

# EARLY GROWTH STAGES IN RHABDOMESOID BRYOZOANS FROM THE LOWER CARBONIFEROUS OF HOOK HEAD, IRELAND

by RONALD TAVENER-SMITH

**ABSTRACT.** A number of specimens of young rhabdomesoid colonies were examined, each carrying a curious conical proximal termination. Sectioning showed that these represent the earliest growth stages, following fixation of the ancestrula. External walls of cones have a two-fold structure comprising outer, primary (recrystallized) and inner, secondary (laminar) layers. The arrangement corresponds with that in the basal walls of encrusting trepostomates. There are reasons for believing that during later development the conical structures were progressively obscured by calcification from an external mantle. Some of the young colonies grew around productid spines or other slender objects, and in such cases an internal 'basal wall' defines an axial tube. In others there is no such complication and zoecial tubes diverge from a simple skeletal axial rod. Differences in the origin and structure of the axial parts of rhabdomesoids and the mesotheca of pilodictyoid cryptostomates suggest that these groups may not have been more closely related to one another than either was to certain trepostomatous stocks.

**ABOUT** a dozen specimens representing what appeared to be minute rhabdomesoid colonies growing from conical structures were recently sent to the writer by Dr. G. Sevastopoulo (Trinity College, Dublin) and Dr. G. Lane (University of California, Los Angeles). The specimens were collected from shales of the upper *Michelinia* Beds of Tournaisian age (Smyth 1930, p. 533) at Hook Head, County Wexford, Ireland. They were particularly welcome, for they promised to shed light on the early developmental stages and mode of growth of this common but little-studied group of bryozoans. The Sub-order Rhabdomesoidea is one of three major divisions of the Cryptostomata proposed by Astrova (1964). It comprises ramose forms with slenderly cylindroid growth habit and (almost always) radial symmetry. Although the group ranges from the Ordovician to Permian, these fossils are particularly well known from certain Lower Carboniferous strata where they occur as fragments of colonies up to 30 or 40 mm long by 1 or 2 mm wide. Specimens of complete colonies or of the attachment regions between colony and substrate are, to the writer's knowledge, as yet unrecorded. Rhabdomesoids constitute the greater part of the group sometimes loosely referred to as 'stick bryozoans'.

*External morphology.* The specimens varied from 1.3 to 3.0 mm in length and from 0.7 to 0.9 mm in diameter. On examination they proved to be early growth stages of rhabdomesoid bryozoans and each showed at its proximal end a conical structure. These were on average 0.8 mm long and, originating from a slender tip, each expanded distally, curving slightly along its length (Pl. 16, figs. 1, 2). Microscopic examination showed that the external surfaces carried closely spaced transverse growth wrinkles. The distal (wide) end of each of these cone- or horn-shaped structures showed a gently lobate or scalloped margin, which was thickened into a notable rounded rim marking the limit of growth of the cone. Each lobe around the rim formed the lower margin of one of the first series of zoecial apertures of the new colony. The two other sides

of each initial aperture combined to form a vaulted shape above the lower rim, so that the complete aperture has a rounded-triangular appearance and a basal width of about 0.2 mm. The position of each zooecial tube within the cone is evident, for it forms a rounded surface swelling with a linear shape narrowing proximally (Pl. 16, figs. 1, 2). There are five to eight apertures in the first cycle around the rim of the cone. They are succeeded by others having a polygonal outline, commonly hexagonal or rhombic (Pl. 16, fig. 3), though the exact shapes have in many cases been obscured by minor recrystallization or silicification. Numbers of large acanthopore nodes, 0.03 to 0.05 mm in diameter and of about the same height, project from zooecial walls at the zoarial surface.

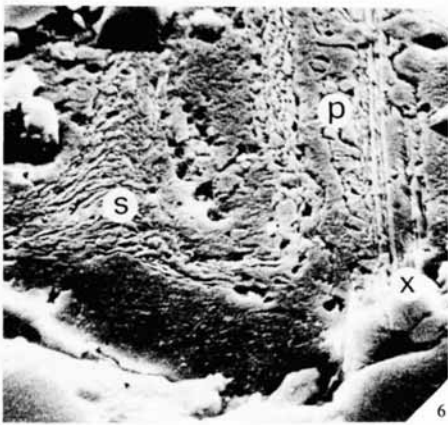
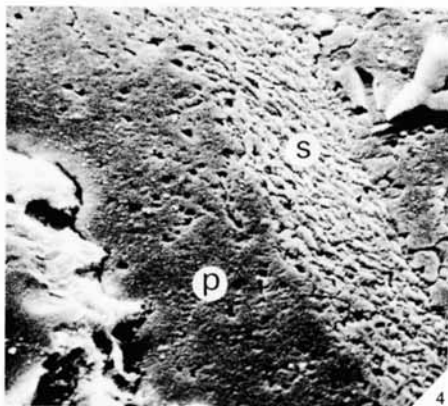
Although most of the cones studied show perfect horn shapes, a few depart from this pattern to varying degrees. In an extreme case the colonial origin is attached to a fragment of *Cladochonus* stem, the 'cone' being quite asymmetrical and tending to wrap around its tubular substrate (Pl. 16, fig. 3). The young rhabdomesoid colony growing from this distorted origin nevertheless assumed an orthodox cylindroid form which grew forward parallel with and close to the *Cladochonus* stem. One well-developed cone with zooecial tubes just emerging showed a terminal surface with an evenly convex curvature, distal extension not yet having given rise to a cylindroid shape. The convex zooecial growth surface comprises a peripheral cycle of initial apertures, eight in number, occupying lobate projections of the cone rim. Within these are other apertures, twenty-nine in all, which become progressively smaller and more closely spaced towards the apex of the convex terminal face. It is clear that even at this early stage a vigorous growth zone, involving active subdivision to initiate new zooecia, was already established at the distal tip of the young colony.

*Internal structure.* This was investigated using specimens embedded in an epoxy resin which were cut to provide one or more oriented surfaces. These were polished, etched with EDTA, shadowed with gold-palladium, and subsequently studied using a Cambridge scanning electron microscope. A few specimens were disappointing, for incipient silicification had destroyed much of the skeletal detail, but in others this was well preserved and permitted a full interpretation of the microstructure and growth sequence.

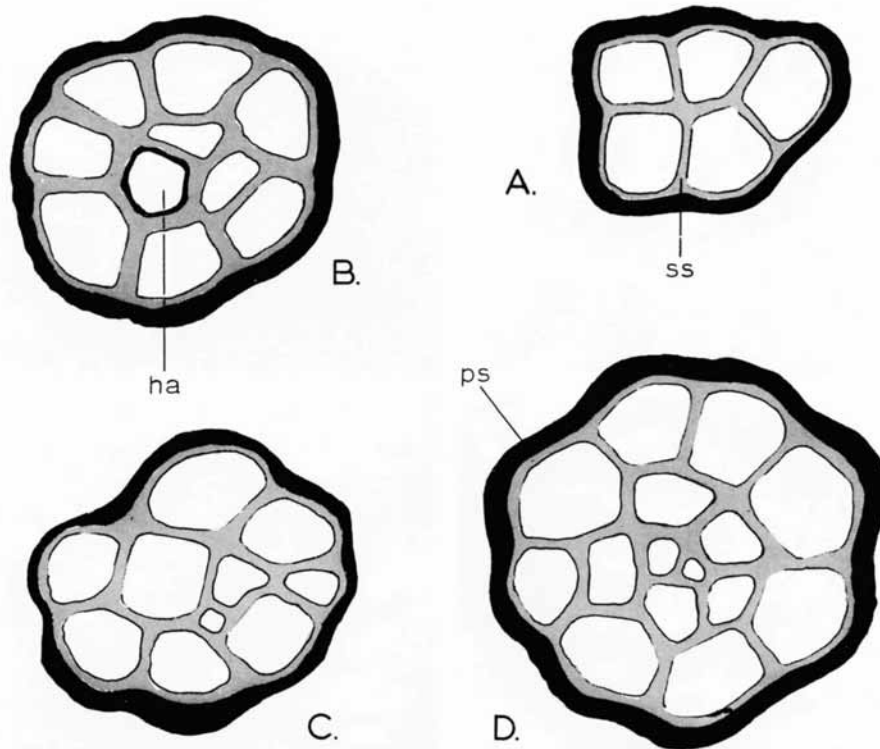
Transverse sections close to the proximal apices of cones (text-fig. 1A) showed a small number (three to five) of the initial cycle of zooecial tubes, but the ancestrula could not be positively identified. In one case (text-fig. 1B) the tubes were arranged

#### EXPLANATION OF PLATE 16

Figs. 1-6. Scanning electron micrographs of whole mounts or polished sections of young rhabdomesoid (bryozoan) colonies. 1, Initial cone with zooecial apertures at distal end.  $\times 77$ . 2, Cone showing transverse growth ridges, viewed from proximal end.  $\times 70$ . 3, Distorted 'cone' resulting from growth of the earliest-formed zooecial tubes over a *Cladochonus* stem (c). Commencement of the ramose part of the colony, with zooecial apertures, is also seen.  $\times 75$ . 4, Longitudinal section through the peripheral wall of a cone, showing the recrystallized primary (p) and laminar secondary (s) components.  $\times 1450$ . 5, Detail of peripheral wall of cone showing secondary fibres arranged in laminae oblique to the junction between primary and secondary layers.  $\times 2900$ . 6, Longitudinal section at proximal end of the cone showing primary (p) and secondary (s) layers of the peripheral wall passing inward as an investment around a productid spine, only one side of which is visible (x).  $\times 1450$ .



TAVENER-SMITH, young rhabdomesoid colonies



TEXT-FIG. 1. Transverse sections of initial growth cones. A, near proximal end. B, C, about midway along cone length. D, near distal end. Abbreviations: ha, hollow axial tube; ps, primary skeleton; ss, secondary skeleton.

around a central cavity which was not a zooecium or ancestrula, but may have represented some foreign structure, perhaps entirely soft-bodied, around which the cone had developed. More distal sections showed an increase in the number and diameter of zooecia, with a few small, new tubes appearing in the axial region (text-fig. 1C). Close to the wide distal end of the cone transverse sections clearly showed the peripheral, large diameter tubes of the first cycle, and within them a considerable number of smaller tubes, decreasing in diameter towards the centre (text-fig. 1D). It was evident from these transverse sections that zooecial walls within the cone were structurally continuous with the peripheral walls. This left no doubt that the cone was, in fact, an integral part of the bryozoan, and constituted an initial cup from which the mature colony took its origin. Longitudinal sections confirmed this, and showed the outer walls of the cone to be of two-fold construction: an outer, finely granular layer from  $12\ \mu\text{m}$  to  $36\ \mu\text{m}$  wide passes internally into a laminated layer with an average width of  $24\ \mu\text{m}$  (Pl. 16, fig. 4). The granular layer shows no obvious structure and may

be recrystallized. The laminar one consists of large numbers of roughly parallel fibres averaging about  $5\ \mu\text{m}$  wide and  $600\ \text{nm}$  thick, arranged in layers, one upon the other (Pl. 16, fig. 5). The resulting laminae are inclined at angles of 25 to 30 degrees to both the junction with the granular layer and the internal surface of the laminar wall. At the distal extremities of a cone sections showed that the granular layer becomes attenuated, but the laminar one thickens considerably to form the greater part of the peripheral rim. The two layers of the cone wall, granular and laminar, will hereafter be referred to as the primary and secondary layers, respectively, for they undoubtedly originated in that order. It is clear that the walls of the cone are identical in structure with the basal walls of encrusting trepostomatous colonies, and also with outer walls in many other members of the *Stenolaemata* (Tavener-Smith and Williams 1972).

Internal zooecial walls within the cone, as well as those in later-formed parts of colonies, show the kind of ultrastructure commonly associated with such walls in the *Trepostomata* and *Cryptostomata*. Apart from certain exceptions mentioned later, they are constructed entirely of secondary fibres with widths of 3 to  $5\ \mu\text{m}$  and thicknesses of between  $350\ \text{nm}$  and  $1\ \mu\text{m}$ . Laminae formed from successive layers of such fibres show a distally arched arrangement within walls (Pl. 17, fig. 2), and in their axial parts successive laminae commonly exhibit a selective thickening. Zooecial walls are relatively thin (average width about  $9\ \mu\text{m}$ ) within the cone and in the axial part (endozone) of the fully formed cylindrical stem beyond it. Where zooecial walls form the outer surface of the cylinder beyond the limits of the cone, however, it is clear that once the diameter of the initial cone had been attained these walls commenced to thicken, signaling the commencement of the exozone. Primary tissue is absent from zooecial walls in the endozone, though finely granular tissue not of primary origin constitutes the axial parts of large acanthopores in the exozone.

Three of the specimens sectioned longitudinally showed evidence of the original presence of foreign structures within the young colony. This was particularly clear in one case where a short section of a productid spine in an early stage of growth had been lapped around and overgrown by the extending bryozoan tissues (text-fig. 2). The stump of the spine projected slightly from the pointed proximal end of the cone and sections showed that, in contact with it, the primary and secondary layers of the cone outer wall curve round and pass upwards on both sides, forming a complete sheath around the spine (Pl. 16, fig. 6). The latter lies wholly within the cone occupying a roughly axial position: it is probable that it provided support for the young colony and helped to maintain it in a suitable growing position. The calcareous wall secreted by the bryozoan colony as an investment around the productid spine has a structure (Pl. 17, fig. 1) identical to that of the cone outer wall, with which it is continuous. The thickness of this internal investing wall varies from 7 to  $20\ \mu\text{m}$ , averaging  $12\ \mu\text{m}$ . The primary wall component ranges in thickness from 4 to  $16\ \mu\text{m}$ , being most commonly about  $8\ \mu\text{m}$ , and secondary laminae constitute the rest. Fibres composing the secondary laminae compare in dimensions with those of the outer wall of the cone.

In the specimen referred to, one end of the productid spine is embedded within the young colony, and at this end it is apparent that the spine had been broken before being overgrown by the investing tissues, which unite beyond it (Pl. 17, fig. 4). Many zooecial walls in this colony originated from the laminar secondary layer on the inner side of the wall around the productid spine (Pl. 17, fig. 1). This is a natural

consequence of the formation of successive new zooecial tubes (perhaps on the pattern of a helicoid spiral around the spine) from the axial part of the developing colony. Beyond the inner end of the spine the investing walls merge to form a poorly defined axial rod (text-fig. 2) which may, nevertheless, be traced to near the distal apex of the young colony. This structure commonly follows a somewhat irregular path, being slightly offset alternately to right and left. It is slightly wider (9 to 11  $\mu\text{m}$ ) than the zooecial walls which arise from it on either side. The structure of the axial rod is similar to that of zooecial walls, the main difference being that axial thickening of the distally arched laminae may be locally pronounced (Pl. 17, fig. 6). In transverse sections this leads to the appearance of granular tissue (not of primary origin) in the medial part of the axial rod, and this may extend for short distances into zooecial walls which diverge from it.

The morphology of these young rhabdomesoid colonies includes many features strongly reminiscent of ramose Trepostomata, to certain of which the Rhabdomesoidea as a group may have been closely related. These include tubular zooecia (though not as long as is general in the Trepostomata, and lacking diaphragms), the presence of recognizable endozonal and exozonal regions, large acanthopores and zooecial walls with laminar structure, the laminae being convex towards the exterior. As with so many rhabdomesoids and ptilodictyoids (bifoliate cryptostomates), differences from the Trepostomata are mainly matters of degree, rather than the presence of distinctive new structures or the entire disappearance of old ones.

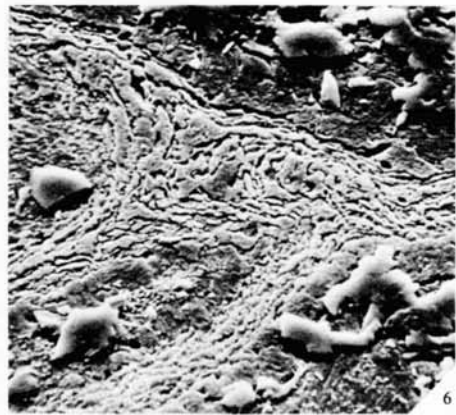
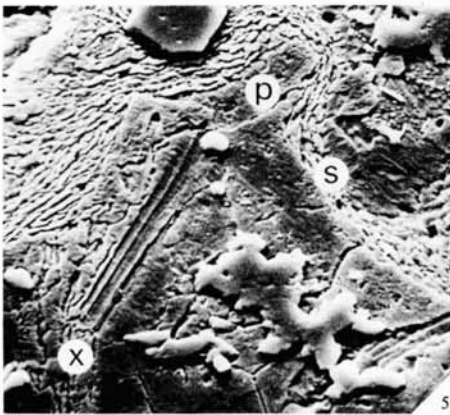
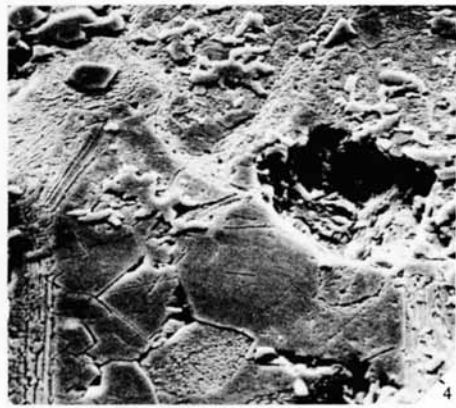
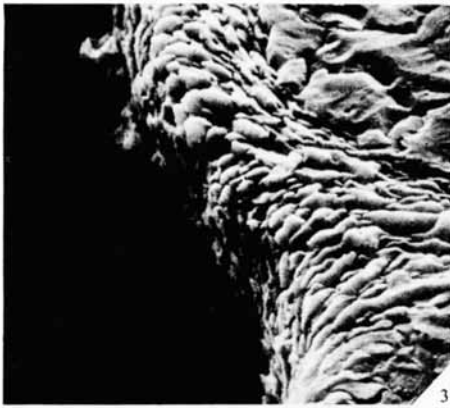
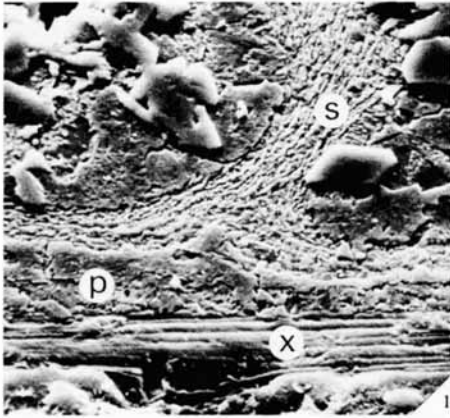
*Mode of growth.* It is clear from the situation and structure of the outer wall of the cone at the proximal end of each specimen, that this corresponds morphologically to the attached base of an encrusting stenolaemate colony. It is as if, centred on the ancestrula, a circular basal plate had been reflexed away from the substrate. There may be comparable cases among certain arthrostylid genera (for example, *Arthrostyleocia*, *Ulrichostylus*, and *Sceptropora*) which seem to have similar cone-like structures at their proximal ends (Bassler 1953, pp. G128, G130). Parallels between the outer cone wall and an attached colonial base emerge still more clearly if the circumstances and mode of their formation are considered.

The external walls of the initial cone are also the external walls of the first cycle of zooecia that lay within it. These walls must, therefore, have been secreted from the cellular epithelium which lined the zooecial tubes and represent the calcification of

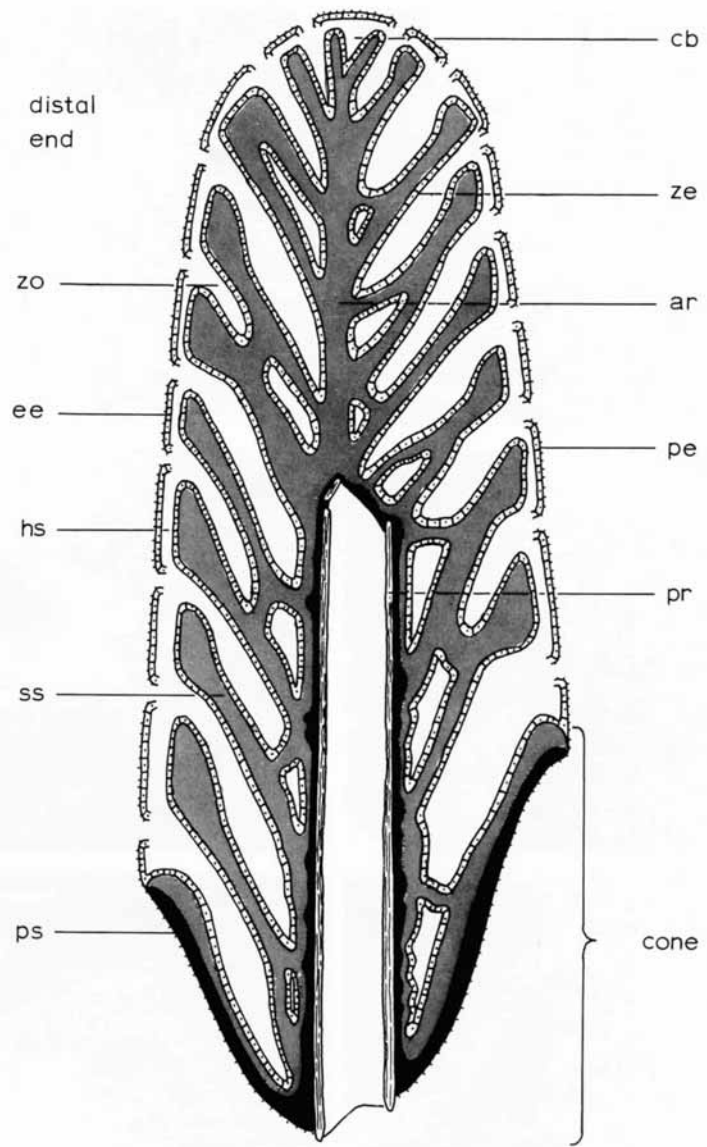
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#### EXPLANATION OF PLATE 17

Figs. 1-6. Scanning electron micrographs of polished longitudinal sections through young rhabdomesoid (bryozoan) colonies. 1, Primary (p) and secondary (s) bryozoan wall tissue overlying one side of a productid spine in the axial region of a colony. The secondary tissue forms the proximal part of an internal zooecial wall.  $\times 1400$ . 2, Typical zooecial wall structure, showing the distally convex secondary skeletal laminae.  $\times 2800$ . 3, Three-dimensional view of the edge of a zooecial wall, showing the fibrous nature of the units composing each lamina.  $\times 3000$ . 4, A view showing the continuity of bryozoan skeletal tissue around the distal end of a productid spine in the axial part of a colony.  $\times 700$ . 5, Detail of Fig. 4 showing primary (p) and secondary (s) wall components overlying the fractured extremity of the productid spine (x).  $\times 1400$ . 6, Part of the axial rod showing medial thickening of distally arched laminae.  $\times 1400$ .

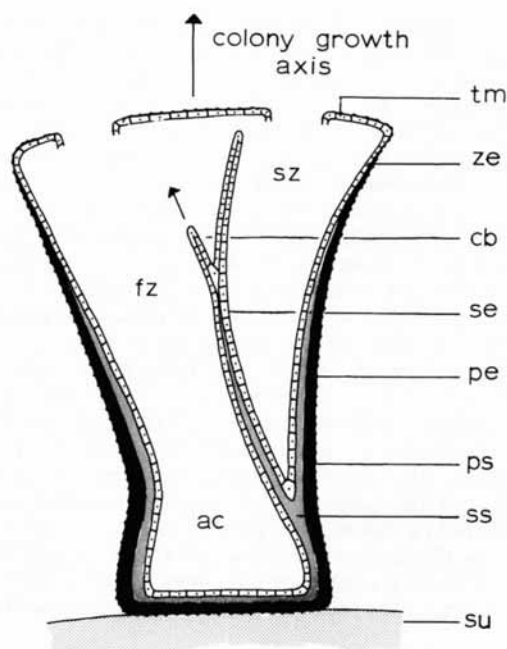


TAVENER-SMITH, young rhabdomesoid colonies



TEXT-FIG. 2. Medial longitudinal section of young rhabdomesoid colony with proximal cone, showing main skeletal layers and reconstructed position of epithelium. Abbreviations: ar, axial rod; cb, common bud; ee, eustegal epithelium; hs, hypostegal space; pe, periostracum; pr, productid spine; ps, primary skeleton; ss, secondary skeleton; ze, zooidal epithelium; zo, position of zooid.





TEXT-FIG. 3. Reconstruction of earliest stages of growth from the ancestrula in a rhabdomesoid colony. Abbreviations: ac, ancestrula; cb, common bud (initiated in axial position); fz, first zooid, growing directly from ancestrula; pe, periostracum, or external 'cuticle'; ps, primary skeleton; se, septum, calcified proximally to form the first internal zoocial wall; ss, secondary skeleton; su, substrate; sz, second zooid; tm, terminal membrane; ze, zooidal epithelium.

the originally soft limiting layer of the young colony (text-fig. 3). By analogy with modern cyclostomatous bryozoans (Borg 1926, pp. 191-194) this would have comprised an ectodermal epithelium, sealed on its outer side by a polymerized acellular exudation here called the periostracum. Walls within the cone which served as an immediate investment around a spine or other foreign structure must also have originally been bounded by periostracum, for they are continuations of the outer wall and structurally identical with it (text-fig. 2). From an anatomical point of view such walls must be considered 'external' and, by their direct adhesion to foreign objects, they demonstrate the same relationship as that between the basal wall of an encrusting colony and its substrate. Walls between zooecia within the cone and beyond it differ from those already mentioned both in structure and derivation. They consist entirely of laminar secondary skeleton and there is no reason to suspect the former presence

of primary tissue or a periostracal layer at any stage. These walls are continuous with and derive from either the inner secondary lining of the peripheral wall or from an axial rod composed of the same material. The uniform construction of common zooecial walls from superimposed, distally arched laminae which persist to the exozonal extremities, makes two clear demands in interpreting the origin of these structures. They are, firstly, that the wall was completely enclosed within a cellular envelope which must have been the zooidal epithelium; secondly, that the wall grew in length by the successive apposition of calcite laminae at the distal end. The epithelial envelopes within which mineralized zooecial walls necessarily had their inception must have arisen as plate-like invaginations of the epithelial layer lining the peripheral wall of the cone (text-fig. 3). Furthermore, the configuration of laminae at the distal terminations of shared zooecial walls indicates that the epithelium was continuous across the distal end, and therefore also between adjacent zooids. From this several further inferences may be made, namely: that the distal margins of zooecial walls were not in direct contact with the frontal wall of the colony; that they were separated from this by what can only have been a narrow coelomic space which allowed physical continuity between the body cavities of neighbouring zooids; that, lacking skeletal evidence to the contrary, the frontal surface of the colony was entirely composed of soft tissues; and that, by the nature of their origin and construction, zooecial walls were essentially *internal* partitions. A logical corollary from the above is that the frontal membrane of the colony, with the associated lophophore and ancillary apparatus of individual zooids, can only have been a continuation of the epithelial-periostracal layer which, in the proximal region, secreted the outer wall of the cone (text-figs. 2, 3).

Arrangements of the above kind, in which mineralized zooecial walls did not meet the frontal membrane and individual zooids were not entirely separated from one another, have been and are common to many groups of bryozoans. They are known to occur in certain cyclostome stocks (Ceramoporoidea, Cerioporina, Cancellata, and Rectangulata) and probably did so throughout the Cystoporata, Trepotomata, and Cryptostomata. They are likely to have been the rule rather than the exception and the condition, though at first sight complex, is probably primitive rather than advanced (Tavener-Smith and Williams 1972, p. 155). The arrangement and structure of walls comprising the initial cone leave no doubt that the manner of 'budding' off new zooids in these colonies was essentially the same as that described by Borg (1926, p. 256) from modern Cyclostomata. The same pattern may well have been general throughout the Stenolaemata. It involves the repeated division of a continuously growing cavity or cavities by calcareous septa fabricated within sheet-like invaginations of the zooidal epithelium in the manner described earlier for zooecial walls (text-fig. 3). In this way successive daughter cavities (new zooecial tubes) were formed. As this process continued and newly formed tubes lengthened, the cavity which underwent repeated division (the 'common bud' of Smitt 1865, p. 6) remained at the focal point of an increasing group of slightly divergent tubes. In this way an axis of active growth was established, with the continuous presence at the distal tip of the developing colony of a group of lately formed zooecial tubes of small diameter.

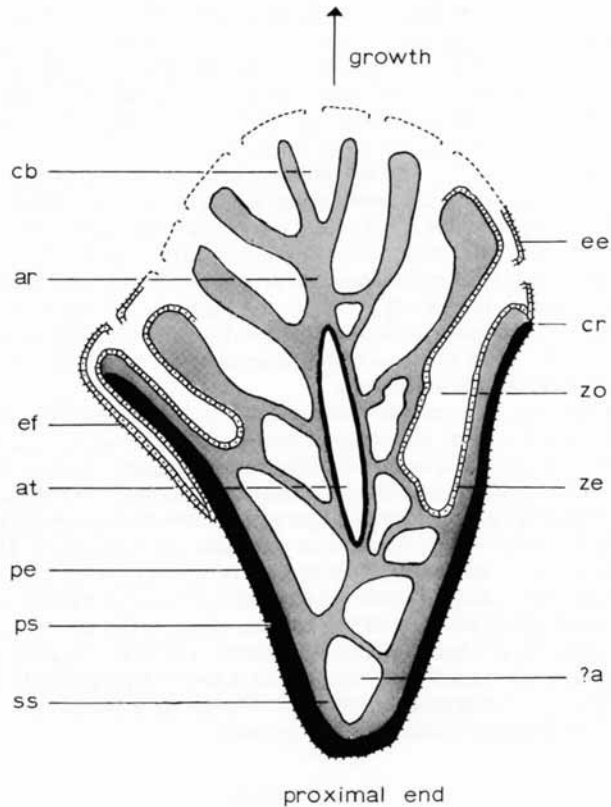
On the basis of the observed skeletal structure of the specimens, and the reconstruction of secretory tissues which that permits, and in the light of what is known of

growth processes in modern bryozoans, a developmental sequence may be suggested to account for the morphological features of the colonies examined. Settlement and fixation of the larva to form an ancestrula must have been followed by the distal growth and distension of the latter, and the formation within it of the first septum (internal zooecial wall). This duly divided the available space into two parts, connected only across the distal margin of the septum, which just failed to reach the terminal membrane (text-fig. 3). One of the chambers so formed would have constituted the first autozoid of the new colony, the other being the common bud which repeatedly divided in the same way to form a succession of slightly divergent zooecia. As these tubes lengthened and increased in diameter their outer walls, at first delimited only by combined layers of epithelium and periostracum, became mineralized. First granular, and later (more slowly, and by the addition of successive increments) laminar material was deposited to form the solid outer wall of the cone. This must, as an inherent result of its mode of origin, represent the greatly lengthened and distended apertural rim of the ancestrula.

The walls of the cone continued to extend distally, as indicated by successive transverse growth wrinkles, until the zooecial tubes of the first cycle had attained their mature, genetically ordained length. At this stage the diameter of the future zoarial cylinder was provisionally determined and zooecial extension largely ceased, though some thickening of the cone rim took place (the inception of the exozone) due to the continued deposition of calcite in more or less static circumstances. This continued as long as the zooecia were occupied by functional zooids. By the time the first cycle of zooecia, whose outer sides constituted the walls of the cone, had attained maturity it seems that repeated subdivision of the 'common bud' in the axial part of the young colony had already given rise to many more immature tubes. As each generation of these lengthened and attained maturity, so the colony length also extended and the ramose cylindroid shape gradually emerged. The tapering distal apex continued to mark the region of active subdivision and growth.

#### DISCUSSION

These specimens show early stages in the formation of rhabdomesoid colonies. In each of them an ancestrula gave rise to a small number of slightly divergent zooecial tubes. In growing distally these formed an initial cone from which the characteristically cylindroid main part of the colony originated. In some specimens it seems that the cone developed from the basally attached ancestrula without external support to help maintain it in a favourable growth position. This is surprising, considering the minimal nature of the attachment area. Other specimens showed a slender axial hollow within the cone (text-figs. 1B, 4), suggesting that temporary support may have been derived from the overgrowth of some soft-bodied organism which later decayed. In others the initial zooecia grew against, and then around spinose or tubular substrates which were skeletal parts of other organisms, so that these became incorporated within the cone. In all these instances only the earliest formed parts of colonies are concerned, and it is relevant to inquire whether such arrangements for attachment and support were adequate in fully developed colonies, or whether considerable modification would be called for in the course of subsequent growth.



TEXT-FIG. 4. Median longitudinal section through an initial cone containing an axial hollow outlined by a thin layer of primary skeleton. The epithelium is reconstructed to show (left side only) how an external flap, or mantle, might have permitted calcification of the basal region from the exterior. Abbreviations: ar, axial rod; at, axial tube; ?a, possible ancestrular chamber; cb, common bud; cr, rim of initial cone; ee, eustegal epithelium; ef, external flap; pe, periostracum; ps, primary skeleton; ss, secondary skeleton; ze, zooidal epithelium; zo, position of zooid.

Modern cheilostomatous colonies with slenderly ramose forms comparable to that of rhabdomesoid cryptostomates assume an erect growth habit in quiet water of moderate depth (Stach 1936, p. 62; Lagaaij and Gautier 1965, p. 52). Schopf (1969, p. 236), although in general agreement regarding the habitat of the erect Cheilostomata, suggested that at the depths at which they are commonly found (100 to 150 m) water movement may be appreciable. Cheetham (1971, pp. 7-12) examined

the mechanical implications of lateral stresses generated by water movements upon developing colonies of erect growth habit. He recognized that as a colony extended distally the load resulting from the weight of the structure itself and the torsional stress due to laterally directed water pressure would increase. Also, that these forces would be most pronounced at the base of the colony, and that therefore the need for greatest skeletal support would be in that region. He concluded that the skeletal pattern manifested by many of the erect Cheilostomata represents a mechanically efficient means by which such colonies may support themselves and counter water pressures acting against them by permitting a degree of controlled flexibility. Such arrangements most commonly incorporate a strongly calcified attachment zone at the base of a pillar-like colony, the latter having a rigid outer frame (frontal walls of successive zooids) thickening progressively towards the base, and a relatively light internal structure.

Fragments of rhabdomesoid colonies and of the ramose *Trepotomata* show what was probably an equally effective skeletal arrangement, embodying the same mechanical principles but differing in design. In these groups a thin-walled endozone is bordered peripherally by the more massive walls of the exozone, which were progressively added to while the colony lived and extended distally. The structural similarity to the ramose Cheilostomata strongly suggests that these colonies also were adapted to withstand stresses of the kind associated with an erect growth habit, and that they too had rigidly attached bases.

In view of these considerations it is unlikely that unmodified cones of the kind seen in the proximal regions of the specimens examined would have provided adequate means of attachment or support for fully developed ramose colonies. They would have been inherently weak, and it is therefore reasonable to suppose that the basal attachment was progressively reinforced and strengthened during the later life of the colony. Such additions would have been made most effectively from the exterior, and this may well have been accomplished by secretion from the inner surface of an external mantle, formed as a flap-like proximal extension of epithelial layers from the rim of the cone (text-fig. 4). Mineralization on this pattern, in conjunction with exozonal thickening and possibly the eventual sealing of zoecial tubes in the basal region, could have provided a strongly calcified zone of attachment, as in hornerid and fenestellid bryozoans. Whether this in fact took place will not be known until specimens showing the proximal parts of fully developed rhabdomesoid colonies are available, but if such was the case it is certain that the early developmental stages shown by the present specimens would have been concealed and lost for study purposes in the early stages of overgrowth.

Longitudinal sections of cones and subsequent cylindrical parts of the colonies examined showed certain variations of internal structure. In some sections zoecial walls took their origin from an axial rod which represented successive positions of the inner wall of the 'common bud' chamber. In such cases the axis of the young colony was solid (text-fig. 1A, C, D). In others zoecial walls could be traced back to the inner side of an axial tube which, as indicated earlier, was in effect an invagination of the peripheral wall of the cone. In some instances this tube was the basal bryozoan investment around a productid spine, but in others no such foreign structure was present and an axial hollow or tube existed within the developing colony (text-figs. 1B, 4).

Such a space may originally have been occupied by some soft structure, used as a temporary support in the earliest growth stages, which later decayed.

One specimen showed a tubular internal 'basal wall' enclosing a productid spine and closing beyond its broken end, so that the tube was succeeded by an axial rod (text-fig. 2). Although no instance was seen, it would presumably be possible for an axial hollow to pass into a solid-cored zoarial cylinder in the same fashion. This is of interest when it is recalled that the currently accepted difference between two largely contemporaneous and commonly coexisting ramose cryptostomatous genera, *Rhabdomeson* Young and Young and *Rhombopora* Meek, is the presence in the former of an axial tube which is not found in the latter.

Good examples of the early developmental stages of bryozoan colonies are not common, particularly among palaeozoic genera. Such specimens are of great interest, for they may yield structural information of value in assessing phyletic relationships between groups. This is especially important in the Cryptostomata, for stratigraphic data give little help in interpreting the affinities of the three major divisions of the Order, either to each other or to the Trepostomata, to which they are related. Certain aspects of the colonies examined seem to provide useful pointers in this connection. It is clear that the morphology of the juvenile colony was determined by budding from an attached ancestrula on a narrowly divergent pattern. The initial form evolved was therefore a cone. Subsequent cyclic budding from the distal end of the cone initiated new, tubular zooecia, each originating in the axial region and diverging towards the periphery. These zooecia were essentially similar to those of the Trepostomata and their continuous, systematic addition resulted in the emergence of a ramose, cylindrical form with radial symmetry.

Although the cone may superficially suggest an encrusting colonial base reflected away from the substrate, it cannot have originated in that way. The development of a particular three-dimensional shape in stenolaematous bryozoans is largely dependent upon the size and situation of the 'common bud' area, that is, the part of the periphery possessing the capacity to subdivide unspecialized colonial spaces by the development of internal septa (Borg 1926, p. 256; Illies 1968, p. 225; Brood 1972, p. 41). To permit the formation of a basal disc of encrusting zooecia it is prerequisite that each of a cirlet of tubes originating from and spreading radially over the substrate around the ancestrula should have possessed that ability. In the specimens examined it is clear, however, that the capacity to proliferate by fission was entirely restricted to a zone lying *within* the first-formed cycle of zooecia which was itself directed *away* from the substrate. In these circumstances an encrusting colonial base cannot possibly have formed.

In contrast it is instructive to consider the organization of a typical ptilodictyoid such as *Stictopora* Hall. Here the symmetry is bilateral, not radial, and the zoarial form a flattened, bifoliate frond. Zooecia arise on either side of a medial partition, or mesotheca, and, due to the restricted width of the frond, are shorter and more compact than in the Rhabdomesoidea. Zooecia of this kind are closer to the more specialized and advanced zooecia of the Fenestelloidea than are those of the rhabdomesoids. The mesotheca differs in structure from zooecial walls and bears strong resemblances to that of the basal walls in many stenolaematous bryozoans, in that both primary and secondary tissue is present (Tavener-Smith and Williams 1972,

p. 149, pl. 28, figs. 182-184). The former is mostly seen as a series of disconnected, medially disposed lenses or pods, called 'tubules' by some authors (Phillips Ross 1960, p. 1063; Karklins 1969, p. 7). Superficially the appearance suggests two basal walls that were united face to face with one another, and then stretched so that the originally continuous primary layer was separated into a series of discrete lenses. However, these primary lenses show no trace of a medial partition which would have marked the position of the fused periostraca in such a case. Careful consideration of the ultrastructure makes it seem altogether more likely that the mesotheca formed within an epithelial fold drawn up from the inner side of an already partly calcified encrusting basal lamina. This being so, it follows that the periostracum was at no stage involved in the structure, which does not correspond to a doubled basal wall. A comparable case has been observed in the transverse zooecial walls of the modern cheilostome *Umbonula* (Tavener-Smith and Williams 1970, p. 249, fig. 34), which also contain separated lenticular pods of primary tissue. It would therefore appear that the establishment of a flat basal encrustation was an essential prerequisite for the development of a ptilodictyoid frond.

If it may be assumed that the young rhabdomesoid colonies examined in this study were developmentally similar to others of the same group, it would follow that certain fundamental differences separate them from the Ptilodictyoidea. These relate to the colonial symmetry; the presence or otherwise of an initial basal encrustation as a necessary astogenetic stage; the lack of structural and developmental correspondence between mesotheca and 'axial rod' (or internal tube wall); and, finally, the general aspect of the zooecia themselves. The ptilodictyoid attributes are such as to suggest that the group may have had close affinities with the more advanced (and stratigraphically later) fenestelloids. But it seems unlikely that the ptilodictyoids were more closely related to the rhabdomesoids than was either group to the Trepostomata, from which both may have been independently derived.

Unsectioned specimens from the original collection are deposited in the Sedgwick Museum, Cambridge (SM E 20056-20069).

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R. TAVENER-SMITH  
Department of Geology  
The Queen's University of Belfast

Present address  
Department of Geology  
University of Natal  
King George V Avenue  
Durban  
S. Africa

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