

THE PHYLOGENETIC AFFINITIES OF FENESTELLOID BRYOZOANS

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ABSTRACT. In this paper suggestions are made as to the affinities and derivation of the cryptostomatous sub-Order Fenestelloidea. Diagnostic features of the group are held to be the presence of zooecial apertures on the obverse of a colony only and 'longitudinal striae' on the reverse; also the presence of a primary axial complex within branches. Longitudinal striae are recognized as a fundamental and significant part of the skeletal structure. In *Pseudohornera* it can be seen that the striae are vestiges of formerly existing interzooecial walls which are homologous with range partitions in the Ptilodictyoidea. If longitudinal striae are vestigial interzooecial walls then their presence on the reverse of fenestelloid fronds suggests that this group was originally bifoliate. If, in bifoliate ancestral forms, zooecia grew back-to-back against a medial lamina, this must be represented in fenestelloid branches by the flattened primary axial skeleton on which zooecial bases rest.

Fenestelloid skeletal rods are structurally identical with acanthopores in the Trepostomata and in view of their size must be considered micracanthopores. The carina of biserial fenestellids represents a preferentially developed interzooecial wall, and carinal nodes are megacanthopores of outstanding stature. The latter structures must have exercised a protective function but it is probable that micracanthopores were concerned with the stabilization of the outer, soft colonial layers.

There is a strong body of evidence linking the Fenestelloidea with the Ptilodictyoidea and a complete morphological series bridging the gap between these sub-Orders can be assembled without difficulty. The structure of the medial lamina in *Pseudohornera* is closely linked on the one hand with the primary branch skeleton of the Fenestellidae and on the other with the mesotheca of the Ptilodictyoidea. Other lines of evidence provide further reasons for believing that the fenestelloids were derived from the ptilodictyoids, with the phylloporinids representing an intermediate stock.

CURRENT problems posed by Palaeozoic bryozoans include the need to understand the relationships of the subdivisions of the Order Cryptostomata to one another, and to the Trepostomata with which all show undoubted affinities.

From many points of view it is not an easy matter to differentiate satisfactorily between the Trepostomata and the Cryptostomata and thorough investigation shows that there is, in fact, no clear-cut means of distinguishing between them. The differences which undoubtedly do exist are essentially matters of degree. Features such as monticules, acanthopores, mesopores or diaphragm-bearing, tubular zooecia with endozones and exozones which are typically associated with the Trepostomata are also found in cryptostomatous forms. But they are not universal among the Cryptostomata and, where present, are developed only to a limited extent. All the signs indicate, therefore, that these two Orders accommodate different but fairly closely related stocks.

Within the Cryptostomata a three-fold division into the sub-Orders Rhabdome-soidea, Ptilodictyoidea, and Fenestelloidea, as suggested by Astrova and Morozova (1956, p. 661), is not only acceptable but is also eminently defensible on grounds both of external morphology and internal structure. Reasons have been given elsewhere (Tavener-Smith 1974) for believing that the rhabdomesoids are a primitive branch of the Cryptostomata and for considering that this sub-Order and the Ptilodictyoidea were independently derived from the Trepostomata, to which both show strong

structural similarities. In this paper attention is focused on the phylogenetic affinities of the remaining sub-Order, the Fenestelloidea, and suggestions are made regarding its derivation and relationships.

STRUCTURAL CONSIDERATIONS

General

Bassler (1953, pp. G120–G147) included within the Cryptostomata a number of diverse groups and it was these (together with the Phylloporinidae) that Astrova and Morozova placed in the three sub-Orders already mentioned. Before proceeding further it is advisable to inquire into those characteristics which may be considered to circumscribe the Fenestelloidea and to distinguish them from other cryptostomatous groups. In this connection the following might commonly be cited:

- (i) An upright, fenestrate colonial skeleton with cup-like, fan-like, or foliaceous habit.
- (ii) The common presence of compact, box-like zooecia.
- (iii) The presence of zooecial apertures on one side of the skeletal meshwork only, the reverse showing parallel, longitudinal striations.
- (iv) The presence of a primary skeletal layer forming a ramifying axial component in all branches and an envelope around individual zooecia.

The first consideration, though at first sight fundamental, does not apply throughout the sub-Order; *Penniretepora*, *Diploporaria*, and *Thamniscus* are obvious exceptions. On the other hand, members of other groups undoubtedly do manifest this aspect: some ptilodictyoids have a fenestrate structure (e.g. *Clathropora*, *Coscinella*) and the same growth habit is also known among the Cyclostomata (e.g. *Coscinotrypa*) and Cheilostomata (the Reteporidae). Nor is the presence of compact, box- or sac-shaped zooecia truly diagnostic, for this is common among the Cheilostomata. Also this characteristic is not shown by most phylloporinids which the writer, in agreement with the Russian authors, would include in the Fenestelloidea. Furthermore, some species of *Fenestella* itself have short tubular zooecia.

Items (iii) and (iv) are, however, found to varying extents in all fenestelloids and seem to represent the fundamental attributes of the group, being peculiar to it. Both therefore merit further attention.

Emplacement of the primary layer

By 'primary layer' in this context is meant the first-formed component of the mineralized skeleton at any point in the colony, whether beneath the initial attachment disc or at the tips of growing branches. This first-formed component is designated *primary* to distinguish it from the differently constructed *secondary* skeleton which was subsequently added and is commonly much thicker. The primary layer has distinctive and characteristic features under either the light or electron microscope. Examination with the light microscope shows primary tissue as an apparently structureless layer of clear calcite, while the much higher magnification in the electron microscope reveals a disorganized granular structure with either vestigial organic investments around the grains, or a complete absence of organic matrix (Tavener-Smith and Williams 1972). These features contrast with the well-organized arrange-

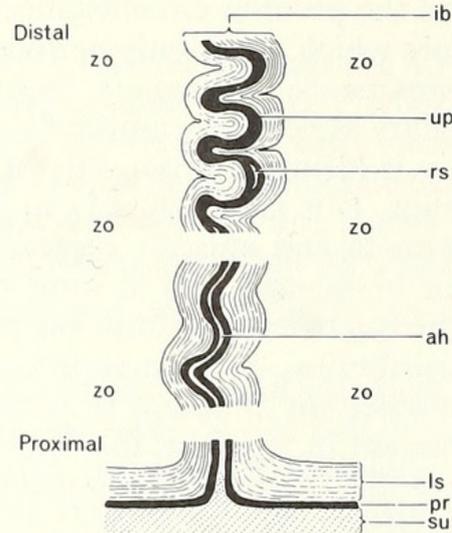
ment of mineral fibres in the secondary layer, which show marked laminar structure and an organic envelope around each crystallite. It seems probable that the poor organization of the primary layer reflects relatively rapid and ill-concerted deposition of an initial mineral investment to secure the immediate support and protection of the newly formed soft parts. The primary layer is, therefore, the first-formed part of the colonial skeleton, and the peculiar circumstances of its formation impressed upon it a distinctive structure which commonly permits differentiation from subsequently added skeletal components. Though in themselves distinct the junction between primary and secondary skeleton is commonly of a gradational nature.

The primary skeletal layer is identifiable not only in the fenestelloids but also in other cryptostomotous groups. It is also regularly to be found in members of the Trepostomata and Cyclostomata and must be regarded as a fundamental skeletal constituent of all Palaeozoic bryozoans, and in some of later date (Tavener-Smith and Williams 1972). But whereas in other groups the primary skeleton has in most cases a strictly localized distribution, being mainly confined to the basal areas of attachment, in the Fenestelloidea the situation is quite different. In that group the primary layer is not only present in the basal disc but also forms a ramifying axial plexus extending throughout all structural components of a complexly branching skeleton (Elias and Condra 1957, p. 26).

A transverse section of any fenestelloid branch examined under the microscope shows the primary skeleton forming a basal platform on which the zooecial chambers rest. The lower limit of the primary layer in such a section commonly exhibits a number of projections, giving it a toothed appearance, while on its upper surface thin extensions of primary material extend upward to form the medial elements of walls between zooecia (Pl. 1, fig. 1). In three dimensions it will readily be appreciated that such medial elements form a cup or envelope around each zooecial chamber that is complete except in the apertural region. The immediate question then is: by what developmental sequence did a primary skeletal component, which must have originated as the basal layer of an attachment disc in fenestelloid ancestors, come to form the axial component of branches in ramifying fenestrate colonies?

The beginnings of an answer seem to lie in certain stocks in which the primary skeletal layer shows a tendency to rise from the substrate on which it originated. This is seen in specimens of early stage rhabdomesoid colonies studied by the author (1974) in which the basal primary layer rises to form an insulating sheath around foreign axial supports. It is also clearly seen in many ptilodictyoid colonies as the medial element of the mesotheca which rose from an encrusting base as a centrally placed lamina within the erect, bifoliate frond. It is true that transverse sections of the mesotheca commonly show the primary layer to be represented only by a system of closely spaced rods (Pl. 2, fig. 2). These are the *median tubules* of earlier authors (e.g. Karklins 1969, p. 7). In some cases these structures show a distinct tendency to lateral flattening, being lenticular in the plane of the mesotheca (Pl. 2, fig. 6), while in others they are united into a continuous medial sheet, shown as a black line in Karklins (1969, p. 23, fig. 6) (see also Pl. 2, fig. 3). The main point, however, is not whether the primary tissue forms tubules or sheets, but that it is demonstrably rising from its original prone position adjacent to the substrate. An excellent illustration of the power of a flat-lying, primary layer to rise locally from the substrate to form a potential medial lamina

within an upright frond is shown in a thin section of *Alveolaria semiovata* Wood (lectotype in B.M. (N.H.) Collection) of Pliocene age. In this case the basal lamina clearly consists of primary and secondary components. Both of these are doubled in the 'mesotheca' which is essentially an erect invagination of the basal lamina (text-fig. 1). There can be no doubt, therefore, of the potential ability of a basal primary



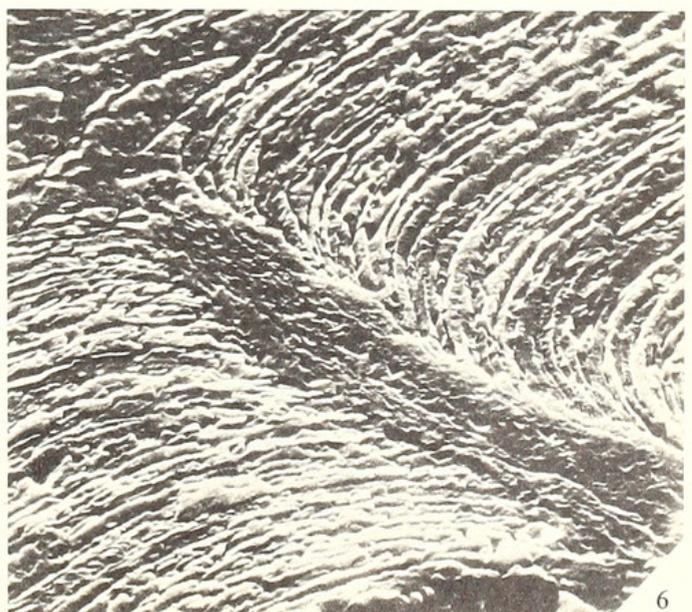
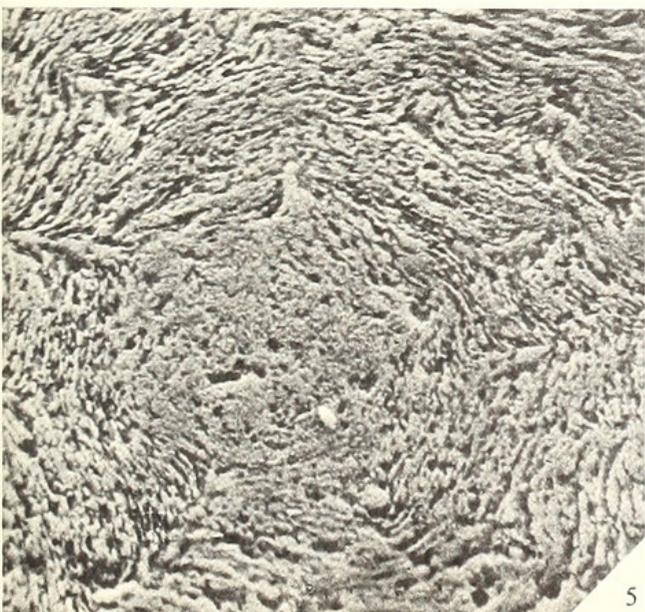
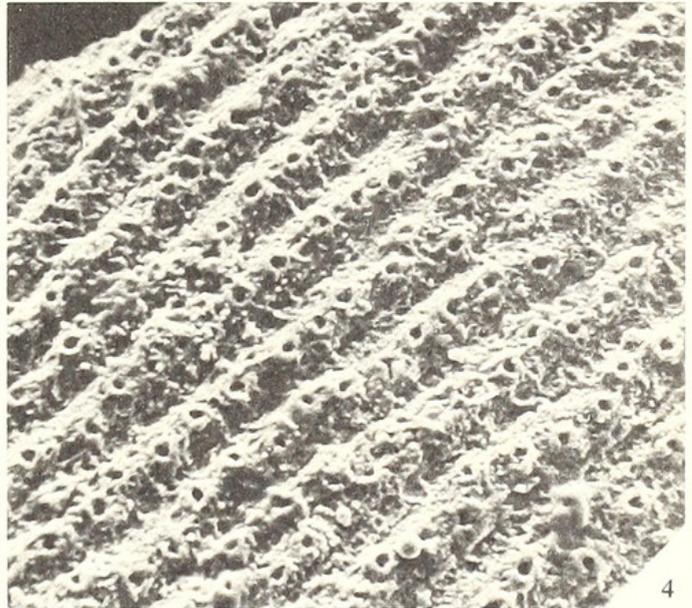
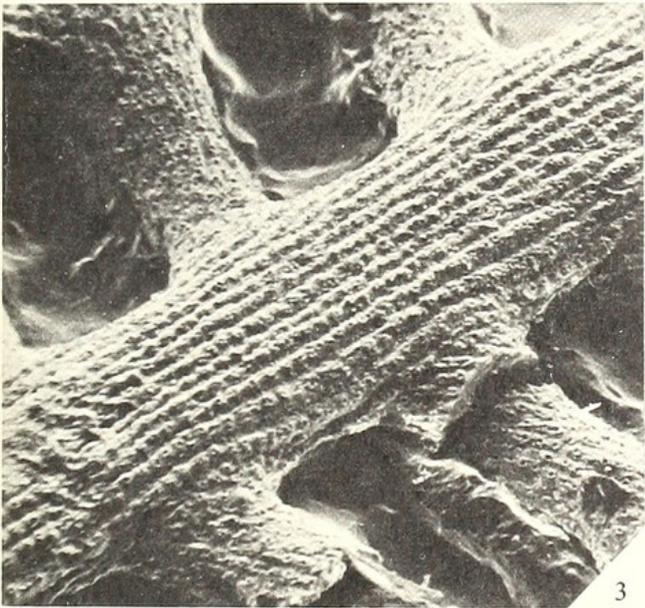
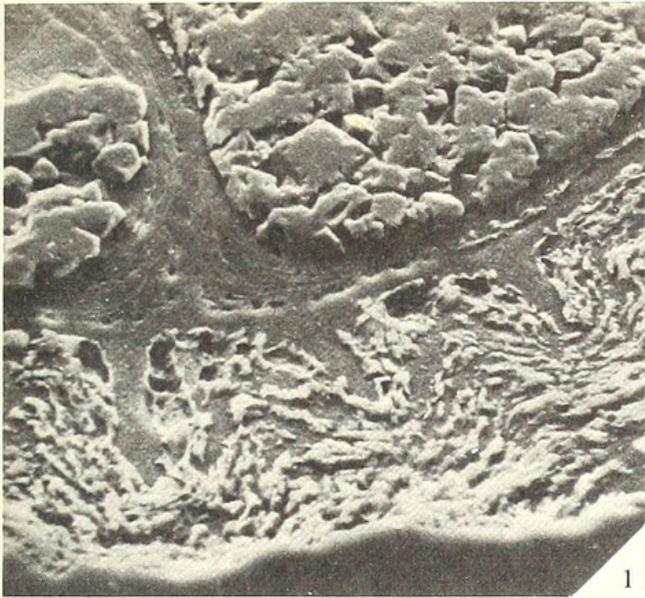
TEXT-FIG. 1. Transverse section of *Alveolaria semiovata* Wood showing three stages in the formation of a doubled wall which rises from the basal plate to form an erect medial lamina within the sub-globular colony. Drawn from thin section of lectotype D6905 in the B.M. (N.H.) Collection.

ah: axial slit within doubled 'basal wall'; ib: invaginated basal wall forming medial lamina; ls: laminated secondary wall component; pr: primary basal layer (stained yellow to brown in the section); rs: residual slit in distal part of invagination; up: united primary layers forming a single unit; zo: positions of zoecia flanking the medial lamina.

EXPLANATION OF PLATE I

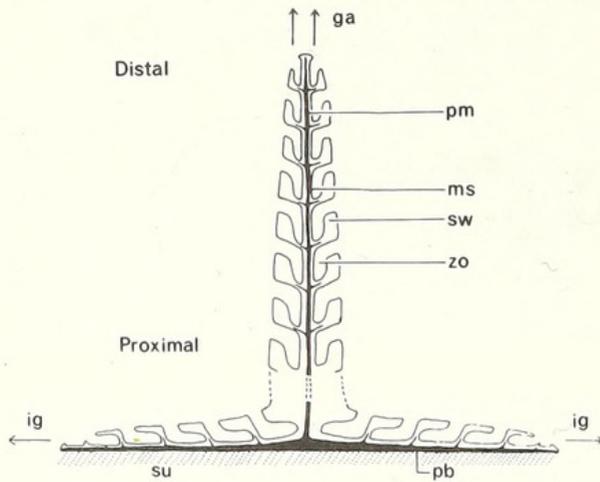
All figures are scanning electron micrographs of whole mounts or polished sections.

- Fig. 1. *Polypora dendroides* McCoy. Tournaisian, Hook Head, Ireland. Part of transverse section of a branch. The bases of zoecial chambers rest on a primary skeletal layer which shows a digitate lower surface, $\times 310$.
- Fig. 2. *Fenestella polyporata* (Phillips). Viséan, Black Lion, Ireland. Detail of transverse section of a branch. Primary layer beneath zoecium showing digitate process encased by laminar secondary tissue. The process gives rise to two incipient skeletal rods, $\times 2700$.
- Fig. 3. *Ptylopora pluma* McCoy. Tournaisian, Hook Head, Ireland. Reverse of colony midrib showing longitudinal striae which extend on to dissepiments, where skeletal rods are clearly visible, $\times 64$.
- Fig. 4. *Ptylopora pluma* McCoy. Tournaisian, Hook Head, Ireland. Detail of fig. 3 showing ends of skeletal rods as pits (result of differential weathering) aligned along crests of longitudinal striae, $\times 275$.
- Fig. 5. *Fenestella cf. albida* Hall. Viséan, Florence Court, Ireland. Transverse section of carinal node showing granular primary core surrounded by closely spaced secondary laminae. Obliquely directed off-shoots from the core penetrate secondary layers, giving a stellate pattern, $\times 1300$.
- Fig. 6. *Penniretepora pluma* McCoy. Viséan, Florence Court, Ireland. Detail of transverse section of colony midrib. Primary tissue in the core of a skeletal rod is flanked by cone-in-cone secondary laminae. Base of a zoecial chamber is top left and branch periphery to bottom right, $\times 2400$.



TAVENER-SMITH, fenestelloid bryozoa

layer to enter into the axial structure of subsequently formed parts of a bryozoan colony which may adopt an erect posture. It must be pointed out, however, that the structure of primary components of mesothecae in ptilodictyoids does not support the idea that such structures were formed as simple invaginations of the type described above. In these forms (text-fig. 2) the *basal* part of the primary layer is continuous and



TEXT-FIG. 2. Diagram of a typical erect bifoliate ptilodictyoid frond growing from a small basal encrustation. Width of primary skeleton greatly exaggerated.

ga: main growth axis; ig: direction of initial growth to form encrusting basal plate; ms: mesotheca; pb: primary layer of basal plate; pm: primary medial layer of mesotheca; su: substrate; sw: secondary wall tissue; zo: zoecium.

Most ptilodictyoid colonies consist of one or more broad, flattened bifoliate fronds and in a few genera growth at the frond margin was differential. In *Clathropora* this gave rise to an initially dentate pattern, the prominences of which grew onward and reunited, leaving behind rounded fenestrules. Repetition of this process led to the formation of a fenestrate frond. In *Taeniodictya* the initial projections grew onward independently of one another and formed ribbon-like branches. In both instances the broad, flattened branches which resulted contain a mesothecal element incorporating a median lamina of primary tissue, the latter in some cases showing the beginnings of extension into interzoecial walls.

It has been stated that in the Fenestelloidea primary tissue forms a continuous axial complex within all branches of a colony. It constitutes a blade-like base beneath zoecial chambers from which upwardly growing flanges encase the chambers to a varying degree. This primary axial structure ('colonial plexus' of Elias and Condra 1957, p. 26) persists to the distal extremities of growing branches, and the means of its propagation has already been discussed by the writer (1969*a*, pp. 294-299; 1973, pp. 356-357). A clear parallel exists between the situation of primary tissue forming the broad axial plate beneath zoecia in the Fenestelloidea and that within the mesotheca of those ptilodictyoids which develop a fenestrate frond or flattened, ribbon-like branches. The main differences are that whereas the fenestelloids bear zoecia on only

only the *upper* section was drawn upward into the mesotheca, the primary component of which shows no ultrastructural evidence of having been formed by the union of originally separate layers. In the ptilodictyoids, therefore, the initiation of the mesotheca by upward invagination from the primary basal plate took place only during the later stages of the formation of the primary skeleton (Tavener-Smith 1974). A final point to be made in connection with ptilodictyoid mesothecae is that in some sections examined it was clearly evident that primary tissue of the median lamina extended laterally for short distances on both sides into the walls between adjacent zoecia (Pl. 2, fig. 4). In other words, there are shown the beginnings of a tendency for the primary layer of the mesotheca to extend into the axes of interzoecial walls as cup-shaped bases supporting zoecial chambers.

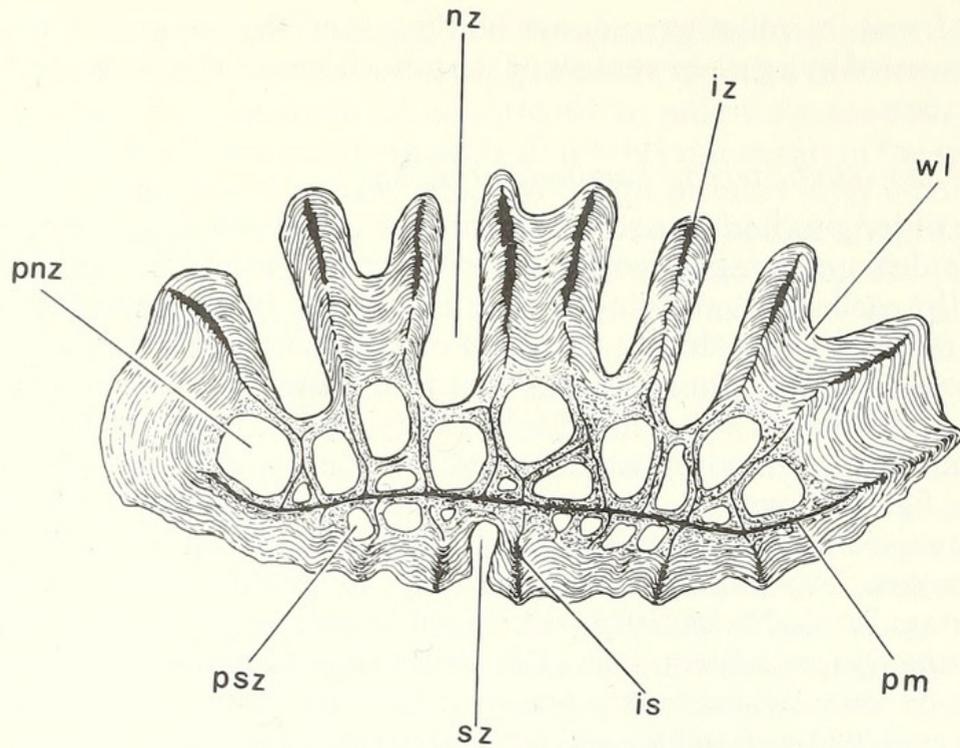
one side of a frond the ptilodictyoids are bifoliate, and that whereas the fenestelloid zooecium is invested by a primary envelope the ptilodictyoids show only the beginnings of such structures.

The structure and significance of longitudinal 'striae'

The presence of longitudinal 'striae' on the reverse of branches is a unique feature of the Fenestelloidea, not being evident in other bryozoan groups. Its presence has been remarked on by earlier writers going back to the time of Phillips and McCoy, but no serious inquiry has been made into its origin or significance. The 'striae' are a series of closely spaced, parallel, linear ridges which are always most prominent on the reverse surface of a frond (Pl. 1, fig. 3). But they are not confined to that side, for careful examination commonly reveals them on the obverse also (Tavener-Smith 1969a, pl. 53, fig. 5) though in *Fenestella*, the best-known genus of the group, they tend to be obscured by more strongly developed features such as zooecial apertures and carinal nodes. The same is true of all other fenestellid genera having biserial apertures. Striae also tend to be clearly developed on colonial structures not associated with zooecia and their apertures, such as dissepiments and the larger spinose developments. Striae on such structures are always continuous with ones on branches and they must be regarded as fundamental skeletal characteristics.

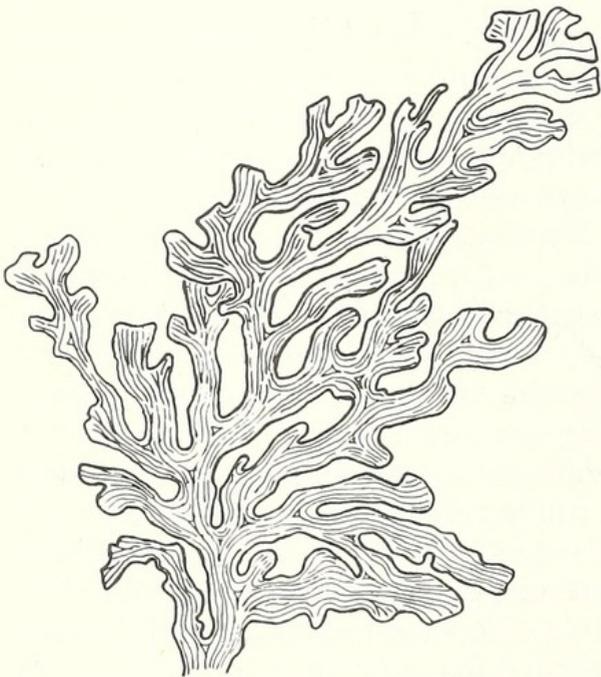
The occurrence of striae as longitudinal lines paralleling the axes of branches means that they cannot have originated as growth lines. This being so, the most natural structures with which they may be associated are the longitudinal dividing walls separating adjacent rows of zooecia. Such walls are also parallel with branch axes and examination of many groups of bryozoa, both ancient and modern, consistently shows that walls between adjacent linear rows of zooecia are more strongly developed and of greater morphological significance than those between successive zooecia in the same row (Levinsen 1909, p. 11; Karklins 1969, pp. 12-16).

Proof that longitudinal striae do indeed represent relics of formerly existing inter-zooecial walls is provided by the structure of the phylloporinid *Pseudohornera*. This genus, together with the rest of the family to which it belongs, was assigned to the Trepostomata by Bassler (1953, p. G115) but other writers have preferred to regard these forms as a primitive fenestelloid stock (Larwood, Medd, Owen and Tavener-Smith 1967, p. 384; Brood 1970, p. 196). Transverse sections across branches of *Pseudohornera diffusa* Hall, the type species, show a unique arrangement. Bisecting the lenticular branch along its major axis is a feature identical in position and structure with a ptilodictyoid mesotheca. This is flanked on one side (the obverse) by a number of short tubular zooecia with well-developed separating walls showing strongly laminar characteristics. On the opposite side of the mesotheca (reverse) the structure is fundamentally the same, but the zooecia are stunted and obsolete (text-fig. 3). Views of the reverse surface of a colony (text-fig. 4; see also Bassler 1953, p. G188, fig. 26) show that the branches bear marked longitudinal striae, and close examination indicates that these correspond in number and position with the vestigial interzooecial walls seen in transverse section. It is therefore clear that in this instance the striae on the reverse are relics of what were originally interzooecial walls, and there seems no reason to doubt that the same is true of fenestelloids in general. *Pseudohornera* therefore illustrates an important intermediate instance in which some



TEXT-FIG. 3. *Pseudohornera*: transverse section of a branch, approximately $\times 44$. Drawn from an acetate peel of *P. diffusa* (Hall) in the U.S.N.M. Collection.

is: obsolete interzoecial wall forming a stria on reverse side; iz: interzoecial wall; nz: normal zoecium; pm: primary medial layer of mesotheca (extensions from this ramify into interzoecial walls); pnz: proximal tubular part of normal zoecium; psz: proximal part of suppressed zoecium; sz: suppressed zoecium; wl: secondary wall laminae.



TEXT-FIG. 4. Reverse of *Pseudohornera* colony showing ribbon-like branches and well-developed longitudinal striae. Drawn from a specimen of *P. diffusa* (Hall) in the A.M.N.H., New York, Collection. Approximately $\times 2$.

essentially ptilodictyoid characters, for example, the tendency towards a flattened, potentially bifoliate branch with mesotheca, are combined with others peculiar to the fenestelloids, for example, zooecial apertures confined to one surface and longitudinal striae on the other.

Study of the ultrastructure of longitudinal striae in fenestelloids and range partitions in ptilodictyoids like *Stictopora* (Pl. 2, fig. 1) shows that the arrangement is fundamentally the same in both cases. (Range partition was defined by Karklins (1969, p. 7) as 'A linear segment of laminated calcite in the exozone of a zoarium between the adjacent ranges of zooecia'.) In transverse sections the primary plate enveloping fenestelloid zooecia shows on its outer side a dentate margin which is most strongly marked on the reverse: the side on which longitudinal striae are most marked. It is important to realize that the tooth-like projections seen in such sections are not spine-like but are thin flanges running the length of the undersurface of each branch. Each flange-like projection from the outer surface of the primary plate is encased by numerous laminae of the secondary skeleton, all of which faithfully follow its outline (Pl. 1, fig. 2). The image of the projection is therefore transmitted through the thick, outer, laminar tissue until the periphery of the branch is reached, where each convexity receives positive expression as a rib-like longitudinal 'stria'. The structure of range partitions in stictoporid ptilodictyoids is virtually the same, for they also consist of numerous superimposed, secondary laminae which are strongly convex outward from a primary origin in the form of a projection from the medial mesothecal layer.

The fundamental importance of longitudinal striae in fenestelloid wall structure is particularly evident in cases where normal branches degenerate at their tips into long, spinose structures devoid of zooecia. In that part of the branch bearing zooecia the striae are virtually restricted to the reverse surface, but beyond the point at which the zooecia terminate striae are strongly developed on *all sides* of the spinose tip. Transverse sections of such spiny branch terminations show a scalloped pattern similar to that seen in a section across a strictoporid stipe, except for the absence of zooecia. The inference to be drawn from this seems to be that although longitudinal striae are closely related to the presence of zooecial chambers they are in a sense even more fundamental to the colony than the zooecia. The axial, primary branch continuation in the above example, together with its outer casing of secondary laminae, are clearly colonial rather than zooecial structures. This is exactly the state of affairs on the reverse side of a normal fenestellid branch where, in spite of the absence of zooecia, primary and secondary tissue of *colonial origin* have combined to form longitudinal striae (Pl. 1, fig. 3). It would appear perfectly logical to deduce from this that, just as the striae on the obverse side of the spiny branch termination are clearly related to the zooecial walls which lie proximal to them, so the striae on the reverse of fenestelloid branches are indicative of the former presence of zooecia on that surface.

The obscure development of striae on the obverse of normal fenestelloid branches is also interesting. In *Polypora* and other multiserial forms such striae may be evident as low ridges, straight or sinuous, separating adjacent rows of zooecial apertures (Miller 1963, p. 169). They are the surface expression of longitudinal interzooecial walls. In *Fenestella* and other biserial forms, however, vestigial striae may be seen

either in association with the median keel (carina) or towards the lateral margins of the obverse surface in cases where zooecial apertures are placed close to the keel. Such striae commonly show a sinuous pattern, following the outline of the apertures, and are seen to be continuous with striae on dissepiments. If striae represent the surface expression of former interzooecial walls, and the presence of such striae immediately adjacent to one another reflects the suppression of the zooecia which formerly separated them, then two conclusions must be drawn:

That biserial forms such as *Fenestella* and its allies evolved from multiserial fenestelloids by the suppression of one or more rows of zooecia.

That in some cases it was the inner rows which were suppressed (leaving, for example, three longitudinal striae associated with the keel, as in *Levifenestella* Miller), while in others it was the outer rows, leaving closely spaced, parallel striae at the branch margins. It may therefore be that biserial fenestelloid genera are of polyphyletic derivation.

For the reasons stated it would seem that the features known as longitudinal striae, which characterize fenestelloid bryozoans and are particularly evident on the reverse side of branches, are relict structures. They appear to represent longitudinal walls which originally separated adjacent rows of zooecia that were at some phylogenetic stage suppressed. If this is so it must be concluded that such rows of zooids occupied the reverse side of branches in ancestral fenestelloids. It is therefore probable that the ancestral forms were bifoliate, the opposed sets of zooecia backing on to a medial platform-like structure or lamina, now represented by the flattened part of the primary skeletal component occurring beneath zooecial chambers. There appears to be a substantial body of evidence suggesting that the fenestelloid basal plate and the ptilodictyoid mesotheca are homologous structures.

Skeletal rods, carinal nodes, and allied structures

Skeletal rods are structures which are considered to be an integral part of the mineralized colonial wall of those bryozoan groups in which they occur (Tavener-Smith 1969a, p. 290; Tavener-Smith and Williams 1972, p. 135, etc.). In fenestelloid genera they are almost invariably situated along the crests of longitudinal striae where they commonly form well-defined single or multiple rows (Pl. 1, fig. 4). Likewise, in ptilodictyoids most skeletal rods are situated along the range partitions, though the arrangement is less regular than in fenestelloids (Pl. 2, fig. 5). If fenestelloid longitudinal striae represent vestiges of formerly existing interzooecial walls then the position of acanthopores (structurally identical with skeletal rods) in many genera of the Trepostomata is the same, for these also occur as minute prominences along the distal extremities of interzooecial walls. In terms of the range of acanthopore size, fenestelloid skeletal rods (Pl. 1, fig. 6) with diameters of 10 μm –20 μm , must be considered micracanthopores.

The carinal nodes in *Fenestella*, *Fenestralia*, *Moorephyloporina*, and other genera have posed problems as to their origin and affinities for many years. Likharev (1926, p. 1032) observed that carinal nodes showed the same basic microstructure as the rest of the branch skeleton around zooecial chambers, and Elias and Condra (1957, p. 19) concluded that 'carinal spines are part of the primary skeleton or colonial

plexus in Fenestellidae'. Miller (1961, p. 223) suggested that carinal nodes might possibly be homologous with acanthopores in the Trepostomata. The writer is in general agreement with all these observations. Carinal nodes in the Fenestellidae are situated along the medial keel or carina on the obverse of branches. Consideration of its position and internal structure leaves no doubt that the keel corresponds in all respects except size with interzoecial walls separating rows of zooecia in multiserial genera such as *Polypora*. In other words, it is a preferentially developed interzoecial wall—the *only* longitudinal wall of this kind present in biserial fenestellids—and as such it is homologous with longitudinal striae on the reverse of branches, and with range partitions in the Ptilodictyoidea. In *Polypora* and associated genera corresponding structures are seen on some specimens as low, commonly sinuous ridges between zooecial rows. Such ridges may also bear nodes along their length, but these are always less prominent than in biserial forms with a single median keel.

Carinal nodes in biserial fenestellids are of similar structure to skeletal rods in that they consist of a roughly tubular core of granular tissue buttressed by a peripheral zone of closely spaced secondary laminae. The primary material of the core is in direct continuity with that of the axial branch skeleton and the secondary laminae are deflected distally to constitute a clear cone-in-cone structure around the core. One minor difference between the structure of carinal nodes and skeletal rods is that in the former the primary axial core may show slender off-shoots directed distally at oblique angles. These off-shoots penetrate the enveloping secondary laminae (Pl. 1, fig. 5). As a result of this arrangement medial longitudinal sections of carinal nodes may present an appearance reminiscent of a Christmas tree. The relationship between the primary core and flanking laminae is always gradational (Tavener-Smith 1969*b*, p. 94).

Carinal nodes therefore correspond structurally with skeletal rods and also with acanthopores. They must, however, in terms of size, rank as megacanthopores of outstanding stature. Smaller nodes, which may be present on interzoecial ridges in *Polypora* and other multiserial fenestellids, must also be considered to be megacanthopores and homologous structures are found in the Ptilodictyoidea and Rhabdomesoidea. To summarize: it may be said that the carina and its nodes in biserial fenestellids represent the strongly preferred development of a longitudinal interzoecial wall, together with its skeletal rods.

The development of diversified structures from the distal ends of carinal nodes represents a sophisticated trend in biserial fenestellid stocks and several variations of this kind appeared at a relatively early stage in the evolution of the group. They include the geometrically patterned superstructures of *Hemitrypa*, *Loculipora*, and *Isotrypa* which undoubtedly fulfilled a protective function, preserving the delicate extruded tentacles of the lophophore from the attentions of predatory organisms. Structures such as these provide impressive illustrations of the capacity for evolutionary experiment and diversification in the vigorously developing fenestellid stock. The case of *Cervella*, a later genus of Permian age, is different. Here it is possible that the exotic appearance, due to the multiple branching of the distal ends of carinal nodes, is a gerontic feature indicating the senescence of this branch of the stock.

Whereas the function of megacanthopores and their ramifications must have been essentially protective (and this applies equally to the Trepostomata: see, for example,

the strong apertural spines in *Tabulipora*) the same cannot be said of micracanthopores. It has been suggested elsewhere (Williams 1956, p. 252; Tavener-Smith 1969a, p. 292) that skeletal rods may represent surfaces of attachment for tendons which served to anchor and stabilize the external mantle, a possibility that receives support from the common occurrence of those structures as circlets around the rims of zooecial apertures (Miller 1963, pl. 23, fig. 3). Due to the repeated extrusion and retraction of the lophophore it is in precisely this position that stabilization of the outer mantle tissue would be most necessary, and indeed within the Trepostomata this is the only situation in which micracanthopores occur. The more general distribution and much more numerous occurrence of skeletal rods in the Fenestelloidea may well be associated with the presence of far more extensive areas of branch surface between zooecial apertures. Over these areas it would be essential for the external mantle to be held firmly in position. Finally, it is perhaps relevant to add that the only cases of the occurrence of skeletal rods in bryozoa outside the Trepostomata and Cryptostomata known to the writer occur in the cyclostomatous families Lichenoporidae and Horneridae, in both of which an external mantle of soft tissue is known to exist (Borg 1926, pp. 195-197).

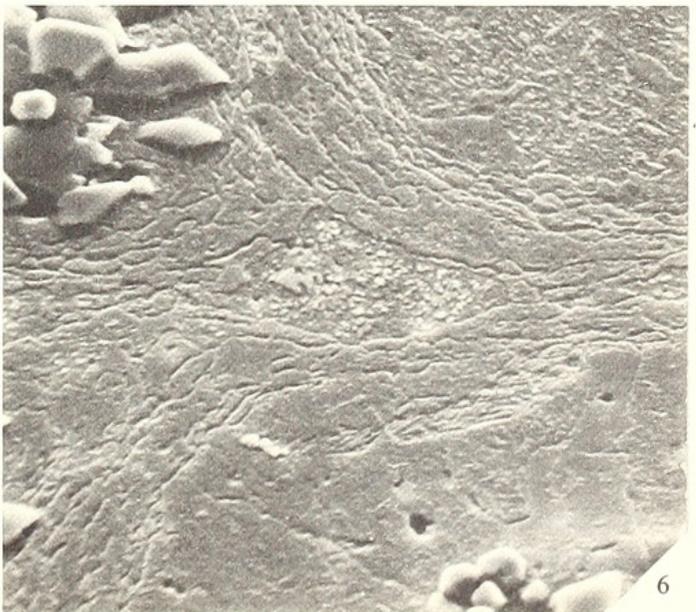
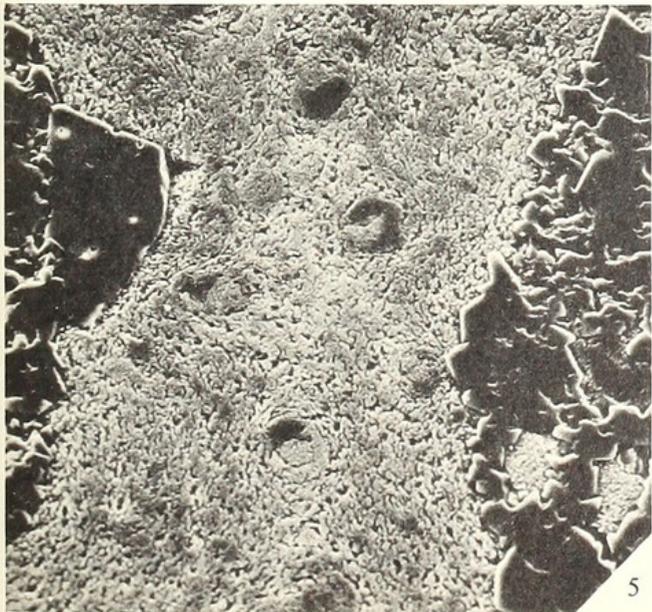
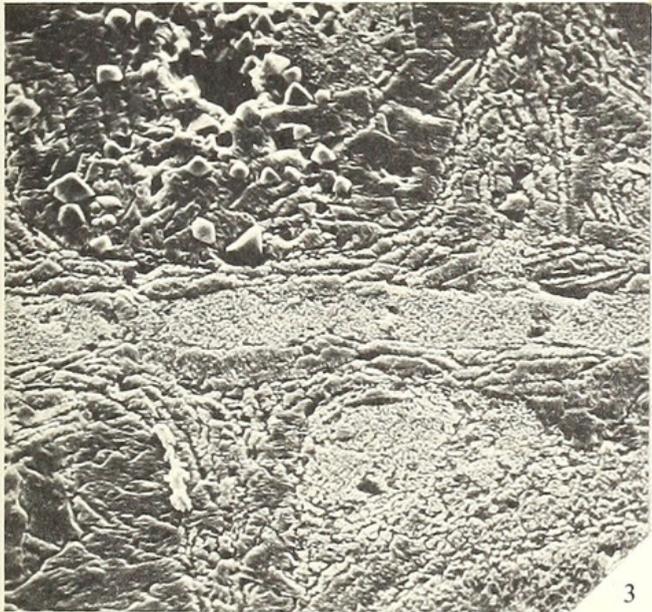
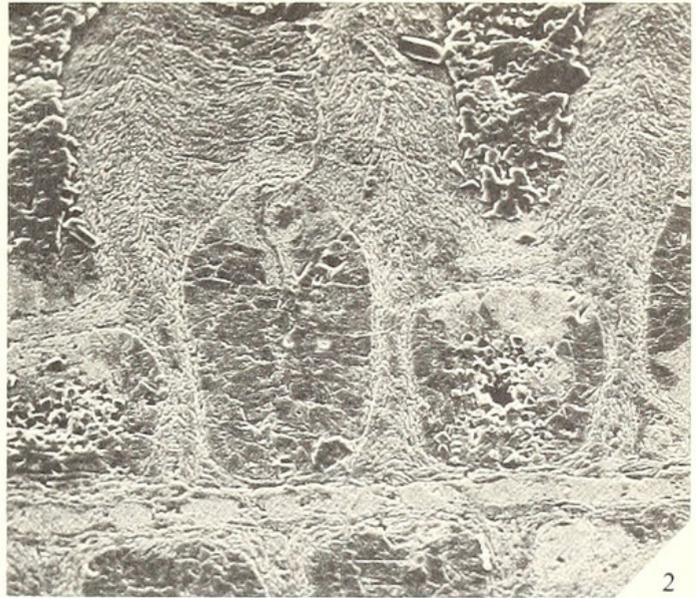
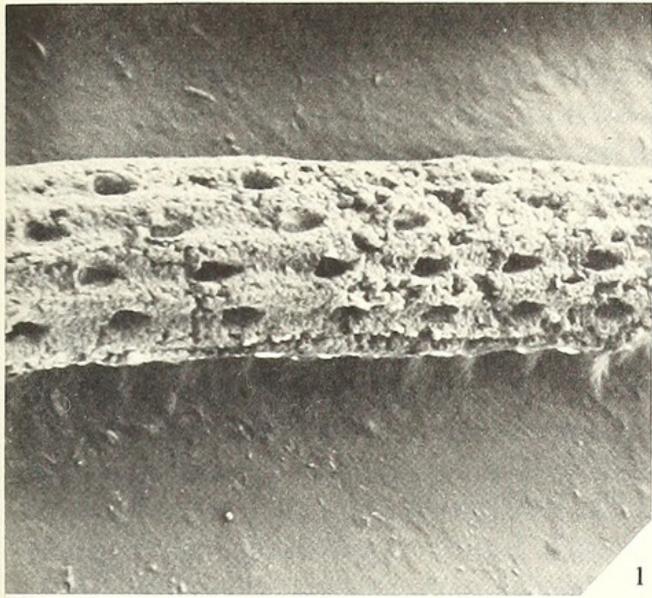
INTERPRETATION OF RELATIONSHIPS

The thesis adopted in this paper is that the origins of the Cryptostomata are to be found within the Trepostomata, or else that both stocks sprang from a common ancestry. There are too many morphological and structural similarities for it to have been otherwise. The common presence of acanthopores and mesopores; the occurrence of tubular zooecia showing endozonal and exozonal regions and bearing diaphragms; these and other features point clearly to a common origin. On the other hand, the general absence of ovicells and of mural pores set these two stocks apart from the other great Palaeozoic group, the Cyclostomata.

EXPLANATION OF PLATE 2

All figures are scanning electron micrographs of whole mounts or polished sections.

- Fig. 1. *Stictopora mutabilis* Ulrich. Ordovician (Decorah Shale) St. Paul, Minnesota. Part of colony showing prominent range partitions separating longitudinal rows of zooecial apertures, $\times 30$.
- Fig. 2. *Stictopora mutabilis* Ulrich. Ordovician (Decorah Shale), St. Paul, Minnesota. Part of transverse section of a frond showing zooecia and mesotheca. The latter has a medial layer of more or less discrete primary rods, $\times 260$.
- Fig. 3. *Stictopora mutabilis* Ulrich. Ordovician (Decorah Shale), St. Paul, Minnesota. Detail of fig. 2 showing that primary mesothecal rods locally coalesce to form a continuous medial layer, $\times 650$.
- Fig. 4. *Astreptodictya fimbriata* (Ulrich). Ordovician (Decorah Shale), St. Paul, Minnesota. Transverse section showing a primary rod of the mesotheca with an extension which enters medially into an adjacent interzooecial wall, $\times 2850$.
- Fig. 5. *Stictopora mutabilis* Ulrich. Ordovician (Decorah Shale), St. Paul, Minnesota. Near-surface tangential section of a branch showing distribution of skeletal rods along a longitudinal range boundary wall between zooecia, $\times 600$.
- Fig. 6. *Astreptodictya acuta* (Hall). Ordovician (Decorah Shale), St. Paul, Minnesota. Transverse section showing a lenticular primary medial rod with long axis in the mesothecal plane and a lateral prominence directed towards an adjacent interzooecial wall, $\times 1325$.



TAVENER-SMITH, fenestelloid bryozoa

Within the Cryptostomata it has been maintained (Tavener-Smith 1974) that the Rhabdomesoidea and Ptilodictyoidea represent separate lines derived from trepostomatous forebears. If this is so then the Order Cryptostomata is at least biphyletic. The origin of the Fenestelloidea remains to be accounted for and although Bassler (1953), by placing the Phylloporinidae within the Trepostomata, implied that fenestelloid ancestors were in direct relationship with that Order, his contention is not accepted here. Nor does it seem likely that fenestelloids were derived from the Rhabdomesoidea for the long, tubular, diaphragm-bearing zooecia of that group with their well-defined endozonal and exozonal regions are primitive in comparison even with relatively early fenestelloid chambers. In addition, the colonial architecture of the Rhabdomesoidea, with its strongly ramose habit of cylindrical branches and zooecial apertures opening over the whole surface, suggests no affinity with the fenestelloids. Finally, the organization of proliferation fronts, involving in the rhabdomesoids a single 'common bud' at the distal apex of each branch, is difficult to reconcile with that of the Fenestelloidea (Tavener-Smith 1973, p. 356). Another significant difference is the fact that basal attachment discs are unknown in the Rhabdomesoidea though they are the rule among fenestelloids (Cumings 1905, p. 171).

On the other hand, there is a strong body of evidence suggesting a close link between the Fenestelloidea and Ptilodictyoidea. At superficial level, considering only gross morphology, it is not difficult to assemble a continuum of forms which bridge the gap between the two sub-Orders. Typical members of the Ptilodictyoidea form colonies consisting of erect, broadly flattened bifoliate fronds. In a few genera (e.g. *Clathropora*) the frond margin, which in typical ptilodictyoids is smoothly curving, underwent differential growth resulting in a number of stubby prominences which gave rise to a dentate pattern. In *Clathropora* these prominences subsequently reunited to form a crudely fenestrate frond. In other cases, such as *Taeniodictya*, the prominences grew onward without uniting and resulted in a number of flattened, ribbon-like branches. In both genera the branches are bifoliate, with zooecia arranged back to back against a localized and restricted mesotheca.

The phylloporinid genus *Pseudohornera* shows a similar colonial form and internal structure to that described for *Taeniodictya*, with the important modification that zooecia are stunted and obsolescent on one side of the medial lamina. On that surface, however, the interzooecial walls persist as clearly defined linear ridges identical in structure and situation with the longitudinal striae of other fenestelloids. The persistence of vestiges of zooecial structures is also seen on the reverse side of branches in other fenestelloid genera, for example *Fenestrapora* and species of *Septopora*, in the form of scattered pits or 'accessory apertures' which open into blindly ending tubes.

From a form such as *Pseudohornera* it is a short step to the generalized fenestelloid form. This was achieved by the loss of remaining zooecial elements on the reverse side, the consolidation of tubular zooecia into more compact shapes (with the concomitant loss of diaphragms), and the organization of branches into a sub-parallel pattern. At first sinuous branches were connected laterally by anastomoses but, as evolution proceeded and branches straightened, the points of anastomosis were drawn out to form specialized, bar-like dissepiments. This enabled branches and the

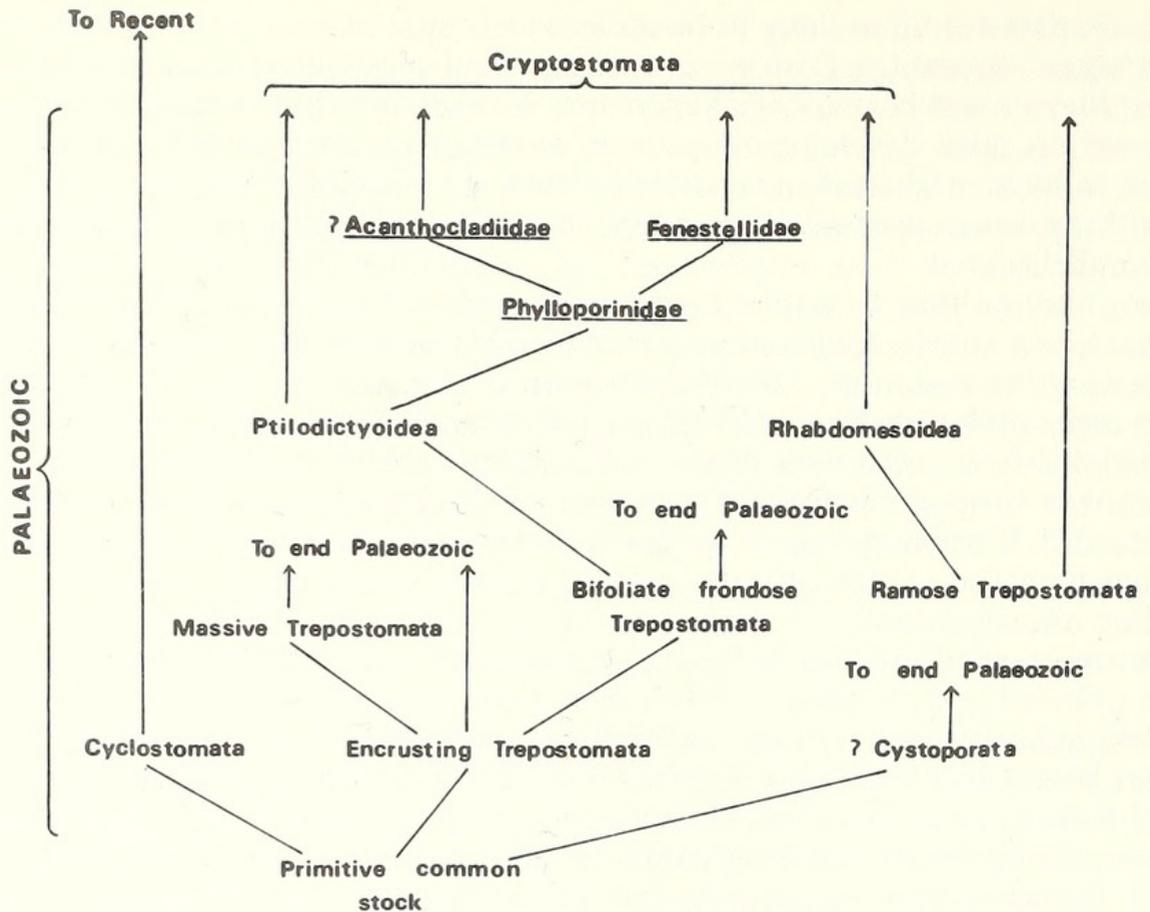
zoecial apertures upon them to be more widely spaced, which probably conferred an ecological advantage. Dissepiments within the Fenestellidae are invariably sterile, that is, they do not bear zoecial apertures. Connecting struts which do carry apertures were a later development and are confined to the Acanthocladiidae. They appear to have originated quite independently as a result of the union of opposed lateral branches in pinnate forms where the main branches grew in close proximity and parallelism.

The objection that a morphological series such as that outlined above cannot be shown to be a stratigraphic one and therefore has no evolutionary significance does not destroy the argument, for what *has* been demonstrated is that the *potential* for such a series undoubtedly existed. This is important, for the emergence of the earliest fenestelloid stocks with their distinctive characteristics probably took place before the bryozoa formed mineralized skeletons and is therefore not documented in the fossil record. It is commonplace, however, that evolutionary patterns may be repeated through time and in this case the pattern of later events contributes to an understanding of earlier ones.

The structure of the medial lamina of *Pseudohornera* appears identical with that of the ptilodictyoid mesotheca, with which it corresponds in situation and function. It seems logical to believe that such a structure was the forerunner of the primary skeletal layer beneath zooecia in fenestelloid branches, to which it gave rise by the loss of zooecia on one surface. The interzoecial walls on that side have persisted as vestiges, giving rise to the longitudinal striae on the reverse of fenestelloid meshworks. There is, therefore, also a distinct and strong case resting, not on any morphological series, but upon the generalities of skeletal structure, for believing that the sub-Order Fenestelloidea (including the Phylloporinidae) was derived not from the Trepostomata but from early ptilodictyoid stocks. Accordances of zoecial shape and structure support this contention, for fenestelloid chambers have notably stronger affinities with those of the Ptilodictyoidea (many of which show a tendency towards a consolidation in length and reduction or loss of diaphragms) than with chambers of the Rhabdomesoidea or Trepostomata. Zooecia of the Phylloporinidae, with their tubular shapes, diaphragms, and the presence of mesopores in some forms, provide all necessary morphological intermediates between ptilodictyoids on the one hand and the Fenestellidae and Acanthocladiidae on the other.

There can be little doubt that phylloporinid cryptostomes represent an early fenestelloid stock (text-fig. 5) for they manifest an amalgam of primitive and advanced characteristics. That they are themselves true fenestelloids is made plain by their possession of the two critical diagnostic features, namely, a unifoliate frond with longitudinal striae on the reverse side and the presence within branches of a primary axial complex which also forms an investment around zoecial chambers.

The loss of zooecia from one surface of branches was of crucial importance in the emergence of the distinctive fenestelloid growth habit, and contributed significantly to the success of the group. It permitted the increased secretion of skeletal substance on the reverse side of branches which, in conjunction with the longitudinal ribbing of the striae, resulted in greater mechanical strength. This in turn permitted an increase in the size of fronds which was, in the most successful forms, accompanied by a straightening of branches and reduction in branch width (following a reduction of



TEXT-FIG. 5. Suggested phyletic relationships between bryozoan groups during the Palaeozoic era. The three families comprising the Fenestelloidea are underlined.

the number of zoecial rows on a branch). Larger fronds extending higher above the substrate and composed of slender branches bearing more widely spaced zoecial apertures represented ecological advantages which must have contributed powerfully to the immense success of the biserial fenestellids. *Fenestella*, in its sheer numerical abundance, reflects the acme of success among fenestelloids in responding to the demands of environment.

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