median wall they may be more abundant on one side; autozooecial walls are compound and autozooecia in the same longitudinal row are commonly in contact when recumbent, but become isolate when mature. Basal diaphragms and hemisepta occur occasionally.

Vesicles are structurally simple, bilamellar, initially thin walled and forming hemispherical units close to the median wall, where autozooecia are recumbent, but soon become thick walled and completely infilled with stereom toward the zoarial surface.

Autozooecial apertures are of variable size, circular to oval, commonly with upraised rims, developed at their proximal margins into lunaria. They are alternately arranged in adjacent longitudinal rows in quincunx. Longitudinal ridges occur commonly between the rows of apertures.

Range

Silurian to Permian.

Genus Sulcoretepora D'Orbigny 1849

Type Species

Sulcoretepora parallela (Phillips, 1836)

Diagnosis

Sulcoreteporidae with zoaria forming simple pinnate expansions of elliptical bifoliate branches, with branches irregularly dichotomising, and lateral branches also developed. Branches are bissected by a typically undulatory compound median wall from one or both sides of which autozooecia are developed; when developed from both sides of the median wall they may be more abundant on one side. Autozooecia are arranged in well defined longitudinal rows, and are box-like with a long recumbent portion, and a short distal portion where they curve orally towards the zoarial surface at high oblique angles. Basal diaphragms and hemisepta are uncommon.

Initially vesicles are fairly thin walled and form hemispherical or more box-like units close to the median wall where autozooecia are recumbent, but soon become thick walled and completely infilled with stereom towards the zoarial surface. Autozooecial apertures are large, oval, commonly with lunaria at their proximal extremeties. Narrow upraised ridges usually occur between the rows of apertures.

Range

Devonian to Permian.

TAXONOMIC PROCEDURE

External Morphological Characters

Zooecial Parameters

Number of Autozooecial Apertures in one square millimetre (Z1): recorded as in the Fistuliporidae.

Number of Autozooecial Apertures in a 2 mm line (Z2): recorded as in the Fistuliporidae.

Longitudinal Autozooecial Apertural Diameter (LAD): measured as in the Goniocladiidae.

Transverse Autozooecial Apertural Diameter (TAD): measured as in the Gonocladiidae.

Interapertural Distances (ID): measured as in the Goniocladiidae.

Zoarial Parameters

Branch Width (BW1): measured across a branch transverse to its growth axis, parallel to the largest dimension of a branch.

Branch Width (BW2): measured as in the Goniocladiidae.

Sulcoretepora parallela (Phillips, 1836)

Pl. 186, figs. a-c; Pl. 187, figs. a-c; Pl. 188, figs. a-c;
Pl. 189, figs. a-c; Pl. 190, figs. a-c; Pl. 191, figs. a-c.

1836 Flustra? parallela Phillips, p. 200, Pl. 1, figs. 47, 48.

1844 Vincularia parallela (Phillips); McCoy, p. 198.

1849 Sulcoretepora parallela (Phillips); D'Orbigny, p. 152.

1854 Sulcoretepora parallela (D'Orbigny); Morris, p. 105.

1880 Ptilodictya (?) parallela (Phillips); Vine, p. 231.

1883 Arcanopora parallela (Phillips); Vine, p. 204.

1885 Cystodictya parallela (Phillips); Vine, p. 95.

1887 Sulcoretepora parallela (Phillips); Young, p. 461.

1889 Cystodictya parallela (Phillips); Vine, p. 74, Pl. 3, figs. 1-13; Pl. 4, figs. 18-26.

1953 Sulcoretepora parallela (Phillips); Bassler, p. G142, fig. 103.1.

1969 Sulcoretepora parallela (Phillips); Owen, p. 265, Pl. 23, figs. E, F.

Type

Phillips type material of Flustra(?) parallela is lost and a neotype should be erected. However, during the tenure of the present study it has not been possible to visit Phillips type locality at Whitewell, and it is not yet possible to erect a neotype for this taxon.

Diagnosis

Sulcoretepora forming fairly large pinnate expansions of slender elliptical bifoliate branches, with branches bifurcating at irregular intervals, and lateral branches also developed. Autozooecial apertures open on both sides of branches with between three and seven longitudinal rows equally developed on each side; apertures are large and oval, with upraised rims that are developed into collar-like lunaria at their proximal margins; narrow ridges separate the longitudinal rows and these are papillate. Internally, the median wall has a well defined zig-zag shape; autozooecia have a very long recumbent portion; vesicles are small, only developed close to the median wall, and on autozooecia, elsewhere they are completely infilled with stereom.

Description

External

Zoaria form large, simple pinnate expansions of slender acute elliptical bifoliate branches, up to 5 cm in length, with branches dichotomising at irregularly and widely spaced intervals, lateral branches are also developed.

Autozooecial apertures open on both sides of branches with between three and seven longitudinal rows equally developed on both sides. Autozooecia open onto the zoarial surface at high oblique angles. Apertures are large and oval, with well rounded low prominent peristome-like rims which at their proximal margins are significantly elevated to form a low collar-like lunarium. Apertures in a longitudinal row are closely spaced between half and one total diameter apart, and apertures in adjacent longitudinal rows are alternately arranged, in quincunx.

Between adjacent longitudinal rows of apertures there is a very prominent, straight narrow ridge, which may in part help to form part of the rims of apertures. The ridges are commonly ornamented by very small papillae arranged in a closely spaced uniserial row. Autozooecial apertures occur in all the 'furrows' between the ridges, except in two furrows situated on both sides of the lateral branch margins.

Internal

Autozooecia are budded in well defined longitudinal rows on both sides of a 'median wall', that has an undulatory to distinctly angular 'zig-zag' appearance with autozooecia alternately budded on either side. The median wall is compound with a central thin dark grey granular layer bounded by lighter thicker pale grey granular-prismatic layers.

On each side of the median wall autozooecia are budded in alternately arranged longitudinal rows parallel to the growth direction of branches. The autozooecia have a very long recumbent portion, comprising almost two-thirds of their total length, before curving outwards towards the zoarial surface at high angles between 60° and 80°. The recumbent portions of autozooecia in a longitudinal row are in contact.

Autozooecial walls are thin and compound and are developed by the regular bifurcation of the compound 'median wall' which due to the alternate budding of autozooecia on opposite sides of the median wall, has a distinct zig-zag appearance.

The distinct, straight compound narrow longitudinal walls which separate adjacent longitudinal rows of autozooecia are formed by the compound lateral interzooecial walls of alternately arranged box-like autozooecia in adjacent longitudinal rows.

In transverse section interzooecial walls have a well developed wedge-shape. They are thinnest immediately after development from the median wall and increase greatly in width towards the zoarial surface. The wedge shape is developed by the bifurcation of a thin compound interzooecial wall, close to the median wall, into two new compound walls that diverge toward the zoarial surface at low angles of between 20° and 40°. These walls extend above the zoarial surface as the narrow ridges which separate the longitudinal rows of apertures. The manner of bifurcation results in the alternate arrangement of autozooecial apertures on the zoarial surface, with autozooecial apertures opening at similar levels on each side of the wedge.

Vesicles are structurally simple and are bilamellar. They are fairly thin walled adjacent to the median wall and on the walls of recumbent autozooecia, and form small or moderately sized hemispherical box-like to elongate rectangular irregularly stacked units. Here their bilamellar structure is well defined, with a lower thin primary dark grey granular layer, and an upper thicker secondary granular prismatic layer. However, vesicles soon become thick-walled and throughout most of the zoarium towards the zoarial surface are completely infilled with stereom. Their bilamellar structure is not evident, as the lower primary dark grey granular layer is rarely developed. There are occasionaly very small irregularly distributed cavities, and the lower primary dark grey granular layer may then be developed.

<u>Dimensions</u> (N = 18)

	Mn	Mx	$\bar{X}$
BW1	0.73	1.35	1.00
BW2	0.35	0.53	0.46
Z1	6	8	-
Z2	4	5	-
LAD	0.21	0.28	0.25
TAD	0.15	0.20	0.17
ID	0.54	0.64	0.57

Discussion

Sulcoretepora parallela (Phillips) is recognised by its slender elliptical bifoliate branches, on both sides of which autozooecial apertures are developed equally; its large oval apertures with lunaria at their proximal margins; and the occurrence of narrow papillate ridges separating the longitudinal rows of apertures.

Although all Phillips material of *Flustra* (?) *parallela* is presumed lost, from his description it is obvious that his species is conspecific with the material referred to *Sulcoretepora parallela* in the present study.

Phillips' description is as follows:

> "Linear, longitudinally and deeply furrowed;
> cells in the furrows, in quincunx and their
> apertures oval, prominent; (side furrows
> without apertures)"

There are two other species of *Sulcoretepora* in British Carboniferous strata: *Sulcoretepora raricosta* McCoy (1844, p. 198), and *Sulcoretepora robusta* Young and Young (1877b,p. 166)..

Sulcoretepora raricosta is distinguished from *S. parallela* by the occurrence of autozooecial apertures on one surface only, the other being non-poriferous. *S. robusta* is not so elongate with a more equidimensional octagonal cross-section. Autozooecial apertures are smaller than in *S. parallela*, also without rims or lunaria, and are more abundant on one branch surface than the other. Basal diaphragms occur also, usually with about one per autozooecium. Vesicles are better developed than in *S. parallela*. They are commonly developed at the zoarial surface, and on weathered speciments, occur as small pitted areas between apertures. These small weathered pits were interpreted as pores by Young and Young (1877b, p. 167).

Material

ABAF -2 to 4, -15 to 33	Orton Group, Knipe Scar Limestone (Asbian), Ashfell Road Cutting, Near Kirkby Stephen, Cumbria.
ABAF -214, -216 to 221,-224,-227 to 229,-231,232.	Thin sections, Locality and horizon as above.
ABHR 15	Cavity slide with 32 zoarial fragments. Shales above the Main Limestone (Arnsbergian), Hurst, N. Yorkshire.
ABRE 201, 202.	Thin sections. Orton Group, Seventh Limestone, (Holkerian), Redmain, Nr. Cockermouth, Cumbria.
ABMG -40 to 43	Hardraw Shales (Brigantian), Mill Gill, Nr. Askrigg, N. Yorkshire.
BMNH D.65	Hairmyres (Brigantian), Lower Limestone Shales. G.R. Vine Collection.
BMNH D.206	labelled *S. parallela* Hurst, (Arnsbergian?). G.R. Vine Collection.
BMNH D.257	Holker Park. N. Lancs. G.R. Vine Collection
MBNH D.258	Yoredale Series, Furness, Lancs. G.R. Vine Collection.
BMNH D.329	labelled *S. parallela*, Hurst (Arnsbergian), G.R. Vine Collection.
HM D.113	Cavity slide with 5 zoarial fragments. Lower Limestone Group, Hosie Limestone (Brigantian), E. Kilbride. J. Young Collection. 9 thin sections and 18 acetate peels have been prepared from 4 specimens by F.K. McKinney.
HM D.114	Cavity slide with 13 zoarial fragments. Locality and horizon as above. J. Young Collection.

HM D.115	Cavity slide with 20 specimens labelled as *S. parallela* Phillips and *S. raricosta* McCoy. Locality and horizon as above. J. Young Collection.
HM D.365/1-5	Cavity slide with 5 zoarial fragments. Lime Kilns E. Kilbride, Main Hosie Limestone, (Brigantian). J. Young Collection.
YM 1983/659F	Gilmerton, Edinburgh, Reed Collection.

Stratigraphical Range

Holkerian - Arnsbergian.

Occurrence

Sulcoretepora parallela is quite common in British Lower Carboniferous strata, and has a fairly wide geogrphical distribution being recorded from the Midland Valley of Scotland, North Yorkshire, Cumbria, Lancashire and Northern Ireland.

S. parallela is restricted to mudstone facies, where it lived in a tranquil environment in association with a fauna of bryozoans, brachiopods and crinoids.

The Double-Walled Concept as a Model for Cystoporate Growth

All available evidence suggests that cystoporates were double-walled bryozoans. The main reasons for this are discussed below and are based on personal observations and on the definitive work of Utgaard (1973) on Cystoporates.

(a) In double-walled cyclostomes the whole frontal wall may be considered as representing a much widened and highly complicated common bud, and new autozooecia may develop not only at a budding edge but over the entire surface of the colony. In many cystoporates new autozooecia develop at budding edges on a basal lamina or median wall, and also in the exozone in virtually any part of the colony on older autozooecia or on extra zooidal vesicular tissues. This feature of cystoporates strongly suggests the occurrence of colony-wide budding control by an external outer membrane.

(b) The partial or total isolation of the newly developed autozooecia suggests colony-wide budding control by an external outer membrane and the occurrence of a colony-wide coelomic cavity to enable nutrient distribution across the colony.

(c) Autozooecial walls in most cystoporates are compound, secreted from both sides, like the interior walls in modern cyclostomes, and similarly were probably secreted by infolds of an inner epidermis into the hypostegal coelomic cavity. Some fistuliporids do have lateral and distal sides of an autozooecium composed of superimposed stacks of vesicle walls so that part of an autozooecium becomes simple walled. In such cases the inner zooidal epithelium simply curves up and out to continue as the inner hypostegal epithelium below the hypostegal coelom.

(d) The nature of extra-zooidal vesicular tissue and stereom in fistuliporids suggests they were double walled forms. In most forms vesicle walls and roofs are essentially single curved structural units and were deposited as simple curved plates. Most vesicle walls and roofs are structurally simple, and must have been deposited from the outer side at the zoarial surface. The simple bilamellar nature of vesicles suggests that they contained no living tissue, and there is no space of relatively constant shape or size for zooids to develop. The occurrence of thick walled roofs or stereom at the zoarial surface in many forms is further indication of colony wide control of deposition from an epithelium on the outside of the vesicles.

(e) The development of autozooecial walls on the outer side of vesicle roofs in the exozone requires an epithelium on the outer side. Vesicle walls may be developed on the lower sides of lunaria.

(f) The relatively uniform level of the outer surface of colonies suggests a colony-wide epithelium and colony-wide control of growth. The individual, isolated autozooecia, do not project significant distances above the general surface of the colony in cystoporates as they do in some single-walled cyclostomes.

(g) Small stylets are present in some cystoporates, and it is thought that these may have functioned as stabilisers or loci of attachment of an external outer membrane to the skeleton.

Applying the double-walled model of growth in recent hornerid and lichenoporid cyclostomes it seems likely that a colony-wide inner hypostegal epithelium and its internal equivalent the zooidal epithelium (with which it was continuous) secreted all of the calcareous skeleton. An externally situated coelomic cavity was probably responsible for nutrient interchange between the isolated autozooecia across the colony. The occurrence of communication pores in ceramoporid cystoporates was evidently another means of nutrient interchange between autozooecia in addition to the coelomic fluid in the hypostegal coelom. External to the coelomic cavity an outer eustegal epithelium secreted only the cuticular cover of the colony, including the terminal vestibular membranes of zooids.

Discussion of the Coefficients of Variation Values of selected parameters measured on taxa within the Order Cystoporata.

(see Table 4)

External Morphological Characters

Zooecial Parameters

Branch Width (BW1, BW2): This was measured on the two erect ramose bifoliate forms Goniocladia Cellulifera and Sulcoretepora parallela. In Goniocladia cellulifera the reticulate expansion is composed of branches apparently all showing the same degree of development. Consequently although only small colony fragments have been examined in the present study, the values of CV's are considered to reflect the true degree of within and between colony morphological variance. Within colony CV's are low 5.15 for BW1 and 3.42 for BW2, and are a reflection of the high degree of genetic control on zoarial growth. Between colony CV's are significantly higher 13.36 for BW1 and 5.31 for BW2 and reflect the degree of genetic variability and the effects of such exogenous influences as microenvironment.

In Sulcoretepora parallela the calculated CV values do not reflect the true degree of morphological variability shown by a colony. In the present study generally only small fragments of branches has been examined. Individual branch fragments are of fairly constant diameter as shown by the very low within colony CV's of 3.83 for BW1 and 2.19 for BW 2. However, colonies are pinnate expansions, with branches bifurcating and lateral branches also developed. New branches are typically thinner after bifurcation, and lateral branches are usually significantly thinner than the parent branch. Consequently, with such a variability in branch width in a colony, within colony CV's should be significantly higher than

	BW1			BW2			Z1			Z2			LAD			TAD			LID			TID			ID			LT			LW			FL			FW			MS		
	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T	CV^W	CV^B	CV^T
tulipora rustans	-	-	-	-	-	-	14.37	13.30	14.49	12.98	8.99	10.85	5.64	2.20	2.12	4.73	2.99	4.39	27.37	18.24	38.59	31.41	29.45	37.54	18.56	17.65	18.26	24.56	18.45	22.28	8.78	8.31	9.74	-	-	-	-	-	-	8.20	18.11	-
dopora lensis	-	-	-	-	-	-	10.91	8.88	-	16.85	12.82	-	5.31	2.86	-	8.41	5.92	-	37.81	31.07	-	29.30	26.14	-	15.41	12.65	-	21.31	18.52	-	18.39	14.01		-	-	-	-	-	-	-	-	-
ecrostoma	-	-	-	-	-	-	21.85	19.32	19.38	15.18	13.42	14.10	8.31	6.42	11.04	10.53	9.76	12.31	38.30	31.04	40.43	31.81	27.73	34.36	19.51	15.33	16.30	23.10	14.36	23.40	10.31	6.32	10.75	-	-	-	-	-	-	-	-	-
iocladia tulifera	5.15	13.36	17.92	3.42	5.31	8.73	8.51	15.30	17.49	3.30	5.36	7.45	3.18	4.69	-	3.43	9.51	-	9.46	3.63	10.05	-	-	-	-	-	-	-	-	-	-	-	14.76	14.76	-	-	10.84	-	-	-	-	-
coretepora allela	3.83	18.75	27.40	2.19	13.38	17.50	6.38	14.40	15.30	8.50	6.40	9.87	4.66	7.97	9.56	8.15	9.51	12.84	12.81	5.88	14.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
$\bar{x}$	4.49	16.06	22.66	2.81	9.35	13.12	12.40	14.24	16.66	11.31	9.40	10.56	5.42	4.83	7.60	7.05	7.54	9.85	25.15	17.97	25 79	30.84	27.77	35.95	17.83	15.21	17.28	22.99	17.11	22.84	10.84	9.55	10.24									

those stated in table 4 . However, these calculated values are useful, and their low values reflect the high degree of genetic control of branch growth.

Thus the between colony CV's should probably be lower than the true within colony CV's, because the variability shown by an individual colony is evened out when a number of colonies are examined in a population.

For all the other parameters, the calculated CV values are taken as being a true reflection of the amount of morphological variatio shown within a colony, between colonies in a population, and in the total number of colonies examined in each taxon. For example, although such parameters as Branch Width vary in a colony of Sulcoretepora parallela, parameters such as Apertural Diameter, show no significant variation in dimensions between branches.

Autozooecial Apertures in $1mm^2$ (Z1) and the Number of Apertures in a 2mm line (Z2): In the three fistuliporoids examined in the present study, Fistulipora incrustans, Eridopora beilensis and E. macrostoma, within colony CV's are slightly higher than between colony CV's. Within colony CV's are moderately high ranging between 10.91 and 21.85 for Z1 and 12.98 and 16.85 for Z2. These fairly high values reflect the considerable variation that occurs in the distribution of autozooecia in a colony. Besides being developed at the growing edge on the basal lamina, new autozooecia can develop anywhere on the free colony surface, above the basal lamina, on vesicular tissues or on the recumbent portions of older autozooecia. This variation in the mode of development of autozooecia, with autozooecia being budded over the entire zoarial surface, causes the high variability in the distribution of autozooecial apertures on the zoarial surface. Between colony CV's are only slightly lower, due to the high degree of within colony variation.

Apertural Diameter (LAD, TAD): Apertural dimensions are taxonomically very useful, as shown by the low within and between colony CV's.

In the fistuliporoids apertural dimensions were examined in shallow tangential section. The higher within colony CV's may be accounted for by two factors.

Firstly autozooecia may be budded on a basal lamina at the growing edge, or above the basal lamina on vesicular tissues on older autozooecia over the entire free colony surface. Autozooecia normally increase in dimensions towards the zoarial surface, consequently those developing close to the zoarial surface will have slightly smaller dimensions than those longer tubes that were budded on a basal lamina.

Secondly autozooecial tubes are inclined at high oblique angles to the zoarial surface. As autozooecia commonly have different angles of divergence, and as the zoarial surface is commonly undulatory, the plane of tangential section will cut through autozooecia at different angles.

Between colony CV's are significantly lower and reflect the balancing out of such with colony variation when a number of colonies in a population are examined.

In <u>Goniocladia cellulifera</u> and <u>Sulcoretepora parallela</u> within colony CV's are lower than between colony CV's. In a colony all autozooecia are regularly budded from a median wall in well defined longitudinal rows, and the subsequent pattern of development of all autozooecia is comparable. Consequently, with this high degree of genetic control over the growth of autozooecia in a colony, within colony CV's are low and range between 3.18 and 8.15. Between colony CV's are higher ranging between 4.69 to 9.51 and reflect the genetic variation in the mode of colony development and the effects of such exogenous factors as microenvironment.

Interapertural Distance (LID, TID): In the three adnate fistuliporids interapertural distances are extremely variable, CV's are very high and the two parameters are of very low taxonomic value.

Within colony CV's range between 27.37 and 38.30, and reflect the variation in the mode of development of autozooecia that occurs in a colony. Autozooecia are most commonly developed at a basal lamina at the growing edge, but they may also develop anywhere on the free colony surface above the basal lamina, on vesicular tissues or on the recumbent portions of older autozooecia. This variation in autozooecia development in a colony causes the high variation in the distribution of autozooecial apertures on the zoarial surface and is reflected also in the high within colony CV's for the two parameters of interapertural distance. Between colony CV's are only slightly lower due to the high degree of within colony variation.

In Goniocladia cellulifera and Sulcoretepora parallela autozooecia are regularly budded in well defined longitudinal rows on both sides of a median wall and the pattern of development of each autozooecium in a row is comparable. Consequently, within colony CV's are much lower than those for the three fistuliporids and range between 9.46 and 12.81. The within colony variation which does occur, phenotypic variation, and variation due to such exogenous factors as microenvironment, is evened out when a number of colonies in a population are examined. Between colony CV's are significantly lower, ranging between 3.63 and 5.88. From the low values of CV it is evident that longitudinal interapertural distance is of significant taxonomic value.

Lunarium Dimenions (LD, LT, LW): This was measured on the three fistuliporids. Lunarium dimensions are quite highly variable as shown by the high within colony CV's that range from 8.78 to 24.56, while between colony CV's are slightly lower, ranging between 6.32 and 18.52.

There are two factors that account for this fairly high variability.

Firstly the dimensions of the proximal lunarial wall is highly variable between autozooecia in a colony. The lunarium wall commonly increases in thickness significantly towards the zoarial surface. With the development of autozooecia at different levels in a zoarium, autozooecia that occur on a basal lamina, are the longest and commonly have thicker proximal lunarial walls. The degree of lateral development of the lunarium wall is also extremely variable, but the lunarium wall tends to be longer and thus better developed where the entire autozooecial wall is compound.

The second factor contributing to the high values of within and between colony CV's is related to the fact that the measurement of lunarium dimenions was undertaken using shallow tangential sections.

Autozooecia are inclined at high oblique angles to the zoarial surface, and as autozooeica develop at different levels in a zoarium and are isolated they commonly have slightly differing angles of divergence. The zoarial surface in these Bryozoa also tend to be slighly undulatory. Consequently, the plane of tangential section may not cut across all autozooecia in exactly the same orientation. This may cause the values of lunarium thickness to be occasionally artificially increased, and this factor probably accounts for the fact that lunarium thickness is the most variable of the three parameters with within colony CV's ranging between 21.31 and 24.56.

Lunarium width is the least variable of the three parameters of lunarium dimensions, because it is controlled by apertural diameter, within colony CV's range between 8.78 and 18.39.

For all three parameters between colony CV's are only slightly lower due to the high level of variability of the dimensions in a colony.

Zoarial Parameters

Monticule Spacing (MS); This was recorded only in Fistulipora incrustans. Within colony CV's are low ($\bar{X}$8.20), and reflect the importance of the regularity of monticule arrangement (see Chapter 3, p. 34 , for a discussion on monticule arrangement).

Between colony CV's are higher (18.11) and reflect the degree of genetic variation in zoarial development and the effects of such exogenous factors as microenvironment.

For biometric purposes, and the quantitative statistical comparison of species, the parameters such as Apertural Diameter in the three adnate fistuliporids and Branch Width, apertural diameter and interapertural distances in the two ramose bifoliate forms, which display very low CV's are of obvious taxonomic value. Such parameters as interapertural distance and lunarium dimensions in the fistuliporids are of little value for comparative purposes. However in the systematic description of a taxon it is necessary to examine the total morphological variation that exists and such parameters are useful for this purpose.

CHAPTER IX

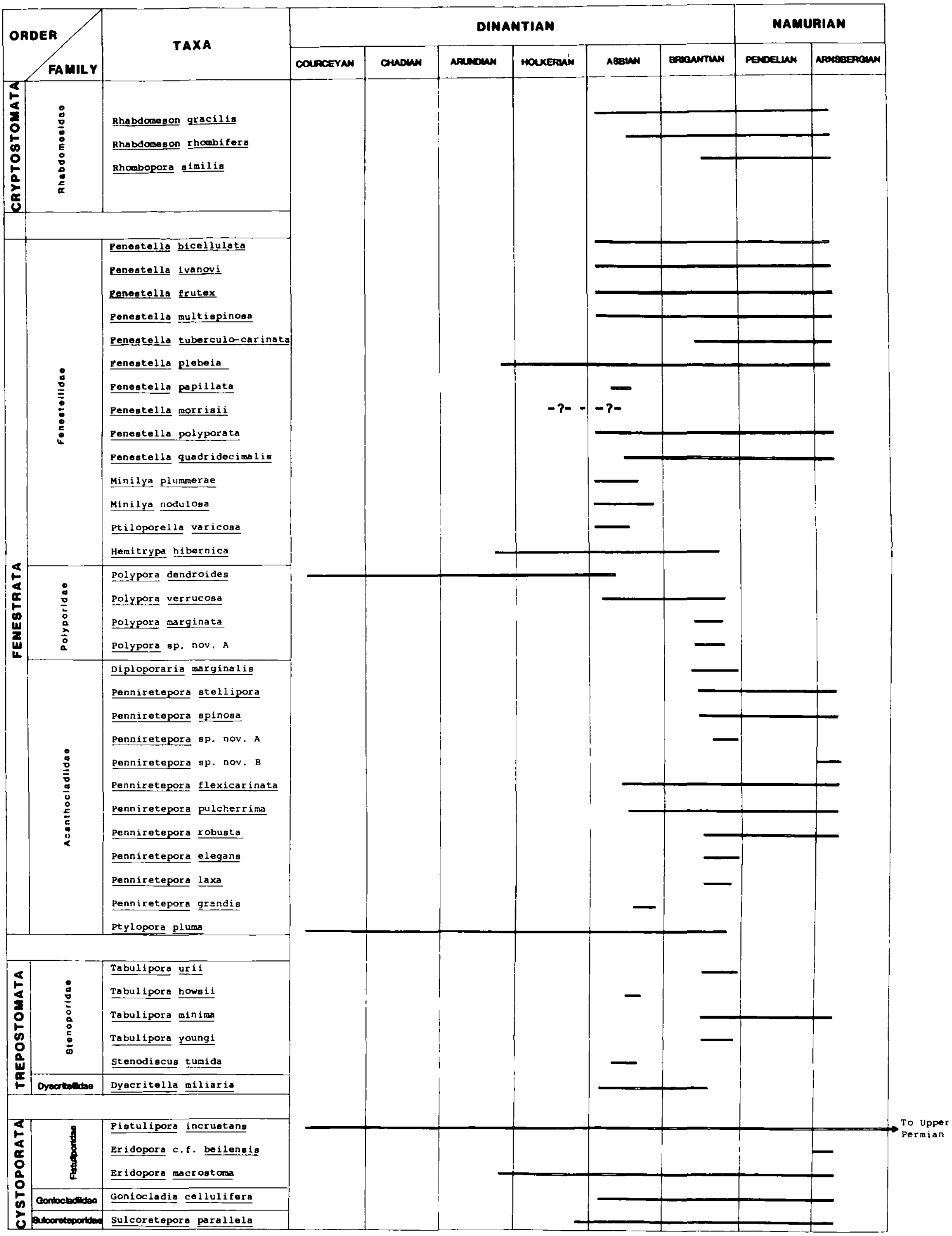
STRATIGRAPHICAL RANGES OF TAXA AND LOCALITY DESCRIPTIONS

Stratigraphical ranges of the taxa examined in the present study.

The present study has encompassed a systematic revision of most of our established species of Carboniferous Bryozoa. Bryozoa have been collected from over twenty localities throughout the British Isles at different geological horizons, ranging from Courceyan to Arnsbergian in age. This material has been supplemented by extensive collections of museum material examined in the present study. By ascertaining the precise stratigraphical horizons of the field collected material and of the accurately curated material in museum collections it has been possible to establish geological ranges for all taxa examined in the present study.

Reference has been made to local and regional geology guides and the stratigraphical correlative book The Dinantian stratigaphy of the British Isles, (George et. al. 1976) in order to find the precise stratigraphical horizons of the material examined in the present study.

The inferred geological ranges of the taxa examined in the present study are illustrated in Text Fig 1.


ORDER
FAMILY
TAXA
DINANTIAN
NAMURIAN
COURCEYAN
CHADIAN
ARUNDIAN
HOLKERIAN
ASBIAN
BRIGANTIAN
PENDELIAN
ARNSBERGIAN
CRYPTOSTOMATA
Rhabdomesidae
Rhabdomeson gracilis
Rhabdomeson rhombifera
Rhombopora similis
FENESTRATA
Fenestellidae
Fenestella bicellulata
Fenestella ivanovi
Fenestella frutex
Fenestella multispinosa
Fenestella tuberculo-carinata
Fenestella plebeia
Fenestella papillata
Fenestella morrisii
-?-
-?-
Fenestella polyporata
Fenestella quadridecimalis
Minilya plummerae
Minilya nodulosa
Ptiloporella varicosa
Hemitrypa hibernica
Polyporidae
Polypora dendroides
Polypora verrucosa
Polypora marginata
Polypora sp. nov. A
Acanthocladiidae
Diploporaria marginalis
Penniretepora stellipora
Penniretepora spinosa
Penniretepora sp. nov. A
Penniretepora sp. nov. B
Penniretepora flexicarinata
Penniretepora pulcherrima
Penniretepora robusta
Penniretepora elegans
Penniretepora laxa
Penniretepora grandis
Ptylopora pluma
TREPOSTOMATA
Stenoporidae
Tabulipora urii
Tabulipora howsii
Tabulipora minima
Tabulipora youngi
Stenodiscus tumida
Dyscritellidae
Dyscritella miliaria
CYSTOPORATA
Fistuliporidae
Fistulipora incrustans
To Upper Permian
Eridopora c.f. beilensis
Eridopora macrostoma
Goniocladiidae
Goniocladia cellulifera
Sulcoreteporidae
Sulcoretepora parallela

Locality Descriptions

The field localities from which Bryozoa were collected for the present study are described below (in alphabetical order).

Locality : Ashfell Edge, (ABA), Near Kirkby Stephen, Cumbria.

(Grid. Ref. NY 736 048)

Horizon : Fell Sandstone Group, Ashfell Sandstone (Arundian).

A large roadside exposure on the A68 Kirkby Stephen to Tebay trunk road on the right hand side at the crest of Ashfell Edge exposes the upper part of the Ashfell Sandstone (Arundian) and the lower part of the succeeding Ashfell Limestone (Holkerian).

The bryozoan fauna was obtained from the Ashfell Sandstone at the base of the exposed sequence in a unit about four metres thick, consisting of red clays interbedded with thin bands of red stained organo-detrital limestones. Text Fig 2. is a logged section of the exposed strata.

The clays contain large colonies of *Lithostrotion martini* Milne, Edwards and Haime , some apparently in growth position. Adnate bryozoans are commonly found encrusting the fasiculate corallites. The following bryozoans were recorded encrusting the corallites.

stenoporid trepostomes s. sp.

Fistulipora incrustans

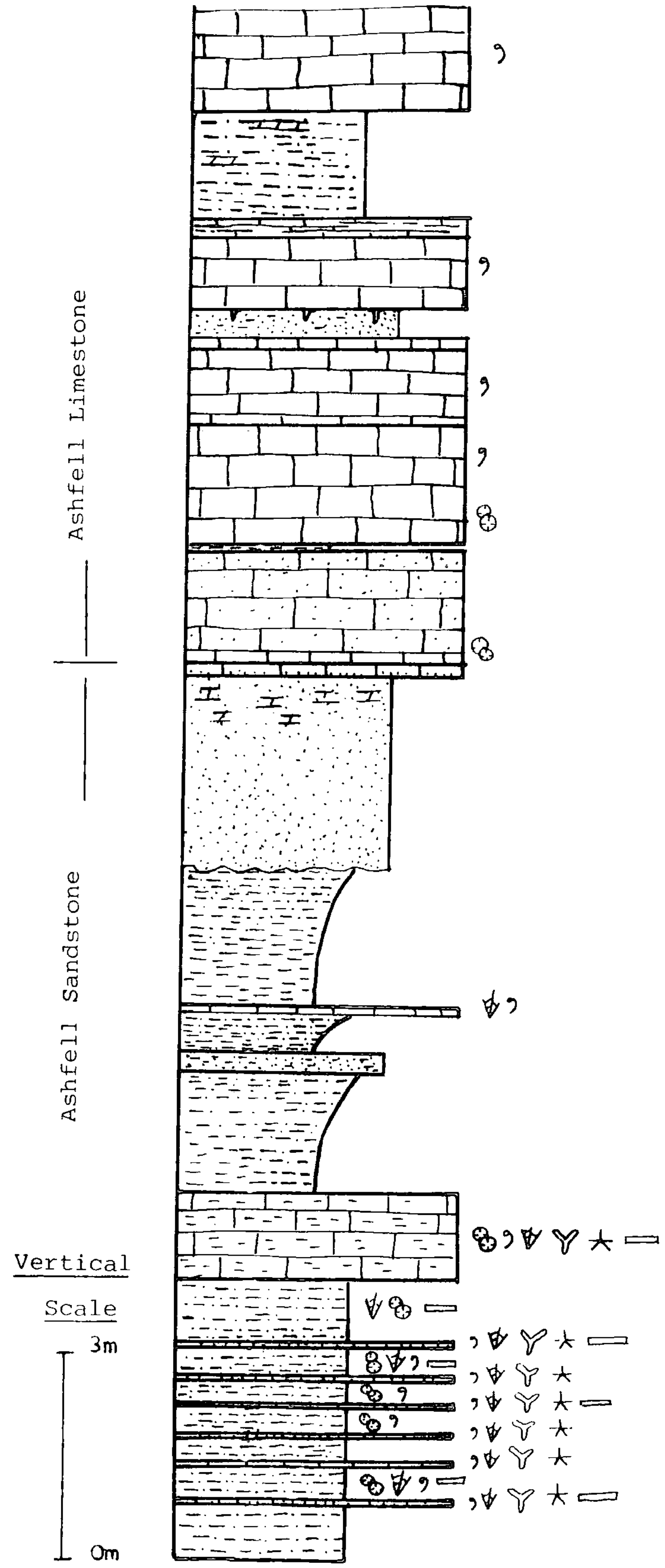
Eridopora macrostoma

The thin organo-detrital limestones are very fossiliferous and contain an abundant fauna of small spiriferid brachipods, crinoids, the tabulate coral *Cladochonus* and Bryozoa. Fenestrate Bryozoa are especially common and their white calcified skeletons contrast sharply with the red colouring of the lithology. The following bryozoan taxa were recorded from the limestones.

Rhombopora sp.

Fenestella s. sp.

F. plebeia


Ashfell Limestone
Ashfell Sandstone
Vertical
Scale
3m
0m

Hemitrypa hibernica
Penniretepora sp.

Adnate stenoporid trepostomes

Fistulipora incrustans

The adnate stenoporid trepostomes and *Fistulipora* were found encrusting the reverse surface of fenestellid branches.

Locality: Ashfell Road Cutting (*ABAF*), Near Kirkby Stephen, Cumbria.
(Grid. Ref. NY 746 054)

Horizon : Alston Group, Knipe Scar Limestone (Asbian).

A small exposure on the A68 Kirkby Stephen to Tebay trunk road on the left hand side 200 metres beyond the Sedburgh turn off exposes the lower part of the Knipe Scar Limestone, of Asbian age .

At the base of the section (see Text Fig 3.) is a massive pale grey biosparrite containing colonies of *Lithostrotion* sp. and productid brachiopods. Above this is a black calcareous mudstone-silty mudstone unit about four metres thick. The lower part of this unit is extremely fossiliferous, containing an abundant and diverse fauna of brachiopods, bryozoans, echinoderms, and occassional tabulate corals and gastropods.

The following bryozoans were recorded from this horizon.

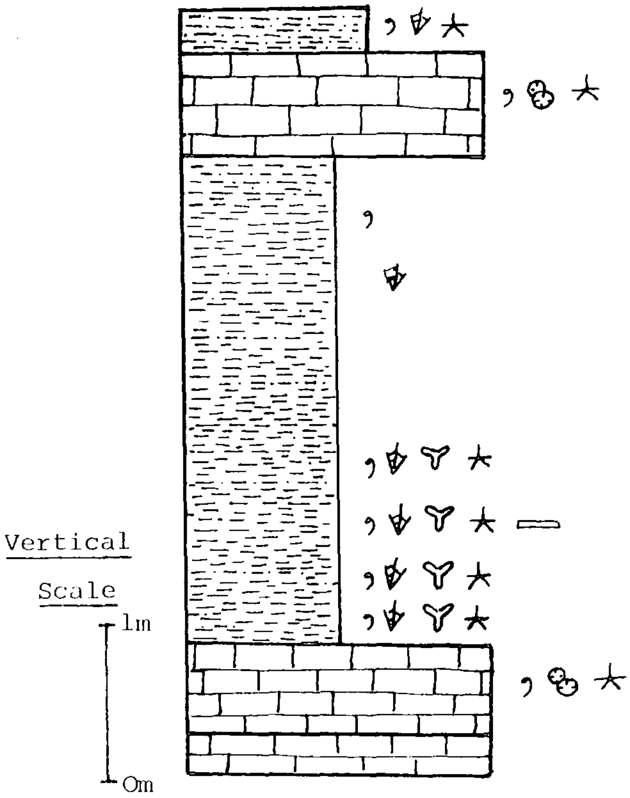
Rhombopora sp.

Fenestella bicellulata
Fenestella plebeia
Fenestella sp.
Minilya nodulosa
Hemitrypa hibernica
Diploporaria sp.
Penniretepora s.sp.

Adnate and erect stenoporid trepostomes

Fistulipora incrustans
Sulcoretepora parallela

Above this unit is another biosparrite containing large silicified


Vertical
Scale
1m
0m

colonies of the tabulate coral Syringopora. This is succeeded by a black calcareous silty-mudstone containing some fenestellid bryozoans.

The fauna collected in the bryozoan rich horizon probably represents a dominantly suspension-feeding community living in tranquil conditions, with bryozoans stabilising a muddy substratum.

Locality : Hookhead Peninsula, County Wexford, Eire. (ABHH)

Horizon : Hookhead Formation, (Courceyan).

At the southern end of the Hookhead Peninsula rocks of Courceyan age outcrop. The rocks are well exposed along the coastline, forming low cliffs and rock benches, the latter best developed in the southern most tip of the peninsula in the vicinity of Slade and the Lighthouse.

The strata consists of an interbedded sequence of dark-grey calcareous mudstones, grey silty-sandstones and dark grey biosparrites. The mudstones and limestones are very fossiliferous and contain an abundant and diverse fauna of brachiopods, bryozoans, crinoids and corals with gastropods, bivalves and trilobites also occurring.

Due to the chemical weathering and erosive action of the sea the fossils usually stand out above the surrounding preferentially eroded bed rock. Bryozoans are extremely abundant and diverse and their white calcified skeletons contrast sharply with the grey to dark grey colouring of the strata. Although large almost complete colony fragments are commonly preserved, and it is apparent that the fauna is buried just about in situ, they are not well preserved and many are considerably weathered and important detail has been removed.

The following bryozoans are recorded from the locality:-

Rhombopora sp.

Fenestella s.sp

Penniretepora s.sp

Diploporaria sp.

Ptylopora pluma
Ichthyorachis sp.
Polypora dendroides
Polypora sp.
Adnate and erect stenoporid trepostomes
Fistulipora incrustans

Locality : Hurst, Near Richmond, North Yorkshire. (Grid. Ref. NZ 044 023)
Horizon : Upper Limestone Group, Shales above the Main Limestone. (Arnsbergian) (*ABHR*)

The locality is a spoil heap, one of hundreds covering an extensive area of the high moorlands above Hurst. The fine dark grey calcareous mudstone in which the bryozoan fauna occurs is heavily weathered and most has broken down to yield a clay. The bryozooiferous lithology is assumed to have come from a horizon just above the Main Limestone. This proposition is based on the occurrence of large ironstone nodules on the spoil heap. A distinct nodular horizon is known to exist just above the Main Limestone, and the fauna collected is comparable to that described by Vine (1883a) from mudstones *in situ* from a horizon just above the Main Limestone.

The mudstone and ironstone nodules contains an abundant and diverse fauna of Bryozoa, also abundant disarticulated crinoid ossicles, and small numbers of small planar spiral and high spired gastropods and small chonetid brachiopods. The following Bryozoa are recorded from the locality:-

Rhabdomeson gracilis
Rhabdomeson rhombifera
Rhombopora similis
Hyphasmopora buskii
Fenestella bicellulata
Fenestella ivanovi
Fenestella frutex
Fenestella multispinosa
Fenestella parallela

Fenestella plebeia
Fenestella polyporata
Polypora tuberculata
Penniretepora stellipora
Penniretepora spinosa
Penniretepora sp. nov. A
Penniretepora flexicarinata
Penniretepora pulcherrima

Adnate stenoporid trepostome sp.
Tabulipora minima

Fistulipora incrustans
Eridopora c.f. beilensis
Eridopora macrostoma
Goniocladia cellulifera
Sulcoretepora parallela

The fauna suggests the palaeoenvironment was one of fairly deep water tranquil conditions especially suited to the suspension filter feeding bryozoans which helped to a stabilise a muddy bottom. The adnate fistuliporids were epiphytic on the crinoids.

Locality : Hudeshope Beck, Middleton on Teesdale, (ABHB)
(Grig. Ref. NY 361 459)
Horizon : Shales above the Three Yard Limestone, (Brigantian)

The locality is a small river bank exposure. A very fossiliferous calcareous mudstone is exposed, and is stratigraphically situated above the Three Yard Limestone (which is exposed at a nearby waterfall, about 10 metres downstream) which of Brigantian age. The strata contains an abundant and diverse fauna of brachipods, bryozoans, crinoids and a few straight shelled nautiloids, high spired gastropods and tabulate corals. Bryozoans, especially fenestellids, are extremely abundant, and the following bryozoans are recorded from the locality.

Rhombopora sp.

Fenestella frutex
Fenestella multispinosa
Fenestella plebeia

Erect stenoporid trepostomes

Goniocladia cellulifera

Locality : Eglwseg Escarpment, Trefor Rocks, Near Llangollen, Clwyd.

(ABL) (Grid. Ref. SJ 429 239)

Horizon : Cefn Mawr Limestone Formation, Upper Grey Limestone, (Brigantian).

The locality is a small scarp face just below the B 5426 Pen-y-cae to Llangollen road that runs along the base of the Eglwseg Escarpment.

At the base of the exposed sequence is a massive pale grey biomicrite This is very fossiliferous and large productid brachipods and fasiculate lithostrotionid coral colonies are common. Bryozoans are uncommon but well preserved colonies of *Rhabdomeson gracilis* and *Fenestella* sp. occur.

Above the biomicrite is a thin calcareous mudstone containing a fairly abundant and diverse fauna of brachiopods, bryozoans, with occasional crinoids and trilobites. Bryozoans are fairly common and the following taxa are recorded;-

Rhabdomeson gracilis

Fenestella sp,
Fenestella frutex
Fenestella plebeia

Fistulipora incrustans

Locality : Mill Gill, Askrigg, Near Richmond, North Yorkshire. (*ABMG*)

(Grid. Ref. SD 938 915)

Horizon : Middle Limestone Group, Hardraw Shales, (Brigantian).

The Hardraw Shales are about five metres thick and are exposed along the length of Mill Gill. It is underlain by the Gayle Limestone and the next major unit above is the Simonstone Limestone. The unit is subdivided by localised nodular biomicrite horizons, not all the unit is fossiliferous and only the finely laminated dark grey calcareous mudstones at the base are fossiliferous. The lower laminated mudstones are extremely fossiliferous, with an abundant an diverse fauna of bivalves, brachiopods, bryozoans, together with a few crinoids, trilobites and rare corals. The following bryozoans are recorded from the shales;-

Rhombopora sp.

Fenestella multispinosa
Fenestella plebeia
Fenestella polyporata
Polypora verrucosa
Penniretepora flexicarinata
Penniretepora pulcherrima
Penniretepora robusta
Penniretepora laxa
Ptylopora pluma

Erect stenoporid trepostome sp.

Sulcoretepora parallela

The suspension filter feeding bryozoans lived in a tranquil environment where they helped to stabilise a muddy bottom inhabited brachiopods, bivalves and crinoids.

Locality : Morpeth Scar, West Burton, Wensleydale, Near Richmond, (ABWB)
North Yorkshire. (Grid. Ref. NY 029 878)
Horizon : Middle Limestone Group, Middle Limestone,
(Brigantian)

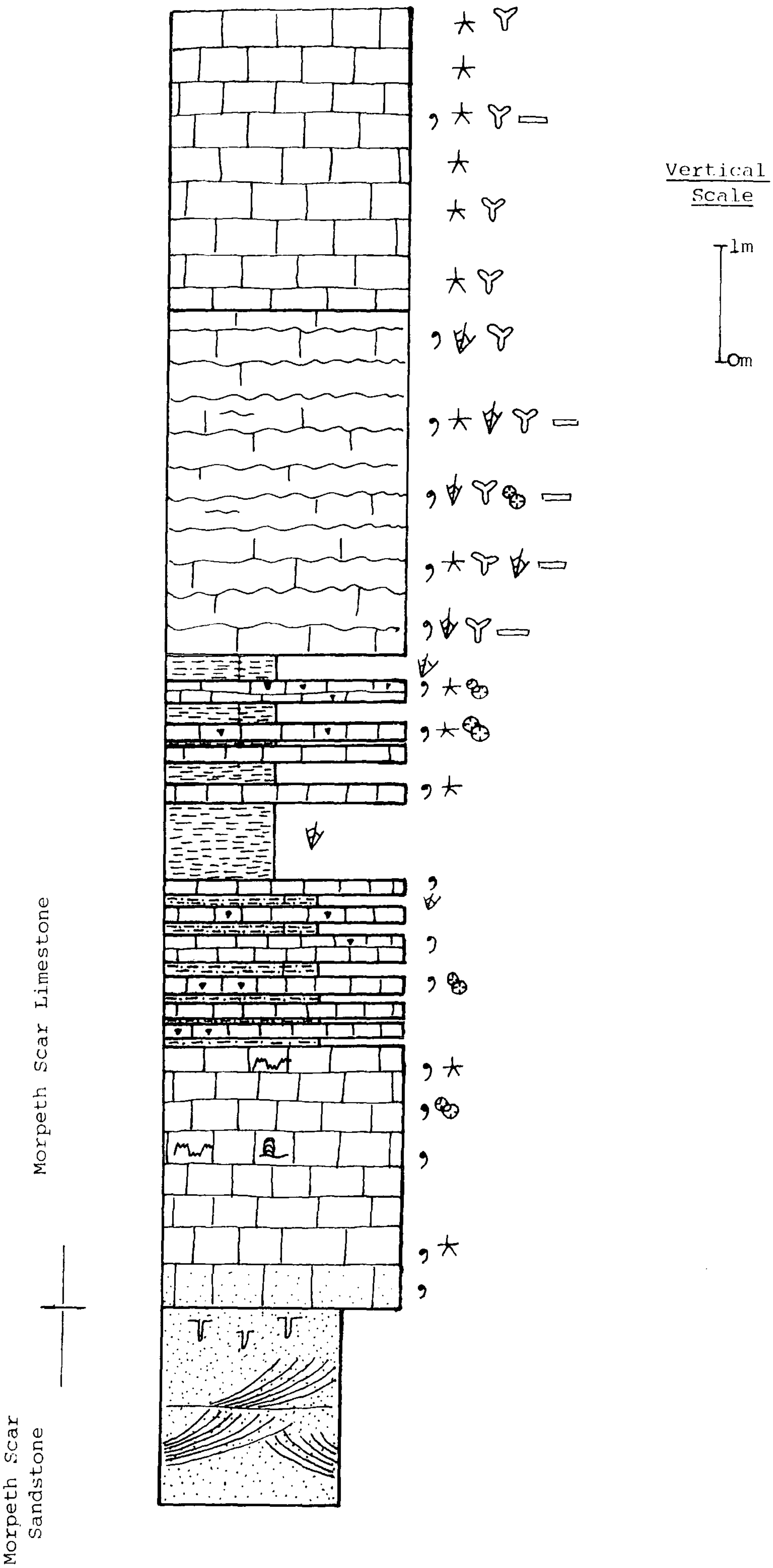
The Middle Limestone known locally as the Morpeth Scar Limestone forms a prominent escarment at Morpeth Scar. A vertical section was logged from a horizon by the side of a track in a small quarry (029 874) to the top of the scar (029 878) , see Text Fig 4.

At the base of the section in the quarry a massive cross-bedded calcarenite, about three metres thick , is exposed. Arenicolites burrows occur near the top of the unit.

Above this lies a massive well bedded dark grey biosparrite which has a sharp erosive base on the sandstone below. The lower part of the unit is matrix supported, being almost a sandy limestone. Corals and brachiopods are common, especially near to the top of the unit, with Lithostrotion sp., Dibunophylum sp. productids and Athyris being common. The occurrence of algal mats in the unit indicates a shallow possibly sub-intertidal environment of deposition.

Above this unit is a unit of interbedded biosparrites, calcareous mudstones and siltstones. The biosparrite bands are very fossiliferous with Gigantoproductus sp. being very abundant. In the shaley horizons between the limestones abundant fenestellid and pinnate acanthocladiid bryozoans occur, with Fenestella multispinosa, Fenestella plebeia and Penniretepora sp. being recorded.

This unit gives way to a massive irregularly bedded pale coloured biosparrite at Morpeth Scar itself. This limestone unofficially known as the Bryozoan Limestone is characterised by the abundance and diversity of bryozoans and could almost be termed a bryozoan coquina. Bryozoans are the most abundant faunal element but some corals, crinoids and


Vertical Scale
1m
0m
Morpeth Scar Limestone
Morpeth Scar Sandstone

brachiopods occur. Very thin mudstone bands occur irregularly throughout the unit, they contain the same fauna but with the notable addition of blastoids.

The following bryozoan fauna was collected from the unit:-

Rhombopora sp.

Fenestella multispinosa
Fenestella plebeia
Polypora verrucosa
Penniretepora sp.

Tabulipora minima ?
Erect stenoporid trepostome sp.
Dyscritella sp.

Fistulipora incrustans
Goniocladia cellulifera

The trepostomes and fistuliporoid cystoporates are especially abundant, *Fistulipora incrustans* encrusts both trepostomes and fenestrates and *Goniocladia cellulifera* is extremely abundant at some horizons, occasionally to the exclusion of other bryozoans.

Above this unit is a massive crinoidal limestone consisting of large loosely consolidated crinoid ossicles up to 15cm in length and 3cm in width. The unit commonly contains crinoids with the exclusion of other fauna, however a restricted fauna of bryozoans and more rarely brachiopods and corals has been collected.

The following bryozoans were recorded from the unit:

Fenestella sp.

Tabulipora sp.
Adnate stenoporid trepostome sp.

Fistulipora incrustans
Goniocladia cellulifera

Locality : Odin Fissure, Near Treak Cliff Cavern, Castleton,
Derbyshire. (ABO). (Grid. Ref. SK 133 834)

Horizon : Bee Limestone Group, Apron Reef Limestone. (Asbian).

The locality is the upper portion of a narrow gulley whose lowest section is known as Odin Fissure. The strata exposed is a fore-reef calcirudite, and is very poorly bedded with an algal framework composed predominantly of Koninckopora inflata with minor local contributions from Chaetetes, Lithostrotion colonies and adnate fistuliporid bryozoans.

The strata contains an abundant and diverse fauna dominated by brachiopods and bryozoans, with bivalves, crinoids, nautiloids and gastropods being less common, corals and trilobites being very scarce.

The following bryozoans were collected from the locality:-

Rhombopora sp.

Fenestella sp.
Fenestella multispinosa
Fenestella plebeia
Fenestella polyporata
Hemitrypa hibernica
Ichthyorachis newenhi
Penniretepora sp.
Ptylopora pluma

Stenopora sp.

Fistulipora incrustans

The algal framework of the strata is suggestive of a shallow water sub-tidal environment, one affected by water currents. The local abundance of the adnate fistuliporid Fistulipora incrustans also suggests this environment. Crinoids are uncommon in the strata and were restricted to deeper water calmer conditions.

Locality : Penruddock Road Cutting, Penruddock, Near Penrith, Cumbria.

(ABP) (Grid. Ref. NY 438 276)

Horizon : Alston Group, Fifth Limestone, (Asbian).

The locality is situated along the right hand side of the A66 Penrith to Keswick trunk road, 150 metres before the Penruddock turn off. The exposure is about 80 metres in length and exposes a sequence about 10 metres thick consisting of interbedded mudstones, siltstones and detrital limestones, which are of Asbian age (see Text Fig 5.).

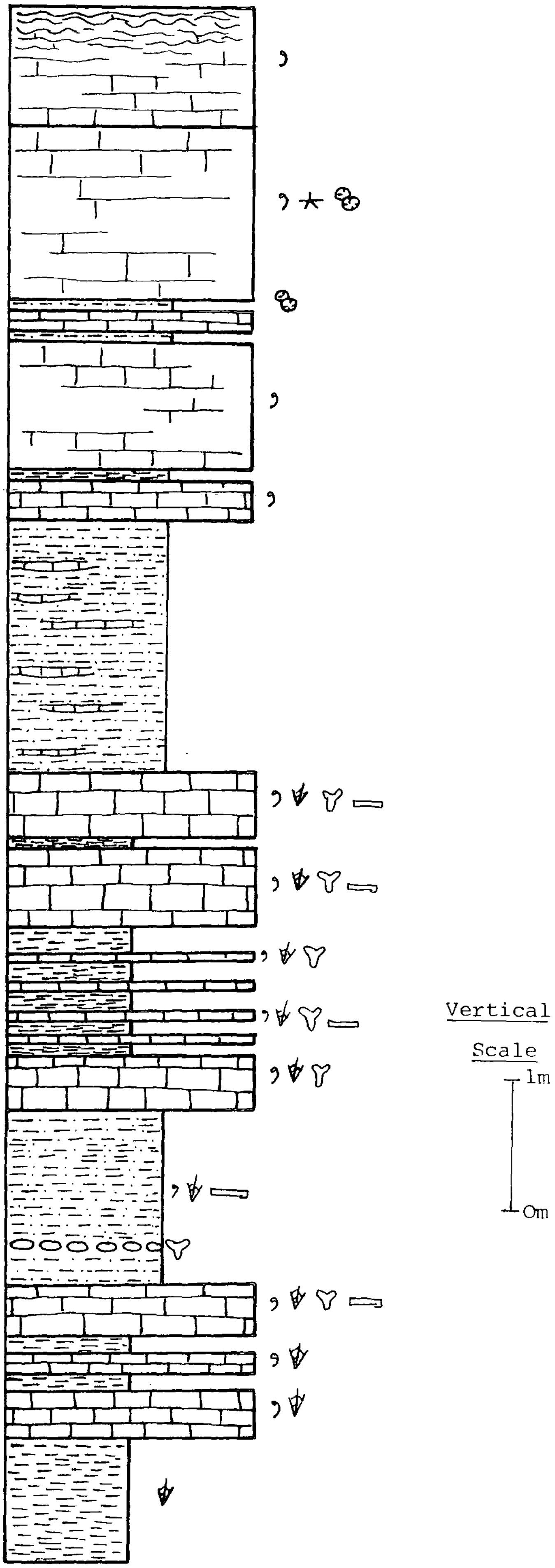
In the fissile calcareous mudstones and siltstones fenestellid and acanthocladiid bryoans are very abundant. The material is well preserved, all having their original calcified skeletons preserved. The following bryozoans were collected from the mudstone and siltstone horizons:-

Fenestella bicellulata
Fenestella frutex
Fenestella matheri
Fenestella plebeia
Fenestella polyporata
Minilya plummerae
Minilya nodulosa
Hemitrypa hibernica
Polypora sp.
Diploporaria sp.
Penniretepora s.sp.

Fistulipora incrustans

Fistulipora incrustans is very common and is found encrusting fenestellid colonies.

A thin nodular horizon occurs in a calcareous siltstone unit in the lower part of the sequence (see Text Fig 5.). The nodules are occasionally encrusted by stenoporid trepostomes and are noted for the occurrence of edrioasteroids on them, often in abundance.


Vertical
Scale
1m
0m

The detrital limestones are noted for their abundant and diverse fauna, with brachipods, bryozoans, crinoids, gastropods, occasional corals and rare bivalves. Bryozoans are very abundant and comprise the dominant fauna in some of the limestone units. The following bryozoans were recorded from the limestone units:-

Rhombopora sp.

Fenestella bicellulata
Fenestella frutex
Fenestella plebeia
Hemitrypa hibernica
Penniretepora sp.

Adnate and erect stenoporid trepostomes
Dyscritella miliaria

Fistulipora incrustans
Goniocladia cellulifera

Locality : Vickers Ltd Quarry, The Steel, Ridsdale, Northumberland.
(ABR) (Grid. Ref. NY 8936 8290)
Horizon : Lower Limestone Group, Redesdale Ironstone and Shale, (Asbian).

The locality is a large disused quarry situated close to the A68 Otterburn to Corbridge road approximately two miles south of the village of Ridsdale.

The quarry has been disused for a number of years and is heavily overgrown. Three units are exposed in the quarry face. At the base is a very weathered poorly exposed dark grey fissile calcareous mudstone which has a very sparce fauna of brachiopods and crinoids. Above this unit is a very fossiliferous iron rich biomicrite known as the Redesdale Ironstone, and is of Middle Asbian age. The fauna is very abundant and diverse consisting of brachiopods, bivalves, crinoids, straight shelled nautiloids, with occasional tabulate corals and fasiculate lithostrotionid corals. Bryozoans are abundant and the following taxa were collected from the ironstone:-

Rhabdomeson rhombifera

Fenestella sp.
Fenestella frutex
Fenestella multispinosa
Fenestella plebeia
Fenestella polyporata
Hemitrypa hibernica
Penniretepora sp.

Stenodiscus tumida

Fistulipora incrustans

Above the ironstone is a calcareous muddy-siltstone the Redesdale Ironstone Shale. The shale is poorly exposed in the quarry, however adjacent to the quarry are many spoilheaps of the shale and ironstone. These are heavily overgrown but the shale has been weathered and broken down and the abundant and diverse fauna it contains is easily extracted. The fauna is similar to that of the ironstone below, consisting of brachiopods, bivalves, bryozoans, crinoids, straight shelled nautiloids together with occasional trilobites, tabulate corals, fasiculate lithostrotionid corals and rare conularids. Bryozoa are very common and the following taxa were collected:-

Rhabdomeson rhombifera

Fenestella sp.
Fenestella bicellulata
Fenestella frutex
Fenestella multispinosa
Fenestella plebeia
Fenestella polyporata
Septopora cestriensis
Diploporaria sp.
Penniretepora sp.
Penniretepora flexicarinata

Tabulipora howsii
Stenodiscus tumida
Dyscritella miliaria
Fistulipora incrustans

Locality : Redmain, Near Cockermouth, Cumbria, (ABRE) (Grid. Ref. NY 145 342)

Horizon : Orton Group, Seventh Limestone, (Holkerian).

The locality is a small trackside exposure a quarter of a mile east of the village of Redmain along a public footpath 300 metres in a south-easterly direction off the Redmain to Blindcrake road. The locality is very small, about three metres long and one metre high, and exposes a massive irregularly bedded dark grey biomicrite of the Seventh Limestone, which is of Holkerian age.

The strata is very fossiliferous but the fauna collected is a very restricted one and is dominated by fenestellid bryozoans with occasional fasiculate lithostrotionid coral colonies also occurring. The following bryozoans were recorded:-

Fenestella s.sp.
Hemitrypa hibernica
Fistulipora incrustans
Sulcoretepora parallela

The fenestellid colonies are of large size and the fauna was obviously buried in situ. Hemitrypa hibernica is especially abundant and all colonies have their superstructure intact above the fenestellid meshwork. Fistulipora incrustans is very common, and is found encrusting the superstructure of Hemitrypa hibernica and the meshwork of the other fenestellids.

Locality : Stenders Quarry, Micheldean, Gloustershire.

(Grid. Ref. SO 659 184)

Horizon : Lower Limestone Shales and Dolomites, (Courceyan)

The locality is a small disused quarry, formerly known as the Micheldean Cement Works Quarry. The steeply dipping well bedded strata exposes rocks of Upper Old Red Sandstone age (Devonian) of the Tintern Sandstone Group which are conformably overlain by marine Courceyan Lower Limestone Shales and Dolomite.

The Lower Limestone Shales are very fossiliferous with bryozoans and disarticulated crinoid ossicles being commonest, a few small brachipods also occurring. Bryozoans occur at two principal horizons, the upper known as the bryozoan bed. Stenoporid trepostomes and rhomboporid cryptostomes are commonest, and the trepostomes are commonly found encrusting crinoid ossicles. Fenestellids are quite common, zoarial fragments may be of large size and the proximal extremeties of conical colonies are not uncommon. The following bryozoans are recorded from the locality:-

Rhombopora sp.

Fenestella s.sp.

Penniretepora sp.

Adnate and erect stenoporid trepostomes s.sp.

The assemblage probably represents a quite water, suspension feeding community that was buried more or less *in situ*.

The following localities were not visited but material from them was donated from museum collections to aid the present study.

Locality : Carrick Lough, Near Derrygonelly, County Fermanagh, Northern Ireland. (*ABCL*).

Horizon : Calp Shale-Upper Limestone, (Asbian).

The litho- and chronostratigraphy of the locality was fully described by Tavener-Smith (1973). The strata consists of interbedded shales and argillaceous limestones which contain reef structures. Bryozoans and small productid brachiopods are the commonest fossils, with horn corals, bivalves, and gastropods also occurring in smaller numbers. Sponge spicules are extremely common.

Apparently the fauna at Carrick Lough is not a life association and the fauna were moved to some extent prior to their deposition and burial (Tavener-Smith 1973). This is suggested by the small size of the fenestellid bryozoan colony fragments and it appears that the material was derived from a nearby reef (Tavener-Smith 1973).

Tavener-Smith (1965a, 1965b, 1966a, 1973) and Olaloye (1974) have described the fenestrate component of the bryozoan fauna, with Tavener-Smith describing the fenestrate forms and Olaloye the pinnate forms. The following bryozoans have been recorded from the locality:-

Rhabdomeson gracilis
Rhabdomeson rhombifera
Rhombopora sp.

Fenestella frutex
Fenestella ivanovi
Fenestella multispinosa
Fenestella modesta
Fenestella hemispherica
Fenestella parallela
Fenestella rudis multinodosa

Fenestella plebeia
Fenestella cf. *arthritica*
Fenestella praemagna
Fenestella fanata carrickensis
Fenestella cf. *spinacristata*
Fenestella cf. *funicula*
Fenestella cf. *filistrata*
Fenestella subspeciosa
Fenestella cf. *albida*
Fenestella oblongata
Fenestella delicatula

Fenestella polyporata
Fenestella irregularis
Levifenestella unidecimalis
Ptilofenestella carrickensis
Minilya plummerae
Minilya nodulosa
Minilya binodata
Minilya oculata
Ptiloporella varicosa
Hemitrypa hibernica
Polypora stenostoma
Polypora dendroides
Polypora verrucosa
Ptylopora pluma parva
Septopora hibernica
Penniretepora pluma
Penniretepora gracilis
Penniretepora frondiformis
Penniretepora normalis
Penniretepora cucullea
Penniretepora cf. *flexicarinata*
Penniretepora sinuosa
Penniretepora elegantula
Penniretepora rotunda
Penniretepora tortuosa

Dyscritella miliaria

Fistulipora incrustans
Goniocladia cellulifera
Sulcoretepora parallela

From the faunal list it is evident that fenestrate bryozoans form the dominant element of the bryozoan fauna present. Although all the material from the locality is silicified a considerable amount of microscopic and internal morphological detail is preserved. Colony fragments of *Hemitrypa hibernica* usually have their superstructure intact and *in situ* above the main fenestellid meshwork, and the small basket shaped colonies of *Ptilofenestella carrickensis* are commonly nearly complete.

Locality : Hairmyres, East Kilbride, Scotland. (ABH)

Horizon : Lower Limestone Group, Hosie Limestone, (Brigantian).

This is the locality from which Prof. J Young and Mr, J. Young collected alot of their material in the latter part of the nineteenth century on which many of their original descriptions of new Carboniferous bryozoan species were based (egs. 1874a, 1874^{b}, 1875a, 1875b)

However the locality is no longer accessible and most of the material examined in the present study belonged to the Young and Young collections in the Hunterian Museum, Glasgow and the Glasgow Art Gallery and Museum. Additional material from the locality was donated from the collections in the Hunterian Museum for the purposes of the present study.

The following bryozoans are recorded from the locality:-

Rhabdomeson gracilis
Rhabdomeson rhombifera
Rhombopora similis
Hyphasmopora buskii

Fenestella bicellulata
Fenestella multispinosa
Fenestella plebeia
Fenestella polyporata
Penniretepora stellipora
Penniretepora spinosa
Penniretepora flexicarinata
Penniretepora pulcherrima
Penniretepora elegans
Penniretepora laxa
Diploporaria marginalis
Thamniscus rankinii
Synocladia carbonaria
Polypora tuberculata

Tabulipora minma

Fistulipora incrustans
Goniocladia cellulifera
Sulcoretepora parallela

CHAPTER X

CONCLUSIONS

The present study has encompassed a taxonomic revision of most of our established species of British Carboniferous Bryozoa. Many of the taxa revised in this thesis were desribed originally during the nineteenth century, and the taxonomic revisions in this thesis owe much to the large well documented Museum collections of type material collected by such people as McCoy, and Young and Young. As these workers did not establish holotypes, lectotypes have been selected from their material for many of the species.

Originally only external morphological characters were employed in entirely qualitative taxonomic descriptions, however, subsequent work has stressed the importance of internal morphological details and the measured parameters. Consequently, in the present study, a quantitative approach has been adopted involving the measurement of zoarial and zooecial morphological characters externally and internally to supplement taxonomic descriptions. An important aspect of the present study has involved the establishment of a standard series of morphological parameters, usually developed at familial level, to enable the precise quantitative assessment of taxa, and to differentiate species.

Internal zooecial characters, and skeletal microstructure, have been examined wherever possible. In the stenoporid trepostomes examined it has proved fairly difficult to distinguish between species solely on external morphological characters, and internal morphological detail is extremely important in species differentiation. Notably such characters as the morphology of the exozone wall, occurrence of basal diagrams, ring septa and the microstructure of interzooecial walls are important in species differentiation. The present study has shown that internal zooecial characters and skeletal microstructure details may be utilised to differentiate fenestrate taxa.

Representative taxa of the four extinct stenolaemate orders have been examined in the present study and it has been possible to elucidate several significant features of skeletal morphology. A reassessment of the structure and function of stylets has been made, and it has been possible to categorise them into three distinct types. The morphology and function of exilazooecia and monticules has been assessed.

In fenestrates several important morphological features have been described. Secondary nanozooids have now been described in a much larger number of genera and species than previously recorded. Ovicells have been described for the first time in the genus Penniretepora. Denticulate autozooecial apertures have been described, and their function inferred. In trepostomes, zoarial growth in the genus Tabulipora has been described, as also has the growth of ring septa in this genus.

The measurement of selected parameters to determine the precise quantitative assessment of taxa has also made it possible to define, and actually to quantify, some unusual aspects of skeletal morphology. For example, the gradation in apertural dimensions around the zoarium in the rhabdomesid cryptostome Rhabdomeson rhombifera has been so quantified. In the cystoporate Goniocladia cellulifera the gradation in interapertural distances between autozooecial apertures in adjacent longitudinal rows in a branch has also been quantified.

Field collection has established an approximate geological range for each taxon described. Although many taxa have long geological ranges, with apparently no significant evolutionary change, some taxa appear to have more limited geological ranges.

Although most of our established species of British Carboniferous Bryozoa have been redescribed and many significant aspects of skeletal morphology considered, there is much scope for further research. The following aspects can be identified as those most in need of study:-

(1) A complete revision of all described Palaeozoic, fenestrate, rhabdomesid, trepostome and cystoporate taxa. The absence of standardised quantitative procedures in species identification, complimented by detailed qualitative descriptions of internal and external morphological characters, has resulted in the high level of conspecificity evident in many genera such as Fenestella and Tabulipora. It is only by utilising standardised quantitative measurement schemes at generic level and by utilising external and internal morphological character states that conspecificity can be eliminated. Through this approach, and utilising internal microstructural details, it will then be possible to analyse the morphological variation within and between taxa, and any phylogenetic relationships or evolutionary lineages can be reasonably inferred.

(2) Further Taxonomic Studies. About twenty British Carboniferous bryozoan taxa remain unrevised. The material collected in the present study has shown that the Carboniferous bryozoan fauna in Britain is more diverse than hitherto realised. In addition to collecting material of established taxa allowing the detailed morphological analysis of the present study, considerable material has been collected of many undescribed species.

(3) Bistratigraphical Applications: It is apparent that although many taxa have long geological ranges and display no significant evolutionary morphological change some taxa have more limited geological ranges and are of biostratigraphical value. It is only by further taxonomic studies and detailed analyses of bryozoan faunas throughout the Carboniferous that their full value in biostratigraphy may be realised.

(4) Palaeoenvironmental Applications. Despite the enormous range of environments in the Carboniferous sequence, bryozoans have not really been utilised in Carboniferous palaeoenvironmental reconstruction and as palaeoenvironmental indicators. Recent work (e.g. Taylor, 1977) has shown that bryozoans have temporal distributions which are largely facies controlled and consequently they could be of great value in such palaeoenvironmental reconstructions.

(5) As cyclostomes are the only living stenolaemates, there is an obvious necessity to develop physiological studies of extant cyclostomes with a particular view to elucidating the relationship of skeletal growth and soft part morphology as a guide to interpreting fossil stenolaemates.

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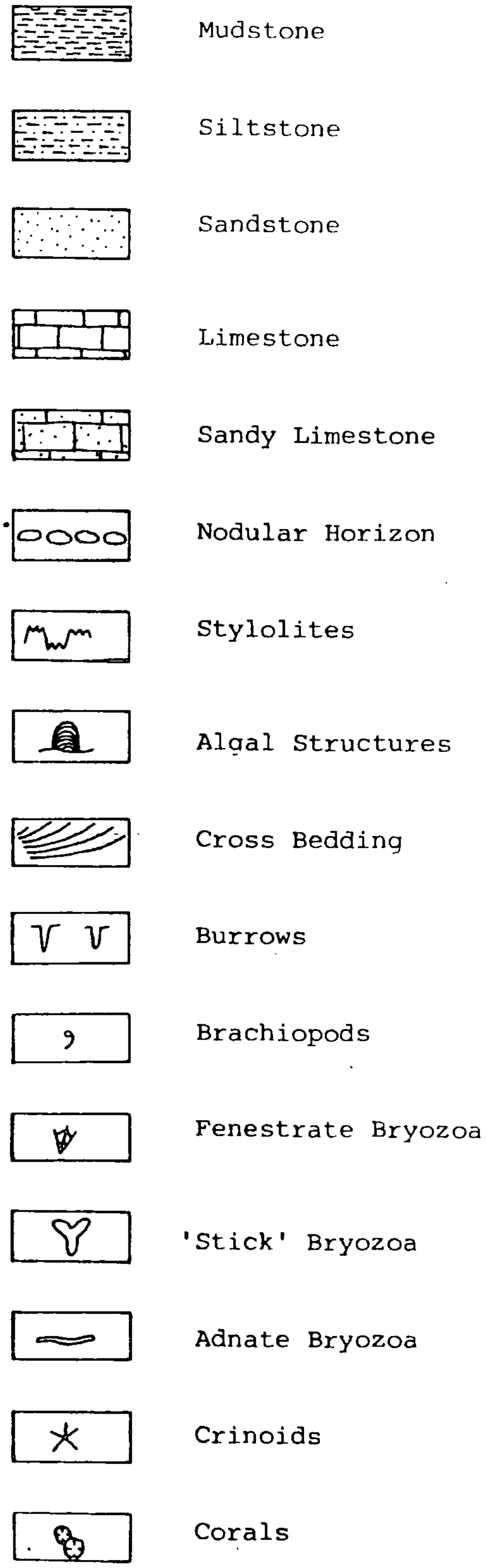
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Brachiopods
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'Stick' Bryozoa
Adnate Bryozoa
Crinoids
Corals