# FENESTRATE BRYOZOA FROM THE VISEA 

 OF COUNTY FERMANAGH, IRELAND
## BY

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## TRUSTEES OF <br> THE BRITISH MUSEUM (NATURAL HISTORY)

# FENESTRATE BRYOZOA FROM THE VISEAN OF COUNTY FERMANAGH, IRELAND 

By R. TAVENER-SMITH

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## SYNOPSIS

This report deals with silicified fenestrate bryozoa from $D_{1}$ limestones at Carrick Lough, County Fermanagh. Thirty-two species belonging to eight genera are described, including two new species and three sub-species. The genus Septopora is recorded from Ireland for the first time.

Sedimentary characteristics suggest that the bryozoans are part of a drift assemblage accumulated in de-oxygenated conditions in water of moderate depth. There are indications that the fenestrate colonies originally grew in a shallower and better aerated environment on the flanks of reef mounds.

A review of the present situation in fenestellid taxonomy suggests a need for increased use of zooecial, as opposed to zoarial, characteristics, and for the use of accepted biometric methods in comparing samples of numerical data. Statistical information included in systematic descriptions is arranged so as to facilitate the latter aim.

## I. INTRODUCTION AND ACKNOWLEDGEMENTS

This bulletin contains systematic descriptions of fenestrate bryozoa from an argillaceous limestone sequence at Carrick Lough, County Fermanagh. The geographic position of the collecting locality, which is about three miles north-west of Derrygonelly village, and about eleven from Enniskillen in the same direction, is shown in Text-figs I \& 3.

Etching of limestone blocks from this locality yielded a silicified fauna which included a profusion of well preserved fragments of fenestrate bryozoa with a range of form exceeding that shown by any comparable collection in the British Isles or, indeed, in all Europe. A unique opportunity was therefore presented to study the structure and systematics of this common, though neglected, group of fossils. Silicified brachiopods from the same general locality and horizon have been described in an earlier Bulletin of this series (Brunton Ig66).

Identification of the fenestrate fossils necessarily involved comparison with type material in other collections, and in this connection I am indebted to the late Dr H . Dighton Thomas of the British Museum (Natural History) ; to Dr J. S. Jackson of the National Museum of Ireland, and to Mr M. Mitchell of the Geological Survey Museum, who provided access to material in their care. In addition, specimens were kindly loaned by the Curators of the United States National Museum; the Sedgwick Museum, Cambridge; the Hunterian Museum, University of Glasgow, and by Dr R. D. Wilson of the Scottish Office, H.M. Geological Survey.

I also wish to thank Messrs C. D. Kemp, Queen's University, and D. H. McNally, Ministry of Agriculture, for useful discussions on statistical aspects of the work; Dr Helen Duncan, U.S. National Museum, for making reference books available on extended loan; and Professor Alwyn Williams for critically reading the manuscript.

## II. STRATIGRAPHY

Although the ground between lower Lough Erne and Lough Melvin has not been mapped since the work leading to the Geological Survey publications of 1885 , neighbouring country to the north and south has received more recent attention (Simpson, 1954; Oswald, 1955; George \& Oswald, 1957). In these areas the Carboniferous stratigraphy is quite well known, and by reference to it the horizon of the collecting locality at Carrick Lough can be determined.

In Leitrim and Sligo the youngest calcareous formation mapped by Oswald is the massive, chert-bearing Dartry Limestone, dated as $\mathrm{D}_{1}$ on palaeontological evidence (Oswald 1955; 180). Below this is the Glencar (or Upper Calp) Limestone, with its distinctive limestone-shale lithology, also considered by Oswald to be of $\mathrm{D}_{1}$ age. The contact between these formations is gradational and both contain reef structures which are, however, commonest in the Dartry Limestone. The latter generally forms a prominent topographic feature, and can be traced without difficulty from Sligo and Leitrim into south Fermanagh and the vicinity of Carrick Lough. Hills on the south side of that lough are part of a locally developed reef complex in a lateral extension of the Dartry, while on the lough shore shales and limestones of Glencar-type are exposed. The junction between the two formations is transitional, as in Oswald's area. The fossil assemblage described in this Bulletin was obtained from beds of argillaceous limestone intercalated with shale below the reef, and is therefore of late Glencar age in terms of the Sligo succession.
Further correspondences are also evident between the succession around Carrick Lough and those of the better known Carboniferous areas to west, north and south. For instance, the country between the collecting locality and the shore of Lough Erne, some three miles away, is underlain by thick, black shales which must be lateral equivalents of the Bundoran and Benbulben (Calp) Shales of the Donegal and Sligo coasts. The Calp Sandstone (Mullaghmore, Kildoney or Mountcharles Sandstones of Oswald 1955, and George \& Oswald 1957) is present within these black shales, though poorly exposed and probably thinner than to the west and north. It outcrops about a mile north-west of Derrygonelly village, and the surveyors of 1885 also recorded it in the vicinity of Monea.
Dark, thick-bedded limestones with thin shale partings are to be seen in many roadside quarries close to the south shore of Lough Erne, between Ely Lodge and Tully Point. They dip beneath the black shales and are locally the lowest visible Dinantian strata. This formation corresponds exactly in lithology and stratigraphic position with the Ballyshannon Limestone of Oswald, which underlies a strip of country a few miles to the west, between Belleek and the coast. The Ballyshannon Limestone of that vicinity is virtually continuous along the strike with Simpson's Pettigo Limestone to the north-east, with which it must be correlated. The Ely Lodge-Tully Point limestone on the south side of Lough Erne is also, no doubt, a lateral equivalent of the Pettigo Limestone, though there is no sign to the south of the Lough of the thick arenaceous formations which underlie the limestone in the Kesh-Omagh area and form the base of the Dinantian there.


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Fig. 2. Relationship of the stratigraphic succession in the Carrick Lough vicinity to that in other parts of north-west Ireland. In some parts of Donegal the succession is very arenaceous in the lower part and much thicker than indicated above.


Fig. 3. Situation of the collecting locality at Carrick Lough. Dotted lines indicate present water levels in the loughs, following recent drainage operations.

Text-fig. 2 relates the succession around Carrick Lough to those of neighbouring areas, as indicated by recent work. In view of the general correspondence between them, and the position of the collecting horizons in the sequence at Carrick Lough, there is little doubt that the fossil assemblage described in this report is of early $\mathrm{D}_{1}$ age.

The beds from which collections were made form an inconspicious series of exposures at the foot of a steep, wooded bluff about half-way along the south side of Carrick Lough. They are also exposed on the adjacent beach, which has formed since the water level in the lake was lowered by deepening the course of the Sillees River. The strike is to the north-east or east-north-east, roughly at right angles to the trend of the shore, and the beds dip north-west, generally at from 25 to 35 degrees.

The strata are essentially alternations of shale and argillaceous limestone, though the proportion between these constituents is not constant. At the south-east (stratigraphically lower) end of the section the beds are mainly mid-grey to buff weathering shale with thin ( 2 to 6 in.) limestone bands. Ascending the succession the latter increase in number and thickness until, at the north-west end, shale is only present as thin partings and there is a passage into the massive, pale, reef limestone of the succeeding formation. In the lower part of the section limestone bands commonly weather out of the shale as flaggy ledges, and this is particularly noticeable on the wide beach. Beds in this situation have been etched by the peaty water of the lough and commonly show prominent, silica-rich, upper and lower crusts separated by a deeply-etched, pale-weathering, calcareous part from which silicified fossils protrude.

Blocks of limestone from beds of the kind described were collected at five separate horizons in a thickness of 240 ft of strata. These were respectively at $24-30 \mathrm{ft}$; $47 \mathrm{ft} ; 87-99 \mathrm{ft}$; IIO-II7 ft and 224-234 ft vertically below the base of the reef which locally represents the Dartry-Glencar contact. Blocks from the four lower horizons were of a dark, flaggy, pyritous nature, while those from the uppermost level were fine-grained, dove-grey, limestone. Such beds, intercalated among predominant argillaceous limestones and shales in the upper part of the section, may represent the lower extremities of lenticular deposits of wave-broken debris which accumulated locally on the flanks of reef mounds, and extended at their lower extremities into deeper water.

## III. TREATMENT OF SAMPLES

About fifteen hundredweight of limestone blocks were collected and etched, using the following technique. Blocks were placed in deep polythene basins and covered with a $20 \%$ solution of hydrochloric acid and hot water. At forty-eight-hour intervals the spent liquor was siphoned off and the blocks carefully washed with clean, warm water. After this the basins were re-filled with acid and hot water. The method was found to promote a continuous and vigorous action until etching was completed.

The nature of the insoluble residue left after etching was found to vary considerably. Argillaceous limestone from the lower collecting horizons yielded relatively large amounts of black sludge, whereas the reef-type limestone produced very little. Some blocks, with prominently weathering fossils and a promising exterior appearance, proved on etching to contain slabby masses of spongy chert, and the fossil yield was disappointing.
The etched fossils and associated muddy residue were, as far as practicable, carefully removed whenever the acid was changed. It was found possible to eliminate most of the mud from the mixture by gently 'panning' it, using a wide, shallow dish and adding clean water at intervals. After this the remaining residue, consisting mostly of fossil material, was transferred a little at a time to petrie dishes for more thorough washing to remove acid traces and mud particles. Larger specimens with mud still adhering were immersed in 100 vol. hydrogen peroxide to which a little caustic soda was added. The ensuing reaction cleansed them of even the finest muddy accretions, and the specimens were then placed on blotting paper to dry, prior to preliminary sorting.

Examination showed the silicified fossils to be delicate, fragile and commonly hollow. Replacement apparently progressed into the fossils from the exterior, for the outer surfaces of many faithfully retain the sculptural detail of the originals, while internal structures are poorly preserved or absent, due to the failure of replacing solutions to penetrate into the axial parts. It is evident from thin sections of limestone that silicification is not necessarily uniform over the whole surface of a fossil. Where replacement was only partial, etching must have resulted in the collapse of a formerly complete fossil into several pieces. This has undoubtedly contributed something to the fragmented nature of the fauna, though there is good reason to believe that breakage was largely of pre-depositional occurrence.

The original skeletal material has been replaced by either chalcedony or quartz. In the former case the internal structure may be well preserved, but it is generally lost where replacement is by quartz. This occurs either as spongy-textured masses, or in a relatively coarsely crystalline form. Replacements of the second kind may extend into the matrix, so that small adventitious masses of quartz adhere to a fossil. These can sometimes be removed with a mounted needle or forceps, though not without risk of damage. A few of the larger brachiopod valves, and secondarily thickened branches of Polypora and Ptylopora showed crude rings of beekite which may obscure a fossil almost beyond recognition. Fortunately this is rare.

## IV. NATURE AND SIGNIFICANCE OF THE FAUNA

Commonest among fossils in the residues are fragmented colonies of fenestrate bryozoa. They are followed by small brachiopods (chiefly productids), non-fenestrate bryozoa and sponge remains, in that order of abundance. With these groups are associated small numbers of simple, rugose horn-corals, lamellibranchs, gastro-
pods and trilobites. Earlier work on silicified faunas (Whittington \& Evitt 1953 : 7; Newell 1953: 172) has shown that certain groups of fossils are more liable to replacement in this way than others, so that an etched fauna may give a distorted impression of the original assemblage from which it was derived. Comparison with unsilicified fossils in strata at the collecting locality suggests, however, that in this case the etched fauna provides a reasonably close indication of the original fossil content of the rocks, both in the groups present and their relative proportions.

The predominant constituents of the etched residues are, therefore, bryozoa and brachiopods. In palaeontology this is a recurring association, and there is ample evidence that in many cases representatives of the two phyla shared a common environment (e.g. Sarle 1901:286; Duncan 1957:788). In spite of this, it seems probable that the Carrick Lough fauna does not represent a benthonic community, that is, a former life assemblage fossilized more or less in situ. Reasons for this belief are given in the following paragraphs.

The attitude of bryozoan fronds, in partly etched blocks and in thin sections, shows that the vast majority did not occupy positions of growth at the time of burial. On the contrary, they lie approximately in the plane of bedding, and rest upon one another in a close-woven tangle of organic debris. This is particularly notable in dark, muddy, pyritous limestones from the lower collecting horizons. The size and shape of fenestrate fronds seen on polished surfaces and in acetate peels from limestone blocks make it clear that fragmentation of the colonies had already taken place before consolidation of the sediment. The breakage may have been caused by predaceous organisms or the action of turbulent water, but is unlikely to have been due to re-working by burrowing organisms, for sedimentary laminae are well preserved in the rocks.

Acetate peels and polished surfaces also show the presence of disoriented fistuliporid colonies and disarticulated brachiopod valves, testifying to the movement of organic debris by wave or current action. Signs of turbulence in the depositional environment are not lacking, and take the form of minor bedding-plane irregularities and the presence, in dark, argillaceous limestone, of ooliths and intraclasts of pale, fine-grained reef material. Schwarzacher (1963) was able to demonstrate bottom current effects by means of oriented crinoid stems in beds of similar age and lithology in Sligo.

Argillaceous and bituminous limestone blocks, of the kind obtained from all but the highest collecting horizon, contain large numbers of fenestrate fragments associated with productoid brachiopods and an abundance of silicious sponge spicules. This is unlikely to represent a life association. Newell (1953: 197) found silicious sponges to be the chief indigeneous faunal element in deep water bituminous limestones and shales from the Delaware Basin. In association with the spicules were productoid and other brachiopods thought to have tolerated relatively de-oxygenated conditions and the presence of suspended mud in the water. Argillaceous limestones and shales of the Carrick Lough section bear a close lithological resemblance to the basin facies of the Delaware region, and probably originated in a similar environment. If present day ecology is an acceptable guide, basin-type conditions would not favour the growth of branching and fenestrate bryozoa, for
contemporary genera of this kind prefer well-aerated water and do not tolerate a high rate of sedimentation (Stach 1936, Lagaaij \& Gautier 1965). In addition, the depth of water may well have been too great. Schwarzacher (Ig6I : i502) concluded that in the Sligo area basin-type sediments adjacent to reef mounds formed in water at least 400 ft deep, whereas present day fenestrate bryozoa flourish best at depths of 80 to 200 ft (Stach I936: 62; Lagaaij \& Gautier 1965 : 54 and Chart I). On sedimentological grounds Elias (1937:428) concluded that fenestellid bryozoa in the Big Blue Series, Kansas, grew at depths varying from 75 to 160 ft .

In view of these considerations it is probable that bryozoan remains in the etched residues were moved to some extent prior to their final deposition and burial. But although it is apparent from their attitude and condition that the colonies did not grow in the situations where they are now found, the size of fragments and common preservation of delicate structures indicate that they were not carried far from the areas of growth. For reasons already given it seems unlikely that fenestrate bryozoa would have flourished in a sea-floor environment such as that represented by dark, bituminous limestones or shales, and an alternative habitat must be sought. Fortunately there is an indication of its whereabouts.

In the Carrick Lough fauna the largest fenestrate fragments were invariably obtained from pale, reef-type beds of the topmost collecting horizon. From their lithology, position and thickness it is probable that these represent the lower extremities of lenticular apron breccias which extended away from reef mounds and became intercalated with muddy deposits on the adjacent sea floor. The recovery of larger fenestrate fragments from these beds suggests that they were relatively closer to the bryozoan growth area than the muddy limestones of the lower collecting horizons. This, together with the likelihood that the bryozoan debris was carried down the sloping reef flanks rather than up them, makes it probable that the original habitat was upon locally existing reefs. In that situation the water would have been better aerated, and environmental conditions would have been generally more favourable than in the deeper, de-oxygenated water of the surrounding sea bed.

Records from many parts of the world relating to occurrences varying widely through time show that bryozoa have commonly been, and still are, associated with reef structures (e.g. Lowenstam 1950, Magdefrau 1933, Theodorovich I94I, Newell 1953). In addition, it has been found that whereas encrusting, massive and stoutly ramose forms inhabit the strongly turbulent water of reef flats, the fore-reef slopes commonly support a luxurient growth of slenderly branching, pinnate and fenestrate colonies. It seems quite possible, therefore, that the masses of drifted bryozoan remains in the limestones from Carrick Lough were derived from the slopes of adjacent reef structures, where these organisms may formerly have lived in great profusion. It is likely that they were fragmented before or after death (mainly the latter) by predatory organisms and perhaps by wave action, and the remains slowly moved into deeper water by gravity and current action. In the somewhat deoxygenated conditions of the sea bed at the foot of the reef slope, where siliceous sponges and muddy water brachiopods formed the indigeneous fauna, the bryozoan debris accumulated and was buried in relatively large amounts.
V. TAXONOMY

The taxonomy of fenestrate bryozoans presents some unusual problems. This is partly the result of a strong tendency for intra-specific morphological variation, and partly because almost all specimens are small fragments of complete colonies. A wide range of zoarial construction has, for example, been demonstrated (Tavener-Smith 1965) within a single species of Ptilofenestella, and it is common knowledge that fenestellid colonies may differ in structure from one part to another. Such variations may be due to differences of age or ecology, or to growth aberrations (Elias \& Condra 1957 : 59). Post mortem fragmentation of zoaria has, therefore, added greatly to the difficulties facing taxonomists in dealing with this group, for many species have been founded on single small fragments.

Fenestellid genera are based primarily on zoarial shape and the morphological character of branches in mature parts of colonies. Specific differences, on the other hand, commonly rest on variations of meshwork texture, and this is particularly so in Fenestella. Ulrich (1886, 1890) popularized the technique of making standard measurements of meshwork dimensions in fenestrate zoaria and using these for taxonomic purposes. He made no allowance for intra-specific variation, however, and in this respect his concept of species was inadequate. The Russian workers Nekhoroshev and Nikiforova, in a series of publications from 1926 onward, recognized the importance of structural variation within a species and sought to express it in numerical form. The arrangement they adopted has become known as the 'meshwork formula' (Condra \& Elias 1944:56-57), or 'micrometric formula' (Miller 1961: 224), and states the range of the number of branches, dissepiments, apertures and carinal nodes per unit distance in a specimen or series of specimens. This attempt to give quantitative expression to intra-specific meshwork variation, and the regular consideration of this factor in comparing data, marked a considerable advance on previous taxonomic practice. Condra \& Elias (1944) introduced the technique to western workers and made great use of it themselves. However, though the micrometric formula may be of use in indexing fenestellid species on the basis of their meshwork characteristics, it has been shown (Tavener-Smith 1966b) quite unsatisfactory in taxonomy. From a biometric stand-point the formula is a crude device and completely inadequate as a basis for the comparison of numerical data. It is not therefore surprising that it commonly yields ambiguous results when used in that way. Furthermore, many formulae are founded on single, small meshwork fragments, and in such cases may fail to reflect the range of structural variation even within the colony to which the fragment belonged. Though the wish to indicate the known limits of morphological variation in defining a species and to utilize this factor in comparing samples was conceptually correct, the application of the micrometric formula towards this end has created much confusion.

Because specific differentiation in Fenestella and its allies has been largely a matter of meshwork structure, a feature that may vary even within a colony, and because species have commonly been founded on small fragments, it is not surprising that large numbers have been erected. There are now more than 500 species in Fenestella alone. Their constantly increasing number causes mounting difficulty in the identification of new material, and several schemes have been devised in an attempt to
provide a more manageable grouping. Simpson (1895:500) divided the species of Fenestella into seven categories based on the nature of the carina, but his scheme was poorly founded and met with little success. Elias (1937) suggested four provisional groups of Pennsylvanian and Permian species, using the number of zooecial apertures per fenestrule and the number of rows of carinal nodes. Trizna (1939: IO3-III), and later Shulga-Nesterenko (I94I : 44), proposed comparable patterns for Permian Fenestella from Russia, while Elias \& Condra (1957: 67-72) suggested an elaborate classification of Fenestella from the Pennsylvanian and Permian of the Glass Mountains, Texas. This comprised thi teen groups based primarily on the arrangement of carinal nodes, number of zooecia per fenestrule and the fenestrule length. Such classifications have a certain pragmatic value in that they facilitate the comparison of new material with the large number of species now in the literature. In doing so they fulfill a similar function to the micrometric formula when used for indexing purposes. These schemes are, however, basically a palliative, not a cure. They do nothing to stem the ever increasing tide of new species, but attempt temporarily to render it more manageable.

It is likely that a major factor in the proliferation of fenestellid species has been the use of meshwork dimensions as the main basis of classification. Such features seem an obvious choice for the purpose, but earlier experience suggests that they may not be the best. Writing seventy years ago about the classification of another group of fenestrate bryozoa, Waters (1896 : 255) commented: 'Our knowledge of the Mediterranean Reteporae is most unsatisfactory, as so many specific names have been given on account of slight differences in the nature of the reticulation it has become quite clear that this is not a satisfactory character', for classificatory purposes. Waters was subsequently proved right (Harmer 1934), and the situation of which he wrote is also that afflicting the taxonomy of the Fenestellidae at the present time.

Among early workers it was the custom to classify bryozoa according to their zoarial shape, an outlook reflected in Canu's (1900:336) dictum that, 'L'individualité bryozoaire est le zoarium.' Since that time workers on living and fossil Cheilostomata have laid increasing stress upon the characteristics of the zooid rather than those of the colony. This change of emphasis, in keeping with the view expressed earlier by Waters, has become so pronounced that Lagaaij \& Gautier (1965 : 39) del'berately misquoted Canu to the effect that, 'L'individualité bryozoaire est le zooecium.' They continued by saying that, 'It is often not the size or shape of the colony, but rather the characters of the individual zooecium that determine the identity of species of cheilostomatous bryozoa.' In the case of the Fenestellidae also it is reasonable to suppose that morphological characteristics relating to zooecial chambers, or to the wall structure, will eventually prove of greater taxonomic worth than zoarial features. The former are likely to have been subject to tighter genetic control, and should, therefore, have greater potential value for specific differentiation. The latter, being essentially a framework maintaining the zooecia in suitable life positions, would predictably be more subject to ecological influence, and perhaps therefore more variable in development. Variation in structures formed by supporting tissue is certainly notorious in the Fenestellidae.

An analysis of more than 17,000 measurements made on fenestellid species by the writer may be interpreted as favouring the reliability of zooecial as opposed to zoarial (i.e. meshwork) characteristics as a basis for classification. Table I shows the coefficients of variation ( $100 \sigma / \mathrm{m}$ ) of 34 fenestrate forms described from the Carrick Lough residues. Examination shows that the least variable characters are inter-apertural space (representing the length of zooecial chambers) and branch width (reflecting the chamber width). The most variable ones are dissepimental width and the distance between carinal nodes, both zoarial features.

A further improvement in taxonomic practice could be effected by the utilization of accepted statistical techniques in comparing numerical data, and the rejection of the micrometric formula for the purpose. This matter has received attention elsewhere (Tavener-Smith 1966b) and will not be elaborated here. Suffice to say that in recent years fenestellid taxonomy has been beset by two major difficulties. These are, firstly, the tendency to base comparisons of fossil material on data from single fragmentary specimens; and secondly, the tendency to look for differences rather than resemblances, and to establish new species on the basis of these. In dealing with fenestrate colonies it is easy to obtain many measurements relating to meshwork features from a single fragment, but the range of these for each dimension only expresses structural variation in the fragment concerned, and has no taxonomic value. Because a single fragment cannot provide adequate data for a numerical comparison it is best, where the identity is in doubt, to refer it provisionally (cf.) to the nearest established species, and not to use it as the basis for a new one. In due course, as more material becomes available, the relationship or lack of it, should be evident and, when a number of similar specimens have accumulated, a valid numerical comparison may be made.

In the past the philosophy of classification in the Fenestellidae has been one of differences. Comparison has been effected with a view to detecting morphological differences between samples, and the erection of new species to accommodate these has led to the present situation. In a group of such morphologically diverse organisms differences are only too easy to find, and the logical end of the present procedures is a classification containing as many, or more, species than there were colonies. Use of the micrometric formula in comparing data has undoubtedly contributed to the proliferation of species, for such comparisons emphasize differences rather than resemblances, and there is no means of knowing whether the former are of taxonomic significance. The mere demonstration of some morphological difference between samples has in many cases led to the introduction of a new specific name, regardless of whether the samples or the means of comparison were adequate. In such a situation numerical methods of proved worth can render valuable assistance (TavenerSmith 1966b). They place the comparison of data on a more objective footing, thus preventing the introduction of new species on spurious numerical grounds, while at the same time facilitating the recognition of genuine morphological differences where these exist. In the systematic descriptions that follow selected morphological statistics are arranged so that comparison with other samples may readily be effected by using orthodox biometric devices such as the $t$-test or the distribution of $\chi^{2}$.
The following account outlines the procedure adopted in classifying fenestrate
bryozoa from the Carrick Lough residues. Faunas from different collecting horizons were at first treated separately, and careful sorting led in each case to the establishment of groups of specimens with a common basic morphology. Further examination showed the presence of an almost identical range of groups in the five collections, which were, therefore, amalgamated. From each of the enlarged morphological groups a sample of between 7 and 30 (generally about 20) of the largest and best preserved fragments was selected for detailed examination. On each specimen of a sample twelve measurements were made for each of twelve variables. The mean or mode (depending on the variate) of each series was regarded as the representative datum for a specimen (Tavener-Smith 1966b : 414, 42I), and from these basic measurements sample statistics were computed. These provide a quantitative statement of the morphological characteristics of a sample, and a basis for objective comparison with others of a similar nature. Where possible specimens of a sample were identified with already established species and, in such cases, the


Fig. 4. Diagram showing dimensions measured for biometric purposes. ap.d., apertural diameter; aps.per fen., number of zooecial apertures per fenestrule; br.w., branch width; diss.w., dissepiment width; f.l., fenestrule length; f.w., fenestrule width; i.ap.d., interapertural distance; i.n.d., internodal distance.
sample data serve to amplify existing descriptions by furnishing a better picture of intra-specific structural variation. When different samples are compared, using a recognized biometric test, and no difference is detectable between them at the 0.05 level of significance, such samples may be considered indistinguishable for the variate concerned. In this way structurally similar groups can be amalgamated to provide larger samples, and species that were initially defined on a narrow basis may be enlarged to include other compatible groups of specimens. Eventually, as a result of this process, more natural groupings may emerge, delimited by statistically established morphological discontinuities.

The chief quantitative features considered in subsequent systematic descriptions are listed below and briefly explained. They are also illustrated in Fig. 4. Because of the nature of the fossil material, peel and thin section techniques were not applicable, and data on matters of wall structure such as the size, spacing and arrangement of skeletal rods, are therefore lacking. These data relate to characteristics of potential value in taxonomy, and it is regretted that, for the species here described, their provision must await future work.

## A. Zooecial Features

I. Inter-apertural distance: Measured between the centres of adjacent apertures in the same row. This dimension may be treated as the equivalent of the zooecial chamber length and is a most valuable diagnostic feature.
2. Branch width: Measured across a branch perpendicular to its axis and away from dissepiments and branch divisions. This dimension gives an indication of the relative width of zooecial chambers, but also incorporates a variable component due to secondary skeletal growth. For this reason the coefficients of variation in branch width (Table I) are appreciably higher than those for inter-apertural space.
3. Apertural diameter: Measured between the inner sides of the rim. This is essentially a zooecial feature, and it would be expected that the size would be constant for a given species, and of great taxonomic value. However, with advancing age there is an undoubted tendency for apertures to be constricted by secondary material, which seriously detracts from the usefulness of the feature. Secondary accretions may also affect the shape and rim ornament of apertures. For these reasons it is best to treat measurements of zooecial apertures with caution when comparing samples, carefully considering the age and state of preservation of the specimens.
4. Zooecial chamber shape and size: The chamber is a three dimensional structure and its shape is not adequately represented by base plan measurements alone. Nevertheless, in many specimens these data are the only ones available. In the descriptions that follow full accounts are given of both shape and size wherever possible, and if not, basal measurements are stated.

Table I
Some coefficients of variation (rooo/m) calculated for fenestellid species collected at Carrick Lough

|  | N. | Diss.w | Ap.d. | B.w | I.n.s. | I.ap.s. |  | F.l. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Fenestella frutex | 25 | 9.03 | 12.05 | 3.93 | $5 \cdot 70$ | $3 \cdot 73$ | $6 \cdot 50$ | . 26 |
| F. ivanovi | 23 | 15.17 | 10.53 | 9.09 | 14.04 | 7.07 | $8 \cdot 70$ | 7.71 |
| F. multispinosa | 24 | 16.38 | 19.58 | $8 \cdot 20$ | 19.89 | 5.03 | 6.71 | 7.50 |
| F. modesta | 20 | $16 \cdot 72$ | $9 \cdot 59$ | $9 \cdot 55$ | 18.87 | $6 \cdot 83$ | $7 \cdot 55$ | $7 \cdot 71$ |
| $F$. hemispherica | 11 | 14.00 | $6 \cdot 53$ | $6 \cdot 99$ | $4 \cdot 69$ | $3 \cdot 68$ | $5 \cdot 83$ | $4 \cdot 28$ |
| $F$. parallela | 20 | $8 \cdot 55$ | $7 \cdot 92$ | $5 \cdot 82$ | 15.93 | $4 \cdot 72$ | $5 \cdot 10$ | 4, 10 |
| F. rudis multinodosa | 22 | $8 \cdot 88$ | 3.93 | $7 \cdot 26$ | 10.88 | $5 \cdot 00$ | 9.04 | $7 \cdot 58$ |
| F. plebeia | 27 | 10.26 | 10.00 | 10.77 | 21.62 | 10.88 | $9 \cdot 17$ | 11.54 |
| F. cf. arthritica | 20 | 14.67 | $9 \cdot 58$ | $6 \cdot 16$ | $8 \cdot 47$ | $4 \cdot 17$ | $8 \cdot 23$ | $5 \cdot 46$ |
| F. praemagna | 16 | $9 \cdot 46$ | $16 \cdot 27$ | $9 \cdot 83$ | 10.56 | $6 \cdot 48$ | $9 \cdot 87$ | $9 \cdot 46$ |
| F. fanata carrickensis | 28 | 17.38 | 10.74 | 8.80 | 15.13 | $6 \cdot 07$ | $8 \cdot 93$ | $8 \cdot 95$ |
| $F$. cf. spinacristata | 25 | 14.69 | $7 \cdot 27$ | $7 \cdot 20$ | 13.53 | 8.02 | $8 \cdot 59$ | $9 \cdot 27$ |
| $F$. cf. funicula | 25 | 10.89 | 10.58 | $7 \cdot 39$ | 17.69 | $3 \cdot 48$ | $8 \cdot 50$ | $8 \cdot 85$ |
| $F$. cf. filistriata | 31 | 14.25 | 12.42 | $6 \cdot 90$ | 16.55 | $3 \cdot 65$ | $7 \cdot 86$ | $9 \cdot 23$ |
| $F$. subspeciosa | 25 | 13.64 | $7 \cdot 55$ | $7 \cdot 24$ | 14.30 | 4.43 | $7 \cdot 03$ | $8 \cdot 02$ |
| $F$. pseudovivgosa | 25 | 14.40 | $9 \cdot 34$ | 7.75 | 15.61 | 7.05 | $7 \cdot 74$ | $9 \cdot 58$ |
| $F$. cf. albida | 25 | 11.76 | $7 \cdot 22$ | 6.89 | 10.64 | $5 \cdot 36$ | $7 \cdot 42$ | 10.50 |
| F. oblongata | 20 | 10.25 | $8 \cdot 33$ | $4 \cdot 62$ | 14.28 | $5 \cdot 84$ | $8 \cdot 51$ | 10.74 |
| F. delicatula | 25 | 14.64 | $8 \cdot 25$ | 7•19 | $27 \cdot 18$ | $7 \cdot 27$ | $9 \cdot 50$ | $9 \cdot 50$ |
| F. polyporata | I | 10•19 | $5 \cdot 35$ | $5 \cdot 51$ | 12.22 | 3.93 | $5 \cdot 16$ | 11.05 |
| $F$. irvegularis | 25 | 13.84 | $5 \cdot 33$ | $7 \cdot 41$ | 10.10 | $4 \cdot 54$ | 10.50 | 9.01 |
| Levifenestella undecimalis | 22 | 15.00 | $7 \cdot 72$ | $6 \cdot 19$ |  | $6 \cdot 32$ | $8 \cdot 26$ | 8.83 |
| Ptilofenestella carrickensis | 55 | $9 \cdot 46$ | 9.41 | $6 \cdot 40$ | 12.08 | $7 \cdot 13$ | $9 \cdot 57$ | $8 \cdot 87$ |
| Ptiloporella varicosa | 30 | 16.77 | 11.19 | $9 \cdot 98$ | 10.96 | $4 \cdot 31$ | $8 \cdot 70$ | 10.51 |
| Minily a plummerae | 10 | $5 \cdot 89$ | $6 \cdot 90$ | 3.91 | 3.42 | $2 \cdot 50$ | $5 \cdot 21$ | $3 \cdot 31$ |
| M. nodulosa | 17 | 10.60 | 9.72 | 11.62 | $7 \cdot 57$ | $5 \cdot 25$ | $7 \cdot 83$ | $7 \cdot 47$ |
| M. binodata | 7 | 10.75 | 11.78 | 2.53 | $2 \cdot 96$ | 1.56 | 3.78 | $2 \cdot 66$ |
| M. oculata | 25 | 13.77 | 9.73 | 3.81 | $4 \cdot 88$ | $3 \cdot 64$ | $8 \cdot 46$ | $6 \cdot 87$ |
| Hemitrypa hibernica | 30 | 24.41 | $7 \cdot 66$ | $6 \cdot 26$ | 6.71 | $4 \cdot 61$ | $8 \cdot 48$ | $8 \cdot 74$ |
| Polypora stenostoma | 15 | $9 \cdot 87$ | 10. 88 | $8 \cdot 16$ | - | 6.00 | $8 \cdot 47$ | $8 \cdot 76$ |
| $P$. dendroides | 6 | 15.92 | - | 15.01 | - | $3 \cdot 18$ | $6 \cdot 13$ | 10.98 |
| $P$. verrucosa | 20 | $10 \cdot 78$ | $7 \cdot 45$ | 7.06 | - | $6 \cdot 46$ | 10.43 | $9 \cdot 09$ |
| Ptylopora pluma parva | 12 | 17.96 | $6 \cdot 18$ | 12.46 | 14.45 | $5 \cdot 66$ | 10.94 | $7 \cdot 57$ |
| Septopora hibernica | ıо | 13.59 | - | $5 \cdot 58$ | - | 3.00 | $9 \cdot 51$ | $7 \cdot 14$ |

## B. Zoarial Features

1. Fenestrule length: Measured parallel to the growth axis between the mid-points of adjacent dissepiments. This is one of the basic dimensions of the zoarial meshwork, and also one of the least variable. The average coefficient of variation for 27 species of Fenestella, each represented by a sample of 20 to 25 specimens, was $8 \cdot 0$. Elias \& Condra (1957: 63) considered this to be the principal diagnostic character in differentiating between species of Fenestella.
2. Fenestrule width: Measured perpendicular to the growth axis and between the mid-points of adjacent branches. This is the other basic meshwork dimension. In the Carrick Lough specimens fenestrule width was slightly less variable than
fenestrule length, the coefficient of variation for the same 27 specimens previously measured being 7.75 .
3. Number of apertures per fenestrule: Recorded as the number of complete inter-apertural distances in a single row between the points where the mid-lines of adjacent dissepiments meet a branch. Elias \& Condra (1957:64) attached much importance to this feature, and to the relative positions of zooecial apertures and dissepiments. In certain species [e.g. Fenestella tenax Ulrich; Minilya nodulosa (Phillips)] the number of apertures per fenestrule and their relationship to dissepiments is regular and of obvious diagnostic value. In the majority this is not so and, because many forms have two or three apertures per fenestrule, the feature loses its usefulness.
4. Internodal distance: Measured between the centres of adjacent carinal nodes in the same row. Examination showed that this dimension may vary considerably within a species, and even within a single fragment. Carinal nodes are among the least regularly distributed of zoarial components, and it is, therefore, to be expected that their taxonomic value is relatively low.
5. Dissepimental width: Measured across the narrowest part of a dissepiment, perpendicular to its length. High coefficients of variation for this dimension (Table I) are due to the presence of secondary accretions of varying thickness on dissepiments. The amount of secondary material is in most cases related to position within a colony. Except in a general way, such as where a form is distinguished by the uniform presence of unusually thick or thin dissepiments, this feature has little taxonomic value.

In addition to quantitative data certain other attributes may also be of value in the classification of fenestellid species. This is particularly so where features reflect, directly or indirectly, zooecial characteristics, or ones fundamental to skeletal structure such as the arrangement of skeletal rods (Tavener-Smith 1969). The three-dimensional shape of zooecia is another attribute of this kind, and so is the disposition of zooecial apertures at branch divisions where they may suggest a budding pattern. The presence of an incipient 'third row' of apertures before bifurcations, as in Fenestella fanata carrickensis, always merits attention, and a single aperture symmetrically placed immediately before the fork may, likewise, have taxonomic significance. The angle between newly-formed branches and the distance taken to regain parallelism, may be a function of the internal branch arrangement, and, therefore, also of diagnostic value-as, for example, in Fenestella hemispherica and $F$. cf. delicatula.

Distinctive fenestrule shapes due to the regular inflation of branch margins by zooecia may be useful in classification, particularly if associated with a symmetrical dissepiment-aperture space relationship (e.g. Fenestella ivanovi). Apparently diagnostic branch surface characteristics such as that mentioned above may, however, become completely obscured by secondary calcification, which militates against the taxonomic use of many seemingly valuable morphological features. Zooecial apertures and peristomial structures are very liable to alteration in this way during astogenetic development, and the same is true of the cross-sectional shape of branches or dissepiments, and the presence of longitudinal 'striae' on the reverse side.

It must be recalled (Tavener-Smith 1969) that external secondary calcification probably commenced close behind the tip of a growing branch, and that deposition continued through much of the subsequent life. Structures in the proximal regions of a colony are, therefore, commonly encrusted by secondary substance, and may differ greatly in appearance from more distally situated equivalent parts. It is completely within the realm of possibility for such differences within a colony to be of sufficient magnitude to have suggested the existence of distinct species had they occurred on separate fragments.

Secondary calcification is a constant hazard in taxonomy, and renders many apparently valuable morphological features useless. Such effects may, however, be largely excluded by the use of carefully considered quantitative attributes. For this reason reliance is placed primarily on these in the present work.

In the systematic descriptions that follow, diagnoses of species are given in the case of new taxa, and where it has been possible to assign samples with certainty to ones already established. These diagnoses are generally stated in qualitative terms, and for maximum effectiveness it is essential that they should be applied in close conjunction with the numerical data.

## VI. ARRANGEMENT OF QUANTITATIVE DATA

In each of the systematic descriptions, measurements made on a stated number of zoarial fragments are given in tabular form. In taking measurements the procedure followed was that outlined in Tavener-Smith 1g66b : 414, 421. The variates used are those mentioned in the preceding section and illustrated in Fig. 4. The following abbreviations are used throughout: F.l., fenestrule length; F.w., fenestrule width; I.ap.s., inter-apertural space; I.n.s., internodal space; B.w., branch width; Ap.d., apertural diameter; Diss.w., dissepiment width. Measurements are in millimetres, and the figures are arranged in four columns lettered A to D. The lefthand column (A) shows the range of specimen mean values within a sample. The mean for a specimen is based on twelve measurements made on that particular specimen. These specimen means are the fundamental data from which statistics given in the other columns are derived. Column B is the sample mean, that is, the average of the specimen means. The third column from the left $(\mathrm{C})$ is the standard deviation of the specimen means, and the right-hand column $(\mathrm{D})$ is their coefficient of variation.

Beneath the tabulated data, a micrometric formula is included in each of the descriptions. This is stated in the conventional manner, that is, figures are given for the number (or range) of branches and dissepiments in a space of 10 mm , and zooecial apertures and carinal nodes in 5 mm . For this purpose twelve measurements were made for each of the four variates on every specimen of a sample. In almost every case variation was encountered, and the observed range is, therefore, stated in the formula for the variate concerned.

Next, an indication is given of the number of zooecial apertures per fenestrule length. In this case also, twelve counts were made on each specimen of a sample, and the results presented in the following manner. Suppose that the number of apertures per fenestrule in a single specimen was found, in the course of making
twelve measurements, to range from 3 to 5 , and that the mode was 4 . This is the specimen mode. In repeating these measurements on each of a sample of 25 specimens it might be found that the range of specimen modes was from 3 to 6 , and that the distribution of modes in each of these four classes was $3, I 2,7$ and 3 respectively. These data would be shown in the following way:

Apertures per fenestrule.
$\begin{array}{lrrrr}\text { Range of specimen modes: } & 3 & 4 & 5 & 6 \\ \text { Distribution of specimen modes: } & 3 & \text { I2 } & 7 & 3\end{array}$
Arrangement of the data in this way facilitates comparison with other samples by means of a $\chi^{2}$ test.

## VII. SYSTEMATIC DESCRIPTIONS <br> Order CRYPTOSTOMATA Vine, 1883 Family FENESTELLIDAE King, I850

Diagnosis. Zoarium a reticulate expansion of branches joined by sterile dissepiments, or by coalescence at opposed sinuous bends so as to form fenestrules; branches rarely free. Zoarium bearing zooecial apertures on one side only. Reverse smooth or longitudinally striate, and may bear small nodes.

## Genus FENESTELLA Lonsdale

Fenestella Lonsdale, 1839 (nom. conserv. ICZN 1962); non Bolten, 1789. Fenestrella D'Orbigny 1850 (non Fenestrellina d'Orbigny, 1850). Actinostoma Young and Young, 1874.

Diagnosis. Zoarium funnel or fan-shaped. Zooecial openings in two rows commonly separated by a median carina bearing nodes or spines.

Discussion. The status of this generic name and the selection of a type species have been under dispute for some years. The first matter has been settled by a decision of the International Commission on Zoological Nomenclature that Fenestella should be a nomen conservandum (Bull. Zoo. Nom., I962). The type species is Fenestella subantiqua d'Orbigny 1850, as revised by Elias (1956; 3I7-324).

Fenestella, used for a group of fenestrate bryozoa, was invalid from its inception, owing to the name being already in use for a living lamellibranch (Bolten 1798). Bolten's name never became established, however, and was later placed in the synonymy of Anomia and, therefore, lapsed. Meanwhile d'Orbigny (1850) had used both Fenestrella and Fenestrellina in referring to the bryozoan group. The first was probably a typographical error, but the second appears to have been an attempt to rectify the irregular position affecting the name Fenestella. He cited Fenestella crassa M'Coy as the type species, Lonsdale not having designated one. The choice proved unfortunate as not only was the species not among those originally named by Lonsdale, but it was also not typical of the genus. Shrubsole concluded from an examination of topotype material that this species did not, in fact, belong to Fenestella, but 'to another fenestrate genus of Polyzoa' ( 188 I : 186 ). Bassler must have been unaware of this when (1935: IIO) he suspended the name Fenestella for
bryozoans, in strict observance of the Rules of Zoological Nomenclature, and suggested that Fenestrellina d'Orbigny be used instead. Several authors (e.g. Crockford from 1943 onwards; Chronic 1949) adopted this usage, but by no means all. Later Bassler became aware that Fenestrellina, as defined by its type species, differed from Fenestella, and in the Treatise on Invertebrate Paleontology, Part G-Bryozoa, he listed the two separately. Fenestrellina is there defined (p. Gi22) as having 'Dissepiments widely separated and fenestrules very long', but being in other respects like Fenestella. Fortunately this ill-defined genus has been rendered invalid by Miller's (1961 : 238) discovery that the type specimen of $F$. crassa M'Coy is undoubtedly a Polypora. The writer has confirmed this.

When Lonsdale introduced the name Fenestella he included four species from the Wenlock of Dudley in the genus. They were (in the original order): F. antiqua, F. milleri, F. prisca, all new species, and Retepora reticulata Hisinger, 1837. Lonsdale's concept of a species was broader than that now acceptable, and he included in the synonymy of $F$. antiqua the earlier form Gorgonia antiqua Goldfuss 1829, from the Devonian of the Eifel. This name, therefore, had priority, and when it later became plain that the two were not conspecific d'Orbigny (1850) re-named Lonsdale's form $F$. subantiqua. In the same year King (1850:35) cited $F$. antiqua (now based on G. antiqua Goldfuss 1829) as the type species, a selection quite in order, but one that has given rise to some confusion, it being uncertain which of the two forms he really intended. According to Toots (1951 : 237) the type of Goldfuss' species is lost and it is impossible to recognize it from the description and figures. It therefore became necessary to adopt a new type species.

Although $F$. subantiqua d'Orbigny was not among the species originally included in the genus by Lonsdale and is, therefore, technically ineligible to be the type species, it is a reasonable choice, being almost certainly the form intended by him as $F$. antiqua. The type specimen in this case also has been lost for many years, and Shrubsole ( $1880: 244$ ), when revising the Wenlock Fenestellidae, concluded that Lonsdale's $F$. antiqua was the same as $F$. plebeia M'Coy from the Lower Carboniferous. He implied that, failing discovery of the type of $F$. antiqua, the common Carboniferous species should be treated as the type species for the genus. This seems to have prompted Ulrich's ( 1890 : 395) statement that $F$. plebeia is the 'accepted type' for Fenestella. This designation has been perpetuated in the literature (Nickles \& Basler 1900:38; Nikiforova 1938:63). However, Elias (1956), working on topotype material from Dudley, succeeded in identifying Lonsdale's species and designated a neotype. This seems a satisfactory end to the matter, particularly as the form concerned fulfils the morphological requirements of Fenestella as at present understood. Spjeldnaes (1957:675) does not, however, favour the adoption of $F$. subantiqua d'Orbigny as the type species on the grounds that a doubt exists as to whether this species was named in place of $F$. antiqua Lonsdale 1839, or Gorgonia antiqua Goldfuss 1829 . It seems most unlikely that the latter was the case, and there are much stronger arguments against the use of either $F$. plebeia M'Coy or $F$. reticulata (Hisinger) as Spjeldnaes proposed.

Type species. Fenestella subantiqua d'Orbigny 1850 ( $=$ Fenestella antiqua Lonsdale 1839).

## Fenestella frutex M'Coy

(Pl. I, figs $\mathrm{I}-9$ )
1844 Fenestella frutex M'Coy; 201.
1878 Fenestella lyelli Dawson; 288.
1887 Fenestella limbata Foerste; 83.
1926 Fenestella limbata Foerste; Nikiforova; 175.
1929 Fenestella lyelli 'mut' Dawson; Bell; $\mathbf{1} \mathbf{1}$.
1934 Fenestella aff. limbata Foerste; Likharev; 155.
1937 Fenestella limbata Foerste; Elias; 318.
1961 Fenestella frutex M'Coy; Miller; 232.
Diagnosis. Close-textured meshwork with branches notably thicker than dissepiments. Keels faint, with small nodes. Apertures bead-like, protruding. Zooecial chambers triangular to hemi-hexagonal.

Material. More than 70 fragments were examined, the largest being $27 \times 13$ mm . PD.5001-7, PD.4892-909.

Measurements made on a sample of 25 zoarial fragments (i.e. $\mathrm{N}=25$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $0.47-0.60$ | 0.556 | 0.029 | 5.26 |
| F.w. | $0.40-0.52$ | 0.461 | 0.030 | 6.50 |
| I.ap.s. | $0.19-0.21$ | 0.201 | 0.008 | 3.73 |
| I.n.s. | $0.20-0.25$ | 0.236 | 0.013 | 5.70 |
| B.w. | $0.22-0.27$ | 0.254 | 0.010 | 3.93 |
| Ap.d. | $0.06-0.10$ | 0.083 | 0.010 | 12.05 |
| Diss.w. | $0.12-0.17$ | 0.150 | 0.013 | 9.03 |

Micrometric formula: 22-28/17-22//24-26/20-24.
Apertures per fenestrule.
Range of specimen modes:
Distribution of specimen modes:

2
23

3
2

Description. Zoarium probably a broad, roughly planar, fan-shaped expansion; branches straight and rigid in the central part, or gently curving outward towards margins of frond. Transverse section of branches sub-circular distally, becoming ovoid in the proximal parts of a zoarium due to secondary accretion. Median keel not pronounced. Branches widen progressively for three to six fenestrules prior to dividing, and may attain a width of 0.5 mm at the point of bifurcation. Immediately beyond this the width of new branches is much reduced, being commonly about 0.22 mm . Reverse side of branches well-rounded and longitudinally striated in the distal parts of zoaria. This surface may show a uniserial row of small nodes roughly coinciding with the disposition of carinal nodes on the obverse, but less regularly spaced.

Dissepiments are initially thin, broadening at either end, moderately depressed below the branch surface on both sides, and having a circular cross section. With progressing age they become encrusted by secondary growth, especially on the
reverse. This leads to development of an ovoid cross section and a relatively shorter and stouter appearance.

Fenestrule shape rather variable. Distally they tend to be rectangular with rounded corners and long sides indented by one or two projecting zooecial apertures. Proximally, fenestrules are smaller (due to secondary thickening of branches and dissepiments) with elongate-oval shapes and no lateral indentations.

Zooecial apertures circular, relatively small and closely spaced. They are surrounded by plain, collar-like peristomes that are higher on the outer side. These may form inflated, cowl-like structures that partly shield apertures and project slightly into fenestrules. Prior to branch division, an incipient third row of zooecial apertures may appear for a short distance. This, with the increase of branch width in such situations, is a distinctive feature. Zooecial chambers are hemi-hexagonal (or pentagonal, see Miller 1961a : 227), in plan, though the two lateral walls may be very short, giving a near-triangular appearance. Average maximum length and width of five chambers was 0.2 mm and 0.121 mm respectively.

Carinal nodes are small and regularly placed. Distally they are circular in cross section, becoming elliptical proximally, with the long axis of the ellipse parallel to that of the branch. These elongate node-bases may unite into a long, thin, strap-like ridge raised only slightly above the branch surface. This is the only indication of a median keel. Where branches divide, carinal nodes cease immediately before the third row of apertures commences, re-appearing as soon as the new branches are established.

Short, relatively stout spines given off sparsely from obverse or reverse, and in some cases bearing recurved barbs, are a characteristic feature. They may be up to 3 mm long and 0.05 mm in diameter at the base. The length was originally greater, as all spines examined were truncated distally by breakage. Barbs are up to 0.2 mm long and sharply recurved. They may be arranged in three or four rows around the circumference of spines. Other spinose processes of comparable dimensions, but lacking barbs, occur at the lateral margins of zoarial fragments as branch continuations.

Discussion. This form is F. frutex M'Coy, as its dimensions compare closely in all important respects with those given for the species by Miller (1961 : 232-3). The micrometric formula given by that author (on the basis of four small fragments: holotype, syntype and two homeotypes) is: 22-31/18-26//24-27/20-24. The only apparent discrepancies between the type material and that from Fermanagh relate to branch and dissepiment width. Miller's measurements of the first ranged from $0.14-0.20 \mathrm{~mm}$, while in the Carrick material the range is $0.22-0.27 \mathrm{~mm}$. Similarly, dissepiments were between 0.06 and 0.09 mm on the type specimens, but from 0.10 to 0.15 mm on the etched ones. It would appear that M'Coy's specimens are from the younger parts of zoaria, while those from Carrick Lough belong to the proximal region where secondary encrustation has given rise to increased dimensions. Fenestrule measurements of the Fermanagh specimens are close to those of Miller, the length varying from $0.35-0.42 \mathrm{~mm}$ against his $0.33-0.39 \mathrm{~mm}$, and the width $0.17-0.25 \mathrm{~mm}$ compared with $0.22-0.33 \mathrm{~mm}$. The shape of zooecial chambers and
the number and arrangement of apertures in each fenestrule are identical with those described by Miller.

There is also a close structural resemblance between the present specimens and F. fenestratum (Young and Young) 1874, from the lower Carboniferous Limestone Series of Scotland. The generic name of that form was originally Actinostoma, a reference to the eight short, regularly placed apertural denticles thought to distinguish it from Fenestella. Later work showed, however, that this feature is also present in other fenestellid species (e.g. Polypora radialis Ulrich; P. septata Campbell) and is unlikely to be of diagnostic value at generic level. Actinostoma was therefore placed in the synonymy of Fenestella by Nickles \& Bassler (1900; 37, 245).

The micrometric formula of $F$. fenestratum (calculated from ten measurements on each of six zoarial fragments) is: 19-28/19-28//19-24/17-30, with which the meshwork of the Carrick Lough specimens closely corresponds. The zooecial chamber shape is also identical in both samples, and tests of branch width and inter-apertural space failed to show a significant difference between them at the o.or level. In view of these important structural resemblances it is possible, not only that the Fermanagh specimens and $F$. fenestratum are conspecific but also that the latter is a junior synonym of $F$. frutex M'Coy. In view of the complete absence of apertural denticles in the Irish forms, however, it would appear premature to merge the species until the significance of this structure has been more thoroughly investigated.

Among American species the Fermanagh material most closely resembles $F$. matheri Condra \& Elias 1944, from the Chester Series of Illinois. The formula for this is (Ibid : 109) : $19-25 / 15-17 / / 22-25 / 19-24$, indicating the presence of larger fenestrules than in the Carrick Lough specimens. No other dimensions were given by Condra and Elias and further numerical comparison is therefore impossible. There appears, however, to be a difference in the chamber shape, that of the American species being described as (p. IIo) 'rectangular, grading to pentagonal near the base'. Both forms occur at about the same stratigraphic level ( $F$. matheri is from the lower Chester) but in view of the above discrepancies and the lack of further information about the American species, they cannot be regarded as conspecific.

Fenestella ivanovi Shulga-Nesterenko
(Pl. 2, figs I-9)
1951 Fenestella ivanovi Shulga-Nesterenko; ioo.
Diagnosis. Fenestella with regular, open meshwork and hour-glass shaped fenestrules. Zooecial apertures occur consistently at ends of dissepiments and mid-way along fenestrules.

Material. Thirty small fragments, the largest being $14 \times 12 \mathrm{~mm}$. PD. 5008, PD.4682-7, PD.4910-25.

Measurements $(\mathrm{N}=23)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $0.45-0.60$ | $0.5 I 5$ | 0.040 | 7.7 I |
| F.w. | $0.40-0.57$ | 0.482 | 0.042 | 8.70 |
| I.ap.s. | $0.2 \mathrm{I}-0.29$ | 0.25 I | 0.018 | 7.07 |
| I.n.s. | $0.2 \mathrm{I}-0.37$ | 0.265 | 0.037 | 14.04 |
| B.w. | $0.15-0.20$ | 0.18 I | 0.016 | 9.09 |
| Ap.d. | $0.05-0.09$ | 0.17 I | 0.008 | 10.53 |
| Diss.w. | $0.07-0.12$ | 0.100 | 0.015 | $I 5 . \mathrm{I} 7$ |

Micrometric formula: $18-23 / \mathrm{I} 7-22 / / \mathrm{I} 7-25 / \mathrm{I} 3-26$.
Apertures per fenestrule.
$\begin{array}{lrr}\text { Range of specimen modes: } & 2 & 3 \\ \text { Distribution of specimen modes: } & 22 & \text { I }\end{array}$
Description. Zoarium probably a small, roughly planar, fan-shaped expansion, not more than 2 or 3 cm across. The delicate meshwork of straight or gently curved branches and slender dissepiments has a characteristically regular, scalariform appearance.

Branches about as high as wide, with an approximately circular cross-section. The obverse of each branch has a poorly defined median keel, on each side of which the surface slopes gently away. Lateral branch margins are undulating owing to the projection of regularly arranged zooecial apertures into fenestrules. Reverse of branches smoothly rounded proximally, but with well-developed longitudinal striae in medial and distal parts of zoaria.

Branches are connected by regularly-placed dissepiments. These are relatively slender, and in most cases half to two-thirds of the branch width. Dissepiments are thin at the centre but wide at each end, where they unite with branches. Because the dissepimental height exceeds its minimum width, broken ends have an oval crosssection. Dissepiments are depressed below branch level on both surfaces.

Fenestrules have a characteristically hour-glass shape, due to the flaring of dissepiments at their ends and the regular indentation by zooecial apertures situated mid-way along each side. This shape is visible on both zoarial surfaces. The outline of the 'hour-glass' varies from roughly quadrate to elongate, according to the spacing of branches and dissepiments. Although this fenestrule shape is distinctive when present, it is not universally developed. A few specimens showed abnormal fenestrules with two apertures per side, only slightly undulating margins and a roughly rectangular shape.

Zooecial apertures are relatively small, round or elliptical, and placed about two diameters apart. They have low, plain, collar-like peristomes. Apertures are in most cases regularly placed: one at the end of each dissepiment and one mid-way between. In the latter situation the side of the branch is slightly inflated so that the aperture above projects into the fenestrule. Where branches divide, there is an aperture placed symmetrically in the angle of bifurcation.

Zooecial chambers have a triangular shape except where branches divide. The chamber situated in the angle may then have a diamond shape and those adjacent to it may also be irregular (commonly four or five sided) as circumstances dictate.

Average dimensions of twelve measured triangular chamber bases were: length parallel to branch axis: $0.15-0.17 \mathrm{~mm}$.; maximum width: 0.12 mm .

Carinal nodes are small and commonly difficult to identify. They are uniserial and not regularly situated relative to dissepiments, though in many cases there are two nodes and rather less than two internodal spaces opposite a fenestrule. Spinose structures are present on many zoarial fragments in this species, and some examples are illustrated. Slender spines from the obverse side may be up to 3 mm long and 0.2 mm in diameter at the base. Some bear small recurved barbs distally. Long spines (up to 5 mm ) also occur as sterile branch continuations. A good specimen of the proximal part of a fan-shaped colony showed a number of these that appear to have functioned as auxiliary supporting structures. In conjunction with a stout basal holdfast they maintained the colony in an upright position. It is of interest to note that the holdfast is welded onto a branch of another fenestrate meshwork, and no doubt the lateral spines were similarly attached. Bryozoan debris on the sea floor seems commonly to have provided a base from which new colonies grew.

Discussion. This Fermanagh form corresponds well with Shulga-Nesterenko's (1951; 100) $F$. ivanovi from the Upper Carboniferous ( $\mathrm{C}_{3}{ }^{\mathrm{ks}}$ ) of Russia, and is assigned to that species. The micrometric formula given by that author is $18 / \mathrm{I} 8 / / \mathrm{I} 8 / \mathrm{I} 8-2 \mathrm{I}$, which is within the range shown by the Irish specimens. The only apparent differences are the occurrence of slightly wider branches in the Russian form ( $0.2-0.25 \mathrm{~mm}$ against $0.15-0.2 \mathrm{~mm}$ ) which also showed an irregular line of nodes along the mid-line of the under-surface. Specimens from Carrick Lough show no trace of the latter, but it is evident from other species that the presence or absence of such nodes has little diagnostic importance. More interesting is ShulgaNesterenko's statement that peristomes in $F$. ivanovi are petaloid, a feature that she also illustrated (195I; IoI, fig. 38). Her thin section (Ibid., pl. XIX, fig. I) shows that the petaloid shape, which may be equated with the 'marginal denticles' of $F$. fenestratum and other species, does not persist below the aperture. Furthermore, the fact that the petaloid shape was associated by Shulga-Nesterenko with the peristome, a secondary structure, could be taken as an indication that such apertural shapes are old-age characteristics. The slightly greater branch width of the Russian specimens as compared with those from Fermanagh would then also be readily explained.

The regular, scalariform meshwork of the Carrick Lough specimens, together with their hour-glass fenestrules, are reminiscent of Foerste's (1887, pl. VII, figs 1oa-d) illustration of $F$. limbatus. Unfortunately Foerste's description is vague and lacks quantitative data, so that it fails to provide a basis for comparison. ShulgaNesterenko ( 195 I ; 79) also recorded the species, however, and included many measurements in her description. She differentiated Foerste's form from $F$. ivanovi chiefly on the basis of meshwork dimensions and zooecial chamber shape. With a formula of: $25 / 23 / / 25-26 / 25$, her $F$. limbatus had a finer textured meshwork; it also had hemi-hexagonal zooecial chamber bases. Dimensions of the specimens from Carrick Lough are closer to $F$. ivanovi than $F$. limbatus and, like the former, have triangular chamber bases.

## Fenestella multispinosa Ulrich

(Pl. 3, figs $\mathrm{I}-9$ )
1890 Fenestella multispinosa Ulrich; 540.
1906 Fenestella multispinosa Ulrich; Cumings; 1278.
1926 Fenestella multispinosa Ulrich; Nekhoroshev; 1245.
1926 Fenestella multispinosa Ulrich; Nikiforova; 178.
1927 Fenestella multispinosa var. karakubensis Nikiforova; 247.
1933 Fenestella multispinosa Ulrich; Nikiforova; 16.
1942 Fenestella multispinosa Ulrich; Kaisin; 93.
1942 Fenestrellina multispinosa (Ulrich); McFarlan; 444
1944 Fenestella multispinosa Ulrich; Condra and Elias; 110.
1948 Fenestella multispinosa Ulrich; Nekhoroshev; 24.
1951 Fenestella multispinosa Ulrich; Shulga-Nesterenko; 85.
1962 Fenestella multispinosa Ulrich; Miller; 121.
Diagnosis. Colonial meshwork similar to F. frutex but slightly coarser and with zooecial apertures protruding less. Branch obverse more flattened, with good median ridge bearing slender nodes.

Material. This is a common form in the Carrick Lough residues. Seventy-four zoarial fragments were examined, the largest being $29 \times 18 \mathrm{~mm}$. PD.4688-94, PD.4926-4I.

Measurements $(\mathrm{N}=23)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $0.55-0.72$ | 0.633 | 0.047 | 7.50 |
| F.w. | $0.45-0.57$ | 0.499 | 0.033 | 6.7 I |
| I.ap.s. | $0.22-0.30$ | 0.250 | 0.012 | 5.03 |
| I.n.s. | $0.27-0.55$ | 0.358 | 0.07 I | 19.89 |
| B.w. | $0.22-0.30$ | 0.250 | $0.02 I$ | 8.20 |
| Ap.d. | $0.07-0.12$ | 0.096 | 0.019 | 19.58 |
| Diss.w. | $0.10-0.17$ | 0.016 | 0.019 | $I 6.38$ |

Micrometric formula: 19-23/13-18//18-23/9-18.
Apertures per fenestrule.
Range of specimen modes: I 2 3
Distribution of specimen modes: I 22 I
Description. Zoarial shape uncertain from the fragments examined. It may have been a fan-shaped expansion of moderate size (several cm across) or a foliaceous meshwork arising from a cup-shaped growth origin.

Branches straight or gently curving; strong and presenting a rigid appearance. A low median ridge on the obverse follows the branch axis and on each side of this the surface slopes sharply away. The reverse also may bear a poorly defined median keel, though proximally this is obscured by secondary material and the surface tends to be broadly rounded. Where a median ridge is present on both sides the branch has a diamond-shaped cross section, otherwise it tends to be angular above and rounded below. Faint longitudinal striae are commonly present on the reverse. Before a branch divides its width increases progressively for a distance of two to
four fenestrules, and at the point of bifurcation the normal width of about 0.25 mm may be doubled. Beyond this new branches are narrower than usual, a width of about 0.17 mm being common. On the reverse of a few specimens there were localized secondary encrustations of unusual thickness. These caused considerable increases in branch width, in some cases to as much as 0.77 mm . The thickenings were particularly evident at branch divisions and also affected adjacent dissepiments.

Dissepiments are slightly depressed below branch level on both sides of the meshwork. They are more slender than branches and thinnest in the middle, increasing in width at either end. Where the reverse of a branch is angular (i.e. has a median ridge) that of adjacent dissepiments may be similar, though the obverse of dissepiments is invariably rounded. Due to the tendency for dissepiments to flare at their ends, fenestrules have rounded extremities. Fenestrule shapes are most commonly rectangular or quadrate, though they may be elongate-oval or elliptical in older parts of zoaria. Fenestrule margins may be gently sinuous owing to the tendency for zooecial apertures to project slightly.

Apertures are circular and commonly have low, plain, ring-like peristomes. Zooecial chambers are hemi-hexagonal in plan. The average dimensions of eleven measured chambers were: maximum length parallel to growth axis: 0.275 mm ; maximum width: 0.137 mm ; width of short lateral walls: 0.075 mm .

Carinal nodes, where well preserved, are slender and up to $0 \cdot 15 \mathrm{~mm}$ high. In most cases they are broken or abraded off and difficult to locate. The spacing of nodes varies considerably between fragments and is unlikely to be of diagnostic value. The reverse of a few specimens bears an ill-defined row of unevenly distributed nodes along the mid-line. These vary in diameter from 0.02 to 0.07 mm . Spinose structures up to 5 mm long are present on some zoarial fragments. They originate from the reverse side or laterally, as branch continuations, and may bear recurved barbs at their distal ends.

Discussion. Zooecial apertures in this species varied considerably in diameter and this is reflected in a high coefficient of variation. The differences appear to be due partly to imperfect replacement of original structures by silica. They may also to some extent be attributed to age differences, as apertures appear to have been progressively constricted by secondary calcareous deposits. Thus the size of zooecial apertures on a fragment tends to be related to its original position in the zoarium.

Some specimens showed evidence of the remarkable capacity of fenestrate colonies to regenerate after sustaining structural damage. One rectangular fragment $22 \times 5 \mathrm{~mm}$ appears to have broken from the parent colony at the proximal end and laterally. Evidence of recovery includes the sealing of broken branch ends by copious deposits of secondary material. Two broken branches subsequently continued their growth but in the opposite direction, in other words, towards the growth origin. One of them divided in the ordinary way but at $180^{\circ}$ to the normal direction. A number of stout trabeculae grew from the damaged ends of adjacent dissepiments to support these aberrant branches.

Another specimen provides an even more striking example of recovery from breakage which, in this case, caused part of the meshwork to diverge from the rest by
about $30^{\circ}$, though still attached proximally. Recovery involved (a) sealing of broken ends of dissepiments by secondary deposits; (b) the development from others of strengthening struts to hold the broken section in a rigid and stable position; (c) renewal of growth in a reverse direction from the broken ends of some branches, including the bifurcation of these in the same direction; and (d) renewal of growth in a normal, forward direction from the broken ends of other branches. Breakage appears to have acted as a growth stimulant in this case. The value of copious secretion of secondary material in effecting structural repairs is very evident. Comparison with established species shows that Fermanagh specimens of this kind are close to Ulrich's (1890:540) Fenestella multispinosa. The micrometric formula of that species, based on Ulrich's description, is: $20-2 \mathrm{I} / \mathrm{I} 4-\mathrm{I} 5 / / 2 \mathrm{I} /$ ?. He made no mention of carinal nodes but it appears probable from his illustrations that the number was between 18 and 23 per 5 mm . Fewer nodes have been counted on specimens assigned by other authors to this species, e.g. 'about 18' (Condra \& Elias I944: II2), I2-I5 (Nikiforova 1927: 246) and 'about 14' (Nekhoroshev 1926: 1245). The Carrick material corresponds closely in node counts and in other dimensions with the last description. Nekhoroshev's illustration (Ibid., pl. XX, fig. 3) shows hemi-hexagonal to triangular base shapes similar to those of the Irish specimens. There are discrepancies in the literature regarding this feature, however. Ulrich's description (I890:540-54I) does not mention chamber shape, but one of his illustrations (Ibid., pl. L, fig. 3d) shows it to be rectangular or just hemihexagonal. Condra and Elias (I944: II2) state that the chamber shape is rectangular, as does Miller (1962 : 122). Shulga-Nesterenko (1951, pl. XVI, fig. 2) shows it as hemi-hexagonal to triangular, mainly the latter. The illustration of $F$. multispinosa var karakubensis Nikiforova (I927, pl. XII, fig. 3) may, however, explain these differences. It shows quite clearly and within the same fragment, chambers that vary in plan from near rectangular, through hemi-hexagonal to sharply triangular. The variations do not seem to be due to sectioning at different levels, but may bear a relationship to branch width, as the shapes are more rectangular in wide branches and triangular in narrow ones.

The Carrick Lough specimens also show resemblances to Ulrich's (i890) F. sevillensis which has the formula: 20/16//16-17/?. An important difference between the two appears to be the wider spacing of zooecial apertures in the American form. Ulrich gave no other useful structural information and, because the species has not been described elsewhere, further comparison is impossible.

## Fenestella modesta Ulrich

(Pl. 4, figs I-6)
I890 Fenestella modesta Ulrich; 550.
1929 Fenestella modesta Ulrich; Moore; 21 .
1962 Fenestella cf. modesta Ulrich; Miller; 124.
Diagnosis. Thin branches and dissepiments enclose relatively large rectangular fenestrules. Good median keels. Apertures small, widely spaced, three per fenestrule. Protruding peristomes may give branch margins a sinuous aspect.

Material. This is not a common form in the residues. Only 40 small fragments were available, the largest measuring $13 \times 8 \mathrm{~mm}$. PD.4695-8, PD.4942-57.

Measurements ( $\mathrm{N}=20$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $0.65-0.92$ | 0.804 | 0.062 | 7.7 I |
| F.w. | $0.50-0.65$ | 0.572 | 0.043 | 7.55 |
| I.ap.s. | $0.22-0.29$ | 0.260 | 0.018 | 6.83 |
| I.n.s. | $0.22-0.40$ | 0.305 | 0.057 | 18.87 |
| B.w. | $0.17-0.22$ | 0.204 | 0.190 | 9.55 |
| Ap.d. | $0.07-0.09$ | 0.073 | 0.070 | 9.59 |
| Diss.w. | $0.09-0.15$ | 0.126 | 0.021 | 16.72 |

Micrometric formula: $15-20 / \mathrm{II}-15 / / \mathrm{I} 8-22 / \mathrm{I} 2-20$
Apertures per fenestrule.

| Range of specimen modes: | 2 | 3 | 4 |
| :--- | :--- | ---: | :--- |
| Distribution of specimen modes: | 6 | I3 | I |

Description. Zoarial fragments have an open-textured meshwork of intermediate size, consisting of relatively thin branches and dissepiments with rectangular fenestrules. Specimens are mostly small, giving no certain indication of zoarial shape, though it is probable that this was of the orthodox planar, fan-shaped kind.

Branches are slender in relation to fenestrule size; they are straight and mostly parallel, except in the proximal region where they bifurcate repeatedly and tend to curve outward. There is a median keel on the obverse. This is clearly marked in distally located fragments but tends to be obscured by secondary encrustation in ones from the proximal part of a colony. In younger fragments the upper surface of a branch slopes sharply away on either side of the keel; more gently in older ones. The margins of branches are in most cases gently sinuous owing to the presence of a slight bulge below each aperture. This is particularly evident on the reverse. The under surface of branches is broadly rounded and commonly shows good longitudinal striae. These may also be visible on the flanks of branches between apertures.

Dissepiments are bar-like, with roughly circular section and do not expand much at the ends. They are slender in the distal region, but shorter and stouter in older, more encrusted parts of colonies. Dissepiments are considerably depressed below the branch crest on the obverse side, but only slightly on the reverse. They bear striations parallel to their length, and on the under side these are continuous with similar markings on adjacent branches.

Fenestrules are comparatively large, commonly $I \frac{1}{2}$ to 3 times the branch width. In most cases they are rectangular with slightly sinuous lateral margins; less commonly they may be almost quadrate (where branches are widely spaced) or elongate-oval to elliptical.

Zooecial apertures small, circular and relatively widely spaced (about $1 \frac{1}{2}$ to 3 diameters apart). Although they show a tendency to regular occurrence in relation to dissepiments, with one opposite the end of each, this is by no means general and they are not 'stabilized' in the sense of Elias \& Condra (1957:70). Apertures are situated on the sloping obverse surface of branches and are directed obliquely
'upward'. Some fragments have branches with a laterally compressed appearance, and in these zooecial apertures may face more or less directly into fenestrules. Plain, collar-like peristomes are commonly present. In some cases the lower margin of the peristome is extended and may project into the fenestrule as a hood, partly obscuring the aperture. The appearance is then reminiscent of the lunaria of Fistulipora and related genera.

Zooecial chambers are triangular or trapezoid in plan. Average measurements of four triangular chamber bases were as follows. Length parallel to branch axis: 0.17 mm ; maximum width: 0.1 mm . Trapezoid chamber bases have slightly larger dimensions (length of longest side: 0.19 mm ; length of shortest side: 0.03 mm ; width: $0 \cdot 13 \mathrm{~mm}$ ).

Carinal nodes are not prominent in this species, the only sign of their former presence commonly being elongate spine bases on the obverse mid-line of branches. Where nodes are preserved they are slender and up to $0 \cdot 12 \mathrm{~mm}$ high. Long spinose structures that are the sterile continuations of branches are present on some zoarial fragments. One of these was 1.77 mm long and had a basal diameter of 0.22 mm . The distal end, truncated by breakage, was 0.17 mm across. Another spine with the same basal diameter was 4.25 mm long, and a third, 2.5 mm long, was expanded at the distal end and attached to another fenestrate colony. These spines, directed laterally from the zoarial margin, appear to have been supporting structures that helped to maintain the colony in its growth position. Other spines, originating from the obverse and reverse of the meshwork, are fewer and less strongly developed than the lateral ones.

Some branches bear a row of small, closely spaced nodes along the mid-line on the reverse side. These are about 0.02 mm in diameter and are spaced one or two diameters apart. Other nodes may be similarly distributed on the under side of dissepiments. One small specimen bore so many strongly developed and closely spaced spines and nodes that it probably represents a pathological condition. The carinal spines are taller and closer than is usual, and several that are particularly well developed branch at their summits, giving rise to clumps of spreading processes resembling the antlers of a deer. Other spines sprout from the flanks of branches above, below and between zooecial apertures. There are also prominent nodes along the reverse mid-line.

Discussion. Specimens of this form compare in all respects with Ulrich's description of $F$. modesta and are assigned to that species. Miller ( y 962 : 124) tentatively assigned a specimen from the Lower Carboniferous Limestone Series at Dalry, Ayrshire, to the same species. It showed most of the features of the American form but had smaller fenestrules which Miller, quite reasonably, attributed to excessive secondary encrustation. Nevertheless, an important discrepancy remains, for his specimen had notably larger zooecial apertures than those observed by Ulrich. Zooecial apertures on the Fermanagh specimens correspond more closely in size and spacing with Ulrich's description.

In the opinion of the writer this form is undoubtedly the Retepora tenuifila described and illustrated by Phillips ( 1836 : 199 and pl. I, figs 23-25) from the

Carboniferous Limestone at Florence Court, Fermanagh, about fifteen miles from Carrick Lough. The horizon from which Phillips obtained his material was almost certainly in the $\mathrm{D}_{1}$ subzone and roughly equivalent to that of the writer's collecting locality. Although Phillips' description is quite inadequate by modern standards, as far as it goes the specimens discussed here respond to it in every particular. His fig. 23 shows the slim, straight branches and dissepiments, and relatively large rectangular fenestrules. This diagram is drawn to natural size, with which the Carrick Lough specimens agree. Fig. 24 illustrates the striated nature of the under side of branches, and 25 shows the gently undulating fenestrule margin with the same number of small, rather widely spaced zooecial apertures as in my specimens. This figure also indicates the keeled nature of the branches, and the fact that they are commonly wider than dissepiments. Phillips' ( $1836: 199$ ) use of the phrase, 'pores small, with prominent edges' presumably refers to the collar-like peristomes surmounting zooecial apertures, and also present in the Carrick material. Elias (MS. 1950: 1) identified specimens in the Hunterian Museum, Glasgow University as 'Fenestella tenuifila Phillips', and gave the micrometric formula: 18-20/11•5-18//1720/16. The present specimens agree well with this. He also recorded the number of apertures per fenestrule as 2.4 to 4 , mostly 3, and the shape of the zooecial chamber as trapezoid, as in the Fermanagh material.

These similarities, taken in conjunction with the stratigraphic equivalence and proximity of the collecting localities, make it seem almost certain that the two forms are conspecific. Nevertheless, the Carrick Lough specimens cannot be assigned to F. tenuifila (Phillips) 1836, for the type material of that species is believed lost. For that reason Miller (1961 : 225) declared the name a nomen dubium and the Carrick Lough material is, therefore, assigned to Ulrich's species.

## Fenestella hemispherica M'Coy

(Pl. 4, figs 7-9; Pl. 5, figs I-4)
1844 Fenestella hemispherica M'Coy; 202.
1881 Fenestella hemispherica M'Coy; Shrubsole; 181.
1961 Fenestella hemispherica M'Coy; Miller; 229.
Diagnosis. A framework of strong, parallel branches joined by short, narrow dissepiments encloses elongate-rectangular fenestrules. A prominent median keel supports regularly spaced nodes. Zooecial chambers hemi-hexagonal.

Material. This form is scarce in the etched residues. Only 17 fragments were examined, the largest measuring $18 \times 10 \mathrm{~mm}$. PD.4699-704, PD.4958-62.

Measurements ( $\mathrm{N}=\mathrm{II}$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | :---: |
| F.l. | $0.75-0.87$ | 0.823 | 0.035 | 4.28 |
| F.w. | $0.47-0.57$ | 0.532 | 0.310 | 5.83 |
| I.ap.s. | $0.24-0.26$ | 0.251 | 0.009 | 3.68 |
| I.n.s. | $0.52-0.60$ | 0.559 | 0.026 | 4.69 |
| B.w. | $0.22-0.27$ | 0.243 | 0.017 | 6.99 |
| Ap.d. | $0.10-0.12$ | 0.115 | 0.007 | 6.53 |
| Diss.w. | $0.07-0.12$ | 0.100 | 0.014 | 14.00 |

Micrometric formula: I8-22/II-I3//I8-20/8-9.
Apertures per fenestrule.

| Range of specimen modes: | 2 | 3 | 4 |
| :--- | :--- | :--- | :--- |
| Distribution of specimen modes: | 2 | 8 | I |

Description. The small fragments available for study, though well preserved, give no indication of the zoarial shape. All belonged to the intermediate parts of colonies and are roughly planar, with parallel branches. They could have come from the medial region of large, fan-shaped meshworks, but it is more likely that they formed parts of cone- or funnel-shaped zoaria of the kind illustrated by M'Coy ( 1844 pl. XXIX, fig. 4a).

Branches are straight, parallel and of moderate width. For two to four fenestrules before a branch divides its width gradually increases, and may reach 0.47 mm at the point of bifurcation. Immediately afterwards this reduces to about 0.2 mm in the new branches. A longitudinal median keel is present on the obverse and in younger fragments the branch surface slopes steeply away from this. On older ones, and approaching branch junctions, the slope is less pronounced and upper surfaces of branches may be almost smoothly convex. The under side is broadly rounded and longitudinally striated.

Dissepiments are characteristically short, thin and depressed below the branch surface on both sides. They have a roughly circular cross-section and, due to secondary accretion, may be comparatively stout in older zoarial fragments. Dissepiments increase sharply in width at their ends.

Fenestrules are commonly elongate-rectangular, with the length varying from $1 \frac{1}{2}$ to 3 times the width. Lateral margins are straight, as zooecial apertures do not project from branches. In most cases fenestrules are as wide, or a little wider than branches; rarely they may be $I \frac{1}{2}$ times the branch width.

Zooecial apertures are circular and from I to $I \frac{1}{2}$ diameters apart. There may be thin, low, rim-like peristomes, but these do not project into fenestrules. At branch divisions an aperture is commonly placed symmetrically in the angle of divergence, but this is by no means always so, and in some specimens the disposition of apertures in this situation is slightly irregular. Zooecial chambers have a hemi-hexagonal base shape and the average measurements of six were: length, 0.25 mm ; and width, $0 \cdot 137 \mathrm{~mm}$.

Carinal nodes are small and regularly placed, though relatively widely separated. They are slender, inconspicuous except in profile view, and up to $0 \cdot 14 \mathrm{~mm}$ high (about half as high as a branch). A characteristic feature seems to be the presence of low, rounded nodes along the mid-line on the under side of branches. These may be situated opposite branch-dissepiment junctions, but not always. They are smooth, rounded swellings up to 0.08 mm high and 0.05 to 0.1 mm in diameter. In one specimen slit-like holes up to o•I mm long and parallel with the branch axis were seen on the sites of nodes that had been removed by breakage or abrasion. Such openings, piercing encrustations of secondary material, denote (like those seen in carinal nodes) the former presence of the primary skeleton. It is, therefore, probable that these nodes are primary structures and not just excrescences associated with secondary encrustation.

Discussion. This form agrees perfectly with M'Coy's (1844:202) description of Fenestella hemispherica from the Irish Lower Carboniferous, and the fragment he illustrated (pl. XXIX, fig. 4b) could well be one of the writer's specimens. With the text of Miller's (196I:229) description there is also close agreement, though the micrometric formula given by that author ( $20-27 / \mathrm{I} 2-15 / / 20-21 / \mathrm{IO}-\mathrm{I} 2$ ) indicates that in his material branches and carinal nodes were slightly more closely spaced than in the specimens from Carrick Lough. Miller's formula was based on only two small fragments however, and they were from a different locality and horizon (top Tournaisean or low Visean). In these circumstances it seems reasonable to attribute the differences to intra-specific variation, and the writer has no hesitation in assigning the specimens described here to M'Coy's species. Because the literature contains hardly any references to Fenestella hemispherica, and in view of the scarcity of fragments of this kind in the etched residue, it must be concluded that the species is uncommon.

## Fenestella parallela Hall

(Pl. 5, figs 5-9)
1881 Fenestella parallela Hall; 26.
1887 Fenestella parallela Hall; Hall and Simpson; 107.
1958 Fenestella parallela Hall; Koenig; 138.
Diagnosis. Similar meshwork to $F$. hemispherica, from which it differs in having broader branches and fenestrules, more widely spaced apertures and more closely spaced carinal nodes.

Material. This form is moderately common and more than 50 fragments were examined. They were mostly quite small but one, from the medial part of a colony, measured $45 \times 22 \mathrm{~mm}$. PD. $4705-\mathrm{II}$, PD. 4963-75.

Measurements ( $\mathrm{N}=20$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $0.75-0.87$ | 0.829 | 0.034 | 4.10 |
| F.w. | $0.52-0.65$ | 0.600 | 0.030 | $5 \cdot 10$ |
| I.ap.s. | $0.25-0.30$ | 0.270 | 0.013 | 4.72 |
| I.n.s. | $0.27-0.05$ | 0.390 | 0.062 | 15.93 |
| B.w. | $0.25-0.32$ | 0.287 | 0.017 | 5.82 |
| Ap.d. | $0.10-0.12$ | 0.110 | 0.009 | 7.92 |
| Diss.w. | $0.12-0.17$ | 0.146 | 0.012 | 8.55 |

Micrometric formula: $16-23 / \mathrm{II}-\mathrm{I} 3 / / \mathrm{I} 7-20 / \mathrm{IO}-18$.
Apertures per fenestrule.
Range of specimen modes: 2
Distribution of specimen modes: 3
Description. Fragmentary specimens examined give no certain indication of the zoarial shape. This could have been a slightly undulose, fan-shaped expansion, or an elongate cone. Colonies must have attained a considerable size, for the largest fragment available was from the medial region and showed no sign of proximal or distal parts.

Branches are relatively stout, straight and more or less parallel (suggesting that the fragments are from the medial or distal parts of colonies). There is a feebly developed median ridge on the obverse, and the branch surface slopes gently away on each side of this. The reverse is broadly rounded and faintly striated, though the striae may be obscured by a coating of secondary schlerenchyma. Branches widen progressively for two to four fenestrule lengths before dividing, and may attain a width of 0.62 mm at the point of division. At the same time the obverse becomes almost flat. Immediately after bifurcation branch width is reduced to about 0.27 mm .

Dissepiments are short, bar-like and depressed only slightly (if at all) below branch level on both sides. The width increases considerably at either end approaching the union with a branch. Coarse ridges and grooves commonly traverse dissepiments along their length and unite with corresponding features on the flanks and under side of branches. Broken ends of dissepiments have a roughly circular cross section, though it may be elliptical in older fragments due to preferential deposition of secondary material on upper and lower surfaces.

Fenestrules are rectangular with rounded extremities, and commonly about $I \frac{1}{2}$ to 3 times as long as they are wide. The width is in most cases slightly greater than that of branches, and lateral margins may be straight or slightly indented by zooecial apertures. The latter are circular and spaced about one diameter apart. They may have plain, circular, rim-like peristomes, though these are not strongly developed. Where a branch widens prior to bifurcation the arrangement of zooecial apertures may be slightly irregular. A few specimens showed a short 'third row' of about two apertures in this position. Zooecial chambers are hemi-hexagonal in base plan. Seven were measured and the average dimensions found to be: maximum length, 0.3 mm ; maximum width, 0.12 mm .

Carinal nodes are small, poorly developed and commonly difficult to identify. Their spacing along the median ridge varies from one specimen to another. Nodes are cylindrical in the distal parts, but proximally are compressed from side to side. The elongate-elliptical node bases are $0.07-0.1 \mathrm{~mm}$ long and parallel with the branch axis. A few specimens had strong spinose structures growing from the reverse side. These were up to 9 mm long with a proximal diameter of 0.4 mm . Some bore recurved barbs up to 0.12 mm long at their distal ends.

Discussion. The presence of long, barbed spines growing from the under surface of branches suggests that the zoarial shape was planar rather than infundibular. Most funnel-shaped colonies of Fenestella have the zooecial apertures on the outer surface (Cumings 1904:72), and that being so, long spines from the reverse would have grown into the funnel. It is difficult to visualize any useful purpose for such an arrangement. With a planar meshwork lying on the sea floor, on the other hand, hooked spines from the under side could have acted as anchors in much the same fashion as the grapnel radicles in species of present day Scrupocellaria (Hinks I880 : pl. 7, fig. 6). However, most forms of Fenestella do not seem to have had a prostrate growth habit, and certainly some specimens bearing barbed appendages had an upright or partly upright posture (e.g. Elias \& Condra 1957 : pl. I7, fig. 4).

Also, barbed spines are not restricted in occurrence to the reverse side of meshworks but in some species grow from the obverse, or arise laterally as branch continuations. It seems likely that in many cases these spines fulfilled their apparent purpose of helping to stabilize colonial meshworks by engaging with other organisms that lay or grew on the sea floor.

Superficial morphological resemblances and similar micrometric formulae (differing only in the number of carinal nodes), at first suggested that these specimens were conspecific with the ones assigned to $F$. hemispherica. Closer examination and the use of t-tests indicated other important discrepancies, however. Statistically significant differences $(\mathrm{P}<0.05)$ between the samples were found to be present in fenestrule, branch and dissepiment width, and also in the spacing of zooecial apertures. As the $F$. hemispherica sample had both thinner branches and narrower fenestrules, these differences could not be attributed to secondary encrustation. In view of this and the lack of correspondence in the spacing of zooecial apertures (hence also in the length of zooecial chambers) it was concluded that the samples were not conspecific.

Comparison with described species of Fenestella showed that the specimens under discussion coincide in all respects with $F$. parallela Hall I881, as recorded from the Chouteau Group (Kinderhookian) of Missouri by Koenig (I958: I38-I40). The micrometric formula given by that author is: $15-21 / 12-19 / / 16-18 / 12-18$. This is within the range of variation shown by the Carrick Lough specimens, which also show close agreement with other dimensions given by Koenig. There is a minor difference in fenestrule length; that of the Chouteau form being 0.55 mm as against an average of 0.6 mm in specimens collected by the writer. It is interesting to note that Koenig (p. I38) gave the zoarial shape as, 'a flabellate expansion', whereas Hall \& Simpson (1887 : 107) stated that it was infundibular. Their illustrations (particularly pl. XLIV, fig; 8 and 9) do not support this statement, however. Hall (1881 : 24) originally recorded the species from the Middle Devonian of New York, Ohio and Alabama, and Koenig's material came from the lower and middle Chouteau, and is probably of Tournaisian age. The Carrick Lough material, therefore, appears to represent a late survival of the species, and extends its range into the Visean.

Although the writer feels in no doubt that these specimens should be assigned to Hall's species, the possibility that $F$. parallela and $F$. hemispherica are closely related and perhaps even conspecific should be borne in mind. The question may be resolved as more material becomes available.

Fenestella rudis Ulrich multinodosa subsp. nov.
(Pl. 6, figs $\mathrm{I}-7$ )
Material. A moderately common form of which 47 zoarial fragments were studied. The largest measured $20 \times 8 \mathrm{~mm}$. PD.4712-16, PD.4976-92.

Measurements $(\mathrm{N}=22)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $0.75-1.07$ | 0.917 | 0.070 | 7.58 |
| F.w. | $0.52-0.82$ | 0.652 | 0.059 | 9.04 |
| I.ap.s. | $0.25-0.31$ | 0.275 | 0.014 | 5.00 |
| I.n.s. | $0.20-0.30$ | 0.255 | 0.028 | 10.88 |
| B.w. | $0.30-0.40$ | 0.334 | 0.024 | 7.26 |
| Ap.d. | $0.12-0.13$ | 0.127 | 0.005 | 3.93 |
| Diss.w. | $0.17-0.25$ | $0.23 I$ | 0.020 | 8.88 |

Micrometric formula: $14-\mathrm{I} 9 / 9-\mathrm{I} 3 / / \mathrm{I} 5-20 / \mathrm{I} 8-25$.
Apertures per fenestrule.
Range of specimen modes: 2
Distribution of specimen modes: I 2I
Diagnosis. These specimens have the typical $F$. rudis meshwork of stout, transversely flattened branches with wide dissepiments and elongate-oval fenestrules. Prominent zooecial apertures are closely spaced, commonly with three per fenestrule. Inconspicuous carinal nodes surmount the median ridge. Though small, these are numerous and distinguish this form from $F$. rudis s.s. Zooecial chamber plan hemi-hexagonal or triangular.

Type specimens. Holotype: PD.47I2, Paratypes: Other zoarial fragments numbered PD. 4713 to PD.47I6.

Description. The specimens appear to have formed parts of zoaria of moderate size (say 3 to 6 cm across), with the form of planar or gently undulating, fan-shaped expansions. The near-parallelism of branches and lack of bifurcation suggests that most of the fragments were from the medial or distal parts of colonies.

Branches are relatively broad, stout and straight. They are rather flat on the obverse, where there is a low but clearly defined median ridge. On each side of this the surface slopes gently away to the fenestrules. In plan the margins of branches show a shallow concave curve between adjacent dissepiments. The reverse is broadly rounded or sub-angular. Branch width increases greatly at bifurcations and may reach 0.85 mm , reducing immediately beyond to about 0.28 mm in each new branch.

Dissepiments are short and stout, thinnest in the middle and rapidly increasing in width at either end. They are regularly placed and may be striated parallel to the length. Dissepiments are notably depressed below branch level on the obverse but only slightly, if at all, on the reverse. On that side secondary encrustation may cause dissepiments to be flush with a branch or even to project a little below it.

Fenestrule shapes are mostly elongate-oval or rectangular with rounded extremities, the latter due to the shape of dissepiments. In most cases the length of fenestrules is about one-and-a-half-times, or twice the width.

Zooecial apertures are relatively large, closely spaced (about one diameter apart) and in two alternating rows placed well out towards branch margins and away from the median ridge. Apertures face obliquely upward and outward. They have only
feebly developed peristomial rims and do not, as a rule, project into fenestrules. At branch divisions an aperture may be symmetrically placed in the angle of divergence. Zooecial chamber bases are hemi-hexagonal or triangular. In the first case the lateral walls are well developed, and in complete chambers are seen to be inclined distally at about $50^{\circ}$. Average dimensions of eight measured chambers were: length parallel to branch, 0.2 mm ; maximum width, 0.21 mm ; length of lateral walls (perpendicular to branch axis), 0.09 mm . Four triangular chambers gave the following average measurements: length parallel to branch, 0.27 mm ; maximum width, $0 \cdot 19 \mathrm{~mm}$.

Carinal nodes are small, and in many cases only identifiable from the position of elliptical basal scars. The spacing varies even within a single zoarial fragment. Node base scars may be pierced by elongate slits, and in a few cases these unite to form a narrow, thread-like cavity along the mid-line of a branch. Such cavities indicate the former presence of the primary skeleton. The arrangement of carinal nodes on many branches is somewhat irregular and not perfectly uniserial.

One or two specimens showed unusually heavy localized encrustations of secondary schlerenchyma on fragments from the medial parts of zoaria. The thickening affected both surfaces, and on the obverse a number of zooecial apertures were occluded and the tips of carinal nodes only distinguishable as fine perforations. On the same side were the truncated stumps of a number of stout, proximally-inclined spines. The maximum length of these was only $I .5 \mathrm{~mm}$ but basal diameters were up to 0.5 mm .

DISCUSSION. In matters of zoarial size, shape and most meshwork characteristics this form corresponds with Ulrich's Fenestella rudis from the Keokuk and Warsaw formations (probably late Tournaisean to mid-Visean) of the United States. It is said, however, ( 1890 ; 537) that dissepiments in that species are 'comparatively weak, rarely half as wide as the branches'. Those of the Carrick Lough specimens are stouter than this, but otherwise of similar character. Dissepimental width is, in any event, a notably variable feature. A more important discrepancy relates to the distribution of carinal nodes, Ulrich's material showing only between nine and thirteen of these per 5 mm Elias ( $1964 ; 378$ ) reduced this range to $10-12$ in his emended description of the species. Although the spacing of nodes is also known to show considerable intra-specific variation, the differences involved here are too marked for the Carrick specimens to be included with $F$. rudis ss. Nikiforova (1926; I78) described a variant, $F$. rudis major, from the Lower Carboniferous of Turkestan. This had fifteen nodes per 5 mm but in all other respects compared closely with the present material. The difference in internodal space (given by Nikiforova as 0.325 mm ) is still too great to allow the two forms to be considered identical, however, and it seemed wisest in the circumstances to introduce a new subspecific name for the etched specimens.

In his recent paper, Elias (1964; 378-379) erected two new species, using specimens originally included by Ulrich (1890) in $F$. rudis. These were $F$. iowensis and $F$. rudiformis, and the formulae of the three stated by Elias, are as follows:
F. rudis s.s.
F. iowensis
F. rudiformis

$$
\begin{aligned}
& \mathrm{I} 6-\mathrm{I} 8 / \mathrm{I} 2 \cdot 5-\mathrm{I} 3 \cdot 5 / / \mathrm{I} 8-2 \mathrm{I} / \mathrm{IO}-\mathrm{I} 2 \\
& \mathrm{I} 4-\mathrm{I} 7 / \mathrm{II}-\mathrm{I} 4 / / \mathrm{I} 8-20 / \mathrm{I} 2 \\
& \mathrm{I} 5-20 / \mathrm{IO} \cdot 5-\mathrm{I} 4 \cdot 5 / / \mathrm{I} 8-20 / \mathrm{IO}-\mathrm{I} 2
\end{aligned}
$$

The species were differentiated solely on minor variations of fenestrule length and zoarial shape. It is difficult to see any reason for the introduction of new names here, as the variations in question are of exactly the type and magnitude that would be expected to occur within a single species.

## Fenestella plebeia M'Coy

(Pl. 7, figs $\mathrm{I}-7$ )
1844 Fenestella plebeia M'Coy: 203.
1844 Fenestella ejuncida M'Coy: 201.
1850 Fenestella plebeia M'Coy; d'Orbigny: 152.
1879 Fenestella plebeia M'Coy; Shrubsole: 278.
188ı Fenestella plebeia M'Coy; Shrubsole: 179.
1895 Fenestella plebeia M'Coy; Stuckenberg: 138.
1933b Fenestella plebeja M'Coy; Nikiforova: 10.
1934 Fenestella plebeja M'Coy; Prantl: 4.
1948 Fenestella aff. plebeia M'Coy; Oakley: 89.
1961 Fenestella plebeia M'Coy; Miller: 226.
Diagnosis. Fenestella with medium-textured meshwork of sub-parallel, straightsided branches bearing strong median keels and closely spaced carinal nodes. Apertures laterally directed, usually four along the side of each elongate-rectangular fenestrule.

Material. Eighty-five specimens of this common, though variable form were examined. They ranged in size from small, virtually complete zoaria about $10 \times 5$ mm , to a large fragment from the proximal part of a colony measuring $22 \times 20 \mathrm{~mm}$. PD.47I7-2I, PD.4993, PD.4995-9, PD.5009-24.

Measurements $(\mathrm{N}=27)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $0.90-\mathrm{I} .57$ | $\mathrm{I} . \mathrm{I} 66$ | 0.134 | $I I .54$ |
| F.w. | $0.55-0.77$ | 0.64 I | 0.059 | 9.17 |
| I.ap.s. | $0.22-0.3 \mathrm{I}$ | 0.260 | 0.033 | $I 2.88$ |
| I.n.s. | $0.16-0.40$ | 0.292 | 0.063 | 2 I .62 |
| B.w. | $0.25-0.35$ | 0.292 | 0.03 I | 10.77 |
| Ap.d. | $0.10-0.12$ | $0 . I I I$ | $0.0 I I$ | 10.00 |
| Diss.w. | $0.12-0.27$ | 0.174 | 0.035 | 20.26 |

Micrometric formula: $13-19 / 7-10 / / 15-20 / 12-25$.
Apertures per fenestrule.
Range of specimen modes:
$3 \quad 4 \quad 5$
Distribution of specimen modes: Io I6 I
Description. The fragmentary specimens indicate that complete zoaria were large, roughly planar, fan-shaped expansions. Several showed parts of basal holdfasts that anchored colonies in position. These vary in size according to that of the colony, larger ones being stout and thickly encrusted with secondary schlerenchyma.

At their lower ends holdfasts may separate into three or four main 'root' processes, with a number of slimmer ancillary ones. The extremities of these expand into thin sheet-like masses that coated objects to which they were attached.

Branches vary in thickness according to age. In the proximal parts of colonies they may be gently sinuous and laterally divergent; medially they tend to be straight and parallel. In most cases branches have a clearly-defined median ridge which, in the proximal region, may be thickly covered with secondary tissue and therefore prominent. The branch surface slopes steeply away on each side of the ridge and, as the under side is shallowly rounded, the cross-section is roughly triangular. Welldeveloped longitudinal striae are commonly present on the reverse, and ridges between these bear numerous tiny punctae or papillae $0.01-0.03 \mathrm{~mm}$ in diameter. These are aligned in poorly defined rows and commonly about 0.06-0.II mm apart. The reverse may be thickly coated with secondary material and as this increased in thickness it appears to have spread up the flanks of branches from below. At a certain stage zooecial apertures, situated between this advancing front and that which enlarged the keel, came to lie in a groove below and parallel with the latter. Some specimens show that the space between apertures later became thickened also, and in such cases the transverse section of a branch is oval.

Dissepiments are characteristically short, and thinner than branches (commonly a half to two-thirds of the branch width). They are roughly circular in section and striated lengthways. The dissepiments are distinctly depressed below branch level on the obverse, but almost flush with it on the under side.

Except in the proximal region and at bifurcations the fenestrule shape is rectangular. Fenestrules are commonly 2 or 3 times as long as they are wide, the greatest relative lengths being found in the proximal region. Distally, branches spread out and the width tends to increase slightly. Fenestrule margins are mostly straight, but may have a sinuous outline where peristomes are strongly developed and project from a branch.

Zooecial apertures are circular and, when well preserved, bear plain, low peristomes. On parts of some specimens the outer sides of peristomes are strongly developed and the flank of a branch below each is slightly inflated. Owing to this condition the branch margin is beaded and not straight. Some branches show a tendency for a regular arrangement of zooecial apertures, with one opposite the end of each dissepiment and 2 to 4 others bordering the intervening fenestrule. This is by no means general, however. Zooecial chambers are mostly triangular in plan, though in some cases the presence of short lateral walls give a shape that is just hemi-hexagonal, and in others the apex of the triangle is truncated so that the shape is best described as trapezoid.

Spacing of carinal nodes on the median keel shows considerable variation from one specimen to another, counts of from 12 to 25 per 5 mm being recorded. Node bases, marking the former position of carinal nodes, are circular or oval (with length parallel to the branch axis) and commonly $0.07-0.1 \mathrm{~mm}$ across. Nodes, where present, are not much higher than wide, though some attain a height of 0.15 mm . In the proximal parts of colonies node bases may appear as a row of dark perforations along the crest of a much-thickened median keel. On the reverse a few specimens
showed a number of low, rounded swellings or nodes. Though not regularly distributed, there is a tendency for these to be situated opposite branch-dissepiment junctions.

Stout spines diverge from the meshwork on both obverse and under sides of several specimens. Their occurrence seems to have been confined to the proximal parts of colonies. Although all such spines have been truncated by breakage, those on the obverse are longer and stouter than the others. On the obverse, spines are up to 6 mm long, with a basal diameter of 0.45 mm , while on the reverse the greatest length is 3 mm , with a diameter of 0.35 mm .

The presence of thick secondary encrustations, particularly in the proximal region, is characteristic of this form and contributes to the unusual degree of dimensional variation shown by specimens. Such encrustation is not confined to the older parts of colonies, however. In two specimens sections of branches were thickly encased in secondary tissue so that the exterior was quite smooth, and numbers of zooecial apertures were completely sealed. On the proximal side of such sections branches were of normal size and apertures unaffected. Another specimen showed a heavily 'calcified' region close to the distal margin of the colony, as indicated by the presence of unbroken branch tips. The reason for such excessive localized secretion of secondary skeletal material is unknown.
Discussion. These specimens agree in all essentials with Miller's (1961 : 225228) revised description of Fenestella plebeia M'Coy, for which he gave the formula 15-20/8-10//17-20/10-20. It will be noted that the specimens measured by Miller ( 4 homeotypes) also showed considerable variation in node count. One of them (NMD. XXVIII, II) was collected at Black Lion, about io miles from Carrick Lough, and from roughly the same horizon ('Upper Limestone') as the specimens discussed here. Miller stated (p. 226) that the shape of the zooecial chamber base is hemihexagonal, but his illustration (pl. 24, fig. I) clearly shows shapes that are here called triangular. Some of the Carrick Lough specimens have larger fenestrules than those measured on the type material by Miller, and call to mind Nikiforova's (1927 : 251) F. plebeia var. longifenestrata from the Lower Carboniferous of the Donetz Basin. However, her illustration (pl. XIII, fig. 2) shows chamber base shapes that approach rectangular and differ greatly from those of the present specimens.

Although Ulrich (1890:537) commented on similarities between $F$. rudis and $F$. plebeia, and Miller (196I : 228) thought that the two might be conspecific, the writer sees closer resemblances between M'Coy's species and $F$. compressa Ulrich. The latter approaches more closely to $F$. plebeia in having rather more carinal nodes and fewer zooecial apertures per unit distance than $F$. rudis, also in having more apertures per fenestrule ( 3 to 4, as against 2), longer and narrower fenestrules, and branches that are slimmer in relation to fenestrule width. Laterally compressed branches with outward-facing apertures, and the presence of a clear median keel in $F$. compressa also invite close comparison with $F$. plebeia, whereas corresponding features in $F$. rudis have a distinctive appearance. F. demaneti Kaisin also shows close resemblances to F. plebeia. Kaisin did not identify the latter species from the Tournaisean of Belgium, though it could reasonably have been expected in those
strata, but Kaisin (1942 : 105) did list $F$. aff. compressa. He differentiated $F$. demaneti from this form only on the basis of its more closely spaced branches (16-17 as against I $_{4}-\mathbf{1 5}$ ). Division of the two might have been rendered more convincing if some indication had been given of the number of specimens measured. In any case, as the range of branches per 5 mm in $F$. plebeia is $15-20$ it seems possible that Kaisin's material really belonged to that species. The micrometric formulae of the forms discussed are as follows:

|  | Br/Io | F/Io | $A p / 5$ | $N / 5$ |
| :---: | :---: | :---: | :---: | :---: |
| F. plebeia. (Type specimens) | 15-20 | 8-IO | 17-20 | 10-20 |
| F. plebeia. (Carrick Lough) | I3-19 | 7-10 | 15-20 | 12-25 |
| $F$. rudis, Ulrich 1890 | 16-18 | 10 | 20-21 | 14-16 |
| $F$. compressa, Ulrich 1890 | 14-15 | $8 \frac{1}{2}$ | I6-18 | about I6 |
| $F$. aff. compressa. (In Kaisin 1942) | I4-I5 | 8-IO | 18 | I6-I8 |
| F. demaneti, Kaisin 1942 | 16-17 | 7-9 | 18 | I7 |

Fenestella cf. arthritica Phillips
(Pl. 7, figs 8-9; Pl. 8, figs I-4)
Material. More than 50 zoarial fragments of this moderately common form were examined, the largest measuring $30 \times 15 \mathrm{~mm}$. Proximal, medial and distal parts of colonies were all represented. PD.4722-28, PD.5025-37.

Measurements ( $\mathrm{N}=20$ ):

|  | A | B | C | D |
| :---: | :---: | :---: | :---: | :---: |
| F.l. | I. $20-1.50$ | I.410 | 0.087 | $5 \cdot 46$ |
| F.w. | 0.80-0.11 | 0.935 | 0.077 | $8 \cdot 23$ |
| I.ap.s. | 0.31-0.35 | $0 \cdot 324$ | 0.013 | 4.17 |
| I.n.s. | 0.45-0.67 | 0.531 | 0.045 | $8 \cdot 47$ |
| B.w. | 0.35-0.45 | 0.414 | 0.025 | 6•16 |
| Ap.d. | 0.10-0.15 | $0 \cdot 120$ | $0 \cdot 115$ | $9 \cdot 58$ |
| Diss.w. | 0.17-0.30 | 0.2II | 0.031 | 14.67 |

Micrometric formula: 10-13/7-9//I4-17/8-1r.
Apertures per fenestrule.
Range of specimen modes:
$3 \quad 4$
Distribution of specimen modes:
$5 \quad 15$

Description. The fragments showed a strong, compact meshwork of medium texture. Their shapes suggested that complete zoaria were more or less planar, fan-shaped expansions of intermediate size (say, 3 to 6 cm across).

Branches are straight or gently curving, with relatively few bifurcations. They are broad for the meshwork texture and flattened on the obverse, though with a strong median ridge or keel. Proximally, branches may be encased in secondary schlerenchyma which in some cases obscures the median ridge and results in a stoutly rounded cross-section. Such branches may have widths up to 0.57 mm .

The reverse is in most cases broadly rounded and may have a fibrous appearance, though longitudinal striae of the orthodox kind were not seen. A few specimens showed rows of minute papillae parallel with the branch axis.

Dissepiments vary considerably in length and width, but are commonly short and about half as wide as branches. The width may, however, be much increased by secondary encrustation and in the proximal part of a colony may attain 0.45 mm . Dissepiments widen notably towards the junction with a branch. They are slightly depressed below branch level on both surfaces and broken ends commonly show an oval cross-section. Because dissepiments increase in width towards the union with a branch, fenestrules are mostly elongate-oval or rectangular with rounded extremities. Their long sides are in most cases straight, but may be slightly indented by protruding peristomes.

Zooecial apertures are circular, relatively small, and directed upwards and away from the branch. Some specimens show apertures with plain, circular, collar-like peristomes, particularly in the encrusted proximal part of colonies. Where peristomes are well developed they may protrude slightly into fenestrules. The zooecial chamber plan varies from hemi-hexagonal to near rectangular, and a prominent hemiseptum is developed. Average dimensions of eight hemi-hexagonal chambers were: length, 0.35 mm ; width, $\mathrm{o} \cdot \mathrm{I} 8 \mathrm{~mm}$. Corresponding dimensions of four rectangular chambers were: 0.32 mm and $0 \cdot 16 \mathrm{~mm}$ respectively.

Carinal nodes, when well preserved, are tall and spaced fairly regularly along the median keel. In profile they resemble the teeth of a saw, and may attain a height of 0.37 mm (about the same as that of a branch). These nodes or spines are cylindrical in the upper part, with a diameter of about $0 \cdot 12 \mathrm{~mm}$, but laterally compressed below. The spine-base is oval with the long axis (about $0 \cdot 17 \mathrm{~mm}$ ) parallel to the branch. The distal ends of spines, which are always broken, may show a hollow axial cavity about 0.05 mm across.

A few specimens had nodular swellings on the reverse of branches. These were commonly about 0.02 mm in diameter and formed a somewhat irregular row along the mid-line, approximately 0.2 mm apart. In some cases distribution appeared to be random. The stumps of stout spinose processes are present on the obverse and reverse of some fragments, particularly in the proximal region, and one or two specimens showed strong lateral spines developed as continuations of ordinary branches.

Discussion. This form bears strong resemblances to Fenestella arthritica Phillips 1841, originally recorded from the Middle Devonian. The types of this species have been lost for many years and the author's description and illustrations are inadequate by modern standards. Nevertheless, the present specimens correspond with them as far as they go. For example, Phillips mentioned the presence of thick branches and dissepiments with oval fenestrules, and his illustration clearly shows the hemi-hexagonal zooecial chambers. Whidborne ( $1895: 170-172$ ) subsequently identified the species from the Middle Devonian of north Devon and his account is valuable, as he was familiar with the type material. Whidborne's description is more comprehensive than that of Phillips and includes some measure-
ments (about 8 fenestrules and $13-15$ branches in 10 mm ) with which the Carrick specimens are in reasonable agreement. He noted that branches are commonly rather narrower than fenestrules, and that they divide only at distant intervals. He also observed the tall carinal spines, though he only saw these in thin section and consequently mistook them for a high, thin keel running the length of the branch. He commented on the presence of nodes on the reverse (pl. XIX, fig. 6) and of 3 to 5 zooecial apertures along each fenestrule margin. Elias (MS. I950 : I) identified $F$. arthritica from the Lower Limestone Group of Scotland and noted the 'pentagonal' chamber base shape and presence of $4-5$ zooecia per fenestrule. He gave the following formula for specimens in the Hunterian Museum collections, Glasgow University: $13 / 7-8 / / 16-17 / 8-10$. The formula for the material from Carrick Lough is close to this and, in view of the similarities noted above, it seems probable that those specimens are related to Fenestella arthritica, if not identical with it. However, because of the absence of type specimens, the imperfections of earlier descriptions and the fact that the original form was Devonian, it seems advisable to leave the identification as a provisional one.

Another species that is morphologically close to the specimens discussed here is $F$. nododorsalis Ulrich, for which Nekhoroshev (1956: 152) gave the formula: $14 / 6 \frac{1}{2}-8 / / 55-16 /$ ? On the basis of Russian specimens he stated the internodal distance to be 0.35 mm (Table 4, pp. I38-I39), suggesting about I4 nodes in 5 mm , a number considerably in excess of that seen on the Carrick Lough material. Ulrich's original specimen, $F$. compressa var. nododorsalis (1890:540) showed only the reverse surface with $12-\mathrm{I} 3$ branches and $7 \frac{1}{2}-8$ fenestrules in 10 mm . The parent species $F$. compressa Ulrich, has the formula: $14-\mathrm{I} 5 / 8 \frac{1}{2} / / \mathrm{I} 6-\mathrm{I} 8 /$ about I 6 , and is similar in several respects to the Irish colonies though with more carinal nodes per unit distance, and thinner and more closely spaced branches. Kaisin (1942 : 105) assigned to $F$. aff. compressa nododorsalis specimens with the formula: 14-16/6-8// I7-18/8-10 and with thicker branches ( $0.4-0.5 \mathrm{~mm}$ ) than those described by Ulrich. This form was not illustrated but, judging from the description, it may be very close to that considered here.

## Fenestella praemagna Shulga-Nesterenko

(Pl. 8, figs 5-II)
1951 Fenestella praemagna Shulga-Nesterenko: 104.
Diagnosis. Small, fan-shaped colonies with open meshwork and lax growth habit. Apertures well separated, usually four per fenestrule. Tall carinal spines branch at their distal ends.

Material. Twenty-six specimens of this form were examined. Almost all were fragments from the proximal parts of colonies. The largest was $8 \times 10 \mathrm{~mm}$. PD.4729-35, PD.5038-46.

Measurements $(\mathrm{N}=\mathrm{I} 6)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $I .05-\mathrm{I} .57$ | $I .384$ | $0 . I 3 I$ | 9.46 |
| F.w. | $0.62-0.85$ | 0.730 | 0.072 | 9.87 |
| I.ap.s. | $0.27-0.35$ | $0.30 I$ | 0.019 | 6.48 |
| I.n.s. | $0.50-0.75$ | 0.665 | 0.070 | 10.56 |
| B.w. | $0.25-0.35$ | $0.3 I 0$ | 0.030 | 9.83 |
| Ap.d. | $0.07-0 . I I$ | 0.095 | 0.016 | $I 6.27$ |
| Diss.w. | $0 . I 5-0.20$ | 0.172 | 0.016 | 9.46 |

Micrometric formula: $12-\mathrm{I} 5 / 6-9 / / \mathrm{I} 4-\mathrm{I} 8 / 6-\mathrm{IO}$.
Apertures per fenestrule.

| Range of specimen modes: | 3 | 4 | 5 | 6 |
| :--- | :--- | :--- | :--- | :--- |
| Distribution of specimen modes: | 2 | 6 | 7 | I |

Description. The specimens indicate that complete zoaria were small, compact, fan-shaped structures probably not more than 2 or 3 cm across. The proximal parts of three colonies, complete with basal holdfasts and supporting processes, show that the growth posture was erect or partly erect, and not recumbent. In one case the holdfast is attached to the obverse side of another fenestrate fragment. The meshwork, composed of stout branches and relatively thin dissepiments, has a rather fine texture and branches commonly show a lax and somewhat irregular growth habit. This may partly be explained by the fact that most of the specimens are from the proximal parts of colonies.

The obverse of each branch bears a fairly well-developed median ridge or keel, from which the surface slopes steeply towards the branch margin. The reverse is rounded and commonly shows a number of fine, closely-spaced, longitudinal striae. In some cases these are also seen on the flanks and upper surface of a branch between zooecial apertures and carinal nodes. Striae in the latter situation are gently sinuous and not strictly parallel with the axis of growth. The broken ends of branches show a transverse section that varies from near-triangular to near-circular.

Dissepiments are relatively slender and bar-like. They do not increase much in width at either end. The cross-section (as seen in broken ends) may be roughly circular or oval, with the long axis either horizontal or vertical, depending on whether the width or height is greater. Dissepiments are slightly depressed below branch level on both sides and may be rather irregularly spaced, as is usual in the proximal parts of zoaria.

Fenestrules are commonly one-and-a-half times to twice the width of branches and their shape is basically elongate-rectangular with rounded extremities. However, due to the lax growth habit of branches and their recurrent division (associated with the proximal location of most of the fragments), and also to the somewhat irregular placing of dissepiments, fenestrule shapes vary considerably and may be rectangular, quadrate or even elliptical.

Zooecial apertures are situated in two rows placed well out towards branch margin and away from the median ridge. Apertures are relatively small, circular and wellseparated (between $I \frac{1}{2}$ and $2 \frac{1}{2}$ diameters apart). Peristomes may be present as
plain, circular, collar-like rims. These may project slightly from the branch margin, giving the latter a sinuous or scalloped aspect. Slight localized inflations along the flank of a branch immediately beneath each zooecial aperture may emphasize this appearance, particularly on the reverse.

The internal structure is poorly preserved and only seven zooecial chambers were measured. Of these, five had a triangular plan (maximum length: 0.3 mm ; width : 0.17 mm ) and the others were trapezoid, with the longest side 0.27 mm , shortest side $0 \cdot 1 \mathrm{~mm}$, and the perpendicular distance between them 0.17 mm .

Carinal nodes are unusually well-developed, and placed at fairly regular intervals along the keel. They are tall, slender, and at their distal ends divide into a number (commonly four) of separate processes, or tines. Although the broken stumps of nodes show the usual axial hollow, the distal ends of unbroken tines are sealed, with no sign of perforation. Complete nodes are taller than the branch bearing them (up to 1.37 mm against 0.32 mm ) and commonly have a basal diameter of about 0.16 mm .

Three specimens with the basal holdfast preserved also show subsidiary supporting processes. These are slender columns up to 4 mm long dividing at their ends into short digitate processes which are attached to the substratum. Such processes and their 'arms' would, if found separately, show a close resemblance to the form genus Palaeocoryne.

In a few specimens small nodes are arranged uniserially along the mid-line of parts of the reverse surface. These pimple-like swellings have a diameter of about 0.05 mm and are spaced about $0 \cdot 12-0 \cdot 17 \mathrm{~mm}$ apart. Larger nodes occur at random on the under side of branches, being most commonly situated in the angle at branch divisions and at branch-dissepiment junctions. They are $0 \cdot 12-0 \cdot 17 \mathrm{~mm}$ in diameter and have the shape of cones up to $0 \cdot 17 \mathrm{~mm}$ high.

Discussion. The well-developed carinal nodes in this form, with their relatively regular spacing and branching ends, suggest an intermediate stage between the simple, pillar-like nodes of most Fenestella and the symmetrical superstructure of Hemitrypa. The coefficient of variation for internodal distance is here 10.56 ; that of specimens of Hemitrypa hibernica was $6 \cdot 71$, while the figure for species of Fenestella is mostly between I3 and 23. Increased regularization in the spacing of carinal nodes and union of branching distal extremities may well have led to the formation of geometrically ordered superstructures, such as that of Hemitrypa. Chronic (1949: II7) described branching carinal nodes in the fenestrate form Cervella cervoidea from the Lower Permian of Peru, and Elias \& Condra (1957: 109) found the same feature in Fenestella cornuta from the Wolfcamp (early Permian) of the Glass Mountains, Texas. In these cases also, authors noted the rounded and imperforate ends of the branching tines, making it appear certain that they did not house acanthopores, as has sometimes been supposed (e.g. Ross I96I: 68).

In appearance and dimensions the present specimens correspond closely with Shulga-Nesterenko's (195I : 104) Fenestella preamagna from the Upper Carboniferous (Gzhelian) of Russia, and are assigned to that species. The formula given by that author is: $13-14 / 6-7 / / I_{5}-16 / 7 \frac{1}{2}-10$, and the number of zooecial apertures per fenestrule 4 or 5. It is stated that $F$. preamagna has oval apertures, but this is not
commonly the case with the Irish specimens, though in one or two fragments apertures were slightly elongated transversely. Shulga-Nesterenko noted the presence of large carinal nodes, but did not mention any peculiarity in their shape. This is not surprising, as her material was not silicified and the spines were probably broken off near branch level.

There is also some similarity between the Fermanagh specimens and Fenestella varifenestrata Elias \& Condra 1957, from the Lower Permian (Upper Leonard) of Texas. However, that species was founded on a single small, poorly-preserved specimen and it is not possible to make a worthwhile comparison. The authors gave the formula: $12 / \mathrm{Io} / / \mathrm{I} 6 / 7-8$, with 2 to 5 apertures per fenestrule. The presence of tall, stout nodes on a weak keel, and small, rather widely spaced apertures are features in agreement with the Fermanagh specimens, but no information was given regarding branch width, zooecial chamber shape or other characteristics, and the illustrations are uninformative (pl. 10, figs $\mathrm{I}-4$ ). It is possible, however, that Elias and Condra's specimen is itself referable to $F$. preamagna.

It would appear that the Fermanagh specimens are most closely comparable with Upper Carboniferous and Lower Permian species. This may, therefore, be a case in which the Carrick residues contain early members of stocks that later became widely dispersed.

Fenestella fanata Whidborne carrickensis subsp. nov.

> (Pl. 9, figs I-9)

Material. This is a moderately common form and more than foo fragmentary specimens were examined. The largest measured $22 \times 24 \mathrm{~mm}$. The form is particularly interesting because of the presence of large numbers of inflated ovicells. These have been described elsewhere (Tavener-Smith 1966a). PD.4736-42, PD.5047-67.

Measurements $(\mathrm{N}=28)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $I \cdot 07-\mathrm{I} \cdot 62$ | $I \cdot 329$ | 0.119 | 8.95 |
| F.w. | $0.70-\mathrm{I} \cdot 02$ | 0.848 | 0.757 | 8.93 |
| I.ap.s. | $0.35-0.45$ | 0.383 | 0.023 | 6.07 |
| I.n.s. | $0.42-0.75$ | 0.555 | 0.084 | $I 5 \cdot 13$ |
| B.w. | $0.33-0.47$ | 0.400 | 0.035 | 8.80 |
| Ap.d. | $0.12-0.19$ | 0.151 | 0.016 | 10.74 |
| Diss.w. | $0.17-0.37$ | 0.233 | 0.040 | 17.38 |

Micrometric formula: 10-13/6-9//IO-I4/6-II.
Apertures per fenestrule.
Range of specimen modes:
34
Distribution of specimen modes: $26 \quad 2$
Diagnosis. Zoarium a flabellate expansion of rigid branches with a distinctive bifurcation pattern and roughly circular cross-section. Keel obsolescent, carinal nodes small and distantly placed. Apertures in two alternating rows placed close
to the median line. Zooecial base shape hemi-hexagonal. This form is distinguished from $F$. fanata s.s. by its distinctly narrower branches (about 0.3 compared with 0.4 mm ), reduced inter-apertural distance (about 0.3 as against 0.383 mm ) and shorter, more compact zooecia.

Type specimens. Holotype: PD.4736. Paratypes: Other zoarial fragments numbered PD. 4737 to PD. 4742.

Description. The sample includes fragments from all parts of colonies except the proximal extremity. They suggest that entire zoaria were roughly planar or somewhat foliaceous, flabelliform expansions, such as that illustrated by Whidborne (1895: pl. XVIII, fig. 6).

The meshwork consists of stout, straight branches and thin dissepiments bounding rectangular or oval fenestrules. A distinctive feature is the presence on branches of globose ovicellular inflations commonly incorporating more than one zooecial aperture. These may be situated at branch-dissepiment junctions, in which case the dissepiment is also variably inflated. Ovicells may be associated in groups on adjacent branches, and pairs are commonly in juxta-position, being partially fused, or conjoined.

Branches are approximately circular in cross-section with no noticeable keel and the reverse may bear faint longitudinal striations. The bifurcation pattern shown by branches and zooecial apertures is distinctive. For two or three fenestrules prior to division branch widths may increase to a maximum of about 0.9 mm . Immediately thereafter the width of each new branch is reduced to about 0.35 mm . The abnormally wide section on the proximal side of the fork is flattened dorsi-ventrally and bears an extra row of apertures. This 'third row' may be up to 4 or 5 apertures long, and the appearance in this part of a branch may be similar to that of Polypora. The arrangement of apertures may be quite regular, with two adjacent rows alternating in the usual manner and an apparently unrelated third row on one side of them, or it may be somewhat irregular. In a few fragments the third row is represented by only a single extra aperture in the angle of bifurcation. In such cases the preliminary expansion of the branch is also much reduced and the pattern resulting from division is more like a wish-bone than a steep-sided V.

Dissepiments are straight and bar-like in the distal parts of zoaria; only slightly expanded at their extremities and moderately depressed below branch level on each side. In the proximal region they are relatively shorter and stouter, with considerably expanded ends and only slightly depressed on the obverse, though more so on the under surface. The transverse section of young dissepiments is roughly circular, though it is commonly oval in older ones. Where an ovicell is situated at or near a branch-dissepiment junction the dissepiment tends to be greatly enlarged over much or all of its length.

Fenestrule shape and size in this form are greatly influenced by age. In the younger parts of colonies relatively large rectangular fenestrules with rounded extremities are bounded by branches and dissepiments of moderate dimensions. In the older parts, the strong, close-textured meshwork is composed of notably stouter elements and, because dissepiments flare at their ends, fenestrules are mostly
elongate-oval. Zooecial apertures never project beyond branch margins and the long sides of fenestrules are therefore straight.

Apertures are mostly circular, but may be semi-oval or reniform. In the last two cases the major convexity is always distal. Apertures are relatively large and the two alternating rows placed close to the mid-line and away from the branch margin. The inner limits of apertures in opposed rows reach the mid-line in most specimens. There is, therefore, no room for a longitudinal median ridge of the orthodox kind, and the crestal part of a branch assumes a zig-zag pattern between the apertures of opposite rows.

The zooecial base-plan is hemi-hexagonal, but at higher levels longitudinal sections show an almost rectangular shape. This is because the base-plan relates only to a proximal chamber about $0.3 \times 0.2 \mathrm{~mm}$ which forms the lower part of a zooecium (Tavener-Smith 1966a: 192, text-fig. IA). Above it the latter is continued as an elongate tube obliquely inclined (at about $25^{\circ}$ ) for most of its length but curving sharply towards the branch surface distally to form the vestibule. The mean length of 20 measured zooecial tubes was 0.85 mm , and the width 0.16 mm . A shelf-like hemiseptum is present at the base of the vestibule.

Carinal nodes are small, distantly placed and difficult to identify. They are low in comparison with branch height ( 0.1 mm compared with about 0.4 mm ). The nodes are uniserial, each being situated on a low oblique ridge separating two apertures in opposite rows. Nodes of unusually large size commonly surmount ovicellular inflations. There may be a single one, centrally placed, or a pair, with one at each end of the swelling.

Discussion. The specimens described are morphologically close to Whidborne's (1895: 165-168) Fenestella fanata from the Middle Devonian of north Devon. The formula of that species, derived from Whidborne's description, is: $10-15 / 6-9 / /$ about I7/?, and the number of apertures per fenestrule 3 or 4 , mostly 4. The zoarial shape, spacing of branches and fenestrules, and the peculiar bifurcation pattern described by that author are identical to those of the Fermanagh specimens. Whidborne particularly commented on the last feature (p. 166) and mentioned a remark by Gregory about the similarity to Polypora at branch divisions. The rounded cross-section of branches, fenestrule shape and virtual absence of median keel and carinal nodes are other important features common to both forms. The hemi-hexagonal zooecial base-shape is another point in common, though comparison with the types (kindly loaned by the Curator of the Sedgwick Museum) shows that the zooecial chambers differ. In the Devonian specimens branches are thinner (average of 24 measured: 0.3 mm ) and the inter-apertural distance less (average of I2 measurements: 0.3 mm ). Zooecia are, therefore, shorter and more compact than in the Fermanagh material, and the hemi-hexagonal shape of the chamber base is continued above, though there is a tendency towards a rectangular shape at the upper levels.

The morphological resemblances noted are, in the writer's opinion, strong enough to justify placing the present specimens in Fenestella fanata, but recognition must be given to the important differences in zooecial size and shape. Hence, it is proposed to introduce a new subspecific name, carrickensis, for the Fermanagh form.

Fenestella cf. spinacristata Moore
(Pl. Io, figs I-6)
Material. Fifty-four fragments were examined, mostly from the proximal and medial parts of colonies. The largest was $20 \times 15 \mathrm{~mm}$. PD.4743-50, PD.5068-84. Measurements $(\mathrm{N}=25)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $I \cdot I 5-I \cdot 62$ | $I .353$ | 0.125 | 9.27 |
| F.w. | $0.65-0.90$ | 0.745 | 0.064 | 8.59 |
| I.ap.s. | $0.26-0.32$ | 0.293 | 0.023 | 8.02 |
| I.n.s. | $0.35-0.60$ | 0.429 | 0.058 | $I 3.53$ |
| B.w. | $0.22-0.30$ | 0.250 | 0.021 | 7.20 |
| Ap.d. | $0 . I 0-0.12$ | 0.110 | 0.008 | 7.27 |
| Diss.w. | $0 . I 2-0.22$ | 0.160 | 0.023 | $I 4.69$ |

Micrometric formula: II-14/6-7//I3-17/6-15.
Apertures per fenestrule.
Range of specimen modes: 34
Distribution of specimen modes: I2 I3
Description. Fragmentary specimens examined indicate that complete colonies were fan-shaped expansions of medium size with an erect or party erect posture. A basal holdfast, of which vestiges are preserved in some specimens, secured each colony in position.

Branches are slender and relatively widely spaced, so that the meshwork has an open texture. They may be gently sinuous, giving a rather lax appearance, but are commonly straight and rigid-looking. Branches are narrow in relation to their height (mean width: 0.25 mm , mean height: 0.3 mm , both of 25 specimens) and on the obverse the surface slopes steeply away from a clearly defined median keel. The under side is rounded, so that in transverse section the shape is that of a high triangle with a rounded base. The pattern formed at branch divisions is distinctive: at first the new branches diverge sharply, but after a short distance they curve into parallelism once more, so that a wish-bone shape is formed. In the proximal region, and whenever a thick coating of secondary schlerenchyma is present, the keel may become greatly thickened and present a prominent, cord-like appearance.

Dissepiments are thin, straight and bar-like. They are commonly little more than half the branch width, show a circular cross-section and do not widen much at either end. Dissepiments are strongly depressed below branch level on the obverse, but flush with it or only slightly depressed on the reverse side. The relatively distant spacing of dissepiments contributes to the open-textured meshwork of this form.

The shape of fenestrules (away from branch bifurcations) is rectangular, though the proportion of width to length varies. In the proximal region, where branches are most closely spaced, it may be as great as I : 4, while in distal parts of the mesh it may be only I: $1 \frac{1}{2}$. Proportions of I: 2 or I: $2 \frac{1}{2}$ are commonest.

Zooecial apertures are circular, or rarely reniform in older parts of colonies, and may show low, rim-like peristomes projecting slightly into the fenestrule. Apertures
are $I_{2}^{\frac{1}{2}-2 ~ d i a m e t e r s ~ a p a r t ~ a n d ~ d i r e c t e d ~ l a t e r a l l y ~ i n t o ~ t h e ~ f e n e s t r u l e ~ f r o m ~ t h e ~ s t e e p l y ~}$ sloping flank of a branch. Viewed microscopically the regular spacing and lateral aspect are reminiscent of port-holes in the side of a ship. Apertures are not stabilized with respect to dissepiments, and from 3 to 6 may occur in the length of a fenestrule. Zooecial chamber bases are trapezoid, the average dimensions of 17 being: long side, 0.17 mm ; short side, $O \cdot 1 \mathrm{~mm}$ (both measured parallel with the branch) ; width, $0 \cdot 15 \mathrm{~mm}$.

A single row of peculiarly-shaped carinal nodes is situated along the median keel. They are relatively small, widely spaced and commonly inclined towards the growth origin. Nodes are about 0.12 mm in diameter at the base and taper upward to about the same height. On the reverse a few specimens show sporadically-developed nodes of small size, $0.15-0.25 \mathrm{~mm}$ apart along the mid-line. These are about 0.04 mm in diameter and of about the same height. They are not present on dissepiments.

Discussion. A strong indication of the growth habit of colonies of this kind is provided by a specimen attached to a Penniretepora stipe. The fenestrate colony originates in a mass of 'calcareous' material that embraces the Penniretepora and acts as a holdfast. Branches radiate from this, and those along one margin of the newlydeveloping colony curve back towards the Penniretepora and re-unite with it for support. It is reasonable to suppose that the stick bryozoan either lay on the sea bed or grew in an upright position. In neither case could the attached Fenestella have been recumbent, and it appears to have had an erect or near-erect posture.

An example of the protective function of the keel and carinal nodes is given by a specimen bearing a small, button-like colony of Fistulipora on the obverse. The under side of the latter is not everywhere welded onto the fenestrate branches, but is only attached at a few points. Elsewhere, there is a clear space between the two and, as the apertures of the Fenestella are unsealed, it is likely that they continued to function in spite of the overlying Fistulipora. Immediately above the keel and nodes on the fenestrate branches there are corresponding depressions in the basal lamina of the Fistulipora, and it seems probable that those features caused the latter to 'keep its distance', thus allowing enough space for the polypides to be extruded. It is easy to see that a uniformly developed superstructure, such as that of Hemitrypa, would perform the same service much more effectively.

Features that distinguish fragments of this kind from other fenestrate species in the residues are (in addition to the meshwork dimensions) the slim branches with steep-sided triangular cross-section, forming an open-textured mesh, the zooecial apertures, suggesting in their close and regular arrangement a line of port holes, and the small, inclined and widely spaced carinal nodes. Among described species the form is closest to Fenestella spinacristata Moore I929, from the Pennsylvanian of Kansas. The micrometric formulae are essentially comparable (that based on Moore's description being: I3-I4/7-9//I4-I6/I2-I4), though the fenestrules in $F$. spinacristata are slightly narrower and the carinal nodes more distantly placed. In both the nodes are laterally flattened and inclined proximally. Moore's specimens had a branch width of $0.45-0.55 \mathrm{~mm}$, however, much in excess of that of the Fermanagh material, though it is possible that his fragments were old and heavily
encrusted. It is felt that although the resemblance to $F$. spinacristata is in some respects marked, discrepancies of branch width and fenestrule size prevent the firm assignment of the Fermanagh specimens to that form.

Another possibility, though remote, is that this form is a variant of $F$. plebeia M'Coy, to which there are certain qualitative resemblances. There is only slight overlap between the formulae, however, due to the more open texture of the present specimens. The existence of significant $(P<0.05)$ statistical differences between the two samples in matters of fenestrule length and width, branch width and interapertural space also make it impossible to equate them.

Fenestella cf. funicula Ulrich
(Pl. Io, figs 7-10; Pl. II, figs I-4)
Material. This is a common form, and more than i20 zoarial fragments were examined. A sample of 25 of the best preserved was selected for measurement. The largest specimen had a size of $26 \times \mathrm{I} 6 \mathrm{~mm}$. PD.475I-59, PD.5085-5100.

Measurements $(\mathrm{N}=25)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $I .07-I .70$ | $I .42 I$ | $0 . I 26$ | 8.85 |
| F.w. | $0.67-0.92$ | 0.776 | 0.066 | 8.50 |
| I.ap.s. | $0.29-0.34$ | $0.3 I 2$ | $0.0 I I$ | 3.48 |
| I.n.s. | $0.47-I .00$ | 0.704 | 0.124 | $I 7.69$ |
| B.w. | $0.30-0.40$ | 0.342 | 0.025 | 7.39 |
| Ap.d. | $0.09-0.12$ | 0.103 | $0.0 I I$ | $I 0.58$ |
| Diss.w. | $0 . I 6-0.25$ | $0 . I 97$ | $0.02 I$ | $I 0.89$ |

Micrometric formula: $10-14 / 5-9 / / 13-17 / 4-9$.
Apertures per fenestrule.
Range of specimen modes: $\quad 3 \quad 4 \quad 5$
Distribution of specimen modes: 8 i6
Description. The complete zoarium appears to have been an approximately planar, fan-shaped expansion. Branches are straight or slightly sinuous, with a median keel that may be prominent and rib-like in the older parts of colonies, due to selective deposition of secondary schlerenchyma. Branch sides slope steeply away from the keel and the under side is broadly rounded. The latter commonly shows fine, closely-spaced longitudinal grooves and ridges, with a row of minute papillae (the 'capillaries' or 'granulations' of Russian authors) at intervals of about 0.04 mm along the crest of each ridge. Clearly defined striations are not seen on the obverse, but this side (particularly the keel) may show numbers of short, sinuous ridges, each bearing a row of papillae corresponding in appearance with those on the under side. In the older parts of zoaria branches may be thickly coated with secondary material showing parallel ridges, each bearing a row of papillae. This external cover may seal up zooecial apertures and give branches a roughly circular cross-section instead of the commoner triangular one. On the reverse of branches there may be a variable number of low nodes or short, pointed spines. These are situated along the mid-line,
particularly opposite branch-dissepiment junctions, or in the angle where branches divide. They are of irregular distribution, and present on only a few specimens.

Dissepiments are from half to two-thirds the width of branches. They have a circular cross-section and widen considerably at their ends. Most dissepiments are clearly depressed below branch level on the obverse, but flush with it, or only slightly depressed, on the under side. There may be a series of closely spaced ridges and grooves along the length of a dissepiment, and these merge at either end with those on branches. The ridges may each bear a crestal row of minute papillae.

Fenestrules vary considerably in shape and size, particularly in the proximal region. They are commonly rectangular or elongate-oval, and about 2 or 3 times as long as wide.

Zooecial apertures are mostly circular but may be reniform in the older parts of colonies. They are small and relatively widely spaced ( 2 or 3 diameters apart). Low, collar-like peristomes surround apertures in some specimens and may project slightly into fenestrules, giving the long sides of the latter a beaded appearance. The zooecial chamber is a box-like structure with hemi-hexagonal plan and walls which (except the outer one) are inclined distally. It is as if the box had received a blow from one side. Average dimensions of 20 chamber bases were: maximum length, 0.32 mm ; maximum width, 0.16 mm .

Tall, stout carinal nodes or spines rise from the median keel and, even when not seen, their former presence may be inferred from elliptical spine-bases. The major axes of these are parallel with that of the branch and $0 \cdot 12-0.2 \mathrm{~mm}$ long. Spines are circular in cross-section and up to 0.82 mm high, though invariably broken at the distal end. Many are seen to be hollow, with an axial cavity about 0.07 mm in diameter extending down into the branch. Spines that are longer and stouter than carinal nodes are present on some fragments. They rise from the median keel and, though broken distally, may attain a length of 6 mm . They have a circular transverse section and on the exterior show a fine ribbing parallel with their length. The ribs, or striae, merge with those of the keel and along their length carry minute, closely spaced papillae identical to those on branches and dissepiments.

One specimen showed an aberrant branch which, possibly because of injury, grew upward from a branch division at right angles to the zoarial plane. After I .5 mm in this direction the branch gave rise, on its dorsal side, to a stout spine of the kind described above. This grew back towards the zoarial mesh at about $45^{\circ}$ and, by uniting with the latter, afforded support to the aberrant branch. Where the supporting process met one of the branches of the meshwork its substance grew over the latter but did not merge with it. This is clearly shown by the ridges and grooves on the spine end: they do not fuse with corresponding features on the branch, but form a number of discrete dactylose processes that clasp the branch and firmly secure the spine to it.

On some fragments spinose processes arise laterally as branch continuations at the zoarial margin. Where a change of this kind takes place zooecial apertures cease, the branch shows a slight decrease in diameter, and the exterior assumes a uniformly striated appearance.

Discussion. The presence of strong carinal nodes with hollow axial tubes recalls the suggestion of some authors (e.g. Condra \& Elias 1944: 26; Ross I961:68; Miller Ig6I : 223) that such nodes housed acanthopores or similar structures. The writer has carefully considered this possibility but concludes that there is no evidence to support the idea. The probability seems to be that the nodes were originally solid (the axial hollow having contained primary skeleton) and their ends imperforate. Being tall and pointed it would appear that their function was to prevent browsing predators from approaching too closely to the extended polypides of the colony.

The presence of nodes on the reverse of some specimens, but not others, strengthens the suggestion that this feature is of no diagnostic importance. Ulrich ( $1890: 540$ ) used it to establish the form $F$. compressa var. nododorsalis on the basis of a single specimen of which only the reverse could be seen. In the Carrick Lough collection several species included specimens with and without such nodes.

External ribs and grooves ('striations') on many specimens are seen to be continuous between branch and dissepiment, but this is not so in the case described above where a spinose process united with a branch of the same colony. The difference seems likely to be due to physiological controls that operated within the colony. The purpose of dissepiments appears to have been the provision of internal support by acting as bracing struts between branches. Therefore, although each dissepiment probably originated as a pair of opposing outgrowths on adjacent branches, these were able to fuse to form the cross-bar, and striae become continuous across them. Spinose processes, on the other hand, are here interpreted as structures intended to afford external support for the colony by attachment to convenient neighbouring objects. Such attachment, for obvious reasons, could not have been attained by organic fusion and was effected instead by the prolific secretion of secondary schlerenchyma. This formed an enveloping crust around the foreign body, or a number of dactylose processes which clasped it. Thus, even when a supporting spine encountered another part of its own colony union was effected as if with some external object. Such unions commonly resulted in appearances closely resembling that figured by Vine (1879 : fig. 203) as 'the base of a Palaeocoryne-like pillar parasitically attached to Fenestella sp.'. It seems likely that Palaeocoryne and its allies are to be explained by such relationships.

The specimens show important resemblances to Fenestella funicula Ulrich I890, from the Keokuk Group (probably lower Visean) of Iowa. The formula of this species is: $14-\mathrm{I} 5 /$ about $5 / / \mathrm{I} 3 /$ about 7 , and there are 4 to 6 apertures per fenestrule. $F$. funicula appears to have longer fenestrules and more widely spaced apertures than the Fermanagh material, though these could be peculiarities of the single small specimen illustrated by Ulrich (pl. LI, fig. 6) and upon which his description appears to have been based. He noted that it was a rare form. Ulrich commented on the strong keel carrying widely spaced nodes, but otherwise the description is uninformative and it is impossible to make more than a tentative assignment to the species.

There are also similarities with the Upper Carboniferous $\left(\mathrm{C}_{3}{ }^{\mathrm{gz}}\right)$ Fenestella ghzelensis Shulga-Nesterenko 195I, from Russia. The formula of this species is: II-I3/7-8//

I5-16/5-6 and the number of zooecial apertures per fenestrule, 3 to 4. Other common features include a strong keel with prominent nodes, and the presence of longitudinal ridges bearing rows of papillae on the reverse. Branches are wider in the Russian form, however, $(0.4-0.5 \mathrm{~mm}$ compared with $0.3-0.4 \mathrm{~mm})$ and the chamber shape appears (pl. II, fig. 3 and pl. IV, fig. 2) to be more commonly 4 - than 5-sided. Also, the Fermanagh specimens do not show smaller nodes between each pair of large ones on the keel, as described by Shulga-Nesterenko.

Fenestella placida Moore 1929 also has similar meshwork characteristics to the Irish specimens. This species, from the Pennsylvanian of Texas, has 4 apertures per fenestrule and the formula is: $10 / 6 / / 55-16 / 3-10$. It appears to differ from the Fermanagh material in having larger fenestrules (average: $1.5 \times 0.6 \mathrm{~mm}$ compared with $\mathrm{I} .2 \times 0.43 \mathrm{~mm}$ ), thinner dissepiments (only $0.06-0.1 \mathrm{~mm}$ wide) and a more flattened obverse branch surface. Carinal nodes are notably smaller and zooecial apertures directed upward rather than laterally, as in the Carrick Lough specimens.

## Fenestella cf. filistriata Ulrich

(Pl. II, figs 5-IO; Pl. I2, fig. I)
Material. This is a moderately common form with a medium-textured meshwork. More than eighty fragments were examined, of which the largest was $23 \times 14$ mm. PD.4760-64, PD.5IOI-5I20.

Measurements ( $\mathrm{N}=25$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $\mathrm{I} \cdot 50-2.10$ | I .776 | 0.164 | 9.23 |
| F.w. | $0.75-\mathrm{I} .00$ | 0.878 | 0.069 | 7.86 |
| I.ap.s. | $0.26-0.32$ | 0.295 | 0.011 | 3.65 |
| I.n.s. | $0.45-0.70$ | 0.555 | 0.092 | $I 6.55$ |
| B.w. | $0.30-0.37$ | 0.340 | 0.023 | 6.90 |
| Ap.d. | $0.06-0.10$ | 0.078 | 0.010 | $I 2.42$ |
| Diss.w. | $0 . I 2-0.22$ | 0.186 | 0.026 | 14.25 |

Micrometric formula: IO-I $4 / 5-8 / / \mathrm{I} 6-\mathrm{I} 8 / 7-10$.
Apertures per fenestrule.

| Range of specimen modes: | 4 | 5 | 6 |
| :--- | ---: | ---: | ---: |
| Distribution of specimen modes: | I | I9 | 5 |

Description. Complete zoaria were probably planar, fan-shaped expansions. There is no certain indication as to whether the growth position was upright or recumbent. In many specimens the meshwork presents a somewhat lax appearance but in others branches and dissepiments are straight and rigid-looking.

Branches are dorsi-ventrally flattened, and the gently curved obverse surface lacks a strong median keel. In its place may be a hair-like ridge bounded by grooves which are in turn flanked by other, fainter ridges and grooves which form a delicate tracery over the obverse of the branch. In some specimens the median ridge is more pronounced and thread-like, and in others it is broader and rounded, forming a low crest from which the branch surface slopes gently to the fenestrule. All gradations between these conditions are to be seen. In the proximal parts of
colonies secondary accretions emphasise the median crest, though it remains low and rounded. The reverse of branches is strongly convex and commonly shows about a dozen fine and closely-spaced longitudinal grooves or striae.

Dissepiments are thinner than branches and of variable length and width, being slender rods in one fragment and short, stout bars in another. Many have well developed ridges and striae along their length. Dissepiments are depressed below the branch crest on the obverse, but only slightly, if at all, on the reverse.

Fenestrules are mostly rectangular or elongate-oval, and of considerably greater width than branches. Their long sides may be straight or beaded, the latter appearance resulting from the slight projection of zooecial apertures beyond branch margins.

Two alternating rows of circular apertures are situated close to branch margins and away from the mid-line. They are relatively widely spaced, being two to three diameters apart and, due to the flattened nature of the obverse surface, face almost directly upward. Each aperture has a ring-like peristome which rises slightly above the general surface and, in conjunction with a slight swelling of the side wall, may cause a lateral projection into the fenestrule. At branch divisions a zooecial aperture may be situated symmetrically in the angle of bifurcation. A short extra row of up to three apertures may occur in such positions, but is uncommon.

The zooecial base-shape is irregularly pentagonal, the chamber itself being divided into two parts by a strong, shelf-like hemiseptum. This originates from the dorsal side and is therefore inferior. It has an arcuate plan, and in curving up the outer wall of the chamber provides this with an internal strengthening. Beyond the hemiseptum the wall must be unusually thin, for in the specimens it is commonly breached and the resultant openings give the impression that apertures are twice as numerous as in reality.

Carinal nodes are variably developed and even when present are weak and of obsolete appearance. In a few specimens they are completely lacking but careful examination invariably shows one or two minute oval node-bases, marking their former position. These are most evident where an axial thread forks at a branch division, and in some fragments are not detectable elsewhere. For the most part these nodes are small, low, irregularly situated and difficult to identify. They would readily be removed without trace by weathering.

A few specimens have spinose processes from the obverse or reverse of the meshwork, or as lateral continuations of branches. They are few in number and do not attain large size. Several fragments showed good examples of regeneration following structural damage sustained during the life of the colony. In such cases displaced and twisted sections of meshwork were stabilized by prolific deposits of secondary tissue in the zones of fracture, and broken ends sealed in the same manner.

Discussion. These specimens are close in appearance and dimensions to Fenestella filistriata Ulrich I890, from the Burlington Limestone (probably lower Visean) of Illinois. The absence of a well-defined keel, wide spacing of zooecial apertures and the striated pattern on the obverse surface are points in common with that species. Structural measurements show a good correspondence except that apertures are more closely spaced in the Carrick Lough specimens ( $15-\mathrm{I} 8$ compared with $13-14$ in
$F$. filistriata). In view of this difference the Irish material is not definitely assigned to Ulrich's species. No mention was made of carinal nodes in Ulrich's description of $F$. filistriata, but small obsolete ones of the kind seen in the present specimens may have been completely removed by weathering.

## Fenestella subspeciosa Shulga-Nesterenko

(Pl. I2, figs 2-8)
1955 Fenestella subspeciosa Shulga-Nesterenko: 121.
Diagnosis. Fenestella with open-textured meshwork and rather lax growth form. Rectangular fenestrules have strongly indented margins due to prominence of cowllike peristomes on apertures. Zooecia mostly trapezoid.

Material. Forty-six zooarial fragments were examined. The largest measured: I7 $\times$ IO mm. PD.4765-9, PD.5I2I-40.

Measurements $(\mathrm{N}=25)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $I \cdot 20-I .60$ | $I .378$ | $0 . I I I$ | 8.02 |
| F.w. | $0.60-0.77$ | 0.697 | 0.049 | 7.03 |
| I.ap.s. | $0.30-0.35$ | 0.321 | 0.014 | 4.43 |
| I.n.s. | $0.45-0.70$ | 0.589 | 0.084 | 14.30 |
| B.w. | $0.2 I-0.30$ | 0.252 | 0.018 | 7.24 |
| Ap.d. | $0 . I 0-0.14$ | $0 . I 22$ | 0.009 | 7.55 |
| Diss.w. | $0 . I 2-0.22$ | $0 . I 68$ | 0.023 | 13.64 |

Micrometric formula: $12-15 / 5-7 / / 13-16 / 6-10$.
Apertures per fenestrule.
Range of specimen modes: 34
Distribution of specimen modes:
IO 15
Description. The specimens appear to have formed parts of small, roughly planar, fan-shaped zoaria between 2 and 4 cm across. The meshwork consists of comparatively slender branches with rather widely spaced dissepiments, and has an open texture. Branches show a slightly irregular or sinuous mode of growth which, combined with the large fenestrules, gives the meshwork a characteristically lax appearance.

The obverse branch surface slopes quite sharply away from a low but clearly defined median keel which may have a thread-like aspect. The reverse is broadly rounded and commonly shows fine longitudinal striae. Transverse sections of branches are mostly oval (long axis corresponding with height of branch), but may be almost circular in older parts which are thickly coated with secondary schlerenchyma.

Dissepiments are from half to two-thirds of the branch width and expand (though not sharply) towards the union with a branch. They are circular in cross-section and depressed below the branch crest on the obverse, though not on the reverse. Many dissepiments show longitudinal ridges and grooves parallel to their length. They are not much affected by secondary thickening and commonly present a marked contrast with branches in this respect.

Fenestrules are mostly one-and-a-half times to twice the width of branches. Shapes vary, but are commonly rectangular with a width: length ratio of $I: 2$ to I: 3. Long sides of fenestrules may be indented by projecting zooecial apertures and show a characteristic beaded or scalloped pattern. This feature is less noticeable on the reverse side.

Zooecial apertures are circular or tear-shaped, with the wider end distally There are three to four opposite each fenestrule and one is always situated centrally in the angle of each bifurcation. All apertures bear a peristome, and the species is characterized by the strong development of this feature, apparently as a result of secondary deposition. Stages in the process appear to be:
I. The presence of a low, rim-like peristome round apertures in younger, distal parts of branches.
2. Increase in height of the peristome rim, and development on its outer side of a strong, basin-like lip that projects into the fenestrule. This must have caused the polypide to be directed obliquely 'upward' rather than laterally.
3. A general thickening and heightening of the peristome to form a collar-like structure that attains, on the inner side, a greater height than the median keel. At this stage the latter has the appearance of a thread lying between alternating peristome rims projecting above it on either side.
4. Further secondary deposition caused the cowl-like peristome to bulge into the fenestrule. The terminal aperture may be constricted or even sealed altogether. The increasing size is manifested as a distinct bulge on the obverse branch surface, and alternating bulges may coalesce across the mid-line so that the keel is obscured or lost, though the tips of carinal nodes remain visible. The obverse now has a knobbly appearance due to the alternating peristomial inflations, and the appearance differs greatly from that of a young branch.
It is notable that in this species secondary skeletal material accumulated principally on the reverse of branches and around zooecial apertures, not along the keel as in many other forms. This leads to a distinctive appearance in heavily encrusted parts of colonies.

Zooecial chambers are triangular or trapezoid in plan, mostly the latter. Average dimensions of twenty chamber bases were: length of longer side, 0.17 mm ; length of shorter side, 0.07 mm ; width between these, 0.15 mm . A single perfectly preserved chamber filling had the appearance of a pear or rounded flask, with trapezoid base and the aperture at the termination of a short neck.

The slender median keel bears small carinal nodes spaced rather widely apart. A few specimens also showed an irregular row of small nodes along the mid-line on the reverse surface. These are commonly $0 \cdot \mathrm{I}-0.22 \mathrm{~mm}$ apart and may also be present on dissepiments. Such nodes are not uniformly distributed and may be present in one part of a specimen but not in another. From some fragments they are altogether absent. A few large spinose processes of the kind that appear to have lent support to colonies or assisted in their attachment were also observed. They are uncommon and of relatively small size.
Discussion. Features that characterize this species are the open-textured meshwork, lax mode of growth and the zooecial apertures that commonly protrude
into fenestrules due to the presence of inflated peristomes. These seem to be developed as a result of excessive localized secondary secretion, but the appearance is reminiscent of peristomial ovicells in certain cheilostomes, and the possibility that the peculiar shape was associated with a reproductive function cannot be disregarded.

The specimens correspond in all respects with Fenestella subspeciosa ShulgaNesterenko 1955, from the Upper Carboniferous (Gzhelian) of Russia, and are assigned to that species. That author's account includes mention of circular or pear-shaped apertures with a well developed 'lunarium', and the chamber base-shape in her species is trapezoid or bluntly triangular.

There is also some resemblance to the Australian F. cerva Campbell 1961. Meshwork dimensions in that species (formula: $10-\mathrm{I} 2 / 5 \frac{1}{2}-6 / / \mathrm{IO}-\mathrm{I} 4 / 6-9$ ) are similar to those of the Fermanagh material though the branches are more widely spaced and the fenestrules, therefore, broader. The Australian form also has a high, sharply defined keel, with zooecial apertures in a groove on either side. Peristomes are present, but they are not of the inflated type. These features, together with 'subpentagonal' chamber bases and the introduction of a short third row of apertures prior to branch division, distinguish $F$. cerva from the specimens described here.

From $F$. praemagna, the Fermanagh material differs in having narrower branches, protruding zooecial apertures, larger rectangular fenestrules and longer, slimmer dissepiments. Another Russian Upper Carboniferous form, F. gzhelensis, is similar in some respects but has wider branches $(0.4-0.5 \mathrm{~mm})$ and a rectangular or hemihexagonal chamber base.

## Fenestella pseudovirgosa Nikiforova

(Pl. 13, figs I-9)
1860 Fenestella virgosa Eichwald: 360, fig. 9a (non fig. 9b).
1938 Fenestella pseudovirgosa Nikiforova: 68.
DiAgnosis. Strong, fan-shaped colonial meshwork. Branches roughly triangular in cross-section. High median keels bear stout, widely spaced nodes. Zooecial apertures large; chambers mostly triangular.

Material. More than 140 zoarial fragments of this common and distinctive form were examined. The largest, from the proximal and medial parts of a colony, was $30 \times 18 \mathrm{~mm}$. PD.4770-7, PD.514I-57.

Measurements $(N=25)$ :


Apertures per fenestrule.

| Range of specimen modes: | 4 | 5 | 6 |
| :--- | ---: | ---: | ---: |
| Distribution of specimen modes: | Io | I2 | 3 |

Description. The zoarium is a planar, flabellate expansion with variable meshwork texture. Branches and dissepiments are much thickened proximally by secondary encrustation, and fenestrules correspondingly reduced in size. Distally, branches are more widely spaced and thinner, with larger fenestrules.

Branches are relatively stout with an approximately triangular cross-section. Their sides slope steeply from a strong median keel on the obverse, while the reverse is broadly rounded. In proximal parts the keel may have a pronounced rope-like aspect due to the selective deposition of secondary schlerenchyma. Lateral thickening of this kind may cause it to overhang zooecial apertures. Secondary material may also thickly coat the reverse and lower flanks of branches so that the apertures come to lie in a groove parallel with the keel and below it on each side. Continued secretion of secondary schlerenchyma near the growth origin may result in the occlusion of apertures, which are sealed by a convex cap. This gives branch margins a beaded appearance that is particularly evident where branches are steep-sided.

The reverse surface commonly shows longitudinal striae, and in well-preserved specimens the fine ridges maybear rows of minute papillae. These are about o.or mm in diameter and spaced $0.03-0.06 \mathrm{~mm}$ apart. Similar grooves and ridges with papillae are seen on the obverse, but there 'striae' are not parallel to the branch axis but sinuous, following the contour of the surface. Ridges with rows of papillae may be very evident on the keel and under side where these are thickly coated with secondary material.

Dissepiments are straight and bar-like, though in older parts of zoaria they may flare considerably at either end. They are depressed below branch level on both sides, have a circular section, and are commonly about half as wide as branches, though there is much variation. Dissepiments may show grooves and ridges parallel to their length. These merge with corresponding structures on adjacent branches and also carry rows of papillae.

The size and shape of fenestrules varies greatly, the commonest shape being an elongate rectangle with rounded extremities. Proximally, fenestrules may be elongate-oval and of reduced size, due to the relatively close spacing of branches encrusted with secondary tissue. Fenestrule margins are mostly straight, but the long sides may show a beaded pattern where apertures are sealed by conical 'caps', or well-developed peristomes are present.

Zooecial apertures are large, circular and spaced about one diameter apart. They are not regularly situated with respect to dissepiments. Plain, narrow peristomes may be present and, particularly on steep-sided branches, these may be accentuated on the outer side so as to project slightly into fenestrules.

The chamber base-shape is mostly triangular, average measurements of twenty being: length parallel to branch, 0.3 mm ; width (perpendicular to branch), 0.16 mm . Some triangles are longer and narrower ( $0.35 \mathrm{~mm} \times 0.14 \mathrm{~mm}$ ), while others are shorter but wider $(0.25 \mathrm{~mm} \times 0.17 \mathrm{~mm})$. In a few cases the apex of the triangle is truncated, to give a trapezoid shape (long side: 0.28 mm ; short side: 0.09 mm ;
width: 0.17 mm ). Walls of zooecial chambers are perpendicular to the base-plane throughout their height.

The median keel bears a row of strong nodes or spines. These are in all cases truncated by breakage but may be up to 0.9 mm high and 0.15 mm in diameter at the base. Small, irregularly distributed nodes are present on the reverse, generally along the mid-line of a branch or close to it. Average space between ten pairs of nodes is 0.82 mm , but there is much variation. The diameter of the nodes is from 0.07 mm to 0.12 mm , and many are no higher than wide, though a few rise to 0.8 mm .

Stout supporting spines may originate from obverse or reverse, or laterally as branch continuations. If well-preserved they show parallel ridges and striae which merge with those of the parent branch; the ridges commonly show rows of papillae of the kind already mentioned. On the obverse such spines grow from positions where a carinal node might otherwise have been expected. They are always broken distally, but may be up to 2 mm long, with a basal diameter of 0.27 mm . Although much longer than carinal nodes, the structure appears to be identical, and it is probable that the spines resulted from the continued growth of certain nodes. Similar spines on the reverse are longer and stouter: up to 6 mm in length and 0.7 mm in basal diameter. Some well-preserved specimens show a radiate internal structure reminiscent of the septa of a rugose coral. Lateral spines may develop either as sterile continuations of branches, or at right angles to the branch axis, in the position of a dissepiment. These spines are up to 7 mm long and 0.52 mm in basal diameter.

Discussion. The radiate cross-section of spinose processes mentioned above is commonly seen in good specimens of these structures. It may occur in conjunction with the concentric pattern of secondary laminae, and the parallel with septa and dissepiments in rugose corals is then particularly evident. The radial elements appear to be silicified skeletal rods which originated from the primary core of a spine and passed through the laminated secondary tissue to the periphery.

These specimens appear to be identical with Fenestella pseudovirgosa Nikiforova I938, from the Russian Upper Carboniferous. This species is not well illustrated ( 1938 : pl. X, figs 6 and 7), but the Fermanagh material appears to agree in all respects with the comprehensive description (Ibid. : 68-70, 228) of the Russian species, to which it is therefore assigned. There is also a strong resemblance to $F$. regalis Ulrich I890, from the Keokuk (probably early Visean) of Kentucky, but this has very wide branches (average 0.7 mm against 0.43 mm ) and hemihexagonal to rectangular zooecial chamber bases. Koenig (1958: 134) assigned specimens with an average branch width of about 0.4 mm to $F$. regalis, which might seem to justify the inclusion of the present material also, but the important discrepancy of chamber base-shape remains. F. eichwaldi Stuckenberg 1895, is another species to which there appears to be a strong similarity, though there are differences relating to branch width ( $0.56-0.67 \mathrm{~mm}$ compared with $0.37-0.5 \mathrm{~mm}$ ) and apertural size (diameter 0.2 mm ). Also fenestrules and dissepiments are wider in the Russian form. The most important difference, however, affects zooecial chamber plan, that of $F$. eichwaldi being hemi-hexagonal to rectangular. It seems possible that this species is conspecific with $F$. regalis, and perhaps the same applies to $F$. crockfordae Campbell I96I, from the Australian Kuttung (Upper Carboniferous).

Campbell's form is much like the Fermanagh one but differs in having an 'irregularly pentagonal' chamber base and a short third row of apertures prior to branch divisions.

## Fenestella cf. albida Hall

(Pl. I4, figs I-6)
Material. This is a fairly common form and more than 80 specimens were examined. They were almost all fragments from the medial part of colonies. The largest measured $34 \times 12 \mathrm{~mm}$. PD. $477^{8-85}$, PD. 5158-74.

Measurements $(\mathrm{N}=25)$ :
A

|  |  |  |  | D0 |
| :---: | :---: | :---: | :---: | :---: |
| F.1. | I.52-2.15 | I. 830 | 0.192 | 10.50 |
| F.w. | 0.75-I.00 | 0.869 | 0.064 | $7 \cdot 42$ |
| I.ap.s. | 0.32-0.40 | 0.350 | - $\cdot 187$ | 5.36 |
| I.n.s. | 0.62-0.92 | 0.742 | 0.079 | 10. 64 |
| B.w. | 0.25-0.30 | 0.272 | 0.019 | $6 \cdot 89$ |
| Ap.d. | $0 \cdot 12-0.15$ | - -138 | o.oio | $7 \cdot 22$ |
| Diss.w. | $0.15-0.22$ | - 170 | 0.020 | 11.76 |

Micrometric formula: $10-15 / 4-6 / / \mathrm{I} 2-16 / 5-8$.
Apertures per fenestrule.
Range of specimen modes: $\quad 4 \quad 5 \quad 6 \quad 7$
Distribution of specimen modes: $\quad 7 \quad$ I2 $\quad 6 \quad 0$
Description. The fragmentary specimens suggest that complete zoaria were fan-shaped expansions with a lax, open meshwork. Branches are relatively thin, and sinuous rather than rigid. There is a distinct, thread-like median keel, on either side of which the branch surface slopes steeply away to the lateral margins. These are gently sinuous or scalloped, due to the presence of a slight inflation below each zooecial aperture. The obverse is strongly ridged and grooved between apertures, and the broadly rounded reverse bears fine longitudinal striae. There may also be a row of small tubercles along the reverse mid-line. Branch divisions are common in the proximal region, and some fragments show zones where adjacent branches divided simultaneously. This contributed to the rapid attainment of the flabelliform shape of colonies. At bifurcations there is a characteristic wish-bone pattern, owing to an initially wide divergence angle between each new pair of branches, which then converge slightly before following a parallel course.

Dissepiments are thin, irregularly spaced and slightly depressed below branch level on both sides. There is no marked increase in width at extremities, and transverse sections are oval, the long axis being parallel with the branch height. Owing to the sinuous growth habit of branches the length of dissepiments is variable: some are slender and bar-like, while others are relatively short and stout.

Fenestrules are large, with much variation in size and shape. Most are elongate rectangles with rounded extremities and beaded branch margins. The ratio of width to length varies between $\mathrm{I}: \mathrm{I} \frac{1}{2}$ and $\mathrm{I}: 4$, depending on the spacing of dissepiments.

Zooecial apertures are prominent, with a circular, oval or (most commonly) pearshape. In the last case the large end is distal, and the long axis slightly oblique. Thin rim- or collar-like peristomes are commonly present and tend to be strongly developed on the outer side. These, in conjunction with localized inflations of the branch margin, may form hood- or lunarium-like structures around the distal ends of apertures. A combination of the features mentioned commonly gives branches a distinctive chain-like appearance on the obverse.

Zooecial chamber bases are triangular or trapezoid. Average dimensions of seven triangles were: length (parallel to branch margin) and width (perpendicular to length), both 0.2 mm . In trapezoid chambers the average measurements of five were: longest side, 0.22 mm ; shortest side, 0.09 mm ; perpendicular width between these, $0 \cdot 17 \mathrm{~mm}$.

Carinal nodes are widely spaced and insignificant rarely exceeding $0 \cdot 12 \mathrm{~mm}$ in height. Nevertheless they may show an unusual development. In one specimen, typical of several, a thick carinal node attained a height of 0.32 mm (about the same as that of a branch), then turned abruptly through $90^{\circ}$ into parallelism with the colonial meshwork. As it grew onward in this direction a number of lateral processes were given off, also parallel with the mesh. The longest of these united with the distal end of another large carinal node situated two branches away from the first, so that the beginnings of a superstructure were formed. This was originally more extensive than at present, for other lateral processes, also showing signs of former union with carinal nodes, are broken off short.

In addition to carinal nodes there are small tubercles on the reverse mid-lines of branches and dissepiments. These are mostly uniserial but the arrangement tends to be irregular, and may be biserial for short distances. Node bases are about 0.25 mm in diameter and spaced about $\mathrm{O} \cdot \mathrm{I}-\mathrm{O} \cdot \mathrm{I} 5 \mathrm{~mm}$ apart.

One small specimen, from the proximal part of a colony, showed a number of lateral supporting spines attached to the reverse of another fenestrate fragment. The spines are short and grew as branch continuations, or from the position of dissepiments. If the second fragment lay reverse-up on the sea floor, the spinebearing specimen must have rested on its side in a plane perpendicular to the substratum. Possibly the growth axis was originally upward but the small colony was displaced for some reason.

Discussion. It is probable that this is the form described by Phillips (1836 : 199) as Retepora undulata. His description is too brief for this to be certain, but it nevertheless includes some of the diagnostic features, such as the presence of thin branches, large fenestrules of variable size and shape, and prominent zooecial apertures. The illustrations (pl. I, figs $16-18$ ) are also insufficient by present standards, but they succeed in calling attention to salient features also shown by the Fermanagh specimens Figure 16 is drawn to natural size (with which the present material corresponds well) and illustrates the open texture, relatively thin branches and dissepiments, and the fact that the latter may be oblique. Figure 17 shows the striated nature of the reverse side, with scalloped branch margins and straight, bar-like dissepiments, while in Fig. 18 the distinctive shape of the zooecial apertures is apparent. These similarities are enough for the writer to consider that
the form discussed here is that described by Phillips. In spite of this it seems inadvisable to refer the material to his species, for the type specimens are lost and the existing descriptions inadequate. Miller (1961:225) declared Retepora undutala Phillips a nomen dubium for these reasons, and there is little hope of reviving the species by describing a neotype, owing to the lack of information about collecting localities (merely given as 'Harrogate, Bolland, Hawes' by Phillips).

Fortunately the species, or a form very close to it, was described from America under the name Fenestella albida Hall 1886. It was collected from the Waverly formation (Mississippian) of Ohio. The Fermanagh specimens correspond well with Hall's description and illustrations except that the apertures are more widely spaced (20 in 5 mm according to Hall), carinal nodes are slightly closer ( 4 per 5 mm in the American form) and branches a little wider ( $0.25-0.3 \mathrm{~mm}$ against $0 \cdot 18-0.25 \mathrm{~mm}$ ). However, Koenig (1958 : 133) assigned to $F$. albida specimens with the formula: $15-16 / 6 / / 16-17 / 4$, and these had rather more widely spaced apertures than Hall's material. The spacing of apertures presents the only important discrepancy between the Irish and American forms, but in view of the diagnostic importance attached to this feature it seems best not to make a firm allocation to Hall's species.

Fenestella oblongata Koenig, 1958
(Pl. I4, figs 7-8; Pl. 15, figs I-4)
1958 Fenestella oblongata Koenig; 132.
1962 Fenestella oblongata Koenig; Miller; 123.
Diagnosis. Cylindroid branches lacking a median keel are united by bar-like dissepiments which may be irregularly spaced. Apertures large; placed well away from the branch mid-line, along which occur prominent, widely-spaced nodes.

Material. Fifty-four fragmentary specimens were examined, the largest being $19 \times 24 \mathrm{~mm}$. PD.4786-93, PD.5175-86.

Measurements $(\mathrm{N}=20)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | I.67-2.62 | 2.054 | 2.200 | 10.74 |
| F.w. | $0.77-\mathrm{I} \cdot 10$ | 0.899 | 0.076 | 8.5 I |
| I.ap.s. | $0.3 \mathrm{I}-0.37$ | 0.338 | 0.020 | 5.84 |
| I.n.s. | $0.67-\mathrm{I} \cdot 25$ | 1.032 | 0.147 | 14.28 |
| B.w. | $0.35-0.42$ | 0.379 | 0.017 | 4.62 |
| Ap.d. | $0.10-0.13$ | 0.120 | 0.010 | 8.33 |
| Diss.w. | $0.17-0.25$ | 0.202 | 0.021 | 10.25 |

Micrometric formula: 10-13/3-6//13-16/4-7.
Apertures per fenestrule.

| Range of specimen modes: | 5 | 6 | 7 |
| :--- | :--- | ---: | :--- |
| Distribution of specimen modes: | 8 | II | I |

Description. On the evidence of specimens examined it is probable that complete zoaria were slightly undulating or foliaceous, fan-shaped expansions a few centimetres across. Due to the gently sinuous growth habit of branches and some-
what irregular spacing of dissepiments, the meshwork commonly has a lax appearance.

Branches are stout, with an approximately circular cross-section. There is no median keel, but along the obverse mid-line is a row of prominent, though widely spaced nodes. The branch surface on both sides is gently convex and bears fine, closely-spaced longitudinal striae. These are straight and parallel on the reverse, but sinuous and less well-marked on the obverse.

Dissepiments are strong and bar-like, not expanding much at the ends. They are about half the branch width and may bear longitudinal ridges and grooves. Dissepiments commonly show irregular spacing and in a few cases two occur close together, as if accidental duplication had taken place. They are quite strongly depressed below the branch crest on the obverse, but not so strongly on the under side.

Fenestrules are mostly rectangular, but there is much variation, due to the sinuous growth of branches and irregular spacing of dissepiments. Shapes vary from broad to narrow rectangles, and may also be elongate-hexagonal or elliptical. The ratio of width to length is between $I: 2$ and $I: 5$. Long sides are mostly straight but may have a scalloped pattern due to projecting apertures.

Circular zooecial apertures are in two rows, placed well out towards branch margins. They are relatively large, and commonly have thin, rim-like peristomes. In some cases the flank of a branch immediately below each aperture is slightly distended and the aperture itself (slightly larger than normal) projects into the fenestrule. This development may be carried a stage further so that the swelling affects not only the outer side, but the whole branch surface around an aperture. The latter is then situated on a localized inflation of the branch margin looking rather like an inverted tea-cup. Such apertures are larger than usual and this appears to be an original feature, as the rims are undamaged. It is possible that the swellings bearing these enlarged apertures had a reproductive function of some kind.

Zooecial chambers have a triangular or trapezoid base-shape. Average dimensions of six triangles were: length, 0.32 mm ; width to apex, 0.2 mm . Eight trapezoid shapes showed the following averages: longest side, 0.27 mm ; shortest side, 0.09 mm ; perpendicular width between these, 0.22 mm . The transverse walls (those not parallel with the branch margin) of chambers are steeply inclined towards the growth origin.

Large 'carinal' nodes are widely spaced along the obverse mid-line, each rising directly from the convex branch surface, as there is no median keel. One of them, which appears to be complete, is 0.25 mm high and $0.2 \times 0.12 \mathrm{~mm}$ at the base. Many have been destroyed, leaving only elliptical base scars (long axes parallel with branch) to indicate their former presence. Between each pair of nodes there is a series of tiny pustules or tubercles, each about 0.02 mm in diameter, and spaced about $0 \cdot 12 \mathrm{~mm}$ apart. They are mostly uniserial but the arrangement tends to be ragged and may locally be biserial.

On the reverse there is an irregular row of small nodes along, or close to the midline. These are up to 0.12 mm high, with about $0.1-0.2 \mathrm{~mm}$ between adjacent node centres. Elliptical base scars are about $0 \cdot 17 \times 0 \cdot 12 \mathrm{~mm}$. There is a good deal of
variation in the size, spacing and distribution of these structures. Some specimens have many, others few.

A few strong supporting spines arise from the meshwork on the obverse and reverse surfaces (one from the latter is 8 mm long), and also laterally as branch continuations (one extended for 6 mm beyond the last zooecial aperture). In the latter kind, longitudinal striae are uniformly developed on the exterior of the spine immediately beyond the last apertures. The same thing has been noted in other species and confirms that these structures are potentially present on the obverse of branches, though commonly obscured by apertures, keel and carinal nodes. One lateral spine was connected to an adjacent branch by normal dissepiments, thus emphasizing the branch-like characteristics of these structures. Some stout spines that are truncated proximally showed good transverse sections with radiate structure in combination with concentric laminae, resulting in a pattern like that of a spider's web.

Discussion. This form shows a close correspondence with F. oblongata Koenig 1958, from the Chouteau Group (probably Tournaisian) of Missouri. The median keel seems to be even less evident in the Irish material than in Koenig's specimens, and the reverse side of branches is not noticeably subangular, as mentioned in his description. Also, dissepiments in the Fermanagh material are somewhat wider ( $0 \cdot 175-0.25 \mathrm{~mm}$ compared with an average width of only $0 \cdot 11 \mathrm{~mm}$ ). However, none of these differences is important enough to warrant separation from Keonig's species, with which in other respects there is the closest agreement. F. oblongata has previously been identified in Ireland by Miller (1962: 123) on the basis of specimens from the Tournaisian of Hook Head, Wexford. These had the formula: 8-14/5-7//I5-20/6-8. Neither Koenig nor Miller gave any account of the shape of the zooecial chamber.

Fenestella cf. delicatula Ulrich
(Pl. 15, figs 5-8; Pl. 16 , figs $\mathrm{I}-3$ )
Material. More than sixty zoarial fragments of this distinctive form were examined, the largest being $19 \times 22 \mathrm{~mm}$. PD.4794-801, PD.5187-203.

Measurements $(\mathrm{N}=25)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | I.55-2.60 | 2.177 | 0.207 | 9.50 |
| F.w. | $0.72-\mathrm{I} \cdot 02$ | 0.844 | 0.080 | 9.50 |
| I.ap.s. | $0.25-0.34$ | 0.295 | 0.021 | 7.27 |
| I.n.s. | $0.47-\mathrm{I} .52$ | 0.848 | 0.316 | 37.18 |
| B.w. | $0.22-0.27$ | 0.247 | 0.018 | 7.19 |
| Ap.d. | $0.09-0.12$ | 0.106 | 0.009 | 8.25 |
| Diss.w. | $0.12-0.22$ | 0.169 | 0.025 | 14.64 |

Micrometric formula: 10-12/3-6//13-17/3-10.
Apertures per fenestrule.
Range of specimen modes:
Distribution of specimen modes:

| 4 | 5 | 6 | 7 | 8 |
| :--- | :--- | :--- | :--- | :--- |
| I | 3 | II | 8 | 2 |

Description. The complete zoarium appears to have been a medium sized, gently undulose, fan-shaped expansion. One specimen with a basal holdfast clearly indicates that colonies grew in an erect position. The distinctive open-textured meshwork is composed of thin, widely-spaced branches and even thinner dissepiments, bounding relatively large fenestrules. Branches divide repeatedly in the proximal region, where they may have a lax pattern of growth, and diverge appreciably to right and left of the colonial origin. In medial and distal parts they tend to be straight and more or less parallel. Branches are steep-sided on the obverse, with a clear median crest that may be thickened and rendered more prominent by secondary skeletal accretion. In extreme cases the keel assumes a rope-like appearance and slightly overhangs the zooecial apertures beneath. The reverse is smoothly rounded but may show fine, closely-spaced, longitudinal striae. In some specimens these are also visible on the obverse, where they are less regular and tend to have sinuous courses, curving round zooecial apertures. There is no noticeable change in branch width before or after bifurcation.

Dissepiments are straight, thin (commonly little more than half the branch width) and distantly placed. They do not expand much at the union with branches, so that fenestrules have good rectangular shapes with sharp angles. Dissepiments are strongly depressed on the upper surface, but flush with branch level on the reverse.

Proximally, fenestrule shapes are variable and commonly irregular, due to the divergent branch pattern and high incidence of bifurcation. In the medial and distal parts they are mostly rectangular, with a length to width ratio of about two or three to one. The long sides of fenestrules are straight and not indented by projecting zooecial apertures.

The relatively small zooecial apertures are spaced one-and-a-half to two diameters apart, and from the steeply inclined sides of branches they face almost directly into fenestrules. The position of apertures in relation to fenestrules and dissepiments is not fully stabilized, though there is commonly an aperture opposite each branchdissepiment junction, and one is always centrally placed in the angle where branches divide. Peristomes are present on a few specimens as plain, low, collar-like structures. They appear to have developed as a consequence of secondary accretion round apertures, the peristomial shape being determined by the path of polypides in extrusion and retraction. Zooecial chambers have a trapezoid base plan, average dimensions of eleven being: longest side, 0.17 mm ; shortest side, 0.07 mm ; perpendicular width between these, 0.15 mm .

The median keel carries a single row of insignificant nodes clearly seen in only a few specimens. Their spacing shows much variation but is fairly constant within a fragment. Where nodes are placed far apart there may be a number of small tubercles between each pair and, since carinal nodes are not large, this adds to the difficulty of obtaining a correct count. Shulga-Nesterenko has described similar features (e.g. 195I : 23 and text-fig. 2a) and commented on the difficulty that may arise in differentiating between true carinal nodes and intervening tubercles. Clearly it would be inadvisable to use carinal nodes for discriminatory purposes in such forms, and counts need to be accepted with caution.

A few specimens have an irregular row of small nodes along the reverse mid-line.

Spacing of these approximates to that of carinal nodes on the same branch. The nodal diameter is commonly about 0.07 mm and the distance between pairs from 0.37 to 0.75 mm .

A few relatively small supporting spines are present on the obverse and reverse of the meshwork. Lateral processes arising as continuations of branches are common and extend for up to 4 mm beyond the last zooecial aperture. Truncated ends of these show a thick zone of closely-spaced concentric secondary laminae traversed by skeletal rods. The latter radiate from an axial canal with toothed circumference, originally occupied by primary skeleton.

Discussion. The slender meshwork and large fenestrules of this form at once suggest Ulrich's ( I 890 : 549) Fenestella delicatula from the Coal Measures of Illinois (probably late Namurian-Westphalian). There is good agreement with the description of that species, in which Ulrich referred to the strong keel with 'occasional very small nodes', features that also characterize the present material. Although zooecial apertures in his specimens were small and widely spaced, they differed from those of the Fermanagh form in having prominent peristomes that projected into fenestrules. The illustration ( 1890 : pl. LII, fig. 2) clearly shows this feature, and the beaded appearance of branch margins is quite different from that of the Irish specimens. This is apparently the only discrepancy and in view of the identity in all other respects the specimens are provisionally referred to $F$. delicatula. In examining the etched residues it was found that differences of peristome development were common between members of a species.

Another form to which the present material shows a close resemblance is $F$. tenuivirgata, Shulga-Nesterenko, 1951, from the Russian Lower Carboniferous. This has thinner branches and dissepiments, but in other respects the two appear to be identical. Ulrich gave no information about the zooecial chamber of $F$. delicatula, but in $F$. tenuivirgata it is triangular or trapezoid. There do not appear to be any discrepancies between these two species that could not reasonably be attributed to intra-specific variation and they are here considered to be conspecific.

## Fenestella polyporata (Phillips)

(Pl. I6, figs $4^{-8}$; Pl. I7, fig. I)

[^1]Diagnosis. Open-textured, fan-shaped colonial meshwork with large rectangular fenestrules. Mostly eight or nine zooecial apertures per fenestrule length. Tall, slender carinal nodes are widely spaced.

Material. This species is common in the etched residues from Carrick Lough. Over a hundred fragments were examined, representing all parts of zoaria. The largest measured $22 \times 17 \mathrm{~mm}$. PD.4802-7, PD.5204-18.

Measurements $(\mathrm{N}=2 \mathrm{I})$ :

|  | A | B | C | D |
| :---: | :---: | :---: | :---: | :---: |
| F.l. | 2.30-3.80 | 3.067 | $0 \cdot 339$ | II. 05 |
| F.w. | I.00-I. 20 | I.105 | 0.057 | 5.16 |
| I.ap.s. | 0.30-0.35 | $0 \cdot 312$ | 0.012 | 3.93 |
| I.n.s. | 0.70-I. 25 | I. 074 | 0.131 | 12.22 |
| B.w. | 0.32-0.42 | $0 \cdot 376$ | 0.021 | 5.51 |
| Ap.d. | O.II-O.I4 | 0-12I | 0.007 | 5.35 |
| Diss.w. | O.I7-0.25 | 0.199 | 0.020 | 10.19 |

Micrometric formula: 9-19/3-4//I4-17/4-6.
Apertures per fenestrule.
Range of specimen modes. $7 \quad 8 \quad 9 \quad$ 1о
Distribution of specimen modes: $\quad 2 \quad 6 \quad 8 \quad 5$
Description. The zoarium was a fan-shaped expansion, probably between 4 and 8 cm wide. The coarse meshwork of straight branches and bar-like dissepiments has a rigid appearance.

Branches are of moderate width with clear median crests from which obverse surfaces slope outward to the fenestrules. The underside is rounded and bears fine, closely-spaced longitudinal striae.

Dissepiments are thin, straight, fairly regularly spaced and do not expand greatly at the ends. They are strongly depressed below branch crests on the obverse, but only slightly on the reverse. Fragments from the distal parts of colonies have slender dissepiments, and in a few cases the junction between the initial 'budprojections' from adjacent branches may be seen. This appears as a slight nick or discontinuity in the surface pattern of longitudinal grooves and ridges. It may be situated mid-way along the dissepiment or be asymmetrical. In one case the union was not quite complete, and the ends of two pairs of ridges, though in contact, are still recognizably lobate.

Fenestrules are rectangular with good shapes, due to the straight-sided branches and bar-like dissepiments. A width to length ratio of about one to three is common.

Zooecial apertures are circular, slightly ovoid (with long axis parallel to branch length) or kidney-shaped. They face obliquely 'upward' and away from the branch surface. Low, plain, rim-like peristomes may be present and tend to be most pronounced on the outer sides. In a few specimens small distensions of the branch margin below each aperture cause peristomes to project slightly into fenestrules.

Many fragments have a short third row of apertures immediately before branch divisions. The additional row commonly consists of only one or two apertures, but may contain three or four, and in one case an extra row of ten apertures extended
for a distance of one-and-a-half fenestrules. Mostly the appearance of a third row is soon followed by bifurcation, but in some cases the extra row aborts after a short distance and the branch, having widened slightly to accommodate it, returns to its normal width.

A few specimens from the proximal parts of colonies show apertures sealed by a translucent, plate-like deposit. Closer examination shows that this is not an oper-culum-like structure, but a continuation of the secondary skeleton over the aperture. The translucent appearance is due to the thin skeletal layer sealing a hollow chamber beneath. In some cases the seal is incomplete, being pierced by a small central orifice, and the appearance is then reminiscent of 'blind cells' in the Cheilostomata (e.g. Bassler 1953 : Gi56). It seems likely that this represents a late stage of the sealing process at which the moribund zooecium may still have functioned weakly.

The zooecial chamber has a hemi-hexagonal base 0.33 mm (max. length) by 0.15 mm (max. width). The short lateral walls are inclined, and the hemi-hexagonal shape relates only to the proximal end of the zooecium. From this the chamber extends distally as an inclined tubular structure terminating at the aperture. The average overall length of nine zooecia was 0.52 mm .

Well-preserved carinal nodes are tall, slender columns up to 0.6 mm high (average height of ten branches: 0.32 mm ). In a few cases the distal ends showed the rounded, lobate extremities of secondary longitudinal ridges surrounding an axial tube (Tavener-Smith 1969 : 301, text-fig. 7c). The latter was originally occupied by the primary skeleton, and the lobed distal ends indicate that the nodes were still growing. Many carinal nodes are missing, their former positions being marked only by slit-like node-bases parallel with the branch axis.

A few longer spines rise from the obverse and reverse sides of specimens. One of these, with a length of more than 3 mm , is only 0.4 mm away from the undamaged tip of a branch. The latter shows little secondary encrustation and if, as seems probable, it was still growing, the length of the spine testifies to the rapidity with which such structures could develop.

Another spine, from the obverse of a specimen, branches at its extremity into a number of processes radiating in a plane almost normal to that of the main shaft. One of these grew strongly, but the others are short and little more than stumps. Outgrowths of this kind are strongly reminiscent of the form-genus Palaeocoryne, supposed by Ferguson (1963) to represent separate organisms growing in close association with Fenestella.

Discussion. The presence of a third row of zooecial apertures proximally to branch divisions indicates a delay between the dual budding of a zooecium, that produced the extra zoids, and the bifurcation that provided more branch space to accommodate them. It commonly happens that on the appearance of extra apertures the normal alternating biserial pattern is lost and a confused arrangement results, only to be resolved when bifurcation takes place. In other examples one series of apertures manages to maintain the usual biserial order, while the other is displaced to one side, usually with a raggedly uniserial appearance. Although this situation is commonly followed by an orthodox symmetrical bifurcation, in some cases the biserial apertures continue into a stouter branch than the other. Where
inequality of this kind is evident it may also happen that the stronger branch continues the original axis of growth, while the other is deflected at an angle. Asymmetry of this kind is the rule in Ptiloporella and distinguishes that genus from Fenestella which was, no doubt, the parent stock.

The specimens are assigned to $F$. polyporata (Phillips) 1836, though there are discrepancies with some of the measurements given by Miller (1961 : 233) in re-describing that species. In general the meshwork of the Fermanagh material is a little coarser than in the two specimens used by Miller: fenestrules are slightly longer, branches and dissepiments are wider. Measurements given by Nikiforova (1926 : 177) and Shulga-Nesterenko (1951 : 30-3I) for the same species bridge this gap to a large extent and seem to justify the inclusion of the present material. The relevant data are:

|  | F.l. | F.w. | B.w. | Diss.w. |
| :---: | :---: | :---: | :---: | :---: |
| Carrick Lough | 2.12-3.55 | 0.67-0.77 | 0.32-0.42 | 0.17-0.25 |
| Miller, I96I | 2.05-2.25 | 0.45-0.60 | 0.22-0.33 | 0.11-0.16 |
| Shulga-N., 1951 | I-90 | 0.80 | 0.35 | 0.10-0.15 |
| Nikiforova, 1926 | 2.00-2.50 | 0.62-0.75 | 0.30-0.37 | O.I2 |

The unusual width of dissepiments in the present material might be due to the fact that many of the specimens are old and encrusted. Local ecological factors, requiring for some reason an unusually strong framework, may also have had some influence. Apart from these dimensions there is complete agreement with Miller's description.

Fenestella irregularis Nekhoroshev
(Pl. 17, figs 2-7)
1932 Fenestella irregularis Nekhoroshev; 56.
Diagnosis. Differs from F. polyporata in having slightly coarser meshwork of wider branches with bi-convex cross-section. Peristomes more strongly developed and commonly indent fenestrules. Zooecial tubes have hemisepta.

Material. This extremely coarse-meshed form is common in the residues, and about a hundred fragments were examined. The largest of these measured $28 \times 15$ mm. PD.4808-I3, PD.5219-37.

Measurements ( $\mathrm{N}=25$ ):

|  | A | B | C | D |
| :---: | :---: | :---: | :---: | :---: |
| F.1. | $2 \cdot 70-3 \cdot 70$ | 3.184 | 0.287 | $9 \cdot \mathrm{OI}$ |
| F.w. | 1.00-1.50 | I 200 | 0.126 | 10.50 |
| I.ap.s. | 0.27-0.37 | $0 \cdot 314$ | 0.014 | $4 \cdot 54$ |
| I.n.s. | I-00-I.50 | I.3I3 | $0 \cdot 122$ | 10.10 |
| B.w. | 0.37-0.47 | $0 \cdot 425$ | 0.031 | 7.41 |
| Ap.d. | 0.01-0.14 | 0.122 | 0.006 | $5 \cdot 33$ |
| Diss.w. | 0.17-0.30 | $2 \cdot 330$ | 0.032 | I3. 84 |

Micrometric formula: $7-10 / 2-4 / / 15-18 / 3-5$.

Apertures per fenestrule.
Range of specimen modes: $\quad 7 \quad 8 \quad 9$ Io II I2
Distribution of specimen modes: $\quad$ I $7 \begin{array}{lllll}7 & \text { Io } & 5 & 2 & 2\end{array}$
Description. The complete zoarium appears to have been a large, slightly undulose, fan-shaped expansion. In one specimen a basal holdfast is attached to the reverse of another fenestrate fragment, and suggests that the growth habit was erect or partly erect, from a substratum of organic debris.

Branches are gently sinuous, giving the meshwork a rather lax appearance. They are stout, with a roughly circular cross-section. Along the obverse mid-line is a low, thread-like keel on either side of which the surface slopes gently to the branch margin. On the reverse are fine, closely-spaced longitudinal striae, and these are also visible to a lesser extent on the flanks and obverse, where they are sinuous rather than straight.

Dissepiments are bar-like and notably thinner than branches. They show little increase in width at their ends, so that fenestrules have sharp, angular extremities. Dissepiments are slightly depressed below branch level on both sides and commonly bear fine longitudinal ridges and striae. In the older parts of zoaria they may be considerably thickened by secondary encrustation.

The large, distinctive fenestrules are mostly rectangular though, due to the sinuosity of branches, they may be elongate-hexagonal. In some specimens the long sides have a beaded appearance caused by the lateral projection of zooecial apertures from branches.

Two rows of alternating apertures are placed close to branch margins and away from the keel. They are mostly circular, though some are elliptical, with the long axis transversely across the branch and others (in the proximal region) kidneyshaped. Prominent collar-like peristomes are commonly present and may give apertures a protruberant appearance. They are particularly well developed on the outer side and may project slightly beyond the branch margin.

The zooecium is basically an elongate tube with a terminal aperture. A distinct oblique septum about one-third of the way from the proximal end separates off a slightly distended, bag-like chamber. This has a more or less hemi-hexagonal plan and short lateral walls that are inclined proximally. The septum is situated further from the aperture than is usual with hemisepta, but if it is a structure of that kind it must be described as 'inferior', being apparently of dorsal origin. Alternatively it may be a diaphragm of the type reported by Miller (1962:543) in the Silurian genus Archaeofenestella. Beyond the septum the zooecium continues as a stout tube inclined at about $40^{\circ}$ to the base of the branch. It is moulded to rest on the proximal chamber of the succeeding zooecium, and against that of its neighbour in the next row. At the base of the vestibule, where the tube turns sharply towards the branch surface, there is a constriction caused by a shelf-like projection from the ventral side. This appears to be a superior hemiseptum. The average overall length of eight zooecial chambers was 0.47 mm , and the length and width of the same number of proximal chambers averaged $0 \cdot 175 \mathrm{~mm}$ and $0 \cdot 15 \mathrm{~mm}$ respectively.

The hemi-hexagonal to triangular zooecial base plan in this species relates only to the proximal extremity of the tube, and gives no indication of the true zooecial
shape. The apparent chamber shape seen in thin sections varies according to the level at which the section is cut, being hemi-hexagonal below and oval to rectangular above.

The thread-like median keel on the obverse of branches bears small, widely separated nodes. These are mostly truncated by breakage, but apparently complete ones may attain a height of 0.5 mm , about equal to that of branches. Node-bases are oval and show slit-like axial cavities. The average dimensions of seven were: length (parallel to branch), 0.375 mm ; width, 0.15 mm . Fragments belonging to this species bear an unusual number of adherent organisms (including Fistulipora, Tabulipora, small gastropods and foraminifera) on the obverse side. Perhaps this is in some way connected with the sparsity and small size of carinal nodes.
Spinose processes may grow from either side of the meshwork, or laterally as branch continuations. In most specimens they are few in number and short, though one fragment carried a slender spine that extended for 6 mm from the obverse mid-line.

Discussion. Comparison of these specimens with those assigned to $F$. polyporata (Phillips) showed statistically significant ( $\mathrm{P}<0.05$ ) differences in branch and dissepiment width and internodal distance. Also the keel is more pronounced in the F. polyporata specimens, in which branches have a triangular rather than a rounded cross-section. Zooecial tubes in both forms show the same general shape, but those of the $F$. polyporata sample do not exhibit the well-developed septa described above. For these reasons the two forms must be differentiated, in spite of superficial resemblances.

Among coarse-textured species of Fenestella the present material is closest to $F$. irregularis, Nekhoroshev 1932, from the Tournaisian of Germany. With the description of this form there is complete agreement, and the specimens are, therefore, referred to it. However, they also bear many resemblances to $F$. quadradecimalis M'Coy 1844, a species originally collected from the 'Carboniferous Upper Limestone' at Black Lion, Co. Cavan, about ten miles from Carrick Lough. From this form, as re-described by Miller ( $\mathrm{g} 6 \mathrm{I}:$ : 231), the specimens differ mainly in having more widely spaced apertures ( $\mathrm{I} 5-\mathrm{I} 8$ in 5 mm and $7-\mathrm{I} 2$ per fenestrule, as compared with $2 \mathrm{I}-22$ in 5 mm and $\mathrm{IO}-\mathrm{I} 3$ per fenestrule). In fact, the Carrick Lough material and $F$. quadradecimalis may have belonged to the same natural species, but in view of the above discrepancy it is necessary to assign the former to the German species, with which there appears to be complete identity. It is relevant to note that Elias (MS. 1950:2) assigned to $F$. quadradecimalis specimens from the Lower Limestone Group of Scotland with the formula: 10/3-3 $\frac{1}{2} / \mathrm{I} 7-18 /$ none, and Io-I3 apertures per fenestrule. He also mentioned the presence of a strong inferior hemiseptum. His material seems morphologically close to that described here, but his notes are very brief and without illustration, so that it is impossible to be certain.

Another coarse-textured form described by Nekhoroshev (1932) from the German Lower Carboniferous is $F$. gracilis. This differs from the present specimens in having more closely spaced and thinner branches, also the inter-apertural distance is greater. F. crockfordae Campbell 196r, from the Kuttung (late Carboniferous) of Australia differs in having more widely spaced and larger zooecial apertures, fewer of these per fenestrule, and a short third row on the proximal side of branch divisions.

## Genus LEVIFENESTELLA Miller, 1961

Diagnosis. Like Fenestella, but lacking carinal nodes and a keel-ridge on the obverse of branches. Instead a single longitudinal thread, or several of these in parallel and placed closely together, form a low median crest.

Type species. Levifenestella maeve Miller 1961a: 494. Lower Carboniferous, Ireland.

## Levifenestella undecimalis (Shulga-Nesterenko)

(Pl. I7, figs $8-9$; Pl. I8, figs $\mathrm{I}-5$ )
1961 Fenestella undecimalis Shulga-Nesterenko; II2.
Diagnosis. Coarse-textured Levifenestella with strong branches, rather flattened on obverse. Fenestrules elongate-rectangular, usually with eight apertures per fenestrule. Apertures commonly transversely elliptical and placed well away from branch mid-line.

Material. This distinctive form is common and more than eighty fragmentary specimens were examined. They were from the medial and proximal parts of colonies, the largest measuring $39 \times 17 \mathrm{~mm}$. PD.4814-20, PD.5238-52.

Measurements ( $\mathrm{N}=22$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | :---: |
| F.l. | $2.20-2.30$ | 2.99 I | 0.264 | 8.83 |
| F.w. | $\mathrm{I} \cdot 00-\mathrm{I} .30$ | $\mathrm{I} . \mathrm{I} 86$ | 0.980 | 8.26 |
| I.ap.s. | $0.30-0.37$ | 0.336 | 0.212 | 6.32 |
| B.w. | $0.45-0.57$ | 0.448 | 0.030 | $6 . \mathrm{I} 9$ |
| Ap.d. | $0.10-0.13$ | 0.116 | 0.009 | 7.72 |
| Diss.w. | $0.22-0.35$ | 0.268 | 0.040 | 15.00 |

Micrometric formula: 8-12/3-4//I3-16/none.
Apertures per fenestrule.

Range of specimen modes:
Distribution of specimen modes:
$\begin{array}{llll}6 & 7 & 8 & 9\end{array}$
I 7 I2 2

Description. Zoarium a near-planar, fan-shaped expansion with open-textured meshwork of stout branches and thinner, bar-like dissepiments.

Branches are more or less flattened on the obverse, with a gently convex profile; the reverse is broadly rounded. The surface is covered by closely spaced longitudinal striae that are straight and parallel on the reverse but gently sinuous on the obverse, due to deflection around zooecial apertures. Along the obverse mid-line are $2-4$ (mostly 3) striae separating narrow longitudinal ridges. These may be strongly developed and form a median strip of distinctive appearance, though an orthodox keel is absent. In some specimens the median strip is slightly raised above branch level and, in the proximal region, it may be accentuated by secondary schlerenchyma and fused into a cord-like crest. This may have a notched profile, so that it is locally discontinuous. Notches are from $0.03-0.05 \mathrm{~mm}$ wide and of irregular occurrence. Their presence suggests that the deposition of secondary calcium
carbonate along the median line was interrupted from time to time, possibly due to temporarily unfavourable conditions. In other specimens the production of secondary tissue in the proximal region was so great that fenestrules are virtually closed and branches welded into a solid mass.

Dissepiments are slightly depressed below branch level on both sides, and show well developed ridges and striae parallel to their length. They are straight, not flaring greatly at the ends, and commonly show some degree of dorsi-ventral flattening, giving an ovoid cross section. In the proximal region dissepiments may be notably thickened by secondary encrustation.

Fenestrules are mostly elongate rectangles with good shapes, though in older parts of colonies the extremities may be rounded. The width of fenestrules is commonly a little greater than that of branches, and the sides are straight or slightly beaded.

Two alternating rows of zooecial apertures are situated close to branch margins and away from the mid-line. The apertures are circular, transversely elliptical (commonest) or kidney-shaped with the convex side distal. They are relatively small, with plain peristomes that rise slightly above the flattened branch surface but do not, as a rule, project laterally into fenestrules. Prior to bifurcation there is commonly an additional row, up to five apertures long, with three or even four abreast where the branches divide. The arrangement in such situations may be confused, and the appearance suggestive of Polypora.

Zooecial chambers mostly have a triangular base, though the development of short lateral walls in some cases gives a hemi-hexagonal outline. Eighteen triangles had an average length (parallel to branch margin) of 0.22 mm ; and perpendicular width (to apex) of 0.25 mm . The triangular-based chamber is only the proximal part of the zooecium, however. From its distal end there is a wide tubular extension to the aperture. This is parallel with the branch and inclined at a low angle, the vestibular portion of one zooecium resting on the proximal chamber of the next. The length of the vestibular part is about 0.32 mm , and the total length in the order of 0.55 mm .

Spinose processes arise from obverse and reverse sides of specimens, particularly in the proximal region. Many have extensive secondary thickening at the base and, away from the spine, this extends as skein-like ramifications along the obverse midlines of branches and dissepiments. Some laterally directed spines that are continuations of normal branches show a constriction immediately after the last zooecial aperture, so that the spine is thinner than the branch. Longitudinal ridges and grooves, particularly those of the obverse mid-line, are continuous from branch to spine, curving gently at the junction in accordance with the decreased diameter.

One specimen of the proximal part of a zooarium includes the basal holdfast, which is attached to another fenestrate fragment. The colony is supported in an upright position by a number of bar-like spines originating from the basal part of the colony and serving as struts between this and the organic substratum.

Discussion. The appearance of a constriction at the base of certain lateral spines suggests that their development may have been initiated by injury to the branch from which they grew. It is as if a broken branch tip was sealed by an overgrowth of secondary schlerenchyma forming a 'stump', and that continued
growth from this resulted in the spine. It is not contended that all lateral spines originated in this way, but only that certain cases suggest it.

These specimens lack a true keel and carinal nodes, having instead a striated median strip. They must, therefore, be referred to Miller's (Ig6Ib : 47) genus Levifenestella. Among described species of this kind only one is similar to the present specimens: L. undecimalis (Shulga-Nesterenko) I94I, from the Lower Permian of the southern Urals. The Fermanagh form agrees in every respect with the description of this species, to which it is assigned without hesitation. In view of the age difference between the Irish and Russian specimens it is possible that there is here a case of homoeomorphy, and that the species did not, in fact, persist from Lower Carboniferous to Lower Permian times. Future work may shed more light on this matter.

The specimens also bear many resemblances to the common Lower Carboniferous Fenestella polyporata (Phillips) 1836 . It was at first thought that they belonged to this species, particularly as the type material came from Florence Court, a few miles from Carrick Lough and at approximately the same horizon. Indeed, it seems likely to the writer that Phillips' specimens (1836:pl. I, figs 19 and 20) were identical with the form here described, and differed from that now known as $F$. polyporata. His fig. 20 shows a specimen lacking keel, with a striated obverse surface and bearing two rows of small apertures placed well out towards the branch margin. These features, in combination with the wide branches and slender dissepiments shown in the figure, present a strong resemblance to the form discussed here. However, Phillips' specimens are lost and Miller (I961a : 233) has re-described the species on the basis of a neotype that was itself the holotype of M'Coy's (1844:203) F. multiporata. Miller considered this name a junior synonym of $F$. polyporata, so that his use of M'Coy's specimen in re-describing the latter was justified. Nevertheless, the writer feels that in reality the two forms may have been distinct. From $F$. polyporata, as re-described by Miller, the Carrick Lough specimens differ in lacking a keel and nodes, also in having much wider branches and dissepiments.

Genus MINILYA Crockford, 1944
Diagnosis. Morphology as for Fenestella with the exception that nodes on the obverse branch surface are biserially arranged. Nodes are regularly disposed so that one corresponds with each zooecial aperture.

Type species. Minilya duplaris Crockford 1944. Lower Permian, Western Australia.

Discussion. Crockford's generic diagnosis (I944: I72) was similar to that given above but also stated that zooecial chamber shapes are triangular. Elias and Condra (1957:66) rightly pointed out, however, that no single chamber shape characterizes all forms in which the nodes are biserial.

Minilya plummerae (Moore)
(Pl. I8, figs 6-8; Pl. I9, figs $1-4$ )
1929 Fenestella plummerae Moore; 19.
?1951 Fenestella praerhomboidea Shulga-Nesterenko; 99.
1961 Fenestella ninae Viskova; 87.
Diagnosis. Fine-textured, geometrically regular meshwork. Fenestrules quadrate or hour-glass shaped. Zooecial apertures at ends of dissepiments and midway between them. Strong peristomes commonly indent fenestrule margins.

Material. This fine-meshed species bears a strong resemblance to $F$. ivanovi, from which it is distinguishable only with care. Both are moderately common in the residues, and about thirty-five small fragments of the present form were examined. The largest measured $\mathrm{I} 4 \times 6 \mathrm{~mm}$. PD.482I-7, PD.5253-5.
Measurements ( $\mathrm{N}=\mathrm{Io}$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | :---: |
| F.l. | $0.45-0.50$ | 0.475 | 0.016 | 3.3 I |
| F.w. | $0.45-0.52$ | 0.482 | 0.025 | 5.2 I |
| I.ap.s. | $0.23-0.25$ | 0.250 | 0.006 | 2.50 |
| I.n.s. | $0.22-0.25$ | 0.242 | 0.008 | 3.42 |
| (in I row) |  |  |  |  |
| B.w. | $0.20-0.22$ | 0.204 | 0.008 | 3.9 I |
| Ap.d. | $0.06-0.07$ | 0.068 | 0.005 | 6.90 |
| Diss.w. | $0.10-0.12$ | 0.114 | 0.007 | 5.89 |

Micrometric formula: 19-25/20-22//20-21/19-24 (in I row).
There were two zooecial apertures per fenestrule in all specimens examined.
Description. In meshwork characteristics and general appearance this form bears a strong resemblance to $F$. ivanovi. Zoarial shape and size were probably similar to those of that species.

Branches are relatively stout in relation to meshwork texture. They show a tendency to widen progressively for one or two fenestrules before branch division, and are narrower than usual immediately afterwards. On the obverse side is a poorely defined median keel; the reverse is broadly rounded and may show fine longitudinal striae.

Dissepiments are similar to those of $F$. ivanovi, though a little shorter. On the reverse side they are depressed below branch level only slightly, if at all.

Fenestrules are mostly quadrate, with well-rounded extremities, due to the increase in width at the ends of dissepiments. The characteristic 'hour-glass' shape seen in $F$. ivanovi is less strongly developed in this form, though paired indentations are present on the sides of many fenestrules. These are less evident on the reverse than on the obverse. Visual comparison suggests that fenestrules are slightly smaller than in $F$. ivanovi, but measurements fail to confirm this. The appearance of reduced size is an illusion possibly promoted by slightly greater branch width in the specimens discussed here.
The position of zooecial apertures in relation to dissepiments is stabilized, with one at each branch-dissepiment junction and one half way along the intervening fene-
strule. In the latter situation apertures may project strongly from the branch margin. Peristomes are more marked than in $F$. ivanovi, and this contributes to a superficial impression (not borne out by measurements) that apertures are smaller in the present species. Zooecial chambers are hemi-hexagonal in plan, the average dimensions of ten being: length parallel to branch axis, 0.2 mm ; maximum width, 0.087 mm .

Carinal nodes in this form resemble those of $F$. ivanovi in their size and obscurity, but differ greatly in arrangement. The insignificant nodes are placed closely together in alternating rows, one on each side of the median keel. One node is situated on the inside of each zooecial aperture, and the close association of keel, nodes and apertures gives the obverse of branches a crowded appearance.

There are also nodes on the under sides of branches. These are small, acuminate, and inclined in the distal direction. They are commonly located at branchdissepiment junctions, but may also occur along the mid-line between these positions. Nodes of this kind are identical in shape and position to those described by the writer (1965:489) in Ptilofenestella carrickensis.

Stout supporting spines originate from the reverse of the meshwork, or laterally as sterile branch continuations. Spines from the reverse are commonly armed with short, recurved barbs arranged in cycles of three around the circumference of the shaft. These barbed spines are a characteristic feature and were not observed in $F$. ivanovi.

Discussion. This form is differentiated from the closely similar $F$. ivanovi by the following:
I. Numerical comparisons of structural data by $t$-tests showed a significant difference ( $\mathrm{P}<0.05$ ) of branch width, that of $F$. ivanovi being narrower.
2. Zooecial chamber bases in $F$. ivanovi are triangular, while those of the present specimens are hemi-hexagonal.
3. Carinal nodes in F. ivanovi are uniserial, while in this species they are biserial and approximately twice as numerous. This difference is not as obvious as it may seem, for in both forms the nodes are weakly developed.
These specimens appear to be conspecific with Moore's Fenestella plummerae from the Pennsylvanian Graham Formation of Texas. Because of the presence of biserial carinal nodes, however, the species must be transferred to Minilya. Moore's holotype measured only $4 \times 3 \mathrm{~mm}$, but in spite of this the present specimens correspond with his description in almost every detail. The only point of difference concerns the branch width, stated by Moore to be 0.25 mm , while in the Fermanagh material it ranges from $0.2-0.22 \mathrm{~mm}$.

The Russian Upper Carboniferous species M. ninae (Viskova) 1961, corresponds so closely in all respects with the description of $M$. phommerae, and with the present specimens, that it is considered to be conspecific with them. The only discrepancies relate to the width of fenestrules and dissepiments ( $0.17-0.25 \mathrm{~mm}$ and $0.15-0.17 \mathrm{~mm}$ in the Russian form) and these are too small to warrant taxonomic attention.
M. praerhomboidea (Shulga-Nesterenko) 1951, is another Upper Carboniferous species probably conspecific with $M$. plummerae. It has a micrometric formula
indistinguishable from that of the American species, though the branches and dissepiments are notably wider ( $0.3-0.4 \mathrm{~mm}$ and $0.15-0.25 \mathrm{~mm}$ respectively), and fenestrules correspondingly shorter and narrower. Such differences could be accounted for by the presence of thick secondary deposits on Shulga-Nesterenko's specimen, and her illustration (pl. XX, fig. I) supports the idea. Despite the difference in branch width the zooecial base shape and size are the same as those of the present specimens.
M. rhomboidea (Nikiforova) 1938, has a slightly coarser meshwork than the Fermanagh material and the zooecial base shape is triangular rather than hemihexagonal. These features serve to differentiate this form, in which zooecial apertures and carinal nodes are also more widely spaced.

As Moore (1929:20) indicated, there is a similarity between M. plummerae and $F$. mimica, Ulrich, but this does not stand up to examination. The second species has a distinctly finer mesh with more apertures ( 24 per 5 mm ), and the carinal nodes are in a single row.

Minilya binodata (Condra)
(Pl. 19, figs 5-7; Pl. 20, fig. I)
1902 Fenestella binodata Condra; 350.
1903 Fenestella binodata Condra, Condra; 66, 1 ıо.
1957 Fenestella binodata Condra, Elias and Condra; 90.
Diagnosis. Compact colonial meshwork. Branch obverse gently convex: keel poorly developed; nodes small, obscure. Commonly an aperture at the end of each dissepiment and two along the intervening fenestrule margin.

Material. This is a rare form, of which only twelve small fragments were available. Several were partly replaced by beekite, and their finer structure obscured. The largest specimen measured $9 \times \mathrm{I} 2 \mathrm{~mm}$. PD.4828-3I, PD.5256-8.
Measurements ( $\mathrm{N}=7$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | :---: |
| F.l. | $0.82-0.87$ | 0.853 | 0.023 | 2.66 |
| F.w. | $0.57-0.65$ | 0.622 | 0.023 | 3.78 |
| I.ap.s. | $0.26-0.27$ | 0.271 | 0.004 | 1.56 |
| I.n.s. | $0.26-0.27$ | 0.270 | 0.008 | 2.96 |
| (in I row) |  |  |  |  |
| B.w. | $0.27-0.30$ | 0.296 | 0.007 | 2.53 |
| Ap.d. | $0.07-0.10$ | 0.078 | 0.009 | $1 I .78$ |
| Diss.w. | $0.12-0.17$ | 0.153 | 0.017 | 10.75 |

Micrometric formula (based on seven specimens only) : $15-\mathrm{I} 6 / \mathrm{II}-\mathrm{I} 3 / / \mathrm{I} 8-20 / \mathrm{I} 8-19$ (in I row).
In the specimens examined there are mostly three, but in some cases two, zooecial apertures per fenestrule.

Description. The available fragments indicate that complete zoaria were symmetrical, fan-shaped expansions. It is likely that colonies were of small size,
probably $2-4 \mathrm{~cm}$ across. The meshwork is strong and compact, consisting of stout branches connected by short, thin dissepiments.

The obverse side of branches is rather flat, with a gently arched median crest but no pronounced keel. The reverse is rounded and faintly striated. There may be thick localized deposits of secondary schlerenchyma on this side, particularly where branches divide. The transverse section of branches is oval, with the long axis in the plane of the meshwork. At points of bifurcation branches may attain a width of up to 0.57 mm , decreasing immediately afterwards to about 0.25 mm .

The relatively short dissepiments are about half as wide as branches, and roughly circular in cross section. They increase considerably in width at either end, towards the union with branches. Spacing of dissepiments is regular, and they are almost level with the branch surface on the obverse, though somewhat depressed on the under side.

Fenestrules are basically rectangular with a length to width ratio of about two to one. They are mostly about one-and-a-half times as wide as branches. Superimposed on the rectangular shape, and to some extent obscuring it, are rounded extremities (due to the rapid increase in width at either end of dissepiments) and two rounded protrusions from the branch margin on each side. The last are most evident on the obverse surface.

Zooecial apertures are circular, close to the branch margin, and spaced about one-and-a-half diameters apart. They are regularly arranged, one opposite the end of each dissepiment and two along the side of the intervening fenestrule. In the latter situation the branch wall below an aperture commonly bulges into the fenestrule, causing the aperture itself to project in the same direction. Peristomes were not observed, but the outer apertural rim may be developed into a hood-like structure that emphasizes the beaded pattern of the branch margin.

The zooecial base shape could not be determined with certainty but it is most likely to be either a parallelogram or elongate-oval. The maximum length of each chamber is 0.17 mm , and the width perpendicular to this, 0.09 mm .

Carinal nodes are insignificant and difficult to identify, minute node-bases commonly providing the only indication of their former presence. Their disposition is in many cases obscure, though basically they are in two alternating rows, with a node corresponding to each zooecial aperture. The arrangement is locally confused and irregular, however, with the biserial pattern deteriorating for short distances into something approaching a ragged single line.

Ovicells similar in structure to those of Fenestella cf. delicatula (see Tavener-Smith, 1966a: 165) are present in some specimens. Each is found on the inner side (i.e. closer to the branch crest) of an associated zooecial tube and has the form of a deep, bowl-shaped concavity about 0.12 mm in diameter. The gonozooecial tube enters the brood chamber from below and to one side. The roof of the latter is invariably missing : no doubt it was of delicate construction and easily destroyed. One specimen showed quite a large number of ovicells grouped together. They are not restricted in occurrence to branch-dissepiment junctions, but generally distributed along the obverse of branches.

Discussion. The specimens appear to correspond closely with Condra's (1902) description of Fenestella binodata from the Coal Measures of Nebraska (Pennsylvanian), and are considered conspecific with that species. Owing to the presence of biserial carinal nodes, however, the form must be transferred to Minilya. Elias \& Condra (1957 : 90) stated that the holotype has elongate-oval zooecial base shapes, and it is possible that in the Fermanagh specimens this is also the case. In describing $F$. binodata var. wolfcampensis, a Lower Permian variety hardly distinguishable from the parent species, Elias \& Condra estimated the size of complete colonies to be 'about $20-25 \mathrm{~mm}$ high and $30-40 \mathrm{~mm}$ wide', figures very similar to those suggested above.

The specimens bear a general resemblance to $M$. nodulosa (Phillips), also found in the Carrick Lough residues (Tavener-Smith 1965a). That form has two and not three apertures per fenestrule, and its zooecial apertures and nodes are notably more widely spaced. It also has shorter but wider fenestrules and much wider branches.
Fenestella triserialis Ulrich 1890 is in many respects similar to the specimens described here, and its dimensions are also closely comparable. That species has triangular zooecial base shapes, however, and Ulrich's illustration (pl. L, fig. 4) clearly shows that the carinal nodes are uniserial.

Fenestella colymaensis Nekhoroshev 1935 and F. benskiensis Shulga-Nesterenko I95I, are other species structurally similar to the present form. In both, however, carinal nodes are uniserial, and Shulga-Nesterenko's form has keeled dissepiments, a feature not shown by the Fermanagh specimens.

## Minilya oculata (M'Coy)

(Pl. 20, figs 2-8)
1844 Fenestella oculata M'Coy; 203.
1961 Fenestella oculata M'Coy; Miller, 229.
Diagnosis. Branches wide in relation to compact meshwork; somewhat flattened, with low, rounded median crests. Fenestrules with broadly rounded extremities. Apertures large, prominent.

Material. This distinctive species is common in the Carrick Lough residues and more than a hundred and twenty fragments, representing all parts of colonies, were examined. The largest measured $23 \times 14 \mathrm{~mm}$. PD.4832-9, PD.5259-75.
Measurements $(\mathrm{N}=25)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | :---: |
| F.l. | $I \cdot I O-I .35$ | $I .222$ | 0.084 | 6.87 |
| F.w. | $0.65-0.90$ | 0.780 | 0.066 | 8.46 |
| I.ap.s. | $0.30-0.35$ | $0.3 I 5$ | $0.0 I I$ | 3.64 |
| I.n.s. | $0.30-0.35$ | 0.328 | 0.016 | 4.88 |
| (in I row) |  |  |  |  |
| B.w. | $0.35-0.40$ | 0.367 | 0.014 | 3.8 I |
| Ap.d. | $0 . I 0-0.12$ | $0 . I I I$ | $0.01 I$ | 9.73 |
| Diss.w. | $0 . I 5-0.25$ | $0 . I 96$ | 0.027 | $I 3.77$ |

Micrometric formula: $12-16 / 8-10 / / \mathrm{I} 5-17 / \mathrm{I} 4-\mathrm{I} 6$ (in I row).
Apertures per fenestrule.
Range of specimen modes: $3 \quad 4$
Distribution of specimen modes:
$21 \quad 4$
Description. Complete zoaria were probably fan-shaped expansions a few centimetres across, and the growth posture (as indicated by a fragment attached to a Rhabdomeson colony) was at least partially erect. The meshwork is strong, compact and of medium texture.

Branches are stout in relation to meshwork texture, and commonly of about the same width as fenestrules. On the obverse there is a well-formed median ridge with a rounded crest; the reverse is broadly convex and without prominent striations. Where present, the latter are faint and widely spaced. In the proximal region the under side of branches may be thickly coated with secondary skeletal substance. At bifurcations the pattern is normally that of a tuning fork, new branches at first diverging at angles of $50-70^{\circ}$, then curving back almost at once into parallelism.

Although in the proximal parts of colonies branch division is mostly regular and symmetrical, departures from this pattern are fairly common. In some fragments a strong and persistent central branch fails to bifurcate for some distance, instead giving rise to a series of lateral branches that diverge at an angle on either side. Such an arrangement is reminiscent of Ptylopora. In other cases a thick central branch bifurcates near the growth origin, the two offshoots then continuing in parallelism for some distance without further bifurcation. However, each produces a series of lateral branches on its outer side, and these bifurcate to complete the flabelliform shape of the colony. This pattern presents obvious similarities to that of Ptiloporella. The width of the major branches in these cases commonly exceeds that of normal ones, and may attain 0.45 mm . An exceptional figure of 0.7 mm was recorded in a heavily encrusted specimen.

In many zoarial fragments creeping stolons of the ctenostome Condranema follow the obverse branch crests and ramify from them. In some cases the slender, silicified stolonic tubes rest on the surface, but in others they are partly immersed, forming deep grooved channels in the substance of branches.

Dissepiments are short and moderately depressed below branch level on both sides. They are commonly slender but, due to secondary encrustation, there is considerable variation in width ranging from about one-third that of branches to near equality with them. From the mid-part of a dissepiment the width increases considerably towards the union with adjacent branches.

Fenestrules are mostly elongate-oval, or rectangular with well-rounded extremities. In the proximal region, where the branch pattern is less stabilized than elsewhere, fenestrules may be elliptical. The long sides are straight or slightly indented by zooecial apertures.

Circular zooecial apertures are commonly large and prominent. Peristomes are mostly lacking (possibly due to post-mortem abrasion) but where present they are plain, collar-like rims, most evident on the outer side where they may protrude slightly into fenestrules. There is no constant spatial relationship between zooecial
apertures and dissepiments. Zooecial chamber bases have an elongate, hemihexagonal shape. The short lateral walls are inclined towards the growth origin. Maximum length of the chamber is 0.4 mm , and the maximum width, 0.2 mm .

Carinal nodes are insignificant, pimple-like structures that in many fragments are poorly preserved and difficult to identify. The only indication of their former presence may be tiny circular or oval basal scars. There is approximately one node per zooecial aperture, and the spacing between nodes in the same row is unusually regular. Although nodes are basically in a double row along the median keel, the strict biserial pattern is not uniformly maintained. Locally the arrangement may be somewhat irregular and even raggedly uniserial. A clear transition from biserial to uniserial was not observed, however.

Some specimens also bear a row of small nodes along the reverse mid-line of branches. The arrangement is uniserial and the structures (each with a diameter of about 0.02 mm ) are spaced approximately 0.12 mm apart.

Supporting spines are present on the obverse or reverse of some specimens, but are small in size and number. Lateral spines growing as branch continuations are common, however, and one of these attained a length of 4 mm . Its width decreased in that distance from 0.55 mm (branch width at the last aperture) to 0.37 mm .

Discussion. This form is M'Coy's (1844:203) F. oculata, which was redescribed by Miller ( 196 I : 229) on the basis of two of M'Coy's examples. Both are very small and unsuitable as type specimens, being tectonically deformed and (in the case of one of them) heavily re-crystallized. In neither specimen is the keel well preserved, and the biserial nature of the carinal nodes is, therefore, not evident. The presence of this feature, here recognized for the first time, requires the transfer of the species to Minilya. In other respects the material described responds well to Miller's description, though the fenestrules are slightly larger. This is probably because both M'Coy's specimens are heavily encrusted with secondary schlerenchyma.

It is fortunate that the Carrick Lough fragments are recognizably conspecific with M'Coy's form, for they are in a much better state of preservation than his material. In addition, by representing all parts of zoaria they provide a better understanding of the specific characteristics. Some specimens in the sample seem at first sight to differ from the holotype, but closer examination shows that they share all its essentials, and are united with it by intermediate forms.

## Genus PTILOPORELLA Hall, 1885

Diagnosis. Like Fenestella, but with branches of two sizes. A few larger or primary ones give rise to smaller or secondary branches on one or both sides. As the frond expands further primaries may arise by bifurcation or lateral growth from earlier ones, and in this way a fan-shaped colony is formed.

Type species. Fenestella (Ptiloporella) laticrescens Hall 1887. Devonian, Ontario.

Ptiloporella varicosa (M'Coy)
(Pl. 2I, figs I-9)
1844 Fenestella varicosa M'Coy; 204.
1961 'Fenestella' varicosa M'Coy; Miller; 238.
Diagnosis. Ptiloporella with distinctive flabellate meshwork of strong branches united by slender dissepiments. Branches have triangular cross section and high median keel. Apertures large; chambers trapezoidal.

Material. The strong meshwork and distinctive branch pattern of this common species differentiate it at once from other fenestrate forms in the Carrick Lough residues. More than eighty fragments were examined, of which the largest measured $35 \times 20 \mathrm{~mm}$. PD.4840-7, PD.5276-97.

Measurements ( $\mathrm{N}=30$ ):

|  | A | B | C | D |
| :---: | :---: | :---: | :---: | :---: |
| F.l. | I. $20-2.00$ | I.513 | -.159 | 10.51 |
| F.w. | 0.75-1.00 | 0.908 | $0 \cdot 790$ | $8 \cdot 70$ |
| I.ap.s. | 0.35-0.40 | $0 \cdot 366$ | 0.016 | $4 \cdot 3$ I |
| I.n.s. | 0.45-0.75 | 0.588 | 0.064 | 10.96 |
| B.w. <br> (Primary) | 0.37-0.60 | $0 \cdot 477$ | 0.053 | II•17 |
| B.w. (Secondary) | 0.25-0.35 | 0.287 | 0.025 | $8 \cdot 80$ |
| Ap.d. | 0.12-0.19 | $0 \cdot 136$ | 0.015 | II•I9 |
| Diss.w. | 0.1I-0.22 | 0.158 | 0.026 | 16.77 |

Micrometric formula: $I \mathrm{I}-\mathrm{I} 7 / 6-9 / / \mathrm{I}_{3}-\mathrm{I}_{5} / 7-\mathrm{I} 2$.
Apertures per fenestrule.
Range of specimen modes: $\quad 2 \quad 3 \quad 4$
Distribution of specimen modes: $4 \quad 23 \quad 3$
Description. The fragmentary specimens examined indicate that zoaria in this species were slightly undulose, approximately fan-shaped expansions. Mature colonies were of fairly large size, probably $5-10 \mathrm{~cm}$ across.

The chief distinguishing features of these specimens are:
I. the peculiar branch pattern intermediate between those of Fenestella and Ptylopora, and
2. the presence of branches of two sizes in the meshwork.

Measurement shows that differentiation into primary and secondary branches is not clear cut, however, and that all gradations exist, from the thickest to the thinnest. Nevertheless, consideration of a large number of branches indicates that the mean widths of the two groups are quite distinct. Most primaries diverge from the growth origin towards the margins of the frond. While their vigour lasts they maintain their dimensions and direction, giving rise to numbers of secondary branches on either side. Distally, however, they tend to become thinner and bifurcate in the manner of Fenestella, eventually losing their distinctive appearance. Lateral, or secondary branches, are initially thin and many remain so throughout their length.

In some cases, however, there is a progressive increase in width until the branch attains the dimensions of a primary. It may then bud off a series of laterals before returning to its original condition, or terminating.
On the obverse of branches there is a well-developed keel-ridge bearing a single row of carinal nodes. On either side of the keel the branch surface slopes steeply away towards the fenestrules. The reverse is broadly rounded, and on this side the difference between primary and secondary branches is particularly evident. A thick coating of secondary tissue commonly obscures longitudinal striae, and these are never strongly developed. Sparsely distributed 'pores' on or near the reverse midline proved to be the base scars of small acuminate spines similar to those present on some species of Fenestella. They are elliptical, with a length of about 0.05 mm .

Dissepiments are thinner than branches and many are slender and bar-like. There is an increase in width at each end, as the junction with a branch is approached. The spacing of dissepiments is somewhat irregular and they are depressed below branch level on both surfaces. The cross-section is roughly circular and in the older parts of zoaria connecting bars are much thickened by secondary deposits.

Fenestrules show much variation in shape and size between specimens, and even within a single fragment. The unusually distinctive characteristics of this group make it evident that all the fragments are conspecific, and the diverse fenestrule sizes and shapes provide an important indication of the range of morphological variation that is possible within a species. The commonest shape is rectangular with rounded extremities, the length to width ratio varying from two to one (about $\mathrm{I} .8 \times 0.9 \mathrm{~mm}$ ) to near equality. In the proximal region, where branches and dissepiments are secondarily thickened, fenestrules may be elliptical and differing shapes and sizes are commonly associated, giving the meshwork an irregular appearance. The long sides of fenestrules are mostly straight but may be slightly indented by projecting apertures.

Large and prominent zooecial apertures have circular or oval shapes and are relatively closely spaced. Although the spacing is regular the number of apertures per fenestrule is rather variable, due to the irregular disposition of dissepiments. Plain, low peristomes are evident in a few specimens but are rarely prominent, though they may cause a slight lateral projection into the fenestrule. Some fragments from the proximal region show apertures occupying shallow grooves on either side of the keel. This is due to heavy secondary accretion on the latter structure and also on the branch sides.

Zooecial chambers are regularly trapezoid in plan, and ten that were measured yielded the following average dimensions: length of longer side, 0.3 mm ; length of shorter side, 0.1 mm ; perpendicular width between these, 0.225 mm . Branch divisions appear to have been preceded by the appearance of a larger, polygonal chamber which budded twice. Simultaneous budding seems to have led to symmetrical branch division, or bifurcation, but otherwise the earlier (more vigorous) bud maintained the original axis of growth, while the other was off-set and gave rise to a lateral or secondary branch. In a few cases 'secondary' buds were displaced abnormally and directed out of the meshwork plane altogether. These produced aberrant branches that are really misdirected laterals. They are thin, weak-looking
and grew from the meshwork at varying angles. For these reasons they could be mistaken for young adventitious colonies of another species. Careful examination reveals the above relationship, however, and it is evident that such branches are essentially similar to the rest of the colony.

Supporting spines up to 5 mm long occur on the obverse or reverse surface but are relatively uncommon. Lateral spines representing the continuation of normal branches are more numerous and attain lengths up to 3 mm . In these there is a marked decrease in branch height (from about 0.65 mm to about 0.42 mm ) immediately after the last aperture. It is as if the zooidal line had for some reason aborted, leaving the outer schlerenchyma to continue and form a sterile spine.

Discussion. This form is M'Coy's Fenestella varicosa, and the data given above may be used to amplify and modernize his description. Owing to the distinctive branch pattern the species must, however, be transferred to Ptiloporella Hall. The branch pattern in question, being intermediate in character between those of Fenestella and Ptylopora, suggests that the three genera were successively evolved. The record of their stratigraphic appearance is entirely in accord with this possibility.

## Genus HEMITRYPA Phillips, I84I

Diagnosis. Like Fenestella, but with a superstructure supported on carinal nodes, and consisting of a planar, honeycomb-textured lattice. One of the hexagonal openings of the lattice lies above each zooecial aperture, and there are, therefore, two rows of hexagons per branch.

Type species. Hemitrypa oculata, Phillips, i84I. Devonian, England.

## Hemitrypa hibernica M'Coy

(Pl. 22, figs $\mathrm{I}-\mathrm{IO}$ )
1844 Hemitrypa hibernica M'Coy; 205.
1893 Hemitrypa hibernica M'Coy; Cole; 138.
1960 ? Hemitrypa reticulata Burckle; 1091.
1927 cf. Hemitrypa burulica Nikiforova; 182.
1962b Hemitrypa hibernica M'Coy; Miller; 314.
Diagnosis. Fine-textured, cup-shaped colonial meshwork of strong, parallel branches and short, stout dissepiments. Fenestrules oval. High keel on branches with regularly spaced spines. Apertures large; closely spaced.

Material. This is the commonest fenestrate species in the etched residues and hundreds of fragments from all parts of colonies were examined. The largest was $83 \times 42 \mathrm{~mm}$ in size. PD. $4848-57$, PD. $5298-3 \mathrm{II}, \mathrm{PD} .5342$, PD.5313-3I7.

Measurements $(\mathrm{N}=30)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | :---: |
| F.l. | $0.52-0.77$ | 0.689 | 0.060 | 8.74 |
| F.w. | $0.45-0.62$ | 0.537 | 0.046 | 8.48 |
| I.ap.s. | $0.22-0.27$ | 0.249 | 0.011 | 4.6 I |
| I.n.s. | $0.35-0.45$ | 0.421 | 0.028 | 6.7 I |
| B.w. | $0.25-0.32$ | 0.287 | 0.018 | 6.26 |
| Ap.d. | $0.10-0.14$ | 0.12 I | 0.009 | 7.66 |
| Diss.w. | $0.11-0.25$ | 0.179 | 0.044 | 24.4 I |
| Sup.1. | $0.22-0.26$ | 0.250 | 0.010 | 4.13 |
| Sup.w. | $0.27-0.32$ | 0.285 | 0.017 | 6.19 |

Note: The dimension 'Superstructure length' refers to the length of one of the hexagons of the superstructure parallel to the branch axis. Measurement was made between the centres of bars at opposite ends of the hexagon. 'Superstructure width' was measured perpendicular to the above, also between the centres of an opposing pair of bars.

Micrometric formula: $18-22 / \mathrm{I} 3-18 / / \mathrm{I} 8-21 / \mathrm{II}-13$.
Apertures per fenestrule.

$$
\begin{array}{lrr}
\text { Range of specimen modes: } & 2 & 3 \\
\text { Distribution of specimen modes: } & \text { I9 } & \text { II }
\end{array}
$$

Description. The presence of a regular and symmetrical superstructure distinguishes this, the only species of Hemitrypa, from other fenestrate forms. Even without the superstructure, the regular branch system, evenly distributed apertures, numerous carinal nodes and commonly occurring ovicellular depressions (TavenerSmith, 1966a: 195) render identification easy.

Many of the larger specimens belonged to a single, more or less complete colony that emerged from the matrix as etching proceeded. It had an upright growth position and consisted of a convoluted, foliaceous meshwork rising at least 70 mm from a cup-shaped growth origin. The diameter was about 60 mm at the rim, and the superstructure external. The general appearance was similar to that of modern fenestrate cheilostomes such as Iodictyum.

Branches are mostly straight, stout and bifurcate rarely except in the proximal region. They are unusually high (average of twelve branch heights: 0.45 mm ) and for this reason the cross-section is commonly oval. On the obverse there is a prominent median keel with a row of strong and regularly spaced carinal nodes, which act as supports for the superstructure. The reverse is well-rounded and may bear fine striae, though these are commonly obscured by thick secondary deposits. Prior to branch division the width increases progressively over a distance of $4-8 \mathrm{~mm}$ to a maximum of about 0.62 mm at the point of bifurcation. Immediately beyond this each new branch is only about 0.25 mm wide.

Dissepiments are short and vary greatly in width; some are slender and rod-like, but the majority are stout. There is always a considerable widening from the midpoint towards the union with a branch. Dissepiments are depressed below branch level on both sides and, because in most cases the height (average of fifteen: 0.25 mm ) exceeds the width, they have an oval cross-section.

Fenestrules are commonly narrower than branches. They are mostly elongateoval, with a length to width ratio of between two and one-and-a-half to one. Zooecial apertures do not, as a rule, protrude into fenestrules, which have straight margins.

Apertures are large, circular and spaced about one diameter apart. Peristomes commonly occur as low rims, and are in some cases more strongly developed to form collar-like structures. These may project slightly beyond the branch margin, but this is rare. Although the spacing of apertures is regular, their occurrence is not stabilized with reference to that of dissepiments.

Zooecial base-shapes are hemi-hexagonal, the average measurements of fifteen being: maximum length, 0.262 mm ; maximum width, 0.15 mm . The short proximal and distal walls of chambers are steeply inclined towards the growth origin.

Carinal nodes, in this genus more properly regarded as pillars supporting the superstructure, are uniserial and spaced regularly along the keel. Their height, from keel to superstructure, is approximately 0.25 mm and the cross-section is circular or oval. Where the superstructure is destroyed the nodes commonly present a strongly serrated appearance in profile. The superstructure itself is a thin, planar, lattice-like expanse of hexagon units associated into a honeycomb meshwork of uniform texture. Two rows of hexagons correspond to a branch, and each one is situated directly above a zooecial aperture. The junction between the hexagon rows above a branch is of stouter construction than that above adjacent fenestrules, and provides attachment points for the ends of the supporting carinal nodes (Miller, 1962b: text-fig. I).

The bars of the superstructure carry axial canals radiating from the distal ends of carinal nodes. In the unsilicified state these canals were occupied by the primary calcareous skeleton, which has not been preserved.

Nodes are also commonly present on the under sides of branches. They may be low, conical structures up to 0.07 mm high and of about the same diameter. Such nodes are sparsely distributed (roughly 0.5 mm apart) near or on the reverse mid-line, commonly occurring opposite branch-dissepiment junctions. On other specimens nodes are of slightly smaller size, but more closely (though less regularly) spaced, the distance between them being $0.7-0.17 \mathrm{~mm}$.

The presence of thick secondary deposits on the reverse side is a characteristic of this species, and dissepiments may be particularly affected causing them to project below branch level. When a number of dissepiments enlarged in this way are roughly in alignment, the thickening spreads across intervening branches to form a continuous rib-like encrustation. One or more such ribs may be present on the under side of a meshwork, particularly in the proximal region. They are roughly concentric with the growth origin, and must have helped to support the large fronds by stiffening them. The local increase of branch height in these cases may be great -from a norm of, say, 0.3 mm up to about 0.75 mm , almost all of the thickening being on the reverse side. Similar massive dissepimental arcs have been described by Koenig (1958) in Fenestella albida, F. alternata and $F$. regalis.

Supporting spines are present on the obverse and reverse of the meshwork and, less commonly, as lateral branch continuations. They may be up to 7 mm long,
with basal diameters up to 0.62 mm . On the obverse spines rise from the superstructure and, at their bases, strands of supporting tissue extend over the surface in many directions. It is notable that the main mass of a spine is derived from this level rather than from the branch. For example, a large spine with basal diameter 0.52 mm at superstructure level could be traced downward into two thickened (and distally amalgamated) carinal nodes whose aggregate diameter was only 0.2 mm . It is not clear which of them (if either) contained the axial material of the spine.

Discussion. This form is Hemitrypa hibernica, as the specimens correspond in all respects with M'Coy's ( 1844 : 205) description, and also with that of Miller (1962b : 314) who gave a revised account of the species. The present data, drawn from a larger sample, are of use in amplifying existing concepts of the species and providing an idea of the degree of variation within it.

The most distinctive feature of Hemitrypa is the honeycomb-patterned superstructure, and there is little doubt that this developed from the carinal nodes and had a protective function. Miller's ( $1962 \mathrm{~b}: 3 \mathrm{I} 8$ ) suggestion that extended polypides actually protruded beyond the superstructure is unlikely to be correct, however. Measurement of the cross-sections of twelve meshworks yielded the following mean figures: height of branch, 0.33 mm ; height of zooecial chamber, 0.175 mm ; height of centre of superstructure above keel, 0.275 mm . It is, therefore, probable that the extruded polypides functioned between branch surface and superstructure, the latter affording a protective screen.
The thickened dissepimental arcs on the reverse of meshworks were most likely formed during pauses in the forward growth of a colony. They therefore represent stages in the colonial development and are crude 'growth lines'. During intervals of this kind zooecial budding appears to have been inhibited and no primary skeleton laid down. Secondary deposition did not cease, however, but continued along a front that remained static, and the massive, arcuate ribs resulted.

## Genus POLYPORA M'Coy, 1844

Emended diagnosis. Planar, funnel or cup-shaped fenestrate expansions of radiating, straight or gently sinuous branches connected by regularly disposed, transverse dissepiments. Branches bear three or more rows of zooecial apertures on one side only; dissepiments are sterile. Obverse of branch smooth or with low longitudinal ridges separating rows of apertures. Ridges may bear low nodes. Reverse smooth, or longitudinally striate, with or without nodes.

Type species. P. dendroides M'Coy 1844. Tournaisian, Ireland.

## Polypora dendroides M'Coy

(Pl. 23, figs I-7)
1844 Polypora dendroides M'Coy; 206. 1963 Polypora dendroides M'Coy; Miller; 167.

Diagnosis. Robust meshwork of strong, roughly cylindroid branches, joined by short, stout dissepiments. Fenestrules oval to elliptical. Branch obverse somewhat flattened, with three to six rows of apertures and sparsely distributed small nodes.

Material. This is an uncommon form in the residues and only eight fragments were available. Six were well enough preserved to provide measurements. Due to the small number of specimens, and to the fact that all may have belonged to a single colony, the statistics given below do not provide an entirely adequate basis for comparison. The largest fragment was $17 \times 15 \mathrm{~mm}$ in size. PD.4865-9, PD.53I8.

Measurements $(\mathrm{N}=6)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $2.00-2.80$ | 2.367 | 0.260 | 10.98 |
| F.w. | $\mathrm{I} .30-\mathrm{I} .60$ | I .467 | 0.090 | $6 . \mathrm{I} 3$ |
| I.ap.s. | $0.37-0.40$ | 0.392 | 0.009 | 2.36 |
| (in I row) |  |  |  |  |
| I.ap.s. | $0.30-0.32$ | 0.312 | 0.012 | 4.00 |
| (diagonally) |  |  |  |  |
| B.w. | $0.75-\mathrm{I} .07$ | 0.088 | 0.013 | 15.01 |
| Diss.w. | $0.45-0.75$ | 0.579 | 0.092 | 15.92 |

Micrometric formula (based on six fragments) : 6-8/4-5//I2-13.
Apertures per fenestrule.
Range of specimen modes: $\quad \begin{array}{lll}3 & 4 & 5\end{array}$
Distribution of specimen modes:
I 32
Number of rows of apertures per branch: three to six, usually four.
Description. The available fragments do not indicate with certainty the original zoarial shape, but it is likely that this was a flat fan-shaped expansion. In several specimens branches divide repeatedly and are thickly coated with secondary material, particularly on the reverse. These appear to have belonged to the proximal region. Branches are in general very stout in comparison with fenestrule width and have a roughly circular cross-section. The obverse is somewhat flattened, notably in the wider part that precedes branch division, and the under side may show numerous, fine, closely spaced longitudinal striae. In some specimens the meshwork is irregular and branches seem to have obstructed one another during growth.

Dissepiments are short and stout (being commonly much thickened by secondary schlerenchyma), and not always uniformly spaced. They have a circular transverse section and are slightly depressed below branch level on the obverse, though more so on the under side. The width of the central part of dissepiments is mostly about half that of branches, though it increases greatly at either end.

Fenestrules vary considerably in size, particularly in length. They are mostly oval or elliptical, and have straight sides uninterrupted by projecting apertures.

Zooecial apertures are in four or five rows on the obverse of branches. The number may increase to six at bifurcations, decreasing to three immediately there-
after. The division into rows is not always clear and locally the arrangement may be somewhat confused. Apertures are circular or oval, but measurement is commonly hampered by thick secondary deposits that partly or wholly obscure the openings. Circular apertures are about $0 \cdot 12 \mathrm{~mm}$ in diameter while in oval ones the major axis has a length of about 0.22 mm .

Zooecial chamber bases are rhombic or lozenge-shaped in the internal rows, while those along branch margins are hemi-hexagonal or irregularly five-sided. Chamber walls are not quite perpendicular to the base, but inclined steeply towards the growth origin.

Carinal nodes do not occur in Polypora, there being no median keel, but sparsely distributed nodes may be present on the obverse, in some cases on low ridges that separate rows of apertures. In the present specimens a few small base-scars and truncated stumps mark the former position of nodes, but they do not appear to have had a regular arrangement.

Another feature of the obverse of several specimens is the presence of stout spines, from the proximal ends of which rope-like strands of supporting tissue ramify over the surfaces of adjacent branches and dissepiments. These anchoring strands are of striated secondary schlerenchyma, and pass distally into the outer investment of the colonial surface. In fragments from the proximal region, the amount of secondary encrustation associated with the spines is so great that fenestrules have been sealed and apertures occluded in considerable numbers. The purpose of the structures, which must have been of considerable size, is unknown but comparison with other fenestrate species suggests that they had a supporting role.

Shorter and less robust spines grow from the reverse surface of some specimens. These are all truncated at the distal ends, but may be up to 5 mm long.

Discussion. The material described here corresponds closely with the type specimens and descriptions (M'Coy 1844: 206; Miller 1963: 167) of Polypora dendroides, and is assigned to that species. The original specimens came from the Tournaisian of Hook Head, Co. Wexford. A thin section used by Miller in redescribing the form shows that chamber bases have the same shape as those described above.

## Polypora verrucosa M'Coy

(Pl. 24, figs I-7)
1844 Polypora verrucosa M'Coy; 206.
1963 Polypora verrucosa M'Coy; Miller; 169.
Diagnosis. Open-textured meshwork of strong branches and slender dissepiments; fenestrules rectangular. Branches flattened on obverse, with three to five rows of apertures. Peristomes may indent fenestrules. Zooecia tubular, with lozenge-shaped or triangular bases.

Material. This is the commonest Polypora and its fragments, present in abundance, constitute a distinctive element of the fauna. More than a hundred and fifty were examined, the largest measuring $28 \times 16 \mathrm{~mm}$. PD.4870-7, PD.5319-30.

Measurements $(\mathrm{N}=20)$ :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $3.30-4.70$ | 4.135 | 0.376 | 9.09 |
| F.w. | $\mathrm{I} .40-2.20$ | I .755 | 0.183 | 10.43 |
| I.ap.s. | $0.35-0.42$ | 0.385 | 0.020 | 5.19 |
| (in I row) |  |  |  |  |
| I.ap.s. | $0.22-0.32$ | 0.26 I | 0.022 | 8.23 |
| (diagonally) |  |  |  |  |
| B.w. | $0.52-0.70$ | 0.630 | 0.044 | 7.06 |
| Ap.d. | $0.10-0.12$ | 0.117 | 0.009 | 7.45 |
| Diss.w. | $0.25-0.35$ | 0.287 | 0.03 I | 10.78 |

Micrometric formula: 5-8/2-3//II-I4.
Apertures per fenestrule.

| Range of specimen modes: | 8 | 9 | IO | II | I2 |
| :--- | :--- | ---: | ---: | ---: | ---: |
| Distribution of specimen modes: | 5 | 6 | 4 | 4 | I |

Number of rows of apertures per branch: Three to five, usually four.
Description. This striking form cannot be confused with any other in the etched residues. The coarse textured and rigid-looking meshwork consists of straight, strong branches connected by relatively thin, bar-like dissepiments. Complete colonies were probably large, roughly planar expansions, but there is nothing to indicate whether the growth habit was erect or otherwise.

Branches are broad, flattened on the obverse, and decorated on that side by gently sinuous, longitudinal ridges and furrows sweeping round and between apertures and nodes. On the reverse both sides slope inward to form a blunt 'keel' that may be accentuated by selective secondary deposition. In cross-section, therefore, branches have the appearance of 'rounded triangles' with the apex downward. The under side is longitudinally striated, with about a dozen fine, closelyspaced ridges, the counterparts of those more prominently developed on the obverse. The striated nature may be obscured by secondary schlerenchyma, particularly on the reverse, where this can be so thick that silicious replacement has taken the form of concentric rings of beekite.

Dissepiments are relatively thin, bar-like and circular in cross-section. There is an increase in width at either end approaching the union with a branch, but it is not great. Spacing is fairly regular, and longitudinal ridges and furrows on the cross-bar curve into continuity with corresponding structures on adjacent branches. Dissepiments are strongly depressed on the obverse, but on the reverse are about level with branches, or even slightly bowed so that they project below them.

The large fenestrules are mostly elongate-rectangular but in some cases elongateoval. On the reverse their lateral margins may be regularly indented by protruding apertures: this is less evident on the upper surface.

Circular zooecial apertures are in four longitudinal rows on each branch, the number increasing to five before bifurcations and decreasing to three immediately afterwards. Peristomes are variably developed and may be prominent. They
appear initially as collar-like rims round apertures, but continued growth results in the formation of a rounded-conical tumidity with a terminal aperture. The latter is, of course, a secondary structure with slightly reduced diameter (average of six measured: o. I mm). The presence of strongly developed peristomes may give a coarsely nodular appearance to branches and, in the case of marginal rows, the structures may notably indent fenestrule margins.

Zooecial chambers are elongate tubes and not box-like. They are inclined at $25-45^{\circ}$ to the lower surface of a branch and, therefore, have relatively small base areas. These are rhombic or lozenge-shaped in the inner rows, with a maximum length of about 0.27 mm , and maximum width about 0.15 mm . In rows bordering fenestrules the shape is triangular, with similar length but slightly reduced width (about $0 \cdot 12 \mathrm{~mm}$ ).

Small and insignificant nodes are present at irregular intervals ( $1 \cdot 25-2.0 \mathrm{~mm}$ ) along the obverse mid-line of branches. They are not on a ridge or keel, but rise directly from the branch surface between the inner rows of apertures.

Discussion. The specimens correspond in all respects to descriptions of Polypora verrucosa by M'Coy ( 1844 : 206) and Miller (1963: 169), and undoubtedly belong to that species. M'Coy's type material came from the 'Carboniferous Upper Limestone' at Black Lion, Co. Cavan, a few miles from Carrick Lough and at approximately the same horizon. The holotype shows the streamlining of ridges and furrows round apertures more clearly than the Carrick Lough material, though the characteristic 'warty' appearance to which the specific name refers is equally well developed in the latter.

Because of the apparent absence of nodes from the obverse mid-line of branches, and the presence of strong longitudinal ridges and grooves on that side, Miller (1963: 169) only assigned this form to Polypora provisionally. He thought these features might have indicated the presence of a separate genus bearing the same relationship to Polypora as Levifenestella bears to Fenestella. However, the present specimens do show an irregular median line of small nodes, and the strongly striated obverse is merely an unusually pronounced manifestation of a condition that, at least potentially, exists in all Fenestellidae. There is, therefore, no reason for the erection of a new genus, and the form is here regarded as typical of Polypora.

Miller's (1963: 166) emended diagnosis of the genus stated that there should be 'regularly spaced, elevated nodes on the central line of the obverse' of branches. This is an innovation, as no such requirement is included in earlier diagnoses, for example, those of M'Coy 1844 : 206; Nickles \& Bassler 1900 : 39; Bassler 1953: GI25; or the Russian Treatise 1960:80. The view of these authorities is adequately reflected by the statement of Nickles and Bassler that in the genus branches 'lack the median keel, though this is sometimes represented by a row of strong nodes or tubercles' (the writer's italics). It is implicit in this statement that not all species of Polypora possess such nodes, and their presence is not therefore diagnostic. The generally-held concept of the genus has not radically changed in recent years, and Miller's requirement in respect of nodes must be rejected as unwarranted and over-restrictive.

## Family ACANTHOCLADIIDAE Zittel, I880

Diagnosis. Zoarium a pinnate or fenestrate expansion, celluliferous on one face only, consisting of strong central stems which give off numerous smaller lateral branches from their margins; the lateral branches are free, or unite with those of the next stem; non-poriferous dissepiments rarely present ; zooecial characters mostly as in the Fenestellidae (Nickles and Bassler 1900: 4I).

## Genus PTYLOPORA M'Coy, 1844

Diagnosis. Fan or funnel shaped, attached by roots from which a strong midrib arises, giving origin on each side to thin, equidistant branches, connected by regular dissepiments; external face of the branches carinate, and bearing two rows of zooecial apertures. (Based on M'Coy 1844: 200.)

Type species. P. pluma M'Coy 1844. Tournaisian, Hook Head, Ireland.
Ptylopora pluma M'Coy parva subsp. nov.
(Pl. 25, figs I-Io)
Material. Only a few small specimens were available, mostly with a welldeveloped primary branch but relatively little of the meshwork. One showed the proximal region with a well-preserved basal holdfast. The broken ends of strong primary branches commonly showed the interior in an excellent state of preservation and yielded valuable information about skeletal structure, which is identical to that of the Fenestellidae. The largest fragment measured $13 \times$ 10 mm . PD.4883, PD.4878-82, PD.533I-5.

Measurements ( $\mathrm{N}=\mathrm{I} 2$ ) :

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | ---: |
| F.l. | $0.85-\mathrm{I} .05$ | 0.954 | 0.072 | 7.57 |
| F.w. | $0.55-0.82$ | 0.635 | 0.069 | 10.94 |
| Primary measurements |  |  |  |  |
| B.w. | $0.47-0.80$ | 0.612 | 0.092 | $15 \cdot 10$ |
| I.ap.s. | $0.30-0.35$ | 0.321 | 0.014 | 4.36 |
| I.n.s. | $0.17-0.35$ | 0.256 | 0.049 | 19.12 |
| Ap.d. | $0.09-0.11$ | 0.104 | 0.004 | 2.06 |
| Secondary measurements | $0.27-0.37$ |  |  |  |
| B.w. | $0.25-0.30$ | 0.283 | 0.031 | 9.82 |
| I.ap.s. | $0.20-0.27$ | 0.235 | 0.020 | 6.97 |
| I.n.s. | $0.09-0.11$ | 0.097 | 0.023 | 9.77 |
| Ap.d. | $0.10-0.22$ | 0.157 | 0.010 | 10.34 |
| Diss.w. |  | 0.028 | 17.96 |  |

Note: 'Primary' measurements refer to the strong midrib, while the others apply to the laterally developed meshwork. Care must be exercised in using the width of the midrib for comparative purposes, for this tapers distally.

Micrometric formula of meshwork: $14-18 / 9-13 / / \mathrm{I} 7-20 / \mathrm{I} 8-25$.

Apertures per fenestrule.
Range of specimen modes: $\quad 2 \quad 3 \quad 4$
Distribution of specimen modes: I Io I
Diagnosis. Small Ptylopora structurally similar to P. pluma, from which it differs in having shorter fenestrules, thinner secondary branches and more closely spaced carinal nodes. Dimensions are stated above.
Type specimens. Holotype: PD.4883. Paratypes: PD. 4878 to PD. 4882.
Description. The zoarial shape was penniform, with a midrib of considerable length (the longest specimen, which was incomplete, measured 28 mm ) supporting a Fenestella-like meshwork on either side. The divergence angle of lateral branches varied from $44^{-68^{\circ}}$, the average in twelve specimens being $60 \cdot 5^{\circ}$. The presence of a specimen with a heavily calcified basal holdfast and supporting processes suggested that colonies grew in an upright, or partly upright position.

The primary branch is strong, straight and distally tapered. A prominent, rib-like median keel, rising abruptly from the somewhat flattened obverse surface, takes up about one-third of the branch width, and close to this on each side is a row of small zooecial apertures. These may lie in longitudinal grooves representing areas of minimum secondary accretion between zones of much greater thickening on either side. The broadly rounded reverse commonly bears about a dozen fine, closelyspaced longitudinal ridges, each with a row of minute papillae on its crest. These have a diameter of about 0.02 mm and are spaced about the same distance apart. The reverse of some specimens is smoothly rounded, however, and without ridges or striations, though there are numerous papillae streamed generally parallel with the branch length.

Ridges and striations are also present on the obverse, though they are hardly visible and have a less regular arrangement. Papillae are numerous but appear to be randomly distributed and do not form rows except along the keel. This commonly consists of three or four closely associated and clearly marked longitudinal ridges, one of which may be accentuated to form the crest. Along it a row of papillae may be visible between successive carinal node bases.

The holdfast is a thickened, stalk-like proximal part of the midrib from which lateral branches have been stripped or where, perhaps, they never existed. Its length, from proximal extremity to the first lateral branch, is 10 mm , and the maximum width, I mm. At its termination the heavily calcified stalk gives rise to a number of supporting or anchoring processes, between some of which there are slender connecting bars.

Secondary, lateral or side branches are more slender than the main one, which projects below them considerably. They diverge from it at intervals of $0.6-0.8 \mathrm{~mm}$ on either side, are more or less straight, and do not bifurcate. On the obverse the sides of branches slope steeply away from a median keel that resembles the ridge of a roof and in this respect differs from the prominent rib-like structure on the primary branch. At junctions with the latter it is evident that the two kinds of keel are not continuous, there being a flat, keel-less area between them. The reverse is rounded and commonly bears closely spaced longitudinal ridges with rows of papillae along
their crests. At junctions the ridges and furrows of lateral branches merge with those on the midrib, and the rows of papillae do likewise.
Dissepiments are short and slender in most cases, though when coated with secondary schlerenchyma they may be relatively stout. There is a considerable increase in width at each end, close to the union with a branch. Dissepiments, which are approximately circular in cross-section, are clearly depressed below branch level on the obverse, but less obviously on the under side. They are axially striated, with rows of papillae along ridge crests, as with branches. Laterally adjacent dissepiments tend to be situated the same distance from the main branch, with their ends roughly in apposition, so that they form a more or less continuous dissepimental zone. There are a series of these zones on either side of the primary branch and roughly parallel with it.

Due to the terminal increase in dissepimental width, fenestrules are mostly elongate-oval, though they may be elliptical or rectangular. The long sides are straight and uninterrupted by projecting apertures.

Two rows of zooecial apertures are situated close to the keel and away from branch margins. They are circular or oval, in the second case measuring about $\mathrm{O} \cdot \mathrm{I} 2$ by 0.07 mm . The apertures are relatively small and spaced from one to two diameters


Fig. 5. Shape and dimensions of zooecial chambers in a primary branch of Ptylopora pluma parva. di., diaphragm; o.s.w., outer secondary wall; pr.br., primary branch; pr.w., primary wall; zo.ap., zooecial aperture; zo.ch., zooecial chamber.
apart; the diameter and spacing being slightly greater on primary branches than on secondary ones. There are no noticeable peristomes.

The zooecium has an unusual plan, consisting of a roughly D-shaped proximal chamber that continues into a broad tube directed at about $45^{\circ}$ to the upright of the D. The tube is separated from the chamber by a well developed hemiseptum, and has the aperture at its distal end. Within a branch the relatively wide proximal part of a zooecium opposes the narrower distal part of the next, so that they fit closely together in alternating rows. The arrangement is shown, together with dimensions, in the accompanying diagram (fig. 4).

Small, though prominent carinal nodes are present on primary and secondary branches. On the former they are about $0 \cdot 12 \mathrm{~mm}$ high, compared with a branch height of about 0.5 mm . The nodes of secondary branches are mostly missing, but their former positions are marked by small, oval, base-scars.

A few obliquely directed supporting spines with broken distal ends are present on the reverse of specimens. They are up to 5 mm long and 0.5 mm in diameter at the base. A single lateral spine, representing the sterile continuation of a secondary branch, extended for I mm beyond the last zooecial aperture and was 0.2 mm wide.

Discussion. The specimens are superficially similar to M'Coy's $P$. pluma from the Carboniferous Slate of Hook Head, Co. Wexford, but there are dimensional differences. The holotype has the formula: 13-16/7-8//I5-18/10-14 and secondary branches diverge from the midrib at $50-55^{\circ}$. Fenestrules are longer than in the Fermanagh specimens (average length: I.I mm compared with 0.95 mm ), secondary branches are wider ( 0.39 mm against 0.3 Imm ) and carinal nodes further apart (average internodal distance on meshwork: 0.425 mm compared with 0.235 mm ). Dissepiments are also much stouter on M'Coy's specimen, and although age differences might explain this, they cannot satisfactorily account for the discrepancy in branch width. It is true that the Fermanagh sample is small and may consist of immature colonies, nevertheless, there are appreciable differences from the holotype and, as the material is from another horizon and locality, it seems advisable to refer it to a separate subspecies. The overall structural similarity with M'Coy's material prompts the writer to retain the specimens within $P$. pluma however, a decision that is strengthened by Dresser's (unpublished thesis, 1960) discovery of specimens with intermediate characteristics in the $\mathrm{C}_{2} \mathrm{~S}_{1}$ of Malahide, Co. Dublin. Her material (also referred to $P$. pluma) had the formula: $15-17 / 8-10 / / 15-18 / 20-25$.

Comparison of data by $t$-tests showed that in the etched specimens there is a significant difference ( $\mathrm{P}<0.05$ ) between the spacing of zooecial apertures on primary and secondary branches, that of the former being greater. The diameter of apertures on primary branches is also significantly larger than that of secondary ones. In view of the greater width of the central branch it seems probable, therefore, that its zooecial chambers are slightly larger than those of lateral branches. Similar statistical tests showed that there is no significant difference ( $\mathrm{P}>0.05$ ) between the spacing of carinal nodes on the two kinds of branches.

Cross-sections of some heavily encrusted branches showed that although the reverse surface may be smoothly rounded and without striae, secondary laminae
within the branch become progressively more corrugated towards the axial region. This tendency reaches its maximum at the contact with the strongly ribbed under side of the basal plate, a part of the primary skeleton. The ribbing seen in crosssections is merely a reflection of the striated or longitudinally ridged condition in solid specimens, and it therefore seems that although the presence or absence of 'striae' on the reverse may be an indication of the age, or the state of weathering of a specimen, it is unlikely to be of taxonomic value.

## Genus SEPTOPORA Prout, 1859

Diagnosis. Zoarium a fenestrate, flabellate or leaf-like expansion; primary branches numerous; increasing by bifurcation or interpolation; the lateral branches unite with those from the adjacent primary branches; apertures in two rows on primary and lateral branches; reverse usually with fine striae and scattered dimorphic pores (Nickles \& Bassler Igoo: 4I).

Type species. S. cestriensis Prout I859. Mississippian, Illinois.

## Septopora hibernica sp. nov.

(Pl. 26, figs I-8)
Material. Only ten specimens were available. They are not in such good condition as those of other species, being encrusted with secondary tissue to an unusual degree, so that surface features are commonly obscured. Some branches lack the entire apertural face, presumably owing to partial replacement, so that only the base and sides remain. It is possible that all specimens belonged to a single colony, and this should not be overlooked in using the following data for comparative purposes. The largest fragment was $42 \times$ I7 mm. PD.4885-9I, PD.5336-8.

Measurements ( $\mathrm{N}=\mathrm{IO}$ ):

|  | A | B | C | D |
| :--- | :---: | :---: | :---: | :---: |
| F.l. | $\mathrm{I} \cdot 20-\mathrm{I} .50$ | I .400 | $0 . \mathrm{IOO}$ | $7 . \mathrm{I} 4$ |
| F.w. | $\mathrm{I} .50-2.00$ | I .640 | $0 . \mathrm{I} 56$ | 9.5 I |
| I.ap.s. | $0.35-0.40$ | 0.375 | 0.0 II | 3.00 |
| B.w. | $0.72-0.87$ | 0.770 | 0.043 | 5.58 |
| (primary) |  |  |  |  |
| B.w. | $0.45-0.67$ | 0.5 I 5 | 0.070 | I 3.59 |
| (secondary) |  |  |  |  |

Note: Data for zooecial apertures are not included as these structures are commonly broken, abraded, or so reduced by coarse grained silicification that original dimensions are not evident.

Micrometric formula: 6-8/7-9//I2-I4/none.
Apertures per fenestrule.
Range of specimen modes: 3
Distribution of specimen modes: IO
Diagnosis. Septopora of unknown zoarial shape, lacking carinal nodes and 'dimorphic pores'. With well developed keel on primary, but not secondary branches. The latter have a variable growth habit, causing fenestrule shapes to be
irregular. Primary branches may show a Ptylopora-like pattern and bear two rows of small, closely-spaced zooecial apertures. Chamber base shapes triangular or hemi-hexagonal with short lateral walls. Structural data as above.

Type specimens. Holotype: PD.4885. Paratypes: PD. 4886 to PD. 4890.
Description. There is no certain evidence of zoarial shape though, judging from the structure of available fragments, it was probably a more or less upright, foliaceous or fan-shaped growth. Two of the larger fragments have a pronounced Ptylopora-like branch pattern and are only distinguishable from that genus by the cross-bars (secondary branches) which bear zooecia.

Primary branches are straight or gently flexed. They are stout and somewhat flattened on the obverse, which bears a prominent, rib-like median keel. In shallow, longitudinal grooves on either side of this are two rows of zooecial apertures. The reverse is broadly rounded and longitudinally striated, the striae serving to separate a number of ridges, each of which bears on its crest a row of minute, rounded papillae. These are about 0.01 mm in diameter and spaced about 0.04 mm apart. From eight to ten parallel ridges are visible on the reverse of a branch.

Secondary branches (corresponding to dissepiments in the Fenestellidae) are variably developed, and their original shapes are commonly obscured by heavy secondary deposits. Where two unite in the chevron pattern characteristic of Septopora, they leave the main branches at angles of about $50^{\circ}$. This arrangement is uncommon in the present material in which, owing to space restriction and irregularities of growth, others predominate. Close to the junction of primary branches secondaries may be short and straight, rather like stout fenestellid dissepiments. In other cases a secondary appears to have developed independently of its partner, forming an oblique cross bar between adjacent primary branches. Bowshapes are of fairly common occurrence, the angular junction between components having been rounded by later schlerenchymal growth. In other examples irregular shapes have resulted from asymmetrical unions between opposing secondary branches. Well developed secondaries have two rows of alternating apertures, but in many cases the arrangement is irregular. Some appear to lack apertures altogether, but this is probably due to sealing by schlerenchymal overgrowth rather than to a genuine absence of zooecia. Secondary branches do not have a median keel and the cross-section is approximately circular. The reverse shows the same characteristics as in primaries.

Fenestrules in Septopora are typically chevron-shaped with rounded extremities, but these are rare in the present specimens. The irregular growth of secondary branches inevitably results in many variations of fenestrule shape, which may be round, oval, rectangular or even triangular. Variable amounts of secondary encrustation cause still further diversity and commonly convert regular to irregular shapes. The relatively small size of fenestrules and their variable configuration might almost be said to characterize the specimens examined.
Zooecial apertures are in two alternating rows close to the keel and away from branch margins. They may be circular, with a diameter of about $0 \cdot 15 \mathrm{~mm}$, or (more commonly) oval, measuring about 0.225 by 0.125 mm . Some are relatively small
and more than their own diameter apart; others are much larger and separated by only a thin bar. Much depends on the amount of secondary encrustation present, for there is no doubt that this has in many cases reduced the size of apertures or even sealed them altogether. On the other hand, many have been enlarged by breakage or incomplete replacement of their rims. Apertures on both kinds of branches were probably of about the same size.

Few zooecial base shapes are distinguishable in the specimens, but it is possible that there is a slight difference in this respect between primary and secondary branches. Those of the former seem to have hemi-hexagonal shapes with a length of about 0.32 mm and maximum width of 0.2 mm . The short lateral walls are about 0.05 mm long. On secondary branches chambers appear to be of similar size but triangular, with the maximum length (parallel to the branch margin) about 0.3 mm and maximum width about 0.25 mm . Only three chamber bases of each kind were seen, however, and it is uncertain whether the observed difference is general or not.

Discussion. This is the first positive record of Septopora in the British Isles, though Whidborne (1895, p. 183) mistakenly assigned a poorly preserved specimen (probably of Ptiloporella) to the genus. Nor has Septopora been found in other European countries, with the exception of Russia where a number of species have been reported in recent years (Nikiforova 1938; Shishova 1952, 1957; Morozova 1955). The genus was introduced by Prout in the United States, and several species were described by Ulrich (1890). A possible reason for the previous absence of Septopora from faunal lists is that, due to lines of weakness provided by the angular junctions between secondary branches, the colonies were particularly liable to breakage. The resultant fragments typically consist of a primary branch with a number of secondaries on each side, all broken at the junction angle. Such fragments are exceedingly difficult to distinguish from Penniretepora stipes (always abundant in Carboniferous bryozoan faunas) and could easily have been described as such in the literature.

Among described forms of Septopora the present specimens are closest to the type species, which is from approximately the same horizon (lower Chester) in Illinois. Common features include a clear median keel on the obverse, about three zooecial apertures per fenestrule and the absence of small accessory apertures ('dimorphic pores'). There are also important differences, however, S. cestriensis having a rather finer mesh (ten or eleven branches and fenestrules in io mm , according to Prout), carinal nodes and apertural peristomes. Ulrich ( $1890 ; 628$ ) recorded the species from the lower and middle Chester of Illinois and Kentucky, but his specimens had an even finer meshwork than those of Prout. He also mentioned the presence of accessory pores on both obverse and reverse, a feature not shown by Prout's specimens or the present ones. The average branch width of Ulrich's material was 0.5 mm , considerably less than that of the Irish specimens, though this might be accounted for by the thick secondary encrustation of the latter. Shishova (1952; 162) found, in the Dinantian of the Moscow region, specimens that she assigned to S. cestriensis. She stated their formula as: $14 / \mathrm{IO}_{2}-\mathrm{I} \frac{1}{2} / / 22-22 \frac{1}{2}$, which differs widely from that of the Fermanagh specimens. Also her material had
lozenge-shaped (rhomboidal) chamber bases, and there were accessory pores on the reverse.

The only other described species which the present specimens resemble is $S$. subquadrans Ulrich, from the upper Chester. This differs from S. cestriensis mainly in fenestrule shape, and has the formula: $7-\mathrm{I} 2 / \mathrm{IO} \frac{1}{2}-\mathrm{I} 2 / / 2 \mathrm{I}$. The number of apertures per 5 mm is greatly in excess of that shown by the Fermanagh specimens, however, and there are accessory apertures on both surfaces (Ulrich 1890; 629).

In view of the lack of correspondence with existing species it is clearly necessary to introduce a new name for the present material. S. hibernica seems appropriate for the first recorded occurrence of the genus in Ireland.

## Other Genera

Note: In addition to the above forms, three further fenestrate bryozoans belonging to the Carrick Lough fauna have been described separately elsewhere by the author. In each case the account given follows the basic pattern used here. The additional species and location of their descriptions are:

1. Ptilofenestella carrickensis gen. et sp. nov. In 1965, Palaeontology 8 : 478-491. 2. Minilya nodulosa (Phillips). In 1965, Geol. Mag. 102 : I35-142.
2. Polypora stenostoma sp. nov. In 1971, Palaeontology 14 : 178-187.

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## PLATE I <br> Fenestella frutex M'Coy

Fig. I. Obverse of large zoarial fragment, with an encrusting stenoporid colony. PD.5001.* $\times 2.9$.

Figs 2, 3, 5, 6. Obverse of small zoarial fragments to illustrate common variations in meshwork appearance. PD. 5002 to PD. $5005, \times 6 \cdot 0 ; \times 5 \cdot 0 ; \times 6 \cdot 7 ; \times 5 \cdot 6$, respectively.

Fig. 4. Stout, barbed spines from the obverse surface to the meshwork. PD.5006. $\times 4.5$.
Figs 7, 9. Detail of the obverse surfaces of morphological variants within this species. PD. $5005, \times 18.0$; and PD. $5002, \times 21 \cdot 0$.
Fig. 8. Reverse side of a zoarial fragment showing longitudinal 'striae' and minute nodes. PD. $5007 . \times 5.8$.

* The serial numbers of specimens refer to the Bryozoa catalogue numbers of the collections of the British Museum (Natural History), where the material is stored.


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## PLATE 2

## Fenestella ivanovi Shulga-Nesterenko

Figs i, 3, 5, 7. Obverse of zoarial fragments to show variations in meshwork pattern PD. $5008, \times 6.0$; and PD. 4682 to PD. $4684, \times 5.0 ; \times 5.3 ; \times 5.0$, respectively

Fig. 2. Proximal part of a zoarium with basal holdfast and lateral supports; the last developed from marginal branches and dissepiments. PD. $4685 . \times 5.2$.

Fig. 4. Zoarial fragment with elongate spinose structures which are 'infertile' branch continuations. PD. $4686 . \times 5.5$.

Fig. 6. Delicate spines with minute barbs growing from the obverse sides of branches. PD.4687. $\times 5^{\circ}$.

Fig. 8. Reverse surface of zoarial meshwork. PD.4684. $\times$ I7.0.
Fig. 9. Detail of obverse side showing the distinctive shape of fenestrules. PD. 4685
I $6 \cdot 0$.


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## PLATE 3

## Fenestella cf. multispinosa Ulrich

Fig. I. Reverse of zoarial meshwork showing longitudinal 'striae' and nodes on the mid-line of branches. PD. $4688 . \times 5.7$.

Fig. 2. Another view of the reverse surface. PD. $4689 . \times 5 \cdot 0$.
Figs 3, 7. Obverse of zoarial fragments with slightly different meshwork characteristics. PD. $4689, \times 5 \cdot 0$; and PD. $4690 \times 7 \cdot 1$, respectively.

Fig. 4. Obverse side showing normal branches passing distally into sterile lateral processes. PD. $4691 . \quad \times 7.2$.

Figs 5, 8. Obverse of meshwork showing localized development of thick, striated, secondary skeleton. PD. $4692, \times 8 \cdot 0$; and PD. $4693, \times 7.0$.

Fig. 6. Reverse of zoarial fragment showing branches passing distally into stout, barbed, lateral spines. PD. $4694 . \times 5.4$.

Fig. 9. Detail of obverse surface. PD. $4689 . \times$ I8.3.


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## PLATE 4

## Fenestella modesta Ulrich

Figs i, 2, 4, 6. Obverse of zoarial fragments illustrating variation in meshwork pattern. PD. $4696, \times 6.6$; PD. $4698, \times 5.0 ;$ PD. $4695, \times 6.8$; and PD. $4697, \times 6.4$, respectively.

FIG. 3. Detail of obverse surface. $\times 25^{\circ}$ o.
Fig. 5. Reverse of zoarial fragment. PD. $4695 . \times 6.8$.

## Fenestella hemispherica M'Coy

Fig. 7. Obverse of zoarial fragment. PD.4699. $\times$ I3.5.
Fig. 8. Reverse surface showing uniserial nodes along mid-lines of branches. PD. 4704. $6 \cdot 3$.
Fig. 9. Large fragment showing typical meshwork pattern. PD.470I. $\times 4.7$.


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## PLATE 5

## Fenestella hemispherica M'Coy

Figs I, 2. Obverse surface of zoarial fragments. PD.4700, $\times 15.0$; and PD. $4702, \times 6.6$.
Fig. 3. Reverse side showing nodes. PD. 4699 . $\times 5.8$.
FIG. 4. Obverse of meshwork showing characteristic mode of branch division. PD. 4704 . I3.8.

## Fenestella parallela Hall

Fig. 5. Reverse of zoarial fragment showing striated pattern. PD.4710. $\times 7.3$. Figs 6, 8, 9. Obverse surfaces showing meshwork characteristics. PD. 4707 to PD. 4709 $7 \cdot 0 ; \times 7 \cdot 0 ; \times 9 \cdot 7$, respectively
Fig. 7. Detail of obverse side. PD.4708. $\times$ I4.5.


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## PLATE 6

Fenestella rudis Ulrich multinodosa subsp. nov.
Fig. I. Detail of obverse of a zoarial fragment. $\times 14.2$
Fig. 2. Obverse of meshwork with localized presence of thick, secondary skeleton which has coated branch surfaces and reduced or sealed zooecial apertures. PD.47I4 (paratype). $\times 8.8$.

Fig. 3. Reverse side of zoarial fragment. PD.47I4 (paratype). $\quad \times 8.2$.
Figs 4, 6, 7. Obverse of fragments showing slight differences of meshwork pattern.PD.47I3 (paratype), $\times 5.0 ;$ PD. 47 I6 (paratype), $\times 7.4$; and PD. 4712 (holotype), $\times 5.0$.

Fig. 5. Obverse of partly silicified fragment showing hemi-hexagonal zooecial chambers.
PD.47I5 (paratype). $\times 7.9$.


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## PLATE 7

## Fenestella plebeia M'Coy

Fig. i. Obverse of zoarial fragment showing meshwork pattern. PD.4719. $\times 3.6$.
Figs 2, 3. Detail of obverse surface. Fig. 3, from proximal part of colony shows thick secondary skeletal envelope. Minute punctae along branch medial lines are carinal node bases. PD.4719, $\times 11.4$; and PD.4717, XII.3, respectively.

Fig. 4. Obverse of zoarial fragment from proximal part of colony. PD.47I7. $\times 4.5$.
Fig. 5. Obverse of partly silicified fragment showing triangular zooecial chambers. PD.4718. $\times 6.0$.

Fig. 6. Zoarial fragment with inflated peristomes projecting into fenestrules. PD.472I. $\times 6.4$.
Fig. 7. Reverse surface of zoarial fragment. PD.47I7. $\times 4.5$.
Fenestella cf. arthritica Phillips
Fig. 8. Detail of obverse surface. PD.4722. $\times$ I5.0.
Fig. 9. Large zoarial fragment giving an impression of the colonial growth form. PD.4728. $\times 2.9$.


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## PLATE 8 <br> Fenestella cf. arthritica Phillips

Figs i, 3, 4. Obverse of zoarial fragments showing characteristics of meshwork pattern. Stout carinal nodes are visible along proximal part of middle branch in Fig. 3. PD.4727, $\times 3.9$; PD. $4726, \times 5 \cdot 0$; and PD. $4724, \times 5 \cdot \mathrm{I}$. respectively.

Fig. 2. Reverse surface of meshwork. PD. $4727 . \times 3.9$.
Fenestella praemagna Shulga-Nesterenko
Fig. 5. Proximal part of a colony with basal holdfast and lateral supporting struts. PD. $473^{2}$. $\times 5.0$.

Fig. 6. Strong carinal nodes, which divide at their distal ends, originate along the obverse mid-lines of branches. PD. $4735 . \times 5 \cdot 1$.

Fig. 7. Proximal part of a colony attached to a Penniretepora branch. PD.4733. $\times 4.7$.
Fig. 8. Obverse of colony showing basal holdfast and supporting processes. PD. 4734. $\times 10.4$
Fig. 9. Detail of obverse. PD. 473 I. $\times \mathrm{I}^{\circ} \mathrm{O}$.
Fig. Io. Reverse side of zoarial fragment. PD.4730. $\times 6 \cdot 1$.
Fig. if. Obverse of proximal part of an old colony, with thick secondary skeletal cover. PD.4729. $\times 7.0$.


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## PLATE 9

Fenestella fanata Whidborne carrickensis subsp. nov.
Fig. I. Obverse of meshwork showing characteristic pattern at branch division. PD. 4736 (holotype). $\times$ IO.I.

Fig. 2. Zoarial fragment with stout lateral spine developed as a branch continuation. PD. 4737 (paratype). $\times 3.5$.

Figs 3, 5, 7, 8. Obverse of zoarial fragments, showing general meshwork characteristics. Specimen shown in Fig. $3(\times 3.9)$ is not preserved. The others are numbered: PD. 4738 (paratype), $\times 5.0 ;$ PD. 4739 (paratype), $\times 3.8$; and PD. $4736, \times 3.5$, respectively.

Fig. 4. Zoarial fragment with ovicells visible in the distal part. PD.4740 (paratype). $\times 3.5$.
Fig. 6. Reverse side of a fragment, showing evidence of damage and subsequent repair during the life of the colony. PD.474I. $\times 3.3$.

Fig. 9. Detail of obverse surface. PD. $474^{2}$ (paratype). $\times 9.9$.


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## PLATE Io

Fenestella cf. spinacristata Moore
Fig. I. Large zoarial fragment showing overall meshwork pattern. PD.4743. $\times 3.8$.
Fig. 2. Reverse surface of meshwork. PD. 4746 . $\times 5 \cdot 0$.
Fig. 3. Detail of obverse side. PD.4743. $\times 9.5$.
Fig. 4. Proximal part of a colony with holdfast attached to a Penniretepora branch. PD. $4747 . \times 6.1$.

Fig. 5. Obverse of zoarial fragment. PD.4744. $\times 7 \cdot$ I.
Fig. 6. Fragment bearing evidence of structural damage and repair during the life of the colony. PD. 4750 . $\times 4.5$.

## Fenestella cf. funicula Ulrich

Fig. 7. Reverse side of fragment from proximal part of a colony, showing a stout spine developed from obverse mid-line of a branch. PD. 4758 . $\times 5.5$.

Fig. 8. Obverse of a zoarial fragment. PD.475I. $\times 5^{\circ} \mathrm{O}$.
Fig. 9. Reverse side of above. PD.475I. $\times 5^{\circ}$.
Fig. Io. Fragment from proximal part of an old colony showing thick secondary skeletal encrustation. PD.4759. $\times 2.9$.


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## PLATE II <br> Fenestella cf. funicula Ulich

Fig. I. Obverse of zoarial fragment showing ovicells in the distal part. PD. $4759 . \times 4.3$.
Figs 2, 3. Obverse surfaces showing general meshwork characteristics. PD. 4753, $\times 6 \cdot 8$; and PD. $4755, \times 7 \cdot 0$.

Fig. 4. Obverse surface of meshwork with strong carinal nodes. PD.4756. $\times 4^{\circ} \mathrm{o}$.

## Fenestella filistriata Ulrich

Figs 5, 7, 9. Obverse of zoarial fragments showing meshwork pattern. PD. $4763, \times 5.3$; PD. $4761 \times 3.8$ and PD. $4762, \times 5.0$, respectively.

Fig. 6. Reverse surface. PD. $4763 . \times 5 \cdot 5$.
Fig. 8. Reverse of zoarial fragment showing longitudinal 'striae' and hemi-hexagonal bases of zooecial chambers. PD.4764. $\times 7 \cdot 0$.

Fig. io. Detail of obverse. PD.4761. $\times 12.2$.


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## PLATE 12

Fenestella cf. filistriata Ulrich
Fig. I. General view of obverse side of a zoarial fragment. PD.476I. $\times 5.2$.

## Fenestella subspeciosa Shulga-Nesterenko

Fig. 2. Reverse surface. PD. $4766 . \times 5 \%$.
Figs 3, 4, 5. Obverse of zoarial fragments showing general meshwork characteristics. PD. $4765, \times 5.0$; PD. $4769, \times 4.0$; and PD. $4767, \times 5.6$.

Fig. 6. Obverse at higher magnification, showing prominent cowl-like peristomes indenting fenestrule margins. PD. 4766 . $\times 5.2$

Fig. 7. Reverse of zoarial fragment showing a stout spine which resulted from continued growth from an abnormally directed dissepiment. This spine later re-united with the meshwork, as shown. $\times 7 \cdot 2$.

Fig. 8. Obverse of above fragment showing a local concentration of secondary skeletal tissue where the aberrant spine (coming from below) rejoined the meshwork. $\times 7.2$.


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## PLATE 13 <br> Fenestella pseudovirgosa Nikiforova

Fig. I. Detail of obverse. PD.4770. $\times$ I5.0.
Fig. 2. Reverse side of meshwork. PD.477I. $\times 2.9$.
Fig. 3. Zoarial fragment showing general meshwork characteristics. PD. $4770 . \times 5.0$.
Fig. 4. The stout spine developed from a branch end in the distal part of this specimen grew back and re-united with the reverse side of the meshwork. PD.4772. $\times 3 \cdot 6$.

Fig. 5. This strong spine resulted from the continued growth of an abnormal dissepiment. PD.4773. $\times 3.7$.

Figs 6, 9. Zoarial fragments from proximal parts of colonies, showing thick deposits of secondary skeletal substance. PD.4774, $\times 5.6$; and PD. $4775, \times 5^{\circ}$.

Fig. 7. Obverse of fragment, showing a strong laterally directed spine. PD. 4776. $\times 4$. I.
Fig. 8. Reverse surface showing longitudinal 'striae', variably developed nodes, and the triangular base of a zooecial chamber. PD.4777. $\times 4.3$.


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PLATE 14

## Fenestella cf. albida Hall

Figs i, 3. Obverse of zoarial fragments showing general meshwork characteristics. PD. $4783, \times 6.7$; and PD. $4780 \times 5 \cdot 0$, respectively.
Fig. 2. Obverse surface showing chain-like pattern due to projection of inflated peristomes into fenestrules. PD. 478 I . $\times 6.4$.
Fig. 4. Detail of obverse. PD. $4780 . \times 15.0$.
Fig. 5. Proximal part of a colony with basal attachment to a Penniretepora branch. PD. 4779 . $\times 3.4$.
Fig. 6. Reverse side of meshwork. $\times 5 \cdot 8$.
Fenestella oblongata Koenig
Fig. 7. Obverse of a zoarial fragment. PD.4790. $\times 7 \cdot 0$.
Fig. 8. Reverse surface showing longitudinal 'striae', small nodes and the triangular base of a zooecial chamber. PD. 479 I. $\times 7.5$.


## PLATE 15

## Fenestella oblongata Koenig

Fig. I. Detail of obverse of zoarial fragment. PD. $4786 . \times 14.8$
Figs 2, 3, 4. Obverse views of fragments showing general aspect of meshwork. PD. $4787 . \times 5.0 ;$ PD. $4789, \times 4.2$; and PD. $4786, \times 6.3$, respectively.

## Fenestella cf. delicatula Ulrich

Figs 5, 6. Obverse surfaces of zoarial fragments illustrating variation in meshwork characteristics. PD. $4797, \times 6.3$; and PD. $4794, \times 7.0$.

Fig. 7. Zoarial fragment with strong spines from the reverse side of a branch. The spines bear minute barbs. PD. $4799 . \times 5.0$.

Fig. 8. Detail of obverse side. PD.4798. $\times$ I6.0.



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## PLATE 16 <br> Fenestella cf. delicatula Ulrich

Fig. I. Reverse side of meshwork. PD.4798. $\times 7.5$.
Fig. 2. Obverse of zoarial fragment. PD.4795. $\times 4.8$.
Fig. 3. Fragment with strong lateral spine developed as a branch continuation. PD. 4798.
$7 \cdot 5$.

## Fenestella polyporata (Phillips)

Fig. 4. Reverse of meshwork showing longitudinal 'striae'. PD.4802. $\times 7.2$.
Figs 5, 7, 8. Obverse surfaces of zoarial fragments showing general features of meshwork. PD. $4805, \times 7.0$; PD. $4802, \times 3.7$; and PD. $4804, \times 5 \cdot 0$, respectively.
Fig. 6. Detail of obverse. PD. $4804 . \times 14.9$.


## PLATE 17 <br> Fenestella polyporata (Phillips)

Fig. I. Obverse of zoarial fragment. PD. 4803 . $\times 7 \cdot 1$.
Fenestella irregularis Nekhoroshev
Figs 2, 5. Obverse of zoarial fragments, showing meshwork features. PD. $4808 \times 7.1$; and PD. $4^{8 \text { II }}, \times 3 \cdot 9$, respectively.

Fig. 3. Detail of obverse. PD.4810. $\times 13 \cdot 0$.
Fig. 4. Reverse side of zoarial fragment. PD. 4809 . $\times 7.5$.
Fig. 6. Obverse of incompletely silicified fragment showing casts of zooecial chambers. PD. $4{ }^{813}$ 3. $\times 8.5$.

Fig. 7. Oblique view of obverse showing strong carinal nodes. PD.4812. $\times 4.5$.

## Levifenestella undecimalis (Shulga-Nesterenko)

Fig. 8. Reverse surface with longitudinal 'striae' and grooves excavated by ramifying Condranema (ctenostome) stolons. PD.4815. $\times 5^{\circ} \mathrm{O}$.

Fig. 9. Detail of obverse. PD.48I6. $\times$ I6.0.


PLATE 18

## Levifenestella undecimalis (Shulga-Nesterenko)

Figs i, 2, 4. Obverse surfaces of zoarial fragments. PD.4817, $\times 6.6$; PD. $4814, \times 4.0$; and PD. $4820, \times 6 \cdot 2$, respectively.

Fig. 3. Reverse of meshwork showing closely spaced longitudinal 'striae'. PD.48ı6. $\times 7.3$
Fig. 5. Obverse of large zoarial fragment which gives an idea of the colonial growth form. PD. 48 I8. $\times 2.3$.

## Minilya plummerae (Moore)

Fig. 6. Small fragment with a stout, barbed spine developed from the reverse surface. PD. $4827 . \times 6.5$.

Figs 7, 8. Obverse of zoarial fragments showing general aspect of meshwork. PD.4825, $\times 6 \cdot 0$; and PD. $4824, \times 7 \cdot 5$, respectively.


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## PLATE I9

Minilya plummerae (Moore)
Fig. I. Detail of obverse of meshwork. Positions of carinal nodes are indicated on a part of one branch. PD. $4823 . \times 22.0$.

Figs 2, 4. Obverse of zoarial fragments, showing general meshwork characteristics. PD. $4823, \times 6.6$; and PD. $4822, \times 5.0$, respectively.

Fig. 3. Reverse surface. PD. 4822 . $\times 5^{\circ} \mathrm{O}$.
Minilya binodata (Condra)
Figs 5, 7. Obverse of zoarial fragments. PD. $4829, \times 7.3$; and PD. $4848, \times 8.5$.
Fig. 6. Reverse surface. PD. $4828 . \times 5.8$.


## PLATE 20 <br> Minilya binodata (Condra)

Fig. I. Detail of obverse, with the positions of some carinal nodes indicated. PD. 4828. $\times 16.5$

## Minilya oculata (M'Coy)

Fig. 2. A fragment from the proximal part of an old colony, with thick secondary skeletal investment. PD.4833. $\times 6.2$.

Fig. 3. Detail of obverse showing the biserial arrangement of carinal nodes. PD. 4838 . $\times 17.5$

Figs 4, 6, 8. Obverse of zoarial fragments, showing meshwork pattern and growth habit. PD. $4834, \times 5.0 ;$ PD. $4837, \times 6.4$; and PD. $4835 . \times 6.9$, respectively.

Fig. 5. Reverse side of zoarial fragment. PD.4839. $\times 6.5$.
Fig. 7. Proximal part of a colony with holdfast attached to a Rhabdomeson fragment. PD. 4832 . $\times 3.9$.


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## PLATE 21

## Ptiloporella varicosa (M'Coy)

Figs i, 2, 3, 6, 7. Obverse of zoarial fragments showing prominent development of primary and secondary branches. PD. 4840 to PD. 4844 inclusive, $\times 4.0 ; \times 4.7 ; \times 5.0 ; \times 2.6 ; \times 2.7$, respectively.

Fig. 4. This specimen, with a midrib and symmetrically placed lateral branches, resembles Ptylopora M'Coy in its growth pattern. PD. $4845 . \times 4.6$.

Fig. 5. Small fragment with strong spinose structures which originate on the obverse midline. PD. $4846 . \times 43$

Fig. 8. Reverse surface, showing the relationship between primary and secondary branches. PD. $4847 . \times 3.9$.

Fig. 9. Detail of obverse. PD.4842. $\times 13.5$.


## PLATE 22

## Hemitrypa hibernica M'Coy

Fig. I. Proximal part of a colony attached to a Rhombopora fragment. Ends of supporting spines are visible. PD.4848. $\times 3.2$.

Fig. 2. Reverse surface of zoarial fragment showing a secondarily thickened 'dissepimental arc'. PD. $4849 . \quad \times 3.5$.

Fig. 3. Proximal part of a colony with enclosing superstructure and stout supporting spines. PD. $4^{8} 50 . \times 5^{\circ}$.

Fig. 4. Obverse side with superstructure removed. PD.485I. $\times 5^{\circ} \mathrm{O}$.
Fig. 5. Obverse with superstructure partly removed to show abnormal branching pattern, possibly a pathological condition. PD. 4852 . $\times 5 \cdot 0$.

Fig. 6. Lateral view showing superstructure supported by carinal pillars. Underside of meshwork is encrusted by a Fistulipora colony. PD.4853. $\times 6.5$.

Fig. 7. Reverse surface with distal parts of a long, branched supporting spine which reunites with the colonial meshwork. PD. $4854 . \times 3.2$.

Fig. 8. Obverse of a large fragment, with young Fistulipora colony encrusting the superstructure. PD. $4855 \times 3 \cdot \mathrm{O}$.

Fig. 9. Obverse of meshwork showing ovicellular concavities. PD.4856. $\times 4.4$.
Fig. Io. Detail of obverse. PD. $4857 . \times$ I8.o.


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## PLATE 23

## Polypora dendroides M'Coy

Figs i, 5. Obverse of zoarial fragments from the proximal parts of colonies. Thick secondary skeletal tissue is particularly evident at the bases of broken supporting spines, $\times 5.4$; PD.4865, and PD. $4866, \times 2.6$.

Figs 3, 4. Reverse of meshwork. Fig. 4 shows the proximal parts of supporting spines. PD. $4867, \times 5.0$; and PD. $4868 \times 2.6$.

Figs 2, 6. Obverse surfaces showing general characteristics of meshwork. PD.4867, $\times 5^{\circ} 0$; and PD. $4869, \times 4.3$.

Fig. 7. Detail of obverse side. PD. $4867 . \times$ I3.0.


## PLATE 24

## Polypora verrucosa M'Coy

Fig. I. Detail of obverse. PD. $4870 . \times 12.8$
Figs 2, 3, 5, 7. Obverse of zoarial fragments showing general features of meshwork and branch surface. PD. $4872, \times 3.4 ;$ PD. $4873, \times 3.8$; PD. $4870, \times 6.6$; and PD. $4874, \times 6.2$, respectively.

Fig. 4. Fragment from proximal part of a colony, showing prominent peristomes with terminal apertures, some of which are sealed by the thick secondary skeletal investment. PD. 487 I . $\times 6.6$.

Fig. 6. Reverse side showing incipient beekitization resulting from the silicification of thick secondary skeletal accretions. PD. $4877 . \times 6 \cdot 0$.


## PLATE 25

Ptylopora pluma M'Coy parva subsp. nov.
Fig. I. Detail of obverse showing midrib and lateral branches. PD. 4880 (paratype). I8.6
Fig. 2. Reverse surface with prominent 'striae'. PD. 4880 (paratype). $\times$ I 8.6 .
Figs 3, 5, 8, io. Obverse of zoarial fragments showing general meshwork characteristics. PD. $4878, \times 5.0 ;$ PD. $4879, \times 6.0 ;$ PD. 488 I and PD. $4882, \times 4.1 ; \times{ }_{4} . I^{\prime}$ (all are paratypes).
Fig. 4. Proximal part of a colony with thick outer secondary investment. The stalk-like holdfast has subsidiary attachment structures at its lower end. $\times 5^{\circ} \mathrm{o}$.

FIG 6. Midrib of a colony with vestiges of secondary branches. PD. 4883 (holotype). $\times 2 \cdot 7$.
Figs 7, 9. Reverse sides of zoarial fragments. Fig. 9 shows a short lateral spine developed from a branch end. PD. 4884 and PD. 4882 (paratype) respectively. Both $\times 4 \cdot 1$.


## PLATE 26

Septopora hibernica sp. nov.
Figs i, 7, 8. Obverse of zoarial fragments. In many places branch surfaces are obscured and zooecial apertures sealed by thick secondary skeletal deposits. PD. 4885 (holotype), $\times 2 \cdot 2$; PD. 4886 (paratype), $\times 6 \cdot \mathrm{I}$; and PD. 4887 (paratype), $\times 3.6$.

Fig. 2. Reverse surface of meshwork. The difference between primary and secondary branches is very marked. PD. 4885 (holotype). $\times 2 \cdot 2$.

Fig. 3. Obverse with thick investment of secondary skeleton. The 'striae' traverse both branches and dissepiments when traced away from the bases of large spines. PD. 4889 (paratype). $\times 4.5$.

Fig. 4. Fragment with Ptylopora-like meshwork of midrib and lateral branches. PD. 4888 (paratype). $\times$ I $\cdot 9$.

Fig. 5. Zoarial fragments with irregular growth habit. PD. 4890 (paratype) and PD. 489 I. $\times 4.5$.

Fig. 6. Reverse surface showing thick deposits of secondary skeleton. PD. 4889 (paratype). $\times 6.4$.


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[^0]:    
    Pre - cambrian
    Fig. I. Generalized map showing the geographical and geological setting of Carrick Lough Inked rectangle near the lough indicates the limits of the area shown in Fig. 3.

[^1]:    1836 Retepora polyporata Phillips; 199.
    1843 Fenestella polyporata Phillips; Portlock; 323.
    1844 Fenestella multiporata M'Coy; 203.
    1879 Fenestella polyporata Phillips, Shrubsole; 280.
    1881 Fenestella polyporata Phillips; Shrubsole; 185.
    1926 Fenestella polyporata Phillips; Nikiforova; 179.
    1927 Fenestella aff. polyporata Phillips; Nikiforova; 251.
    1933a Fenestella polyporata Phillips; Nikiforova; 23.
    1935 Fenestella ex. gr. polyporata Phillips; Nekhoroshev; 69.
    1938 Fenestella aff. polyporata Phillips; Demanet; 44.
    1948 Fenestella cf. polyporata Phillips; Oakley; 88.
    1951 Fenestella polyporata Phillips; Shulga-Nesterenko; 59.
    1956 Fenestella cf. polyporata Phillips; Nekhoroshev; 149.
    1961 Fenestella polyporata Phillips; Miller; 233.

