

## SKELETAL STRUCTURE AND GROWTH IN THE FENESTELLIDAE (BRYOZOA)

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**ABSTRACT.** Branch walls in fenestellid bryozoans are of threefold construction: a granular layer is flanked by inner and outer laminated tissue. The granular component resulted from continuous deposition, while the laminated tissue was formed by regular, discrete additions. Skeletal rods originate from the granular layer and traverse the laminated skeleton.

The granular layer pre-dates the laminated tissue, and use of the terms *primary* and *secondary* is therefore justifiable. The primary and outer secondary zones were secreted by an external (or colonial) mantle, while the inner secondary tissue was laid down by the zooidal ectoderm. The external mantle probably originated as an ectodermal evagination from the vestibular region of the ancestrula, and was subsequently associated with the growth of all colonial structures.

The wall arrangement in carinal nodes, dissepiments, and spinose outgrowths is similar to that of branches, but the inner secondary layer is absent. These structures had no internal communication with zooecial chambers. Massive colonial supports such as those of *Lyropora* and *Archimedes* consist entirely of secondary tissue formed by localized secretion from the external mantle. Calcite deposits of this kind also played an effective part in the repair of structural damage to the meshwork.

FOR a long time species of *Fenestella*, the commonest and best known of fenestrate cryptostomes, were recognized by external features alone. The genus is characterized by a net-like expanse of regularly spaced branches, connected by short, transverse bars known as dissepiments. The dissepiments in *Fenestella* are 'sterile', that is they bear no zooecia, while the branches contain two rows of zooecial chambers. Each zooecium has an aperture, and all apertures open on one side of a frond, the obverse, 'celluliferous' or frontal side. On this surface there is a longitudinal median carina or keel, which in most species is ornamented by uniserial nodes. Branches may show longitudinal ridges and grooves ('striae' of earlier authors), particularly on the reverse, and may also give rise to a variety of spinous outgrowths. Colonies are attached to the substratum by a massively calcified basal holdfast.

Nicholson was among the earliest to section fossil bryozoa, and he published the first illustration of the microstructure of the fenestellid wall (Nicholson and Lydekker 1889, p. 608). He observed that, '... in the family of the Fenestellidae a portion of the polyzoary consists of dense calcareous tissue which exhibits under the microscope a finely punctate appearance. When a sufficiently thin section of this punctate layer is prepared and examined the tissue is seen to be penetrated by innumerable exceedingly minute tubuli ... which run at right angles to the surface of the polyzoary.'

Ulrich sectioned many species of *Fenestella* and related genera and recognized two principal constituents in the skeletal tissue. These were, '... the original basal or germinal plate', and '... the subsequently added layers of calcareous tissue' (1890, p. 352). He pointed out that the two are generally quite distinct from one another, especially when viewed in transverse thin sections of branches. Ulrich did not describe the structure which he called the germinal plate in detail, but observed that, 'almost invariably the lower side of the plate presents a number of tooth-like projections that represent transverse sections of former longitudinal striations'. Although Ulrich said nothing

about the upper side of the germinal plate his illustrations (1890, pl. 54–5) clearly imply that it continued upward between zooecial chambers as a median wall which projected above the obverse surface of a branch to form the carina. The skeletal tissue that enveloped the germinal plate was variously referred to by Ulrich as 'schlerenchyma', 'layers of calcareous tissue', 'dense portions of the zoarium', 'stony deposit', and 'secondary deposit'. He described it briefly thus (1890, p. 353): 'A finely laminated condition prevails throughout, and very delicate vertical tubuli penetrating the laminae can, as a rule, be demonstrated. The tubuli again are generally arranged in series and, though varying in number, are always abundant.'

Simpson (1895, p. 434) described 'tubuli' visible in sections of the thick secondary deposit on the reverse of *Fenestella* but considered them to be merely part of the ornamentation. He did, however, make an important observation, namely that, 'the deposit of calcareous matter continues after the animals in the immediate vicinity are dead, and all ornamentations of the surface are obliterated'. So great, he said, may be the difference in appearance between the younger sculptured portions and the older, smoother parts of a fenestellid frond, 'that, seen in different fragments they would be considered as belonging to two species'.

Cumings (1904), in his classic paper on the development of some palaeozoic bryozoa, was concerned with the pattern of budding in the early stages of colony formation rather than with wall structure. Nevertheless, he distinguished the main skeletal components and made important observations on the origin of the carina in *Fenestella*. He said (p. 64) that, 'the primary carinae first make their appearance in the metanepiastic stage (when the initial circle of zooecia is completed), and are intimately related to the basal plate. In fact the carina seems to originate as an upgrowth or fold of the basal plate'. He pointed out that the carina is a 'triple structure', the axis of which is an upward extension of the basal plate. This is flanked on either side by layers of, 'dense, punctate schlerenchyma' which are a continuation of the outer, secondary skeleton of the branch. These may cause the carina to attain, 'great size and prominence' (1904, p. 61).

Studies of the microstructure of the wall in *Fenestella* and related genera by Russian workers have added greatly to our knowledge of these features. Likharev (1926) examined in detail the wall structure of certain *Fenestella*. He found that the skeleton consisted of outer and inner parts, the inner being lighter coloured. He noticed that the light substance, in addition to forming the germinal plate on which zooecia rested, enveloped them from the sides and formed their roof. It also formed the axial part of dissepiments. The tubercles and outgrowths upon a carina also had a core of 'light substance comparable to that which surrounds the zooecia; and they are covered by a darker peripheral layer' (free translation from the Russian—p. 1025). Likharev's inner layer of light substance corresponds with Ulrich's basal or germinal plate, and his outer, darker or 'porous' layer to the secondary schlerenchyma.

Shulga-Nesterenko (1931, 1941) made a careful investigation of the microstructure of encrusting tissue in *Fenestella* and related genera, and her findings represent an important advance towards an understanding of the fenestrate skeleton. She concluded that 'pores' in the outer substance of a branch were the means by which amorphous calcium carbonate was conveyed from zooids to build the walls. In support of this argument she mentioned the existence of such pores not only between adjacent zooecia, but also directed outward in the wall facing fenestrules. She suggested the presence of a capillary

system permeating branches and composed of elements of two kinds. These were the 'capillary canals' lying parallel to the length of a branch and situated within the striae, ribs, or corrugations on the underside of the germinal plate, and the 'capillary tubules' which originated near the 'crests' of germinal plate ribs and passed through the secondary skeleton to the periphery of a branch. The last-named structures, clearly evident in suitably thin sections (Pl. 54, figs. 1, 2), are the 'tubuli' of earlier authors. Shulga-Nesterenko considered them to be hollow pores or canals that conveyed 'skeletal substance' from zooids to the branch periphery where it was 'deposited in the form of foliaceous, undulating layers constituting the tissue of branches and dissepiments' (1931, p. 77). This author, therefore, introduced the idea that in the Fenestellidae successive skeletal increments were added from the *outside* and over the general surface of a growing branch. Her ideas subsequently underwent some modification, for she later stated (1949, p. 38) that she had abandoned her earlier interpretation of the capillary tubules as carriers of lime to the outer surface of branches, and instead supposed that they conveyed nutrition to a peripheral ectodermal epithelium, the latter precipitating the outer skeleton of the colony. She seems, however, to have envisaged a single external epithelium *immediately overlying* the skeletal substance, which was not the case.

Condra and Elias (1944) in their revision of *Archimedes* (Hall) rejected Shulga-Nesterenko's ideas on the formation of the secondary skeleton. Instead they suggested that (pp. 23 et seq.) *Archimedes* was a consortium of *Fenestella* (forming the spiral meshwork) and an alga-like organism that contributed the axis or screw. On p. 25 they 'suggest that *Archimedes* is made of *Fenestella*, and that the encrusting tissue about it belongs to a different organism in a symbiotic relationship'. The same explanation was proposed for the presence of thick secondary skeletal deposits in other cryptostome genera.

The same authors presented somewhat modified ideas in their (1957) account of '*Fenestella* from the Permian of West Texas'. They recognised three basic skeletal components (pp. 25-45) which were: (1) the colonial or germinal plexus, essentially the germinal plate of Ulrich; (2) laminated schlerenchyma, 'a secondary calcareous deposit whose laminae correspond to the rhythmic growth lines of brachiopods, molluscs and other invertebrates'. This is the substance described in the earlier paper as 'phytomorphic tissue', and supposed to be of algal origin; (3) transverse 'spicules or filaments'. These are the tubuli of early workers and 'capillary tubules' of Shulga-Nesterenko. Elias and Condra (1957, pp. 20-1) maintained, however, that these structures were solid and not axially perforate. The colonial plexus was described as follows (op. cit., p. 29): 'the principal (or basal) cylindrically rolled germinal plate extends upward over all external surfaces of zooecial chambers and also sends out a thin central wall into the narrow space between them. Radial ribs rise from it along the reverse of a branch and along its sides, although the lateral ribs are not as tall as the dorsal ribs. The central platy wall that meanders between the two rows of zooecia usually expands above the latter and furnishes the core of the structure known as carina'. The authors (op. cit., p. 38) drew attention to the fact that, owing to the continuous, foil-like nature of the colonial plexus, the calcareous wall between adjacent zooecia is common to both and not separated into discrete parts. This offers an exact parallel with the general condition in Cyclostomata (Borg 1926*b*, p. 192) but is apparently contrary to that in Cheilostomata (Levinsen 1909, p. 11).

With regard to the laminated outer, or secondary skeleton, it was proposed (Elias and Condra 1957, p. 37) that this, 'was secreted by the ectoderm that stretched externally over the whole zoarium, not by a special "capillary system"'. The writers thus expressed their continued disagreement with Shulga-Nesterenko as to the structure and development of the zoarial wall, but had moved closer to the ideas of Borg (1926*b*) and Harmer (1934) on that subject. Although they no longer considered the laminated secondary skeleton itself to be of algal origin, they continued to regard the 'tubuli' traversing the skeleton in that light. It was suggested (*op. cit.*, p. 44) that these structures were originally algal hyphae or filaments embedded in the outer skeleton of the bryozoan by an algal symbiont. In support of this idea it was contended that the 'spicules', as Elias and Condra preferred to call them, originated on the outer surface of a fenestrate branch and penetrated inward; that they traversed the laminated skeleton only and did not enter the colonial plexus; and that they had no direct connection with the 'striae' or ribs on the reverse of the latter (pp. 41-3). These things being so, said Elias and Condra, it was impossible for the 'spicules' to have fulfilled the functions attributed to them by Shulga-Nesterenko.

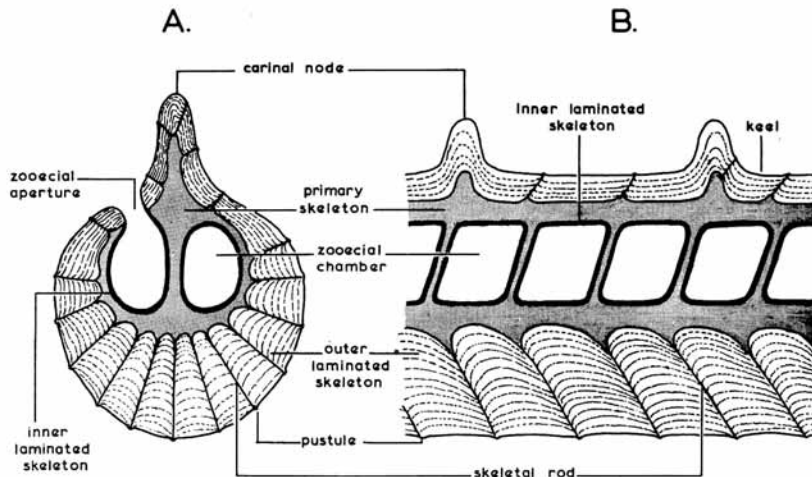
Borg's exhaustive study of cyclostome morphology added much to the knowledge of that subject, not least in respect of skeletal structure. He had the advantage of dealing with modern forms, and was able to examine the soft parts in relation to their calcareous investment. Many of his findings may have general application within the bryozoa, and by careful extrapolation much can be learned about the origin and development of the skeleton in extinct groups such as the Fenestellidae.

Borg (1926*b*, p. 191) found that in most cyclostome stocks the zoecial wall is composed of an external cuticle, a calcareous layer, ectoderm and mesoderm (in that order), the first two being secreted by the ectodermal epithelium of a zooid. In the families Horneridae and Lichenoporidae, however, the structure is more complex and, according to Borg (1926*a* p. 595, text-fig. 6; 1926*b*; p. 196) there are, in fact, two separate walls, an outer one of cuticle lined by epithelium and mesoderm, and an inner, calcareous wall with ectoderm and mesoderm on either side. They are separated by a slit-like space and, since this has mesodermal layers on both sides and is in communication with the zooidal coelom, it must be regarded as a coelomic cavity. Borg termed this the 'hypostegal coelom' because it is extra-zoecial and, though very thin, bounds the colonial skeleton on all sides. The outer membrane of cuticle lined by ectoderm and mesoderm is also common to the whole colony.

Borg (1926*b*, pp. 196-7) pointed out that in the Horneridae and Lichenoporidae, particularly the former, the calcareous wall may attain a remarkable thickness. He went on to say that the zoarial exterior in these families presents, 'an uneven surface with ridges and furrows, contrary to the condition found in other Cyclostomata; in numerous species of *Lichenopora* bristles or spines of calcareous matter are found on the outside of the zoarium. The origin of all these formations is easily understood when one realises that the calcareous layer is covered with an ectodermal epithelium capable of secreting calcareous matter'. In a paper published posthumously Borg (1965) extended his concept of the 'double wall' to certain extinct cyclostome groups, notably the Fistuliporidae and Ceramoporidae, and to some of the Trepostomata.

## WALL STRUCTURE

The branch wall of *Fenestella*, seen in thin section, consists of three basic parts. These are (text-fig. 1), from the interior outwards: a narrow, laminated zone which lines zooecial chambers; an apparently clear and structureless layer enclosing the chambers and their lining; and a wide, outer, closely laminated zone traversed by numerous, slender, radially disposed, skeletal rods.



TEXT-FIG. 1 Generalized structure of a branch in *Fenestella*; A, transverse section; B, longitudinal section.

The middle layer is the germinal plate, or colonial plexus of earlier workers, and has generally been considered the fundamental component of the branch wall. It is less strongly developed than the outer laminated zone, but is invariably present as a continuous structure, completely enveloping zooecial chambers and extending above them as the core of the carina. A distinctive feature is the total absence of laminar structure. Under the electron microscope this wall component has a granular or rubbly appearance (Pl. 55, figs. 3, 5), and differently orientated sections show that the calcite particles, though varying somewhat in shape, are roughly equidimensional. Particle shapes and relationships suggest the former presence of intergranular material, probably proteinous, and this may originally have formed a sheath around each calcite crystal. Diagenetic effects in some cases obscure the granular texture, which is the main characteristic of this layer, so that it appears to be of unitary construction, even under high magnification (Pl. 56, figs. 1-4).

Borg's (1926b) work suggests that there are important parallels between skeletal characteristics in certain cyclostome genera, notably *Hornera*, and those of fenestrate cryptostomes. For this reason an examination was made of wall structure in that genus. In *H. frondiculata*, a living species, the basic arrangement of wall components was found

to be essentially as in *Fenestella*, and a granular layer showing all the features mentioned above occurs in a corresponding structural position (Pl. 55, fig. 2).

The outer, laminated zone of a fenestellid branch is in most cases strongly developed, particularly on the reverse side (Pl. 52, fig. 1; Pl. 53, fig. 1). Each lamina consists of a thin, sheet-like mosaic of calcite particles which show similar narrowly elongate shapes in transverse or longitudinal sections, and must therefore be of a platy nature. Adjacent laminae (and plates within a lamina) are clearly defined, and were probably separated in the living condition by protein films (cf. Wilbur, 1960, p. 16, fig. 2). The relationship of individual calcite plates to cells of the secretory epithelium is, of course, unknown but, to judge from the diameter of the former (commonly 10  $\mu\text{m}$  to 15  $\mu\text{m}$ ), it is unlikely that this was on a one-to-one basis. In *H. frondiculata*, which shows a virtually identical arrangement of plates in the outer laminated skeleton to that of *Fenestella*, there is evidence that two or more calcite crystals seeded and grew within the limits of a single plate. It appears that fusion of material from several growth centres was necessary for the formation of a plate, which must therefore have transgressed cell boundaries. Observed differences in the area of plates may reflect the number of growth centres involved in their formation. Similarly, the apparent absence of a consistent geometrical pattern between plates, such as that found by Williams (1968) in brachiopods, is perhaps attributable to the lack of a simple relationship between plates and epithelial cells.

Skeletal laminae in the outer zone have been recognized by earlier authors (e.g. Elias and Condra 1957, p. 26) as growth phenomena, and Williams (1968, pp. 19, 43) suggested that in brachiopod shells a diurnal periodicity is represented by similar features. Crude estimates based on the number of laminae commonly present on the reverse of a *Fenestella* branch (in the order of several hundreds) and the approximate longevity of the most closely comparable living bryozoa, such as *Hornera*, suggest the possibility of a similar relationship in fenestrate cryptostomes.

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EXPLANATION OF PLATE 52

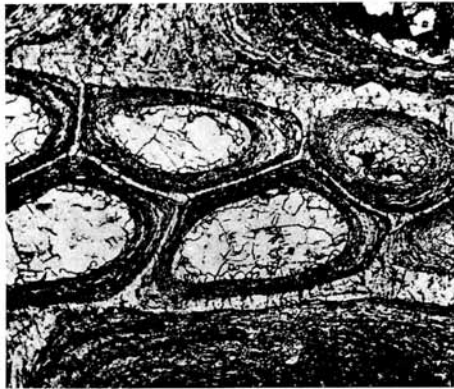
- Fig. 1. *Polypora* sp., Pennsylvanian (Upper Coal Measures), St. Joseph, Missouri. U.S.N.M. 93706,  $\times 100$ . Transverse section of branch showing inter-zooecial walls with core of primary material (light) flanked by inner laminated skeleton (dark). Main wall consists of primary tissue (light) with 'toothed' under side grading into thick outer laminated zone (dark).
- Fig. 2. *Archimedes* sp., Mississippian (Chester group), West Lighton, Alabama. U.S.N.M. 2379,  $\times 170$ . Longitudinal section of branch showing tripartite construction of inter-zooecial walls and well-developed primary layer (light) beneath chambers. Skeletal rods originating from primary layer penetrate the outer laminated zone (dark).
- Figs. 3, 4. *Archimedes wortheni* Hall, Mississippian (Warsaw Beds), Warsaw, Illinois. A.M.N.H., 7525/1A,  $\times 160$ . 3, Tangential section showing chambers with laminated lining. Primary tissue of inter-zooecial walls is continuous with that of main wall, which grades externally into outer laminated skeleton. 4, Shallow tangential section in colonial meshwork close to axial screw. Fenestrule is much reduced in size due to progressive deposition of secondary laminae on adjacent branches and dissepiments.
- Fig. 5. *Lyropora quincuncialis* Hall, Mississippian (Chester group), Chester, Illinois. U.S.N.M. 55742,  $\times 50$ . Longitudinal section of branch within colonial support. Apertural peristomes have extended distally into funnel-like features. White ellipses beneath branch are relics of fenestrules occluded by secondary growth.
- Fig. 6. *Archimedes wortheni* Hall, Mississippian (Warsaw beds), Warsaw, Illinois. U.S.N.M. 44140,  $\times 55$ . Longitudinal section of branch within colonial support. Peristomial funnels show narrow distal terminations. Pale, slender shaft rising from branch between two 'funnels' is an elongated carinal node.



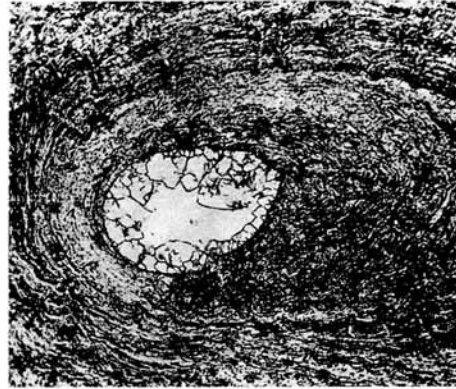
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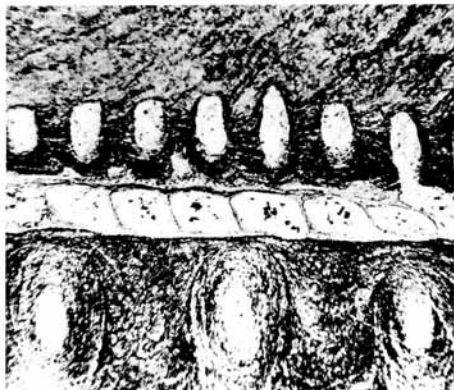
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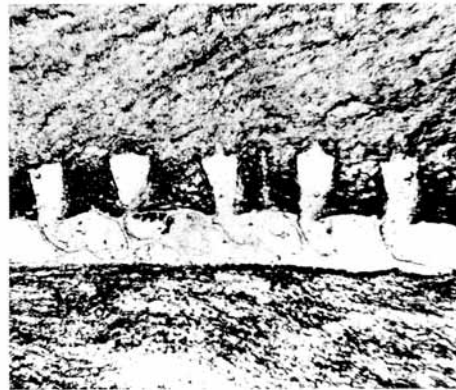
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If laminae were formed as successive skeletal increments laid down during equivalent periods of time, then the rate of growth was not constant. Minor fluctuations in this respect are implicit in width differences between laminae which, though not commonly evident, may be strongly marked. The rate of secretion was also, on occasion, differential from place to place within the same time interval, for though laminae commonly maintain a near-constant width, a rapid increase led, in some instances to the formation of a localized lens or wedge-shaped expansion (Pl. 55, fig. 4). Examination of such structures shows that their formation was attended by certain changes in the shape of component calcite particles. As the width of the lamina increased the platy character of these became less marked, and more stoutly tabular and even equidimensional grain shapes became common. At the same time the originally single-layered structure of the lamina was replaced by an increasingly disoriented arrangement due to the presence of less regularly shaped crystals within the lens. The resultant structure may bear close comparison with that of the granular skeletal layer, but a transitional relationship with adjacent laminae is nevertheless clear.

Earlier workers always considered the 'colonial plexus' and outer 'secondary sclerenchyma' to be quite separate entities, but electron micrographs show that the junction between them is gradational in the most complete sense (Pl. 55, fig. 3). Laminae immediately adjacent to the granular zone are poorly defined, discontinuous, and relatively widely spaced, while further from it they become progressively more strongly and regularly developed. A concomitant change in particle shape from granular to platy accompanies the transition, and follows a similar pattern to that noted in connection with 'lens formation' in the laminated skeleton.

Nevertheless, and in spite of the demonstrably transitional relationship between them, the essential contrast between laminar and non-laminar skeletal layers, with their respective platy and granular textures, is striking, and it is natural to speculate on their significance. It is reasonable to suppose, for instance, that if laminae represent the discrete addition of skeletal fractions (that is, intermittent deposition), then the absence of laminae implies that deposition was continuous. Similarly, since there is a change from platy to granular particle shapes in situations where the growth rate was clearly accelerated (for example, in lenses within the laminated skeleton) it is logical to associate granular shapes with a higher growth rate. Granted these premises, a conclusion seems justifiable, namely, that the granular skeleton was formed as the result of a single, continuous, relatively rapid episode of skeletal growth, while the laminated zone was the outcome of regular and discrete additions over a prolonged period. It would be in harmony with this conclusion to suppose that the epithelium secreting successive laminae was fairly static, since this might be expected to facilitate the formation of platy particles, with large area relative to thickness. In contrast, during the formation of the granular skeleton it might be supposed that the associated epithelium was steadily withdrawing, laying down as it did so particles with a thickness more nearly matched to their other dimensions. Why, under these circumstances, approximately equidimensional forms rather than prisms resulted is not evident, though it is possible that physiological controls of growth dictated regular pauses in calcareous secretion to permit the plasma membranes of epithelial cells to exude protein substance. Such an arrangement would have effectively prevented the formation of columnar crystals.

The inner wall element, that lining zoecial chambers, is of similar appearance and



construction to the outer laminated zone. The banding is, however, more regular (Pl. 55, fig. 1) and in this respect a comparison might be made with the microstructure of productid spines (Williams 1968, p. 42, pl. 22, figs. 3, 4). The inner layer is feebly developed in comparison with the outer zone of corresponding structure. This is readily explicable for, if the chamber lining was secreted from within as would seem most natural, its continued formation would have posed an increasingly urgent and potentially insoluble space problem. It seems likely, therefore, that when the chamber lining had achieved a certain thickness a physiological check operated, and deposition virtually ceased.

Thin partitions between adjacent zooecial chambers are essentially inward projections of the main wall. Each consists of a sheet of granular tissue, continuous with that of the 'colonial plexus', flanked by laminated skeletal material constituting part of the lining of adjacent chambers (Pl. 52, figs. 1, 3). Inter-zooecial walls are therefore bilaterally symmetrical, the laminated component on either side being generally narrower than the granular central layer. The junction between granular and laminated material is moderately well defined and not gradational. Electron micrographs (Pl. 55, fig. 5) show that in detail it is not clear-cut, however, for there is a tendency for adjacent particles of the two kinds to be welded together so that the actual junction is obscured. The character of laminae closest to the contact contributes to the non-gradational appearance, for these are wide and clearly delineated. Further from the junction they assume a progressively narrower and less strongly marked appearance. This arrangement implies that within the inner laminated zone skeletal growth proceeded most rapidly in the initial stages, later declining in inverse ratio to the rate at which the wall thickened. After no great period (to judge from the number of laminae generally present) the addition of further material appears to have ceased.

The above pattern, seen in fenestellid bryozoans, is also present in *Hornera frondiculata* (Pl. 55, figs. 2, 6) where inner laminated tissue was found in chambers close to the tips of growing branches. It is apparent from this that the layer is a fundamental wall component, and not merely a late stage deposit characterizing senility.

A notable feature of the fenestellid skeleton is the presence in the outer (but never the inner) laminated zone of numbers of slender, rod-like elements. These structures are

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EXPLANATION OF PLATE 53

- Fig. 1. *Polypora* sp., Pennsylvanian, Missouri. U.S.N.M. 93706,  $\times 47$ . Transverse section of branches and dissepiment. Primary core of latter is co-extensive with that of branches. Zooecial chambers at either end of dissepiment show attenuation in shape towards it.
- Fig. 2. *Archimedes* sp., Mississippian, Alabama. U.S.N.M. 2379,  $\times 80$ . Transverse section of branch within axial screw. Skeletal rods traversing secondary laminae arise from primary layer of branch. Latter is separated from zooecial chamber lining by a poorly defined zone of dark granules.
- Fig. 3. *Archimedes* sp., Mississippian, Alabama. U.S.N.M. 2379,  $\times 100$ . Longitudinal section of branch at margin of axial screw. Only the narrow, pale band immediately adjacent to zooecial chambers at top-left is primary tissue. Curvature of secondary laminae against skeletal rods is evident.
- Fig. 4. *Archimedes* sp., Mississippian, Alabama. U.S.N.M. 2379,  $\times 180$ . Transverse section showing emergence of skeletal rods at branch surface to form papillae.
- Fig. 5. *Polypora cestriensis* Ulrich. Mississippian (Chester group), Sloans Valley, Kentucky. U.S.N.M. 163,  $\times 37$ . Obverse of branch showing streaming of papillae around zooecial apertures.
- Fig. 6. *Polypora cestriensis* Ulrich. Mississippian, Alabama. U.S.N.M. 163,  $\times 37$ . Reverse view showing arrangement of papillae in bands. These curve onto a dissepiment in the top-centre part of the field.



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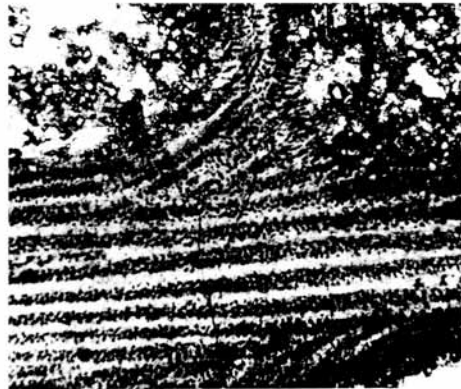
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evident in most transverse sections of branches, particularly on the reverse side, where they diverge from the ribbed lower surface of the granular skeleton ('colonial plexus') and traverse the outer, laminated zone to the periphery (Pl. 54, figs. 1, 2). On the underside of well-preserved branches parallel longitudinal rows of minute pustules, marking the points of emergence of rods, commonly follow the crests of ridges which correspond at the surface to ribs of the granular skeleton (Pl. 53, fig. 6). The rods are also present, though less noticeably, in laminated tissue elsewhere in the skeleton. On the obverse of branches their presence is indicated by sinuous rows of pustules which may be visible between zooecial apertures (Pl. 53, fig. 5). In certain fenestellid species (e.g. *Fenestella cingulata* Ulrich; *F. fenestratum* (Young and Young); *Polypora dendroides* M'Coy) every aperture is surrounded by a cirlet of pustules, each representing the termination of a skeletal rod. The rods are also present in carinal nodes, dissepiments, and spiny outgrowths, where they radiate from granular tissue in the core of the structure and penetrate the external secondary skeleton, giving a radiate or stellate appearance in transverse sections (text-fig. 3A).

Most earlier workers believed the skeletal rods to be hollow, hence the term 'tubules' by which they were known, though Elias and Condra (1957, pp. 20-1) maintained that they were solid 'spicules' of algal origin. There is no evidence to support the last idea, but of the solid construction there can be no doubt. Detailed examination under light and electron microscopes showed no signs of communication, past or present, between the inner ends of rods and zooecial chambers. This would have been a prime requisite, had the structures been tubules performing functions of the kind attributed to them by Shulga-Nesterenko (1941, 1949). Furthermore, if the structures had been hollow, an indication of this might have been provided by the presence of sparry calcite within them. But there is no trace of this. On the contrary, they are composed throughout of calcite particles similar to those of the primary skeleton. Nor is there anything resembling an outer wall and central cavity, which would have been expected if the structures had been tubular. On the other hand it is evident that, where they are in contact with rods, laminae of the outer skeleton are deflected distally to form a succession of close-fitting cones (Pl. 53, fig. 3; Pl. 56, figs. 1-4). This persistent deflection of laminae must have been induced by contact with an *already existing structure*, and this can only have been the solid rod itself. Finally, in the outer laminated skeleton of *H. frondiculata* there are rods that appear to correspond in all respects with those in *Fenestella* (Pl. 56, fig. 5), and it is certain that these are solid.

Detailed examination shows that the skeletal rods originate from the granular wall component, with which they are in direct continuity (Pl. 53, fig. 2; Pl. 54, fig. 3). In addition, it is possible that a few may have derived from lenses of granular-type tissue within the outer laminated skeleton, but this is uncertain. The cone-in-cone structure around rods, caused by the deflection of closely spaced secondary laminae, is continued to the branch surface where it is reflected in the formation of minute pustules (Pl. 53, fig. 4). The core and highest point of each of these is formed by the rod axis and, to judge from the curvature of adjacent laminae, it appears that growth of the rod was always slightly in advance of that of surrounding tissue. Because of the lack of lamination in the rods it is also likely that their growth was continuous, not intermittent. These rods may therefore be considered as solid structures which formed as a result of continuous growth from an infinity of points on the surface of the granular skeleton. They

are therefore integral parts of the colonial wall, and not external in origin as Elias and Condra (1957, p. 44) supposed.

The function of the skeletal rods is a matter for speculation, as they do not appear to have served any obvious purpose. Further study of living hornerids may in due course furnish an explanation. Meanwhile, it is relevant to draw attention to the remarkable similarity between these rod-like structures in fenestellid and hornerid bryozoans and the taleolae of strophomenide brachiopods (Williams, 1956, pp. 251-2; 1968, pp. 39-41). Williams considered it possible that taleolae played some part in strengthening the skeleton by rivetting together the secondary laminae they penetrated. He suggested, however, that their primary purpose may have been to provide anchorage points for tendons lying within the connective tissue. Subsequent discussion will show that such a function could have had great relevance in fenestellid colonies.

Morphological similarities between the skeletal rods of fenestellid bryozoans and so-called acanthopores in other cryptostome groups and the Trepostomata, are also worthy of comment. In both cases a 'tubule' with associated cone-in-cone structure penetrates laminated tissue in the peripheral part of the colonial wall. Future work may well show that these features are homologous.

#### RECONSTRUCTION OF GROWTH PROCESSES

In addition to comprehending the structure of the branch wall it is desirable to inquire into the nature and sequence of the processes responsible for its formation, for these may contribute to an understanding of colonial growth. It is generally recognized that calcareous skeletal structures in invertebrate animals are secreted by closely associated epithelia, and a reasonable *prima facie* inference would therefore be that the fenestellid branch wall was formed by the concerted activity of the ectodermal epithelia of zooids within it. Reflection shows that this is impossible, for the wall, particularly on the reverse side, is commonly many times thicker than the diameter of a zooid. For such a hypothesis

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#### EXPLANATION OF PLATE 54

- Fig. 1. *Archimedes* sp., Mississippian, Alabama. U.S.N.M. 2379,  $\times 45$ . Transverse section of branches at margin of axial support. Laminar structure of secondary tissue forming screw is prominently shown. Skeletal rods radiate from primary layer of branches. Strong carinal nodes are also present.
- Fig. 2. *Archimedes* sp., Mississippian, Alabama. U.S.N.M. 2379,  $\times 45$ . Oblique-longitudinal section of branch at margin of axial screw. Skeletal rods show variously oriented sections in passing towards periphery.
- Fig. 3. *Archimedes* sp., Mississippian, Alabama. U.S.N.M. 2379,  $\times 140$ . Longitudinal section of branch showing derivation of skeletal rods from primary tissue. An irregular band of dark granules separates primary layer from inner laminated zone lining zooecial chambers.
- Figs. 4, 5. *Lyropora quincuncialis* Hall, Mississippian, Illinois. A.M.N.H. 7873/1. 4, Transverse section of part of colonial support and enclosed meshwork. Skeletal rods radiate from branches through secondary tissue of which support is composed. Strong growth laminae visible on the right,  $\times 42$ . 5, Enlargement from previous figure, showing last branch connected by dissepiment to sterile spinose structure. Latter is probably a distal extension of a normal branch and consists of a primary core within secondary laminae,  $\times 160$ .
- Fig. 6. *Lyropora quincuncialis* Hall, Mississippian, Illinois. U.S.N.M. 55742,  $\times 60$ . Transverse section of branches within colonial support. Peristomial funnels are strongly developed and tall, slender carinal nodes are also present.



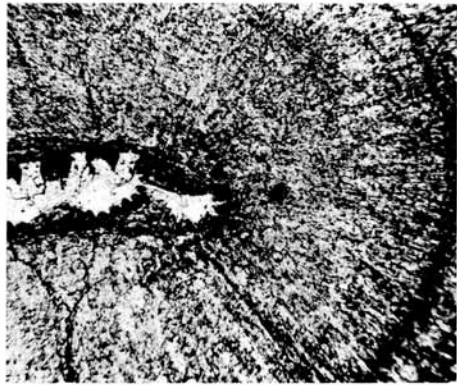
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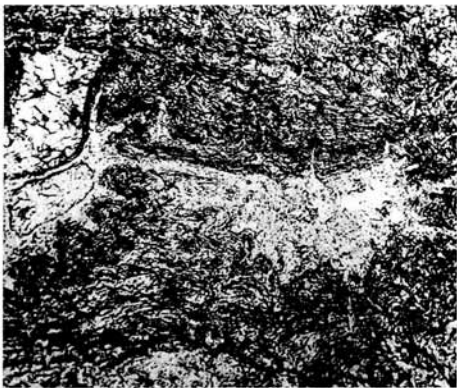
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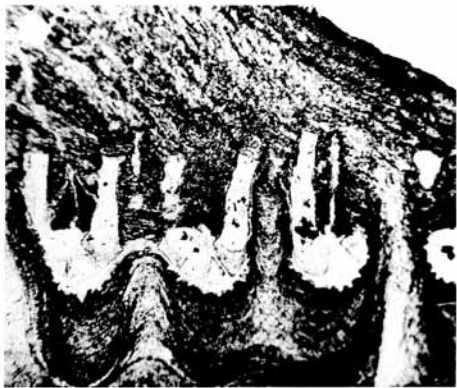
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TAVENER-SMITH, Fine structure of fenestellids

to be workable it would be necessary to suppose that the young zooid was excessively large, and that it progressively decreased in size during life: a clear absurdity. Also, the increase in thickness of the outer laminated skeleton with increasing age suggests that additions were made on the outer, and not the inner side of the branch wall. Further, the gradational nature of the contact between the two outer wall zones, their relative positions, and the fact that skeletal rods originating from the granular layer undoubtedly grew outward through the laminated tissue, indicate with certainty the earlier age of the former. It is also certain, however, from the structure of inter-zoecial walls, that the granular layer pre-dated the inner laminated tissue which lines zoecial chambers. It must therefore be concluded that granular tissue was the earliest formed wall component, and is *primary* in that respect. It will henceforward be referred to as the *primary skeleton*. The outer and inner laminated skeletal components were added later, and are therefore of *secondary* origin. The formation of secondary layers on either side of the primary skeleton indicates the former presence of *two* wall secreting epithelia, and from this it is logical to conclude that in the Fenestellidae the architecture of the wall and associated soft tissues followed a pattern similar to that observed by Borg (1926b) in certain Cyclostomata, notably *Hornera*.

According to that author three epithelial layers contribute to the formation of the calcareous wall in *Hornera*. Of these, the inner (or zooidal) epithelium encloses the polypide, lines the zoecial chamber and secretes the inner part of the calcareous wall. The outer (or colonial) epithelia are separated from the inner one by the thickness of the wall, and form a complete exterior investment of the colony. This external envelope will be referred to as the *external mantle*, for in skeletal secretion it fulfils similar functions to the mantle of brachiopods, from which it differs mainly in its external position. This structure, as described by Borg, is bounded by two epithelia, outer and inner, of which the last is immediately adjacent to the calcareous wall, and partly responsible for its formation. The outer mantle epithelium in most species of *Hornera* (Borg 1926b, p. 197) secretes only a cuticular sheath, but no calcareous substance. This outer layer may, by greatly increasing the area over which gaseous exchange is possible, have performed an important respiratory function (see Ryland 1968, p. 1041). Between the two-mantle epithelia Borg recognized a slit-like cavity which he designated the hypostegal coelom. This common external coelomic space is apparently in communication with the body cavities of individual zooids through a continuity beneath their apertures (Borg 1926b, p. 204) and by means of pores traversing the calcareous wall. It is, therefore, possible for an exchange of coelomic fluid to take place between hypostegal and zooidal cavities, and a circulation of this nature is the most probable means by which cells of the external mantle are nourished. In *Hornera*, as in most cyclostomes, mural pores in inter-zoecial walls further promote the interchange of coelomic fluid between zooids (Borg 1926b, p. 201).

Organization of the wall in fenestellid bryozoans strongly suggests the former presence of an external, membraneous colonial investment, and the suggestion is reinforced by a close similarity to the wall structure of *Hornera*, in which such a feature is known to exist. Other skeletal characteristics of the fenestellid group point to the same conclusion. It is a matter of common observation, for instance, that in the older, proximal parts of colonies secondary laminae encroached upon, sealed, and accumulated to considerable thickness over zoecial apertures. Such tissues must have been deposited from the

exterior, and cannot have been contributed by any single zooid. Again, holdfasts and colonial supports are massive deposits of outer laminated tissue which cannot have been secreted from within. Also, skeletal evidence relating to the growth and development of carinal nodes, dissepiments, and spinose outgrowths can only reasonably be interpreted in terms of calcite secretion from an external mantle.

These considerations appear to establish conclusively the former existence of an outer membranous investment of fenestellid colonies. The presence of such a structure has already been hinted at by Shulga-Nesterenko (1949, p. 38) and Elias and Condra (1957, p. 37), but the latter authors did no more than mention the possibility, while Shulga-Nesterenko was mistaken in supposing that only a single outer epithelium was present. Her concept of a system of 'capillary canals' and 'tubules' which nourished the external epithelium was also in error, for the 'canals' are, in fact, integral parts of the primary skeleton and were not hollow, while her 'tubules' are the solid rods that pierce the outer secondary skeleton. This author (1941, p. 121) also reported the presence in *Fenestella* of mural pores allowing communication between zooids. Such structures must be a rarity, for there is no other record of them nor, in spite of careful search, has the present writer been able to detect any, though they are common in *Hornera*. It is likely that in most fenestellids the only means of inter-zooidal communication was by the circulation of coelomic fluid through the hypostegal space, and that the mantle epithelia were nourished by this means also. Rod-like structures in the outer secondary skeleton, which Shulga-Nesterenko mistakenly believed to be tubules connecting zooecial chambers with the branch periphery, may nevertheless have fulfilled an important function in connection with the external mantle. This consisted of two epithelia separated by a coelomic space, the inner epithelial layer being attached to the calcareous wall on the external side of the latter (text-fig. 2B). Provision would have been necessary to maintain the outer mantle epithelium in a static position relative to the corresponding epithelial layer beneath it, and Williams's (1956, p. 252) suggestion regarding the function of taleolae in strophomenide brachiopods may have a direct relevance here. It is possible that, like the taleolae, the tips of skeletal rods in fenestellid bryozoans may have afforded attachment points for tendons holding the outer epithelium in place. The

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EXPLANATION OF PLATE 55

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. All figs.  $\times 3,000$ ; scale at bottom left of Fig. 1 is equivalent to 1  $\mu\text{m}$ .

Fig. 1. *Hemitrypa hibernica* M'Coy. Transverse section of inner laminated tissue lining zooecial chamber (top right-hand corner). Laminated tissue is in contact with granular (primary) skeleton which occupies the lower-left part of the field.

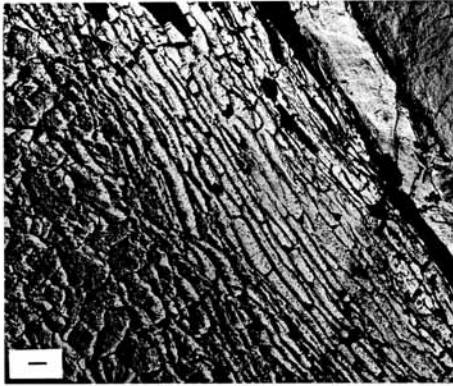
Fig. 2. *Hornera frondiculata* Busk. Transverse section of skeletal layers corresponding to those of Fig. 1, and in a comparable situation (part of zooecial chamber seen at top left). Here the primary layer grades into tissue of the outer laminated zone present in the bottom right-hand corner.

Fig. 3. *Hemitrypa hibernica* M'Coy. Longitudinal section of a branch showing a gradational relationship between granular (primary) and outer laminated skeletal zones.

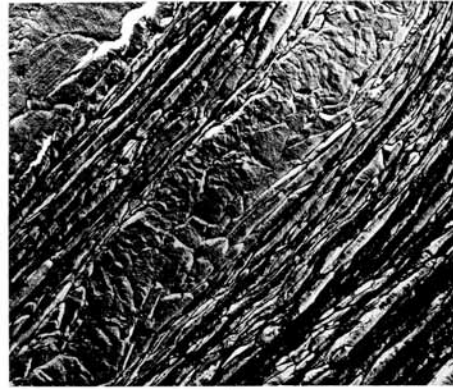
Fig. 4. *Hornera frondiculata* Busk. Transverse section of a branch showing development of a granular lens within the outer laminated zone.

Fig. 5. *Hemitrypa hibernica* M'Coy. Longitudinal section of an inter-zooecial wall showing the core of primary tissue flanked by the inner laminated material lining zooecial chambers.

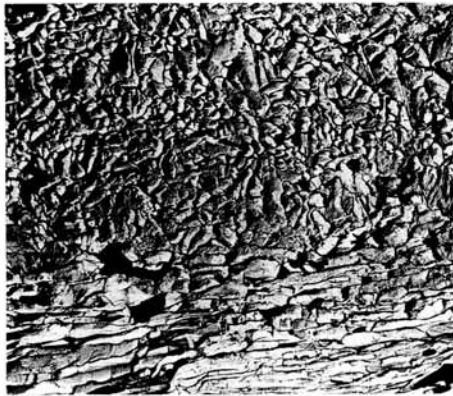
Fig. 6. *Hornera frondiculata* Busk. A typical inter-zooecial wall with tripartite structure similar to that shown in the preceding figure.



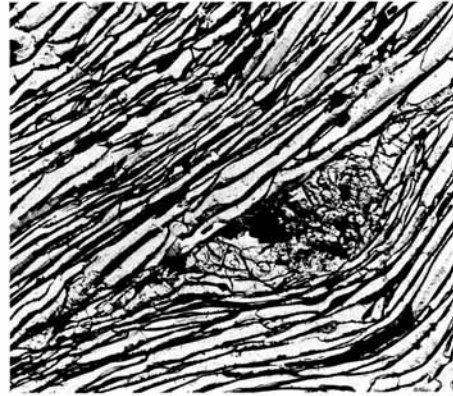
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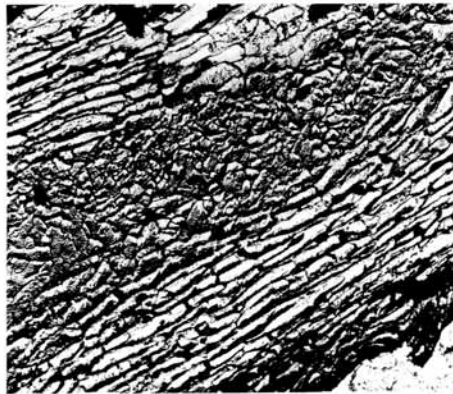
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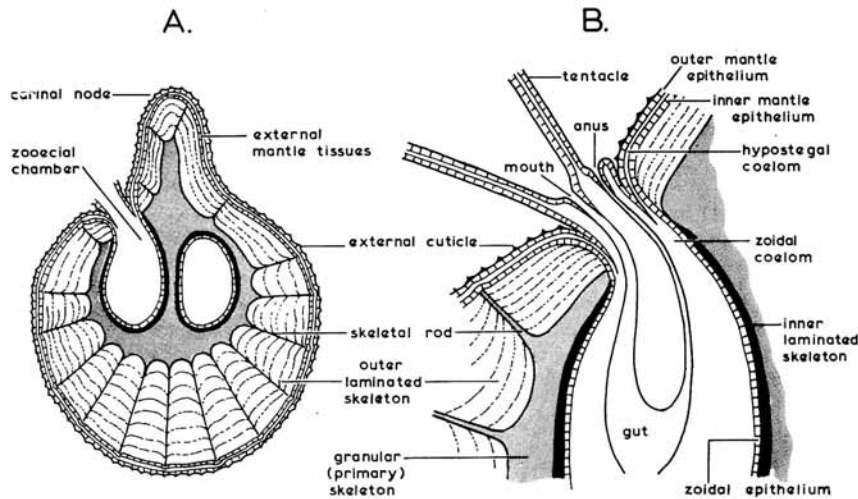
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presence in some species of a circlet of these structures around zooecial apertures appears to emphasize the importance of a stable orientation of the outer mantle wall in that situation.

The association of proteinous cellular exudation with the formation of calcareous skeletal substance is now clearly established, and it is also known that secretory epithelia always produce a cuticular layer before calcite deposition commences. If two such epithelia should be in juxtaposition facing one another, it is therefore logical to suppose



TEXT-FIG. 2. A reconstruction illustrating the probable relationship between wall epithelia and skeleton in *Fenestella*. A, transverse section of branch with external mantle in position; B, exserted polypide showing the mantle components and communication between hypostegal and zoidal coelomic cavities.

that a layer of cuticle, possibly doubled, would separate them. In the formation of the fenestellid (and hornerid) wall such a situation must have arisen with respect to the inner epithelia, and it is implicit in the foregoing account that, after the commencement of calcareous deposition, the position of the cuticular layer was between the inner secondary (laminated) and primary wall zones. This inference, initially based on the absence of a clear gradational contact between those layers, receives support from other considerations. First, the presence in the outer secondary zone of skeletal rods which derive from the primary layer, but the complete absence of such structures from the inner secondary zone. This suggests that the two outer layers had a common origin not shared with the zooecial lining, and the most likely position for a cuticular partition within the wall would therefore be on the inner side of the primary layer. Secondly, carinal nodes, dissepiments and spiny outgrowths consist of a granular core (in continuity with the primary skeleton of the branch wall) enclosed by outer secondary tissue. The inner laminated zone is not present, nor is there any axial space which might have accommodated an epithelium: the core of these structures is quite imperforate (text-fig. 3). It is notable, however, that in the axial position there is commonly a trail of dark

granules extending along the length of the structure concerned. Traced to its origin this is seen to derive from the junction between the primary layer and the laminated lining of the nearest zoecial chamber in the adjacent branch. It is therefore possible that the dark particles mark the former position of a cuticular spindle drawn out from the partition within the branch wall to provide a base for calcite nucleation. If so, the position and derivation of the streams of dark particles confirm the former presence of a cuticle between the primary and inner secondary wall layers. In addition, the occurrence of dark trails in axial positions within carinal nodes, dissepiments, and spines adds weight to the suggestion that the inner laminated skeleton was never present there.

These considerations provide the best available guide to the former position of the intra-mural cuticle but, assuming that the indications are correct, it is perhaps surprising that such a partition did not cause the junction between the two wall zones to be more sharply defined. As an internal cuticle, however, the structure may have been no more than a film, thick enough only to provide a base for the nucleation of calcite crystallites. Proof that intra-mural junctions may be poorly defined in detail, in spite of the original presence of a cuticular layer between the units concerned is afforded by electron micrographs of wall structure in *Hornera frondiculata*, a living species. These show an obvious contact between a laminated skeletal overgrowth and an eroded earlier surface of the same colony (Pl. 56, fig. 6). The overgrowth was laid down by the inner epithelium of the external mantle, and the cuticle associated with that layer must initially have coated the worn surface on which the overgrowth rests. Yet, although the trend of the contact is clear in a general way, it is difficult to trace in detail the junction between particles of earlier and later age, and an interlocking texture between them is locally evident.

For reasons stated above it is probable that the initial non-calcareous branch wall in fenestellid bryozoans consisted of a threefold repetition of ectodermal epithelium and associated cuticle. The inner epithelium provided the immediate investment of the polypide, while the outer ones formed the external mantle, a double-walled envelope over the entire outer surface of the colony (text-fig. 2A). Calcareous wall formation commenced with the secretion of granular tissue from the inner mantle epithelium. Deposition was continuous and relatively rapid as the epithelium migrated progressively outward during growth, taking the outer mantle epithelium with it. In this way the primary wall was laid down.

A decrease in the rate of secretion, accompanied by a change from continuous to intermittent deposition, succeeded the initial phase and is reflected in a transitiona

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EXPLANATION OF PLATE 56

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. All figs.  $\times 3,000$ ; scale at bottom left of Fig 1 is equivalent to 1  $\mu\text{m}$ .

Figs. 1, 2. *Hemitrypa hibernica* M'Coy. Longitudinal sections showing the relationship in peripheral parts of branches between laminae of the outer skeletal zone and rod-like structures which penetrate them. Distal to the right in each case.

Figs. 3, 4. Transverse sections in the outer parts of branches in the above species, showing skeletal rods surrounded by roughly concentric secondary laminae.

Fig. 5. *Hornera frondiculata* Busk. Transverse section of a skeletal rod penetrating outer laminated tissue.

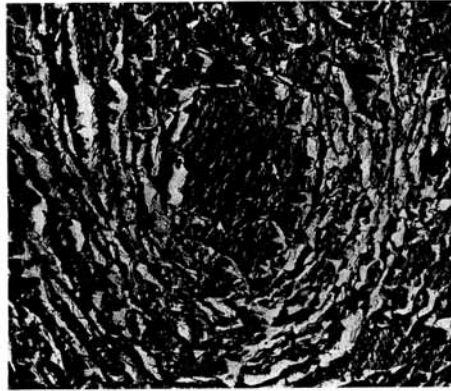
Fig. 6. Longitudinal section in the same specimen showing an 'unconformable' junction in the outer skeletal zone between a slightly eroded old branch surface and a later overgrowth.



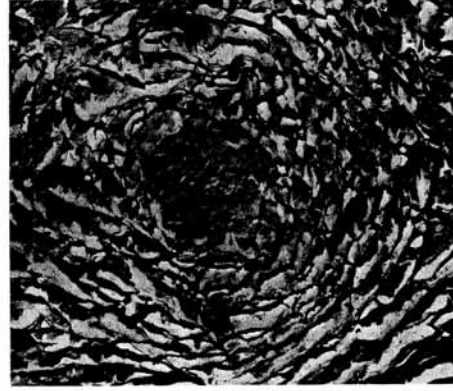
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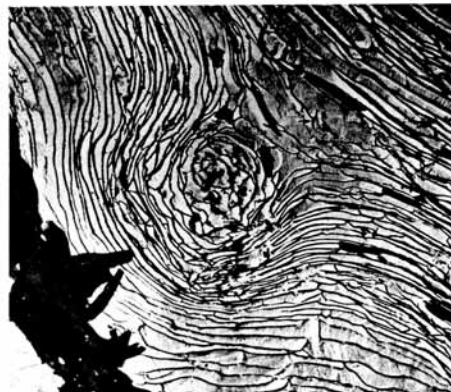
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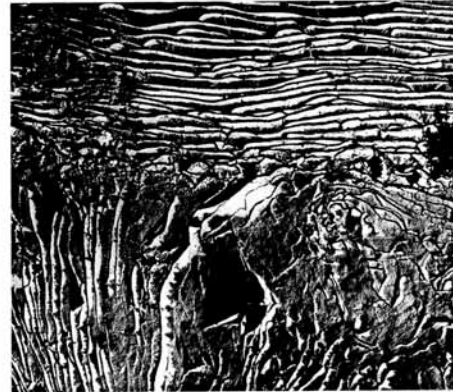
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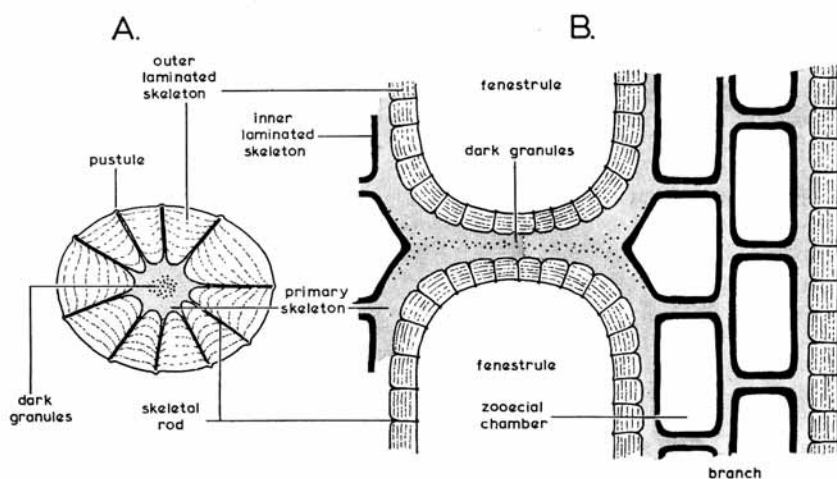
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TAVENER-SMITH, Fine structure of fenestellids

relationship between the primary and outer secondary skeleton (Pl. 55, fig. 3). The outer laminated investment continued to increase in thickness by the regular addition of layers at the periphery as long as the colony lived. At the same time, continuous growth outward from the primary layer persisted at a number of separated points, resulting in the formation of rods and shafts piercing the laminated tissue. Granular calcite for the skeletal rods must have been secreted by special groups of cells of the inner mantle epithelium, in a manner similar to that described by Williams (1968, pp. 39-41 and text-figs. 23-4) for taleolae in brachiopods.



TEXT-FIG. 3. Dissepimental structure in *Fenestella*. A, transverse section; B, tangential view showing distorted chambers at root of dissepiment and axial trail of dark granules.

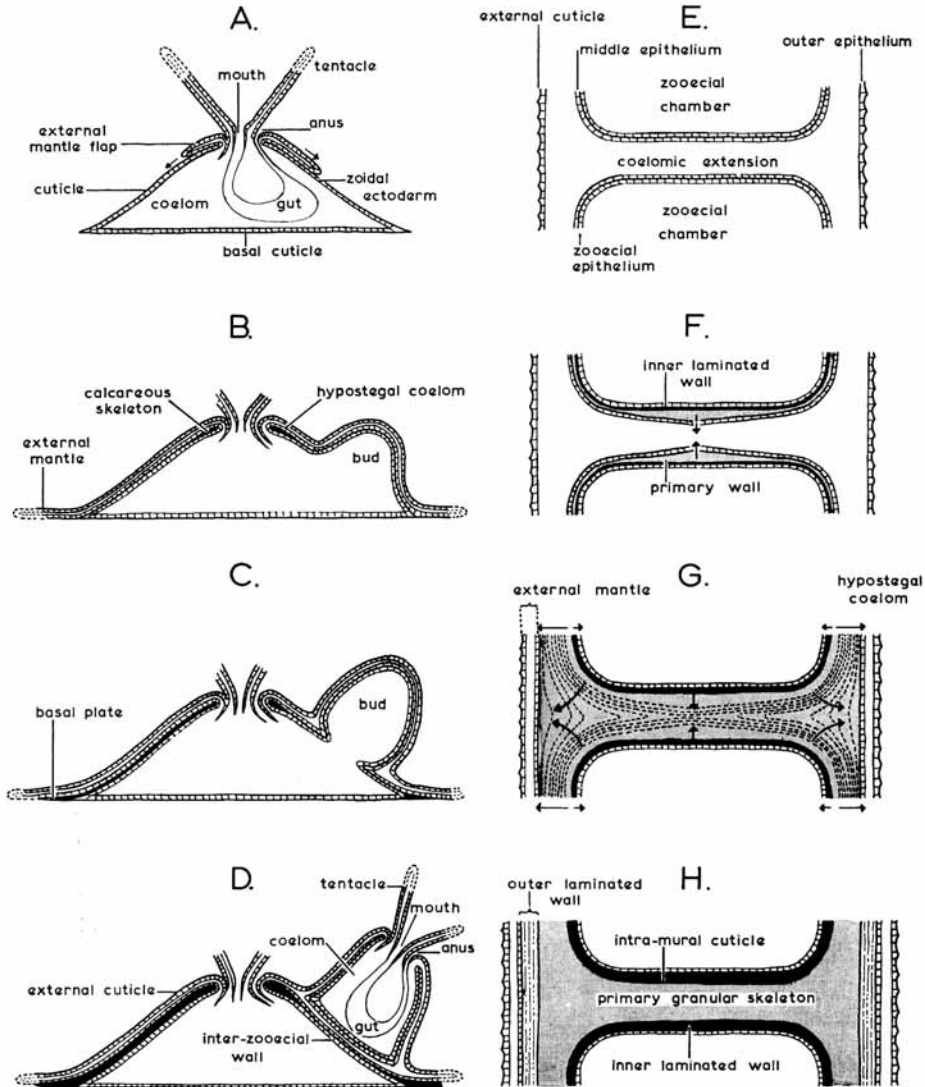
Initial calcareous deposition from the zooidal epithelium (on the inner side of the primary layer, and separated from it by a cuticular sheet or film) probably followed close on the formation of the earliest granular tissue. Rhythmic deposition resulted in a laminate wall structure, but the rate of secretion decreased with time. At the outset it was relatively fast, causing the formation of wide laminae immediately adjacent to the primary wall. A progressive decline in the rate is reflected by narrower additions and, to judge from the number of laminae commonly present, calcareous deposition was not long maintained.

In addition to comprehending the general sequence of events during wall formation, it is necessary to inquire into the origin of the secretory tissues, and the way in which they extended in the course of colonial growth. The nature of the zooidal epithelium is not in doubt for, following the basic principles of budding in bryozoa, this must have been an extension of the ancestrular ectoderm. The origin of the external mantle presents greater difficulty particularly as, in an extinct group, its very existence is hypothetical. On general grounds, however, it seems probable that it originated as a peripheral evagination of ectodermal epithelium from the vestibular region of the ancestrula (text-fig. 4A). The thin but extensive membrane so formed was closely adherent to the

cuticular cover of the ancestrular surface, and commonly extended considerably beyond this (text-fig. 4B). When calcification commenced the inner mantle epithelium (the mid one of the three concerned in wall formation) laid down the relatively extensive, but initially thin, surface encrustation which firmly secured the colony to its substrate, and from which later growth proceeded. This was referred to by Cumings (1904, p. 58, figs. 44-6) as the basal plate. Later additions of thick, laminated secondary skeletal substance from the same epithelium commonly converted this structure and the proximal part of a colony into a massive holdfast. From the earliest stages the inner mantle epithelium was the main secretory layer, and in comparison only a thin wall was formed from within the ancestrula. Cumings (1905, p. 171) found that in basal holdfasts of *Fenestella* the position of the ancestrula was commonly marked by a minute concavity near the centre of the lower surface. In some sections, however, a thin wall could be seen flooring the depression. This must have been formed by the epithelium lining the ancestrula (text-fig. 4D), and contrasts with the massive structure of the surrounding holdfast laid down by external deposition from the mantle epithelium.

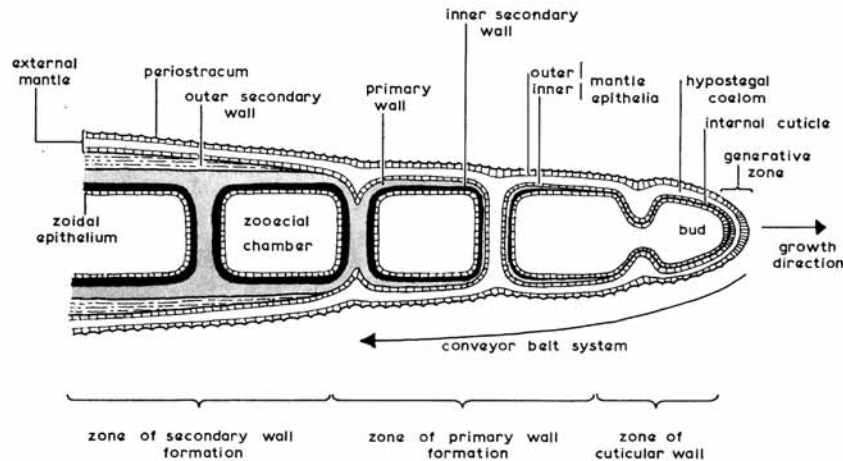
The extension of the external mantle to form a continuous investment over the surface of a growing colony took place as a logical consequence of budding from the first individual. This necessarily involved the expanded original membraneous evagination, and probably followed a pattern like that illustrated in text-fig. 4B-D. As successive zooids were grouped to form incipient branches, the extremities of these were at every stage enclosed within the mantle which, by terminal proliferation, continually extended to form an outer covering pierced only by zooecial apertures. There are strong indications that zooecial buds at the tips of growing branches were, like the ancestrula, initially enclosed in cuticular envelopes, and that calcification commenced only after the attainment of adult size and shape. The tips of perfectly preserved branches from young fenestellid colonies do not, in the writer's experience, show calcified chambers that are partly formed. The last chamber is invariably complete and of adult proportions, though its wall is extremely thin (so as to be translucent in some cases) and consists of primary skeleton with little or no laminated secondary investment. Certain subsequently mentioned features of dissepimental growth also indicate that the inception of calcareous secretion post-dated the achievement of adult form.

In fenestellid colonies, as in modern ramose bryozoans, the tips of branches were the main points of growth, and it is in that situation that the proliferation of epithelial cells and formation of external cuticle must have taken place. Schneider (1963) has shown that this is so, for example, in the modern cheilostome *Bugula*. Skeletal evidence suggests that just behind the advancing tip of a fenestellid branch, where buds had attained adult dimensions, the inner mantle epithelium commenced to secrete granular calcite, and the primary zooecial skeleton was laid down. The secretory phase appears to have operated as long as growth was maintained, and the deposition of granular tissue was, therefore, a continuous process as deduced earlier on other grounds. As forward growth proceeded, earlier formed cells of the inner mantle epithelium were left progressively further behind, and a second change of secretory regime appears to have taken place. The deposition of calcite particles, previously continuous, became intermittent, particle shape changed from granular to platy, and the outer laminated skeleton was formed. Thus it appears that, by physiological adaptation, a single epithelial layer secreted different products during successive phases of growth (text-fig. 5). This offers a striking



TEXT-FIG. 4. A-D, earliest stages of a generalized fenestellid colony, showing the suggested origin of the external mantle from the ancestrula and development of a first generation daughter zooid; E-H, reconstruction of stages in the formation of the calcareous inter-zoecial wall of *Fenestella*; E, early non-calcified stage corresponding to the dividing wall between zooids in D; F, differential secretion of early primary skeleton and initiation of inner laminated wall; G, formation of the primary wall: lines represent the progressive withdrawal of the inner mantle epithelium; H, completely calcified inter-zoecial wall with beginnings of secondary deposition on the branch exterior.

parallel to the 'conveyor belt' principle involved in the construction of the brachiopod shell (Williams 1956, 1968). It is, in fact, apparent that in matters of wall construction there are important parallels between at least some brachiopod groups and fenestellid bryozoans. This is not unexpected, for brachiopods and bryozoans are phyla which, on more general grounds, have long been considered to show certain affinities.



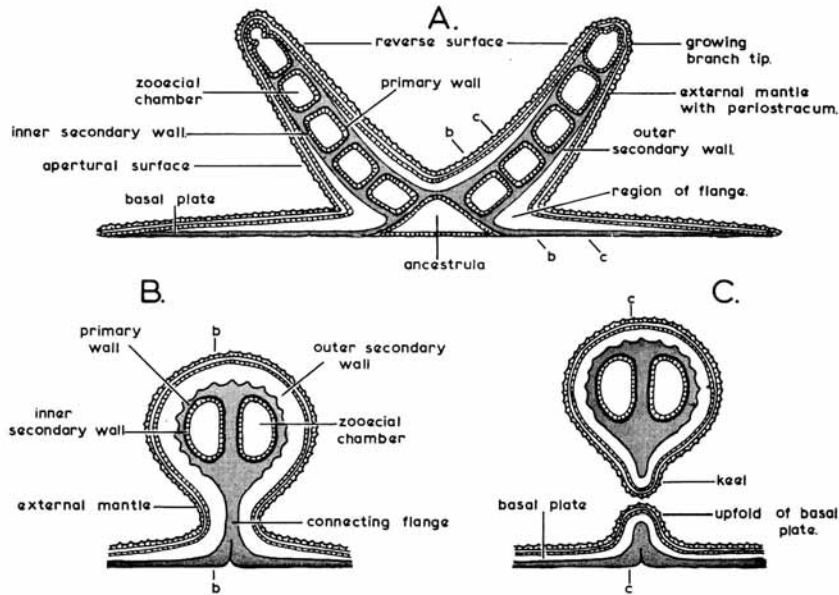
TEXT-FIG. 5. Longitudinal section of a fenestellid branch tip, showing the operation of the 'conveyor belt' principle in skeletal formation.

The sequence of events attending the formation of the calcareous branch wall has already been outlined, but that concerned with inter-zooecial partitions merits further discussion. Initially, the deposition of calcite to form these structures probably took place from the outer surfaces of two layers of inner mantle epithelium occupying back to back positions within the original soft inter-chamber partition. These originated as an invagination of the inner mantle epithelium of the branch wall during the budding process (text-fig. 4 C, D). The formation of inter-chamber partitions by invagination in a similar way is suggested by Lutaud's (1961) illustration of inter-zooidal differentiation in the giant buds of *Membranipora membranacea*. Once primary deposition had commenced, the epithelia appear to have retreated inward, towards one another, laying down granular wall substance as they did so (text-fig. 4F). When the two epithelial sheets were in contact, the coelomic cavity between them having been occluded, fusion probably took place beginning at the central point of the wall. The fused epithelium then developed a central perforation which increased in size in the manner of an opening iris diaphragm, as the doubled epithelium withdrew radially towards the outer wall of the branch (text-fig. 4G). During this process calcite crystals secreted from the tips of the shrinking epithelial lobes filled the central space being vacated and completed the formation of the primary wall (text-fig. 4H). The absence of laminations or growth structures of any kind within the primary core of inter-chamber partitions must be attributed to the continuous nature of the depositional process.

Secretion of the inner laminated wall by the zooidal epithelium probably commenced

at about the same time as, or soon after, the initiation of the primary layer. It then proceeded in the manner already described, and the completed wall, consisting of a granular core buttressed on either side by laminated components, no doubt had relatively strong mechanical characteristics.

In his pioneer work on the early growth of some palaeozoic bryozoa, Cumings (1904, p. 64, figs. 47–62) suggested that the median keel, or carina, on the obverse of *Fenestella*



TEXT-FIG. 6. An early stage in the formation of a cup-shaped colony, showing the flange connecting branch keel and basal plate. A, longitudinal section of colony; B–C, transverse sections of branches at approximate positions shown in A.

branches originated as an upfold of the basal plate. This was in harmony with his observation that in many fenestellids (e.g. *Fenestella*, *Unitrypa*, *Loculipora*, but not *Polypora*) zooecial apertures are on the *outer* face of a cone- or cup-shaped colony. Consequently, the obverse of a branch, close to the growth origin, is directly adjacent to the basal plate (text-fig. 6A). A union between the two in this region would have provided support for the developing branch, and the carina of later growth stages could be considered as a vestige of the earlier connecting flange. The lower part of such a structure would have been secreted from an upfold of the epithelium that laid down the basal plate (i.e. the inner mantle epithelium: that responsible for the formation of the greater part of the skeleton). It would therefore have consisted initially of granular primary tissue, and union with the corresponding epithelial layer of the branch would have led to the formation of a continuous skeletal connecting structure (text-fig. 6B). Subsequent addition of secondary laminated tissue would have completed the process



and, beyond the connection with the basal plate, given rise to the orthodox branch keel (text-fig. 6c).

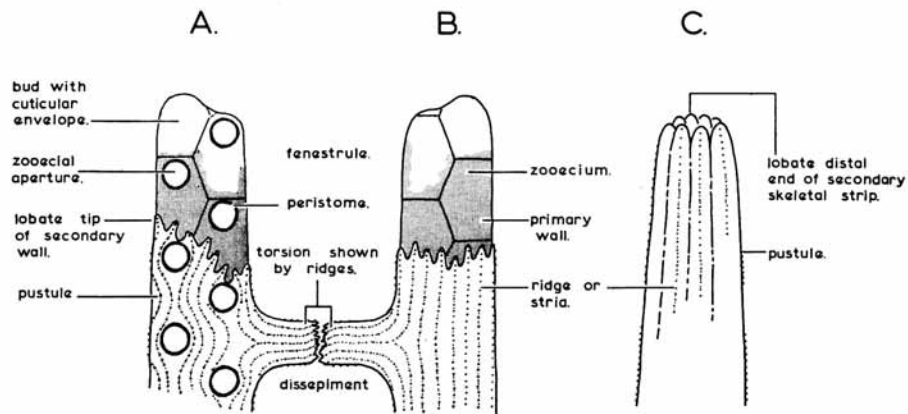
#### THE FORMATION OF OTHER SKELETAL ELEMENTS

A logical explanation of the affinities, origin, and growth of other colonial structures such as carinal nodes, dissepiments, and spinose outgrowths follows from what has gone before. Transverse sections of these show that they consist of a primary or granular core enclosed by outer laminated skeleton. A stellate or 'spider's web' pattern is commonly evident, due to the presence of skeletal rods radiating from the core through secondary tissue to the branch periphery (text-fig. 3A). There is no inner laminated wall component nor any hint of the former presence of an axial perforation that might have accommodated a protoplasmic extension from neighbouring zooids. There is commonly observable, however, a trail of dark particles in the axial region (text-fig. 3), and this may be of organic origin, representing a former continuation into the structure concerned of the cuticular layer separating primary and inner laminated tissue in the adjacent branch. A proteinous axial filament of this kind would have afforded a base for the nucleation of calcite particles.

In the absence of evidence of an internal secretory epithelium it is necessary to conclude that carinal nodes, dissepiments, and spinose structures were laid down from the *outside*, that they had no direct communication with zooids, and that consequently they are *colonial* and not *zoecial* features. This conclusion may have important taxonomic implications, for it is probable that the colonial skeleton (which may be considered as simply a supporting framework for the constituent zooids) was more liable to external influences and less rigidly controlled genetically than the individuals within it. This being so, it is possible that zoecial characteristics in fenestellid bryozoans will ultimately prove of greater diagnostic value than colonial ones, and that the present taxonomic use of such structures as dissepiments and carinal nodes will discontinue. This has lately been happening in other groups of more modern bryozoa (Lagaaij and Gautier 1965, p. 39), and many years ago Waters (1896, p. 255) pointed out the futility of attempting to classify species of Mediterranean reteporids on the basis of slight differences of colonial meshwork.

Dissepiments in *Fenestella* resulted from the union of opposing outgrowths from adjacent branches (Elias and Condra 1957, p. 29). The sequence of events leading to their formation probably commenced with the appearance of buds on the flanks of branches, close to the growing tips. The buds were probably conical evaginations of the outer mantle: the inner (zooidal) epithelium does not appear to have been involved. There is, however, a strong indication that growth of the bud was proceeding vigorously while adjacent zoecial walls were still flexible, for it is commonly observed that the end of a zoecial chamber opposite a dissepiment is drawn out into a shallow cone directed towards the base of the latter (Pl. 53, fig. 1; text-fig. 3B). It is difficult to interpret this as anything but the effect of outward tissue drag due to the growth of the bud. The distortion must have taken place during the earliest stages of wall development, for it could scarcely have occurred after calcification had commenced. From the apex of such a cone a trail of dark granules may continue into and along the dissepimental axis, suggesting that although the inner epithelium did not extend into the dissepimental bud, the cuticular sheet between it and the internal mantle epithelium did so.

The growth of opposing buds towards one another duly led to their contact, and to the fusion of corresponding epithelia. This may have involved a delicate matching up of tissues, for it is not uncommon to find on well-preserved dissepiments signs of rotation, in the curvature of slender parallel ridges, the *striae* of earlier authors. These follow the trend of a dissepiment at its ends, but may show a concerted and localized twist about midway along its length (text-fig. 7 A-B). Condra and Elias (1944, p. 36) suggested that similar torsional features in the 'screw' of *Archimedes* were caused by current action, but in this instance it is more likely that they reflect a physiologically induced



TEXT-FIG. 7. The advance of secondary calcification in growth zones of a fenestellid colony, showing the relationship between distal lobes, longitudinal ridges (or striae) and pustules. A, branch tip, obverse view; B, the same, reverse side; C, the tip of a silicified spinose structure from which the calcareous primary core had been removed by etching.

realignment of epithelial tissue strips at the junction between opposing dissepimental buds. Whatever the precise cause of the rotation, it seems certain that it occurred while the structure was still flexible, and that the pattern was preserved in the subsequently formed skeleton.

Union of the buds was followed by calcification, commencing with the formation of a granular, primary core on a protein base, probably provided by an axial thread. With advancing time the nature of the secretion changed and laminated tissue was laid down, also by the internal mantle epithelium. Skeletal rods originating from the primary core traversed the outer secondary layers and formed minute pustules at the surface. These are commonly in linear series and tend to occur along the crests of longitudinal surface ridges. It seems likely that each of the latter corresponded to, and was secreted by, a definite strip of the underlying epithelium. A similar relationship is evident near the tips of young branches: secondary (laminated) tissue is not present at the branch tips, but makes its appearance as a translucent film perhaps 0.5–1.0 mm. from the ends. Its advancing front is defined by a number of distally directed lobes and behind the apex of each extends a longitudinal ridge bearing on its crest a uniserial row of pustules (text-fig. 7A, B). Borg (1926b, p. 309) noted a comparable arrangement in *Hornera arctica*.

It seems possible that the secondary skeleton was laid down as a number of independent, parallel strips which subsequently became welded together, and that the underlying epithelium was physiologically differentiated to that end.

Carinal nodes, which in many fenestellid species are more suitably described as spines, have essentially the same structure and origin as dissepiments. They rise from the keel at more or less constant intervals and an extension of primary skeleton from the branch wall forms the core of each node. This is enclosed within laminated secondary tissue which is penetrated by radiating skeletal rods. There is no indication of the former presence of soft parts within a node, nor of any internal connection with zoecial chambers. As in dissepiments, however, and probably for the same reason, a trail of dark granules is commonly aligned along the axis.

In thin section the tips of nodes are bluntly rounded and imperforate, though hand specimens commonly show broken carinal nodes which, because of non-replacement or differential weathering, are hollow. This was not the original condition but it has caused some writers (Condra and Elias 1944, p. 26; Bassler 1953, p. G120; Miller 1961, p. 223) to speculate on the possibility that the nodes originally housed acanthopores. This suggestion is quite unsupported by evidence, and seems to have been prompted by the apparent need to protect the obverse of a colony from predators and from larval encrustation. It is probably true that the carinal nodes themselves at least partly fulfilled this purpose by presenting a spiky, unwelcoming aspect. This was particularly so in the genus *Cervella*, in which numerous, closely spaced carinal nodes branched distally, giving a distinctly repellent appearance.

In some genera (e.g. *Hemitrypa*) the distal ends of nodes divided into several geometrically oriented bars in the same plane as the meshwork. These united with corresponding extensions from adjacent nodes to form a regular superstructure. Sections through superstructure elements show them to have basically the same construction as other skeletal outgrowths. Calcareous secretion must have taken place from an external epithelium, there being no trace of an axial perforation to permit the presence of soft tissues internally. These superstructures also, no doubt, served a protective purpose, and their formation by the union of symmetrically disposed projections from the ends of carinal nodes, provides an outstanding example of the closely integrated control that operated during colonial growth. How such control was effected is unknown, but it seems reasonable to connect it with the presence of an external colonial mantle and coelomic cavity for, in the absence of mural pores, the latter presumably afforded the only means of communications between zooids.

Spinose structures, greatly exceeding the length of carinal nodes, are commonly present in considerable number and variety. Fenestellid colonies, like certain modern cheilostomes (e.g. *Adeonellopsis*) had the ability to develop such outgrowths in many situations and for many purposes. Slender spines, up to 1 cm. long, may occur in about equal numbers on the obverse and reverse of a frond, particularly in the proximal region. In many cases they were evidently supporting struts which acted in association with a massively calcified basal holdfast. The skeletal organization of spines is identical to that of carinal nodes, and it appears that a few of the latter developed into spinose processes by continued growth.

Transverse sections of spines show an identical stellate or 'spider's web' pattern to that of dissepiments and carinal nodes: there is a primary core of granular tissue, giving

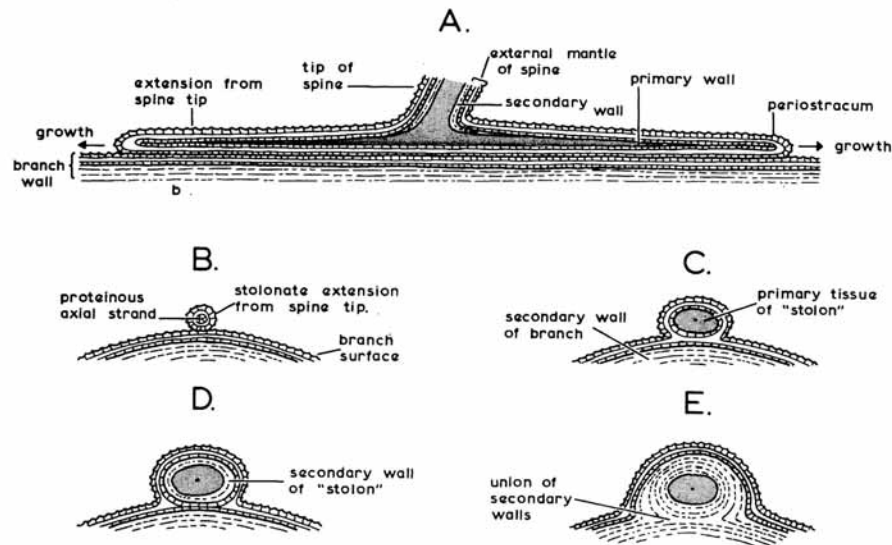
rise to radially arranged skeletal rods which traverse outer laminated substance to the periphery. Rods emerge at the surface as pustules which commonly form uniserial lines, each following the crest of a longitudinal ridge (text-fig. 7c). These parallel ridges, which characterize the external surface of spines, are continuous with corresponding features on the parent branch.

In certain cases spines project laterally from the margin of a fenestrate frond as direct continuations of branches. These are found in areas where branch growth had ceased, and are the 'infertile branches' of earlier authors. The absence of zooecia from these continuations is evident not only in the lack of apertures, but also in a marked reduction of diameter where the 'infertile' part of a branch commences. In the absence of median keel and apertures, longitudinal ridges and grooves are present over the whole surface, as with other spinose structures. These lateral spines must have resulted from the continued forward extension of the external mantle after the budding of zooecia within a branch had ceased. In such circumstances it would not be anticipated that the inner laminated tissue normally lining zooecial chambers would be present within the extension, and this is so (Pl. 54, fig. 5). However, a trail of dark granules may persist beyond the last chamber, suggesting that the associated intra-mural protein layer continued into the axial region of the spine, as in carinal nodes and dissepiments. Increase in length must have taken place, as in productid spines (Williams 1968, p. 42) by the proliferation of new epithelial cells at the tip of the structure. Unlike the brachiopod equivalent, however, the secretory epithelium lay outside the calcareous skeleton, and not within it.

Certain spines, having diverged from a colony, later re-united with it elsewhere. At the point of re-union the spine may be locally thickened, but immediately thereafter it divides to form a number of cord-like (ridged and grooved) extensions that ramify along branches and dissepiments in different directions before becoming attenuated and merging with the meshwork. It is notable that the pattern of longitudinal ridges on an extension from the spine tip commonly fails to coincide with that of the branch surface on which it rests. It would, therefore, appear that a random union between the growing tip of a spine and another part of the same colony did not involve a matching up of epithelial tissue strips (and hence, of surface ridge patterns) like that which accompanied the formation of dissepiments and superstructures. In fact, in these circumstances the tip of the spine seems to have behaved in a manner similar to that of any supporting strut from the colony at its junction with a foreign substrate. It must be recalled that unions associated with the formation of dissepiments and superstructures were between geometrically opposed skeletal outgrowths of identical type, and therefore of quite a different nature.

The most reasonable interpretation, based on skeletal evidence, of the sequence of events when a spine rejoined the colonial meshwork seems to be as follows (text-fig. 8). At the point of contact the external mantle of the spine divided into a number of slender, finger-like lobes which diverged to traverse the surface of the meshwork (text-fig. 8A, B). The outer mantle epithelium of branch and lobe, being in direct contact, subsequently fused, so that coelomic continuity was established between them. It is probable, however that skeletal deposition still proceeded independently leading, in the case of each lobe to the formation of a slender, stolon-like, primary extension of the spine tip (text-fig. 8C). As growth proceeded the addition of concentric secondary laminae enlarged the diameter of this calcareous 'stolon'. The inner mantle epithelium secreting the 'stolon'

was initially separated from its counterpart laying down the branch skeleton by a narrow coelomic cavity but, as development proceeded, this was progressively reduced. Eventually the two epithelia must have occupied back-to-back positions, the coelomic space between them having been completely occluded (text-fig. 8D). At this stage the epithelia probably fused along a median line beneath each 'stolon' and subsequently withdrew to either side, leaving the structure welded to the outer calcareous branch wall. Later deposition must progressively have increased the area of contact between them (text-fig. 8E). In essence 'stolon' and branch wall developed independently, and it is, therefore,



TEXT-FIG. 8. A reconstruction of the morphological pattern at a junction between the distal extremity of a spinose outgrowth and another part of the same colony. A, longitudinal section showing an early-stage relationship between an extension from the spine tip and the branch surface on which it rests; B, transverse section at position *b* in previous diagram; C-E, later stages, suggesting the progressive coalescence of epithelial layers.

not surprising that, in general, their surface ridge patterns fail to coincide. In a few cases, however, deposition continued for some time after fusion occurred, so that later skeletal layers (and their ridge pattern) may be continuous from 'stolon' to branch. Excessive secondary deposition caused the separate entity of the 'stolon' to be progressively obscured by sheets of laminated tissue which, in advanced stages, show a smooth exterior devoid of pattern.

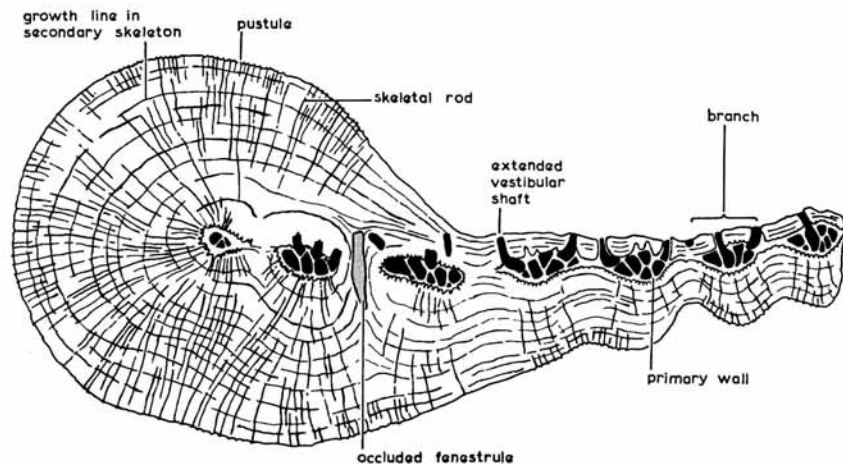
The proximal extremities of fenestellid colonies, particularly those of mature development, commonly show thick, calcareous deposits which weld the skeleton to its substrate and constitute the holdfast. This structure consisted initially of a thin 'basal plate', secreted from the lower surface of the external mantle where this extended over the substratum to which the ancestrula was attached. To the primary granular skeleton there were added, throughout the life of the colony, incremental secondary layers,

resulting in a laminated texture and the attainment of massive proportions. Thick, secondary laminae were also added to adjacent proximal parts of a colony, and branches in this region became generally enlarged. Associated zooecial apertures were commonly sealed by a translucent, plate-like deposit, but close examination shows that this is not an opercular structure, as at first seems possible, but a continuation of the outer, laminated tissue over the aperture. The translucent appearance is due to the fact that there is a hollow chamber beneath the thin skeletal seal. In some cases the seal is pierced by a small central orifice, and the general aspect is then reminiscent of 'blind cells' in certain Cheilostomata (Bassler 1953, p. G156). It is probable that this represents a stage in the encroachment of secondary material at which the moribund zooid was still able to function weakly (Pl. 52, fig. 6). The occlusion of zooecial apertures in this way provides a convincing argument for the deposition of skeletal substance from the exterior and for the former presence of an external secretory mantle.

The presence of an external membrane permitted the effective repair of damage to the colonial meshwork by the rapid, localized deposition of skeletal tissue wherever and whenever necessary. Many fenestellid fragments show evidence of this in the smoothly rounded stumps of what were originally broken branch ends. It seems that after the damage had occurred (leaving a jagged branch end and torn external membrane) the lacerated edges of the mantle grew forward over the fractured surface and coalesced to form an enclosing sheath. The inner epithelial layer then secreted a succession of thin skeletal laminae, resulting in the formation of a smooth stump which sealed the breakage. There is, in this process, a strong hint of the considerable powers of regeneration and mobility possessed by the external mantle. In other cases dislocated sections of meshwork were stabilized by the development of supporting struts, or dissepiments of abnormal length and shape, and by the secretion of masses of secondary calcite which 'welded' broken sections together. In such instances the damage clearly acted as a stimulant to metabolic activity, and the value of copious secretion of secondary material in effecting repairs is evident.

Nowhere is the remarkable ability of bryozoans to secrete masses of calcite for skeletal support better illustrated than in the Fenestellidae. The capacity to do so must be attributed to the presence of an external mantle, which provided a means for the intensive localized deposition of skeletal material at any point on the colonial surface. In *Lyropora*, *Lyroporella*, and *Anastomopora* the framework of branches and dissepiments is supported by a V-shaped marginal rib originating at the basal holdfast. Its formation commenced at an early developmental stage, with the selective deposition of outer laminated tissue on branches at the lateral extremities of a fan-shaped frond. These rapidly increased in diameter, and secondary accretion in due course attained a considerable thickness about zooecial apertures. This led to a progressive increase in the length of vestibular tubes, which eventually assumed the proportions of shafts several times the height of zooecial chambers (Pl. 54, fig. 6). Such a development clearly had an adverse effect upon zooids, for signs of declining vigour are evident in a sharp decrease in the diameter of many shafts at their distal ends. This, in turn, caused a drastic reduction in the amount of water entering the shaft, a circumstance which shortly led to the death of the zooid, for the narrowed entrance did not persist for long before being sealed altogether (Pl. 52, fig. 6). All zooecial apertures on lateral branches were eventually sealed in this way as branch diameters continued to increase by sustained secondary

deposition. With the passage of time other branches close to the frond margins, and associated dissepiments, were also affected. The selective deposition of calcite in these areas continued (Pl. 52, fig. 4) until the greatly enlarged structures came into contact and the fenestrules between them were eliminated. As this occurred the external mantles of branches and dissepiments fused to form a single membrane enclosing the whole developing support. Successive secondary laminae were secreted from the inner epithelium of this soft envelope, until the support was 8–12 times the thickness of the original branches (Pl. 54, fig. 4; text-fig. 9). Half a dozen or more branches were incorporated in



TEXT-FIG. 9. Transverse section of a colonial support in *Lyropora*. Drawn from a peel (U.S.N.M. 43771-1) of *L. subquadrans* (Hall) at approximate magnification  $\times 24$ .

each supporting rib, and between the two extended the normal, fan-shaped fenestellid meshwork. This growth sequence is abundantly documented in thin sections by the laminated structure within supports.

Probably the most impressive example of differential skeletal secretion in bryozoa is provided by the axial 'screw' of *Archimedes*. In this genus a spirally coiled meshwork, in all other respects identical to that of *Fenestella*, is supported by a massive central column with a screw-like flange. Sections show that the frond is continuous through the axis, and on entering and leaving it the outer laminated tissue of branches shows a progressive and rapid increase in thickness. The development of the primary skeleton, on the other hand, remains constant. Careful examination shows that the dense, laminated tissue composing the support is identical in all respects to that of the secondary skeleton of branches, with which it is in direct continuity. The colonial axis is penetrated by innumerable slender skeletal rods, and the origin of these can be traced back to the primary layer of branches (Pl. 53, fig. 2; Pl. 54, figs. 1, 2). As with skeletal supports in *Lyropora*, zooecial chambers of branches within the screw show the development of vestibular 'chimney structures', and their external orifices were eventually sealed by secondary tissue. High carinal nodes, present in some species, were also completely

immersed in the axial region. There is no doubt that, like other supporting structures, the screw of *Archimedes* consists of orthodox secondary skeletal tissue, and only the shape is unique. The structure represents a massive localized secretion at the axis of coiling, and the innumerable laminae composing it can only have been added from the exterior. Sustained selective deposition of calcite in the axial region long after individual zooids within the screw were dead bears powerful witness to the integrated nature of growth in a bryozoan colony. It is also incontrovertible evidence of the former presence of an outer mantle, which provided the means of centralizing calcium carbonate in the axial region and causing it to be deposited there.

#### CONCLUSIONS

1. There is incontrovertible evidence that the major part of the fenestellid skeleton was secreted from the exterior: the available facts will bear no other interpretation. It is therefore necessary to infer the former existence of a soft external mantle from which deposition took place. It is thought that this structure originated as an ectodermal evagination from the vestibular region of the ancestrula.

2. The inner mantle epithelium was the chief calcite-secreting surface and contributed the granular 'colonial plexus' and the thick laminated tissue on its outer side. The ectodermal epithelium of individual zooids, on the other hand, laid down only the thin, laminated lining of zooecial chambers.

3. Study of the wall structure of branches shows that the granular tissue was first formed, and is therefore *primary* in origin, while the inner and outer laminated skeleton, being laid down subsequently, is *secondary*.

4. Secretion of the colonial skeleton in fenestellid bryozoans probably followed the 'conveyor belt' pattern described by Williams (1956, pp. 244-6; 1968, p. 2) for brachiopods, a feature of which is the ability of an epithelium to vary its secretory product with time. The internal mantle epithelium, responsible for the major part of the fenestellid skeleton, appears to have been proliferated at the tips of growing branches, and to have secreted in that region a thin cuticular covering. As the branch tip advanced through growth, and the 'conveyor belt moved to the rear', the same epithelium seems to have laid down in successive phases the primary and then the outer secondary layers of the calcareous skeleton.

5. Skeletal rods which penetrate the outer laminated zone originate from the primary layer and are solid. There is no reason to believe that they were ever tubular. They are an integral part of the wall structure and appear to correspond in all respects with the taleolae of strophomenide brachiopods. Their function may have been to furnish an attachment for tendons which held the outer mantle epithelium in position.

6. Carinal nodes and dissepiments have no internal connection with zooecial chambers, and appear to have been formed quite independently of them. Secretion of these structures took place entirely from the external mantle and they are therefore of 'colonial' not 'zooecial' origin. Spinose outgrowths and superstructure bars have the same basic construction as carinal nodes and dissepiments. Inner laminated tissue, the characteristic secretion of the zooidal epithelium, is absent from them all.

7. Colonial holdfasts and supporting structures, such as those of *Lyropora* and *Archimedes*, were formed by massive, localized deposition of secondary tissue from the inner



mantle epithelium. The repair of damage to a colony was effected by similar means. The ability of fenestellid bryozoans to form thick skeletal deposits where and when necessary suggests a high degree of centralized control of physiological effort. It seems reasonable to associate such control with the external mantle, that being the only unifying factor between the zooids of a colony.

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