Richard S. Boardman

Mode of Growth and Functional Morphology of Autozooids in Some Recent and Paleozoic Tubular Bryozoa

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ABSTRACT

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Most of the diaphragms common to trepostome autozooecia presumably formed floors for living chambers of successive functioning bodies in the degeneration-regeneration cycle. The position of some skeletal intrazooecial structures within living chambers must have been lateral to functioning organs. Mural spines that have a definite distributional pattern might represent calcified attachment points for ligaments or muscles. Skeletal cystiphragms, hemiphragms, ring septa, and autozooecial wall thickenings all seem to be lateral features which provided significant modifications to the shape and size of the autozooidal living chamber. These and other skeletal structures appear to have been developed by zooids growing with colony-wide cyclic coordination so that skeletal structures commonly display a constant relative spacing or size correlation in the growth sequence of a colony. Hemiphragms, cystoidal diaphragms, ring septa, and skeletal cystiphragms and funnel-cystiphragms in some species are perhaps more comparable in cycle with basal diaphragms of autozooecia, suggesting that their distribution might have been controlled largely by degeneration-regeneration cycles. Closely tabulated mesopores seem to provide an expression of the most frequent colony-wide cycles in many species and can be correlated one-to-one with some mural spines and skeletal cystiphragms. Perhaps these most closely spaced structures reflect an increase in length of soft parts during a single functional stage of the degeneration-regeneration cycle.

Some monticuliporid and diaphragmed trepostomes contain a second type of cystiphragm that forms small flask-shaped chambers filled with brown deposits that suggest a concentration of organic material during the life of the colony. These chambers do not preclude retractable lophophores but almost certainly the inflexible necks restrict significantly the room for passage of membranous structures. Because of this restriction and the scattered or thinly cyclic distribution of flask-shaped chambers known from only a few species, a primary food-gathering function does not seem feasible for them. Possibly, these restricted chambers had a reproductive function, conceivably comparable to the male zooids with reduced numbers of tentacles reported in a few species of cheilostome Bryozoa. Regardless of function, if the flask-shaped chambers and their inferred organs were zooids, they represent *intrazooecial* polymorphism, contrasting morphologically with the alternating and consistently present living chambers that presumably contained food-gathering organs. The shape, size, and position of food-gathering organs seem more likely then to be reflected by intrazooecial structures that are repeated regularly in autozooecia, such as basal diaphragms, cystiphragms, hemisepta, ring septa, and annular thickenings of zooecial walls.

Contents

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Introduction

The degree to which the evolutionary history of the Bryozoa can be understood, and the success with which this information can be applied to related problems, such as classification and biostratigraphy, depends primarily on the biologic understanding of both Recent faunas and the available fossil record. As has been demonstrated in other phyla, biologic understanding of fossils comes largely from the extrapolation of knowledge of living forms to fossil forms that have comparable morphology at taxonomic levels low enough to give inferred significance to the comparisons.

Fundamental biologic studies of tubular Bryozoa are few, and published attempts at living to fossil extrapolations are largely fragmentary. As a result, understanding of tubular Bryozoa is lagging and this lack of knowledge is reflected in the basic nature of the questions on mode of growth dealt with in this paper.

Any attempt to learn more about the biology of tubular Bryozoa starts with the work of three authors who have been responsible for the majority of the available biologic interpretations. This paper attempts to integrate and extend their work. Cumings (1904,

Richard S. Boardman, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

1905, 1912) and Cumings and Galloway (1915) made great strides in suggesting approaches and biologic interpretations of Paleozoic Bryozoa, but they were handicapped by lack of morphologic and mode of growth data on living species. Much of the kind of information they needed was supplied some years later by Borg (1926, 1933) working on Recent cyclostomes. While Borg's work on soft parts is detailed and apparently quite accurate, he ignored to a considerable extent the exoskeletal counterparts which are essential to the total growth picture of living forms and extrapolation to fossils. Unfortunately, the work of all three authors had been largely ignored until the past several years.

Tubular Bryozoa are fossil and Recent forms that have generally cone- or tube-shaped zooecia that tend to increase in length during ontogenetic development (Boardman and Cheetham 1969:208). Skeletal apertures are terminal. Present evidence suggests that cuticle (ectocyst of Banta 1969:151) is restricted to the boundary between the colony and the environment and is nowhere incorporated within the exoskeleton. Taxonomically, the informal grouping of tubular Bryozoa includes the Trepostomata, Cystoporata, and Cryptostomata—orders presently thought to have become extinct early in the Mesozoic Era—and the Cyclostomata which is largely Mesozoic to Recent in

1

age. These orders are contrasted with the Cheilostomata that have generally box-shaped zooecia, infolded cuticle and frontal apertures, and the Ctenostomata, commonly held to be closely related to the Cheilostomata.

In Recent Bryozoa, autozooecia can be defined as the skeletons of zooids that have a protrusible lophophore at some stage or stages in their ontogeny (A. H. Cheetham, verbal communication). A lophophore includes tentacles and adjacent supporting structures, including the tentacle sheath (Figure 1) as used here. Functionally, the feeding mechanism always includes a protrusible lophophore. In cheilostomes, a lophophore in addition to being a feeding apparatus can also serve a reproductive function (Silén, 1966:124–129) by allowing the passage of sperm through the two dorsomedial tentacles. Cheilostome autozooids also can have dimorphic lophophores which either alternate in the same autozooecium or occur simultaneously in adjacent autozooecia of similar morphology (Gordon, 1968) ; or, cheilostome autozooids can display dimorphism in adjacent autozooecia and contained lophophores (Cook, 1968). This dimorphism of lophophores correlates with feeding and reproductive function; lophophores that are entirely reproductive (male) in function generally have fewer tentacles than feeding lophophores. In living cyclostomes, different species are known to be monoecious or dioecious, and a range of dimorphism and function comparable to that of cheilostomes can be anticipated hypothetically in fossil tubular Bryozoa.

In fossil tubular Bryozoa, identification of autozooecia, some of which must have contained feeding organs, can be achieved generally for an entire order with little more than the inference that the fossil forms in question were Bryozoa and that these Bryozoa had protrusible lophophores during life that were part of their feeding mechanism. In zoaria in which zooecia of only one morphology are present, some of those monomorphic zooecia must have contained feeding organs for at least a part of their ontogeny, and operationally all of the zooecia in that zoarium are considered to be autozooecia. In related zoaria containing polymorphic zooecia, the commonly occurring zooecia of morphology comparable to the monomorphic autozooecia are operationally considered to be autozooecia. The inference in identification of monomorphic autozooecia with a set of zooecia in zoaria containing polymorphic zooecia is minimal. The different kinds of polymorphic

zooecia usually are easily recognizable, and confusion of the monomorphic autozooecia with one of the kinds of polymorphic zooecia is unlikely.
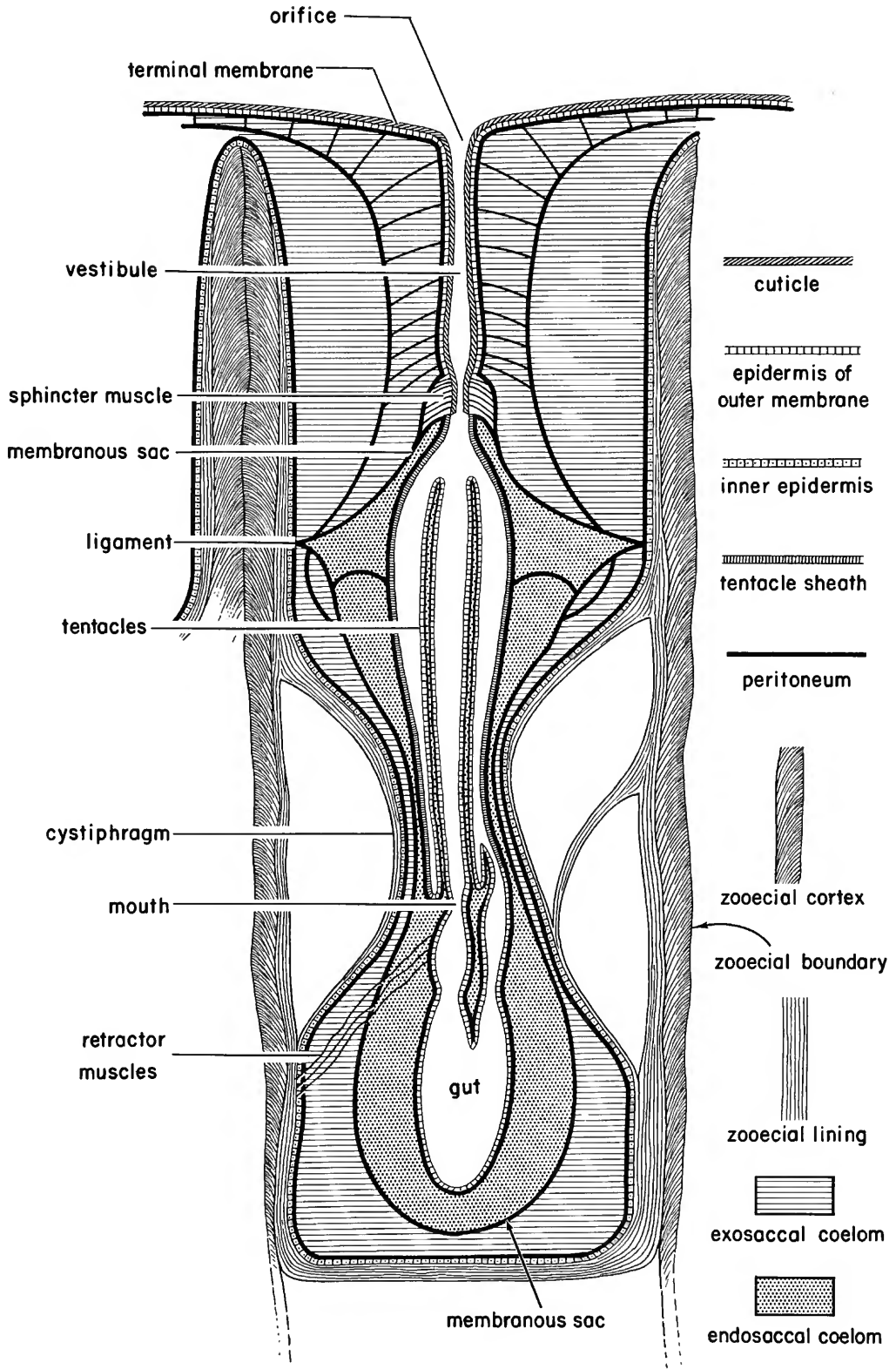
In fossil Bryozoa, therefore, the set of autozooecia that contained lophophores of feeding function is the consistently present set of zooecia in related forms.

FIGURE 1.—Preliminary model of a trepostome autozooid based on the feeding organs of a generalized Recent cyclostome [after Borg (1926: fig. 1; 1933: fig. 26), Marcus (1940: fig. 15), Cori (1941: fig. 379) and Clark (1964: fig. 65)] and a flask-shaped skeletal living chamber of average proportions of the Late Ordovician species *Amplexopora robusta* Ulrich (Plate 9: figures 3, 6). (The preferred hypothesis at the end of this study suggests that something other than feeding organs occupied the relatively few flask-shaped chambers in trepostomes. See text).

For descriptive purposes, the calcareous zooecial wall of a trepostome can be divided into two parts: (1) the *cortex,* occurring in virtually all trepostomes and here defined as the outermost unit of a zooecial wall, in laminated skeletons consisting of laminae that range from inclined to transverse in orientation to the zooecial axis, synonymous with *zone of curved laminae* (Boardman 1960: 22); and (2) the *lining* (Boardman 1960: 23), occurring in many trepostomes and here defined as the calcareous wall unit between cortex and zooecial cavity consisting of laminae generally parallel to the zooecial axis (Plate 8: figure 4).

Laminae of diaphragms and cystiphragms generally continue without break into laminae of the cortex or of the lining, if a lining is present (as shown here). Along the contact between cortex and lining, laminae of the lining can either continue without break into laminae of the cortex (relationship not shown), abut sharply against the cortex, or gradually pinch out on the inner surface of the cortex. These different types of contacts between lining and cortex can be seen along a single zooecium in any combination in some species, or one type is characteristic of other species. Thus, a species might be characterized by one-piece construction of diaphragm-lining-cortex units (Plate 5: figures 4, 5; cystiphragms rather than diaphragms), diaphragm-lining units plus a separate cortex (Plate 8: figures 4, 7), or diaphragm-cortex units if lining is obscure (Plate 8: figure 2; Plate 11: figures 3, 4) either singly or in combination.

The term *cingulum* (Cumings and Galloway 1915: 361) is replaced here by lining only because the original definition restricted the cingulum to secondary thickenings. Diaphragms, cystiphragms, and lining are not considered here to be secondary to the cortex in species in which there is any significant amount of merging of laminate from these structures with cortex laminae to form a single skeletal unit recording a single episode of calcification in the growth of a zooecium. In trepostomes, it has been possible in relatively few species to be satisfied that linings are structurally distinct from cortices all along the zooecia and, therefore, might be considered as entirely secondary. For trepostomes as used in this paper, the term lining is meant to be empirical and not to imply primary-secondary relationships with the cortex.

orifice

terminal membrane

vestibule

sphincter muscle

membranous sac

ligament

tentacles

cystiphragm

mouth

retractor
muscles

gut

membranous sac

cuticle

epidermis of
outer membrane

inner epidermis

tentacle sheath

peritoneum

zooecial cortex

zooecial boundary

zooecial lining

exosaccal coelom

endosaccal coelom

In trepostome zoaria containing polymorphic zooecia, the autozooecia that must have included feeding organs are among those in the set of longer zooecia of larger cross-sectional area which occurs consistently between monticules. The identification of autozooecia is virtually a certainty if trepostomes were Bryozoa with protrusible lophophores as part of the feeding mechanism, and need not be further defended except in the context of evidence for or against the bryozoan affinities of trepostomes.

The function of individual autozooids of which fossilized autozooecia were parts may have been either feeding, reproductive, or both, throughout life or during certain ontogenetic stages. A second set of autozooids of different zooecial morphology may have existed (exilapores in species of trepostomes are a possibility). Investigations of problems, such as function or autozooecial dimorphism that can vary at the lower taxonomic levels, necessarily produce inferential results for fossils that are more or less supported by evidence unique to each investigation.

Investigation of the nature of soft parts that were included in Paleozoic autozooecia is necessary if useful inferences are to be made about mode of growth. Most such inferences must be based on microskeletal studies, because recognizable remnants of soft anatomy in Paleozoic Bryozoa are understandably rare. A search of over fifteen thousand thin sections in the collections of the Department of Paleobiology of the National Museum of Natural History revealed two to three hundred that contained membranous remnants, and few of those showed enough form to support minimum interpretation. These relatively small structures are difficult to interpret unless the plane of the thin section is near the axis or center of the structure, or the section is left thick enough to reveal the structure in three dimensions.

Among Paleozoic Bryozoa, the great majority of indications of soft parts were found in trepostomes. This could be due in part to the protection afforded by the relatively long autozooecia and capping diaphragms so prevalent in the order. Many of the structures interpreted here as remnants of soft parts or the more fragile skeletal indications of soft parts were found well within zoaria under one or more calcareous diaphragms or protective overgrowths.

Material examined for this paper also includes several thin sections from each of approximately two dozen colonies of Recent cyclostomes containing preserved soft parts. The cyclostome sections (Plates 1–3) are epoxy impregnated and ground with abrasives (Nye, Dean, and Hinds, in press) retaining both hard and soft parts without relative displacement, thus permitting direct study of relationships among those structures. The brief study of Recent cyclostomes included here and the cited findings of Borg provide the ground rules for inferences about mode of growth and nature of soft parts in Paleozoic Bryozoa.

The initial assumptions on which the inferences in this paper are based include:

1. Paleozoic forms studied (largely trepostomes) are Bryozoa. This is a generally accepted point that has been questioned less than perhaps it should have been (Boardman 1960:23–25). Most of the evidence is of an indirect nature with the possible exception of the work of Cumings (1904, 1905, 1912). The weight of the evidence indicates, however, that the only reasonable assumption at present places the trepostomes in the Bryozoa. For the purposes of this paper then, trepostomes are considered to be Bryozoa and therefore coelomate with membranous walls sealing off coelomic spaces, and with a protrusible lophophore as part of the feeding mechanism.

2. If similarities exist between Recent cyclostomes and Paleozoic tubular Bryozoa in mode of growth and morphology of feeding and reproductive organs, those similarities can only be inferred by comparison of skeletal microstructure, and shape and relative size and position of known organs and structures in Recent forms to the morphology of Paleozoic forms. Comparable morphology in fossil and Recent forms presumably indicates degrees of similarity in function and mode of growth in proportion to phylogenetic affinity. Empirical comparisons of this kind are inherent in the study of extinct forms and certainly give no assurance or direct measure of correctness. At best these comparisons should provide a series of logical inferences which approximate generally to an unknowable degree the real similarities. This kind of interpretation, therefore, must remain inferential and open to question as new evidence is obtained.

3. Differences in morphology and function are expected between Paleozoic trepostomes and Recent cyclostomes, but within the assumed concepts of the phylum. Minor differences of function can be suggested for Paleozoic forms—even if unknown in Recent Bryozoa—if the fossil evidence seems to require them.

Interpretation of fossil structures not found in Recent forms, however, is necessarily speculative.

4. Differences in morphology and function must be expected within the trepostomes themselves. The morphology of membranous structures found in an exceptionally preserved specimen should not be assumed for the entire order or for a major subdivision of that order.

Determination of Living Chambers

An early step in attempting to understand something of the soft parts of Paleozoic Bryozoa is to determine the extent of possible living chambers of the different polymorphs as delineated by the skeleton. In autozooecia (as the term is applied to Paleozoic Bryozoa), diaphragms are the partitions that extend transversely across zooecial cavities dividing them into segments. Skeletal laminae of calcified diaphragms (Figure 1) extend outwardly toward the apertures into supporting autozooecial walls or less commonly attach outwardly to cystiphragms or other intrazooecial structures. The laminae, therefore, if deposited sequentially, were necessarily deposited on outer sides of the diaphragms. It is assumed, then, that the depositing epidermis and zooidal soft parts were on the outer sides of diaphragms, that at least some of the diaphragms in an autozooecium were the floors of living chambers, and that some of these living chambers must have contained the feeding organs.

Determination of the outer end of a living chamber is more difficult. The obvious starting place is the last-formed chamber of an autozooecium. Unfortunately an undeterminable amount of the end of an exposed autozooecium is commonly removed by abrasion. In some specimens it is possible to suggest the minimum length of the living chamber from a particular diaphragm by tracing the maximum outward extension of the laminae from the diaphragm into the zooecial wall or the lining along the zooecial wall. This assumes that the continuous laminae from diaphragm into wall or wall lining were deposited during the existence of a functional lophophore and gut. The tracing of laminae throughout their length is generally an uncertain procedure, however, and if diaphragm laminae become part of a zooecial lining there is no direct method for determining how far the cortex (Figure 1) extended beyond the lining to complete the total length of the skeletal living chamber.

A better approach to determining the extent of living chambers appears to be through observations of autozooecia under protective incrusting overgrowths, especially under the small patches of intrazoarial overgrowth within an exozone (Plate 5: figure 3; Plate 8: figures 3, 4; Plate 9: figure 5; Plate 11: figures 2, 4). Protection from mechanical wear by the overgrowth after death commonly preserves intact the last developed living chambers (Cumings and Galloway 1915: 353, fig. 40). A survey of the Museum collections indicates that apparently unworn autozooecia under overgrowths have outer living chambers ranging in length from approximately one and one half to five zooecial cavity diameters. Comparison with unprotected autozooecia in the same zoarium indicates that significant lengths of the outermost living chambers are commonly removed by abrasion, giving foreshortened impressions of living chamber lengths, as well as erroneous concepts of zoarial surface features.

In trepostomes, comparison of length of living chamber with distances between adjacent diaphragms in the same autozooecium generally indicates little or no relationship between the two distances. Most commonly, the spaces between diaphragms are considerably less than living chamber length, making it evident, if living chambers are sequential without intervals of diaphragms and unoccupied interspace between, that the floor of a newly developed living chamber was established well within the last living chamber in that autozooid.

Recent Cyclostome Bryozoa

To begin reconstructions of soft parts of Paleozoic trepostomes it would be most helpful to have some idea of: (1) the size of the soft parts of autozooids relative to skeletal living chambers; (2) the organs that are membranous or cuticular and therefore which might be preserved under exceptional conditions; (3) the shapes of these organs, their function, and positions relative to each other; and (4) positions of these organs relative to the skeleton.

MODEL.—To provide a preliminary guide to the possible generalized appearance of a trepostome autozooid, a model (Figure 1) was drawn with the soft parts of a generalized Recent cyclostome placed in a living chamber of a Late Ordovician trepostome. The approximate linear proportions of the soft parts along the autozooidal axis were retained. In the retracted

position this placed the mouth just below the constriction of the cystiphragms with the alimentary canal in the expanded space below the neck and the tentacles passing through the neck outwardly. The width of the soft parts at right angles to the zooidal axis was increased slightly to fill the living chamber. An alternative fit for the retracted position might possibly have brought most or all of the length of the tentacles below the constriction of the cystiphragm.

The choice of the order Cyclostomata as the source of soft parts for the reconstruction of a Paleozoic trepostome zooid is based on the concept of the order Stenolaemata (Borg 1926:490) and the tentative concept of tubular Bryozoa (Boardman and Cheetham 1969:208), which suggest that the cyclostomes are the closest living relatives to the Palezoic trepostomes. The double-walled concept of Borg (1926:195–198, 304–319) seems consistent with available evidence and is followed for the arrangement of soft parts and generalized mode of growth (Boardman and Cheetham 1969: fig. 1) in the cyclostomes and trepostomes included in this study.

MODE OF GROWTH.—According to Borg's interpretations of Recent double-walled cyclostomes, the inner membrane (inner epidermis plus adjacent peritoneum of Figure 1) is immediately adjacent to and presumably deposits the entire calcareous skeleton of a zooid and colony. Together, the inner membrane and skeletal elements were considered to be one wall of his double-walled concept and were termed a cryptocyst by Borg (1926:198, fig. 55). Extrapolating back to Paleozoic trepostomes, spatial relationships and skeletal microstructure make it possible that a corresponding inner membrane could have deposited the entire trepostome skeleton, including basal diaphragms, lateral cystiphragms and hemiphragms, and other intrazooecial skeletal structures that are joined to zooecial walls. The compound skeletal walls (walls grown from two sides) produced by the inner membrane in double-walled cyclostomes are interpreted to be without cuticle by Borg (1926:192) but are epidermal in origin; therefore the entire autozooecium and zoarium are considered to be exoskeletal.

The second wall, the outer membrane or gymnocyst of Borg, also extends over the entire colony and comprises an outermost cuticle, an epidermis, and a peritoneum. The outer membrane includes terminal and vestibular membranes of autozooids (Figure 1) and is attached to and presumably produces the membranous

sac described by Borg with its contained structures, including the lophophore (tentacles, adjacent supporting structures, and tentacle sheath), gut, and sex organs.

Borg's concept of mode of growth for his generalized double-walled cyclostome colony (best illustrated in Borg 1926: fig. 55) starts with the basal disc of the ancestrula (Plate 3: figures 1, 4) that has a simple, external exoskeleton consisting of a calcareous layer and an outermost cuticle (Figure 2). The exoskeleton is simple in that it is grown from one side only, the inner side, by epidermis of the inner membrane. It is external in that it has an outer cuticle that is immediately adjacent to the external environment. This simple exoskeletal layer extends distally from the basal disc to a fold or notch that partly or entirely encircles the ancestrula at this early growth stage. The fold reverses the direction of the exoskeletal layer, and that layer is extended radially outward from the ancestrula to become the basal layer of the colony.

The exoskeleton of the ancestrular zooid is extended distally beyond the fold in the external wall by compound internal walls (Figure 2). In addition, new zooids arise from the basal layer of the colony and their exoskeletal walls are also compound and internal (Plate 3: figure 2). In Borg's double-walled cyclostome, all of the skeletal walls above the basal layer in a colony are compound, internal, and exoskeletal. The walls are exoskeletal because they are produced by a simple infolding of the inner depositing membrane; they are compound because they are grown from both sides of the infolded membrane; they are internal because they are not immediately adjacent to the external environment.

Skeletal walls of zooids in double-walled cyclostome colonies can arise by intrazooidal infolding of epidermis from either the basal skeletal layer or from walls of parent zooids above the basal layer. Skeletal walls above the basal layer apparently are all compound and internal. They lack a cuticular layer because there is no apparent way for simple infolding of inner epidermis from the already formed basal wall to incorporate portions of the external cuticle of the basal layer into the internal walls above.

This epidermal infolding method of budding in a cyclostome colony appears to be flexible enough to produce most of the different growth habits of colonies of Paleozoic tubular Bryozoa by varying the number and position of new zooids within parent zooids. In
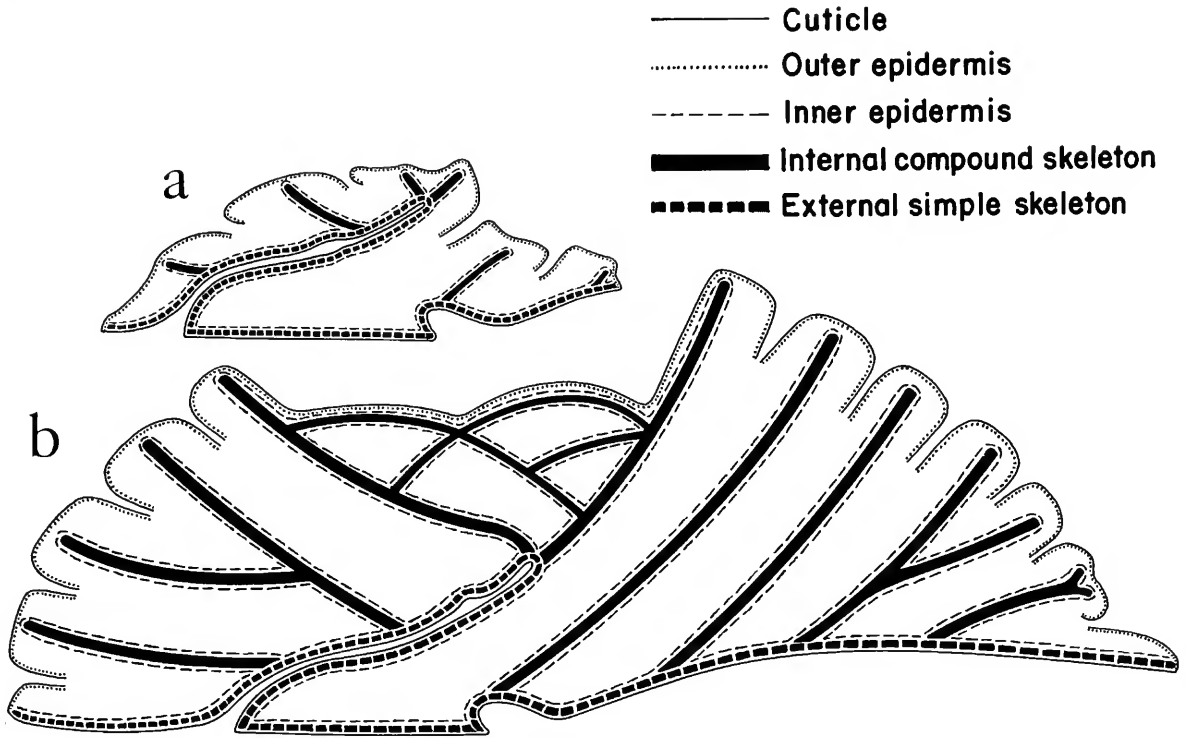
FIGURE 2.—Idealized diagrams of longitudinal section through center of young lichenoporid colony after Borg (1926: fig. 55). The central zooid with flattened basal disc is the ancestrula. The smaller diagram (2A) is a hypothetical earlier growth stage with no attempt made to establish actual relative rates of growth of different zooids. It shows early growth of internal compound skeleton from external simple skeleton by an infolding of inner epidermis. The fold of external skeleton provides a basal skeletal layer for autozooids to left of ancestrula in diagrams. The notch on the right side of basal disc is continuous with fold on the left in three dimensions. Cystose central region of larger colony (2a) depicts brood chambers. (See explanations and figures of Plate 3: figures 1–4)

some trepostomes (rhombotrypids; Boardman and Cheetham 1969: 215, fig. 3) new zooids are centered on zooecial corners of the preceding generation rather than starting from within a zooecium. Preliminary interpretations suggest that this apparent interzooidal budding is feasible without greatly modifying the double-walled arrangement. It seems reasonable that more complexity and different arrangements for budding can be expected to be found among tubular Bryozoa as three-dimensional studies accumulate.

An alternative mode of growth has been suggested for fenestellid colonies (Tavener-Smith 1969: figs. 4A–D) based partly on Borg's work on cyclostomes and apparently also on the assumption that development of a cuticular layer always accompanies deposition of a calcite layer (Tavener-Smith 1969: 293). The fenestellid contains an hypothesized intramural cuticle

(Tavener-Smith 1969: fig. 4H) in what would be a compound internal wall according to Borg's growth model. Borg's work on cyclostomes, however, did not reveal intrazooecial or interzooecial cuticle associated with compound internal walls. Also, it seems unlikely that a cuticle occurred within compound zooecial walls of Paleozoic trepostomes and post-Paleozoic cyclostomes in which zooecial boundaries are smoothly merging and zooecial linings are lacking (for example, the stereotoechid wall, Boardman 1960: 30). Such a zooecial wall is reduced to a cortex (Figure 1) jointly shared by adjacent zooids without indication of longitudinal lineation of any kind as seen under a light microscope. It is important to know whether the less complex mode of growth suggested by Borg could have produced the skeletal morphology of a fenestellid colony.

SIZE AND SHAPE OF FUNCTIONAL ORGANS.—A general idea of the extent to which a living chamber of an autozooecium might have been occupied by a functional gut and lophophore is essential in interpreting the scant evidence of soft parts to be found in Paleozoic Bryozoa. In a reconstruction of a Mississippian trepostome based on an exceptional specimen, McKinney (1969: fig. 1) suggested that the membranous sac assumed to surround the lophophore and gut in life had been preserved and that it passed without significant change in diameter down through the central openings in the diaphragms or ring septa. The reconstruction extends the living chamber through the entire length of the autozooecium and shows a small cross-sectional area for the membranous sac relative to available zooecial area.

To have some concept of the possible range of relative size of soft and skeletal structures in tubular Bryozoa, a number of thin sections were made of epoxy-impregnated autozooids of four genera of Recent cyclostomes in which both soft and hard parts remained intact (see Plates 1–3 and plate descriptions for details). Even though the sample was small, the sections show a wide range of soft-part size relative to enclosing zooecia. Together, the terminal membrane, vestibule, and membranous sac enclosing the gut can vary in relative size in the retracted position from stout masses nearly filling shorter zooecia to similar masses occupying only the outer ends of longer zooecia (see hornerid, Plate 2: figure 4a), or to long and thin masses (see lichenoporid, Plate 2: figures 1, 2). If comparison of these cyclostomes with Paleozoic trepostomes has validity, the relatively small cross section of the suggested membranous sac as it passed through opening in ring septa shown in the reconstruction by McKinney is within reason. The study of these few Recent cyclostomes suggests only that the determining factor for minimum size of soft parts relative to skeletal living chamber is the size of individual cells making up the organs, and the only initial assumption concerning maximum size is that tentacles and gut be small enough to be retractable entirely within the living chamber of the autozooecium, to be consistent with the present concept of the phylum.

Of most use in recognizing possible remains or skeletal indications of soft parts in Paleozoic trepostomes is a generalized concept of the shape of structures in Recent cyclostomes, their relative positions, and mode of development. It is assumed that the cuticle or membranes of organs can be preserved in fossils under the most favorable conditions. It would also seem more likely that original shapes and positions of membranous structures will be recognizable, if at all, in organs that are fixed to the skeleton in some way.

Recent whole specimens that have been air dried and then sectioned were found to have brownish membranous vestiges of lophophores, membranous sacs, and brown bodies, all severely shrunken and misshapen. Nothing was seen of the inner epidermis and very little of the outer wall. It is assumed that early preservation of most fossils was in an aqueous environment which is more likely to preserve original size and shape of membranous structures.

Structures that appear membranous and possibly preservable in the Recent cyclostomes studied include the cuticle of the outer membrane covering the outer surfaces of the colony, and the membranes of the vestibule, tentacular sheath, and membranous sac (Figure 1 and Plates 1–3), all continuous with the outer membrane. These structures are held in place directly or indirectly by lateral ligaments (Plate 2: figure 3b) that are attached to the inner membrane or to the skeleton near the top of the membranous sac and tentacular sheath. The inner cell layer that deposits the skeleton appears to have a substantial membranous layer in only one of the genera studied, a disporellid (Plate 3: figure 5) in a degenerated state. The inner wall has been reported by Borg (1926:194, 196) to have ". . . an extremely thin, endothelium-like film."

Shapes of soft parts than can generally be looked for in fossils then include: (1) outwardly opening funnels formed by combinations of terminal-vestibular membranes; (2) the flask, sac, or cylindrical shapes of the inner end of the membranous sac containing the gut; and (3) the spherical-to-formless shapes of the sex organs and brown bodies enclosed by parts of the membranous sac (see figures and description of Plate 2: figure 1, 3a, 4a). Because a membrane lining the living chambers adjacent to the skeleton is present at least in the nonfeeding part of a disporellid colony (Plate 3: figure 5) it is feasible to look also for something in a similar position in fossils.

Paleozoic Trepostome Bryozoa

PRELIMINARY COMPARISONS WITH RECENT CYCLOSTOMES.—Structures of strikingly comparable size and

shape occur in tubular Bryozoa of greatly differing ages (Plate 1: figures 1–4, all ×100). At first glance, these structures appear to be analogous. Plate 1, figures 3*a* and *b* show whole mounts of the outer ends of single autozooids of a Recent heteroporid cyclostome displaying double funnel-shaped membranous structures of the feeding organs. The outer, more nearly transparent funnel is the terminal-vestibular membrane (Figure 1). The darker, inner funnel is the mass of cells around the sphincter muscle, and the wider dark mass at the bottoms of the figures are the outer ends of the tentacles.

Plate 1, figure 2, shows a pair of funnels of comparable size and shape in a Devonian trepostome. The specimen is essentially a whole mount prepared from a thick section treated with hydrochloric acid and then impregnated with an epoxy. The funnels are considered to have been originally membranous and are still organic in composition as they resist both hydrochloric and hydrofluoric acids (see section on Devonian Antarctic species below).

Plate 1, figures 1*a* and *b*, show thin sections from a Middle Ordovician trepostome passing through funnels and flask-shaped chambers within abandoned living chambers which are surrounded by overlapping skeletal cystiphragms. The dark grains in the chamber are actually reddish brown in color and presumably are an iron oxide. Accumulations of these grains (referred to as brown deposits in this paper) are regularly contained in comparable chambers and have been interpreted, in similar specimens, as indicating the presence of original organic material (Cumings and Galloway 1915:353). The comparable shape, size, and position relative to inclosing skeleton suggest that the Ordovician funnels reflect membranous structures which might be parts of functional autozooids, analogous to those in the Recent cyclostome.

Obvious differences arise immediately between these fossil and Recent funnel-shaped structures, however, as attempts are made to draw more detailed comparisons between them. Close examination of many Ordovician funnels in section reveals that the walls of most of them have the same microstructure as associated skeletal material. Interpretation of these funnels as skeletal structures makes direct comparison with terminal-vestibular membrances seem impossible (see section on monticuliporids below).

The most obvious interpretation of the outer funnels of the pairs in the Devonian forms seems to be as terminal-vestibular membranes. In the Devonian species, both funnels in a pair are attached by their outer rims to the zooecial wall and are positioned well down in the zooecial cavity and living chamber. In Recent double-walled cyclostomes (Plate 1: figures 3*a*, *b*) the outer end of the terminal-vestibular membrane is generally considered to be just beyond the outer end of the skeletal wall (aperture) and not attached there. Comparison to cyclostomes of the zooecially attached inner one of the pair of funnels in the Devonian form seems difficult also because the inner funnels seen in the whole mounts of the Recent heteroporids are not attached to the skeleton at their outer rims.

Comparison of the heteroporid whole mounts with thin sections of congeneric specimens (Plate 1: figures 5*a–d*) indicates that the rims of the inner funnels in the whole mounts are not at the points of ligament attachment of the membranous sac, but that the flare of the funnel is actually the mass of cells surrounding the sphincter muscles at the level where the vestibular membrane, tentacular sheath, and membranous sac are joined (Plate 1: figures 5*b–d*, level B). The lateral ligaments are appreciably lower in the zooid (Plate 1: figure 4 and level A of figures 5*b–d*; Plate 2: figure 3*b*). Further, the shape of the sphincter muscle mass is considerably altered by the extent of extrusion of the tentacles. Extrusion can be judged by the position of tentacle ends relative to the fixed points of the lateral ligaments, as in the series showing progressive extrusion in Plate 1, figures 5*b–d*. Note the change in outline of the sphincter muscle mass (Plate 1: level B of figures 5*b–d*) as the tentacles were extruded. It is not convincing to compare that organ, relatively free of skeletal attachment and variable in shape even in death, with the seemingly attached and regularly shaped inner funnel of the Devonian species. The similar appearing funnels in the Recent and fossil forms figured then apparently do not represent wholly analogous structures, and more detailed evidence is needed.

DEVONIAN ANTARCTIC SPECIES.—The most convincing indications of soft parts (Plate 1: figure 2; Plate 4) in the trepostomes were recognized belatedly in a species from the lower Devonian of the Antarctic, *Leptotrypella? praecox* Boardman (1965:248–251, pl. 1). All intrazooecial structures, including diaphragms, cystiphragm-like partitions, funnels, tubes, and linings of the cavities, are noncrystalline and nonlaminated, and are brown to yellow and translucent

in section. They are insoluble residues after treatment with hydrochloric and hydrofluoric acids. The composition of the intrazooecial structures then must be organic (verbal communication, Kenneth M. Towe) when consideration is given to their general position and morphologic comparison with known bryozoan membranous structures.

Thickness of much of the organic material (Plate 4: figures 2a, b, d) is considerably greater than the thickness of membranes of structures in the Recent cyclostomes studied. It is reasonable to expect some diagenetic change accompanied by change in volume of the original membranes. After extensive treatment with hydrochloric acid the organic layers lost their glassy luster and appeared slightly thinner, suggesting that some constituents might have been removed by the acid. An electron microprobe analysis before acid treatment indicated that the organic material was rich in phosphorus (see also Martinsson, 1965) relative to the calcite of the skeleton and zooecial cavities, and approached concentrations found in apatite. Analyses for calcium, nitrogen, iron, sulfur, and carbon showed no significant differences between the calcitic skeleton and organic material. The phosphorus could have been either biogenic or secondarily inorganic in origin, so it provides no direct indication of diagenetic change. The microstructure in the organic layer lining a closed chamber (Plate 4: figure 2f) is rare in the sections and conceivably could be reflections of cells. Nothing seen in recent cyclostomes, however, seems likely to produce such an appearance.

The most compelling Antarctic specimen (Plate 4: figures 1a, b) has membranes comparable in thickness to those of Recent cyclostomes and shows a nearly symmetrical funnel leading down to a large mass assumed to be the tentacle-gut complex. The funnel has apparently undergone some shrinkage and pulled away from the skeleton. The outward extension of the membrane beyond the expanded bell indicates that the orifice of the funnel was an appreciable distance below the skeletal aperture. Just under the bell of the funnel is a transverse membrane apparently attached to the skeleton and neck of the funnel (Plate 4: figure 1b, see arrows). Empirically this membrane could be the remains of an inner funnel, or it could be a skeletal attachment structure functionally comparable to the attachment ligaments in cyclostomes. Neither interpretation is convincing, however, and nothing of

comparable shape and position has been seen in Recent cyclostomes.

Attached funnels occur either singly or in pairs in the Antarctic specimens. Either all zooids had two funnels and the outer one was not always preserved, or funnels were grown sequentially. The longitudinal distance between the inner funnel and bottom of the living chamber in double-funneled specimens (Plate 4: figures 2a, b) compares with the distance between the funnel and bottom of the living chamber in the single-funneled specimens (Plate 4: figures 2d, e, and 3). These measurement comparisons suggest that the funnels in the single-funneled specimens correspond to the inner funnels of the more complex specimens. Unfortunately, the Devonian material did not reveal living chambers protected by overgrowth, with or without funnels, so no direct evidence of funnel position relative to skeletal aperture is presently available from the fossils. All of the funnels are well within zooecial cavities that had undergone subsequent growth.

The relationship of the outer edges of the terminal-vestibular membrane to the skeleton of an autozooid is of major importance to the coelomic organization of the zooid and the colony. In Recent double-walled cyclostomes, according to Borg, the terminal-vestibular membrane is part of the outer membrane which covers the surface of the colony above the basal layer. It acts as the protective outer wall of the continuous coelomic space beyond the ends of the zooecia and is not attached directly to the ends of the zooecia. This outer coelomic space, then, and the communication pores through zooecial walls provide two possible avenues of coelomic communication among zooids in a cyclostome colony.

Membranous partitioning of coelomic space within a zooid occurs in Recent cyclostomes. The membranous sac is entirely closed, dividing the coelomic space of a zooid into two parts which Borg termed exosaccal and endosaccal (Figure 1). Another method of coelomic partitioning is suggested by the apparently doubled terminal-vestibular membrane shown in the specimen illustrated (Plate 1: figure 5a). Interpreted from the two dimensions of the thin-section, the inner funnel appears to be continuously attached around its rim to the skeleton, dividing the exosaccal coelom into an inner space and a smaller outer space beyond the inner funnel.

Another kind of attachment of soft parts to skeleton in Recent cyclostomes is the ligament attachment of the membranous sac and tentacular sheath discussed

above. In ligament attachment, the plane of a thin section generally does not pass through a ligament as it does in the specimen in Plate 2, figure 3b, and open coelomic space is seen between the sac and the skeletal wall (Plate 1: figure 5b; Plate 2: figures 1, 2).

In the Devonian Antarctic specimens the connection of funnels to skeleton seems generally to be a continuous one similar to the inner funnel of the Recent specimen of Plate 1, figure 5a. This suggests membranous partitioning of coelomic space and the possibility that the Devonian funnels can represent terminal-vestibular membranes.

Inward from the assumed gut (arrow) of the specimen in Plate 4, figure 1a, the thin tubular membrane extending down to the dark mass at the bottom of the figure cannot surely be traced to the mass of the gut, although the positioning of the structures suggests that they were connected. It is not entirely clear, therefore, whether this specimen includes only parts of one elongate membranous complex or parts of two or more generations. The well-shaped, elongate masses of Plate 3, figures 6a, b, are from the same colony and indicate the presence of possible digestive or sexual organs long enough for the specimen of Plate 4, figure 1a, by comparison, to be one continuous complex (Figure 6).

The inner ends or bases of living chambers appear to be delimited by membranous diaphragms (Plate 4: figures 2a, b, d, e, and 3) in most of the Antarctic specimens. Some traces of membranous cystiphragm-shaped structures occur laterally around the shorter living chambers. Neither the membranous basal diaphragms nor the cystiphragms seem to have counterparts in the Recent cyclostomes studied. These membranous structures probably were analogous to the skeletal diaphragms and cystiphragms that are common in many trepostomes. Under normal conditions of preservation, the Antarctic species would appear without any indication of cystiphragms or diaphragms and would be considered to lack these structures for taxonomic purposes. Significantly different taxonomic treatment might well result if the investigator knew that functional membranous diaphragms or cystiphragms had existed in the species and that all that was lacking in the living animal were the calcified supports.

Most zooecia of the Antarctic species are lined by a membranous layer (Plate 4: figures 2a, b, d). Presumably this membrane is analogous to a membranous

part of the inner wall (Plate 3: figure 5) or cryptocyst of Borg, and had to do with deposition of the calcareous skeleton. Quite unexpectedly, some of the chambers formed by membranous diaphragms closing off segments of the zooecial cavity behind the functional feeding organs were found to have a complete inner lining of material (Plate 4: figures 2c, f) similar in appearance to that of the cystiphragms and diaphragms. These linings remained after severe treatment with hydrochloric acid, so apparently they are all of modified organic material and are not an inorganic diagenetic development as their position suggests. Nothing like these linings was found in the Recent cyclostomes studied, partly because they do not show basal diaphragms in series to form closed compartments.

MONTICULIPORIDS.—The monticuliporids (Family Monticuliporidae Nicholson, 1881, largely Ordovician in age) are of importance to the problem of trepostome soft parts because the generally overlapping skeletal cystiphragms (Plates 5–7) characteristic of the group impart a roughly funnel-shaped configuration to presumed living chambers, suggesting some reflection of soft-part shape. The overlapping cystiphragms are considered skeletal because they have the same microstructure as the zooecial walls and are thickened inward extensions of segments of those walls (Plate 5: figures 4, 5).

In three dimensions, skeletal cystiphragms generally form inner collars that extend partly or entirely around the zooecium, depending on whether the enclosed living chamber is eccentric (Plate 6: figures 2a, 3) or is centered in the zooecium (Plate 6: figures 2c, d). Cystiphragms commonly form closed cystose chambers filled only by secondary calcite. They are attached at their inward edges to earlier formed cystiphragms, diaphragms, or zooecial wall. In a few species, cystiphragms, as customarily defined, include structures that do not form closed chambers but terminate inwardly within the zooecial cavity (Plate 5: figure 2), sometimes with strongly serrated edges (Plate 5: figures 1, 2, arrows).

Typical cystiphragms thin inwardly from their origin in the zooecial wall (Plate 5: figures 4, 5) indicating a progressive decrease in calcification toward the inner end of the cystiphragm. Physical continuity with segments of zooecial wall indicates that these cystiphragms were deposited at essentially the same time and by the same epidermis that deposited the con-

nected segment of zooecial wall, presumed to be the epidermis of the inner membrane or cryptocyst of Borg. These cystiphragms then must be considered to be outside the coelomic cavity in a position similar to those in Figure 1.

Presumed living chambers are readily observable under protective intrazoarial overgrowths in Ordovician monticuliporids (Plate 5: figure 3). Living chambers are commonly floored at their inner ends by diaphragms which are attached to one of the several cystiphragms in the overlapping series. The outermost and presumably last-formed cystiphragm in a zooecium is commonly just inside the end of the zooecium so that the living chamber is lined with cystiphragms for most of its length. If the functional organs of the zooid had any appreciable length in the zooecium, the outermost cystiphragms at least were lateral to the organs.

As suggested by Cumings and Galloway (1915:354, 355) the observable function of cystiphragms is to restrict intrazooecial space. They also impart a generalized shape to the space. The ratio of the diameter of the available living chamber to total zooecial diameter in Ordovician monticuliporids is considerably less than that for Recent cyclostomes or diaphragmed trepostomes (Plates 4, 8, 9). The absolute size of the different living chambers can be generally comparable, however, as indicated by the specimens in Plate 1: figures 1–3, all × 100.

Cystiphragms apparently were used to maintain living chamber shape and orientation in growth disruptions of the enclosing autozooecial walls. The two specimens of *Prasopora* (Plate 7: figures 2, 3) show a change in direction of growth of autozooecial wall (arrows). Cystiphragms compensate for the irregularity in zooecial configuration by changing shape (best shown in figure 3), seemingly to provide a living chamber of relatively constant shape in which flask-shaped chambers that span the directional change can be developed subsequently. The rare example of skeletal repair of an apparent mechanical injury (Plate 7: figure 1) suggests that cystiphragm formation can be developed to return injured regions to a functional size, even in species in which cystiphragms are rarely formed.

More delicate cystiphragms, here termed funnel-cystiphragms, which form the necks of smaller flask-shaped chambers (Plate 6) can be found within the chamber defined by the commonly occurring over-

lapping series of skeletal cystiphragms. These funnel-cystiphragms provide morphologic detail within the living chamber that should reveal something of the shapes and sizes of membranous organs. In Ordovician monticuliporids it seems necessary to assume that living chambers in autozooecia defined either by skeletal cystiphragms or the more delicate funnel-cystiphragms, or possibly both, enclosed feeding and reproductive organs, because no other space of reasonable size occurs in the zoaria (Plate 7: figures 5b, 7).

Specimens of Ordovician age of at least four genera of monticuliporids, *Peronopora* Nicholson, 1881 (Plate 5: figures 4, 5); *Prasopora* Nicholson and Etheridege, 1877; and *Prasoporina* Bassler, 1952 (Plate 1: figures 1a, b; Plates 6, 7); and *Atactoporella* Ulrich, 1883, display funnel-shaped cystiphragms and flask-shaped chambers within chambers defined by skeletal cystiphragms. The immediate interpretive question is whether these more delicate structures were orignially skeletal or membranous, or a combination. The walls of most of the funnels do not show the brown or yellow color common in the Devonian Antarctic species. Those funnel-cystiphragms in the Ordovician forms that have walls thick enough display a crystalline microstructure similar in appearance to adjacent skeletal material. It seems unlikely that most of these microcrystalline structures were originally membranous and then became calcified during the fossilization process. Acid treatment of specimens of *Prasopora* left organic residues of segments of funnel-cystiphragms and laminae within assumed skeletons, indicating only that both contained some organic material.

In *Peronopora*, funnel-cystiphragms appear skeletal throughout (Plate 5: figures 4c, 5) or skeletal at the outer funnel end and membranous inward (Plate 5: figures 4a in which funnel-cystiphragm is filled by pyrite at outer end, 4b, 4d). These funnel-cystiphragms were apparently skeletal at least in part and formed large, elongate chambers now containing calcite crystals which generally lack visible impurities, as is typical of chambers behind skeletal cystiphragms. The space within the flask-shaped chamber defined by the funnel-cystiphragm is filled with fossilized brown deposits and impurities, suggesting that soft parts of the autozooid including the coelomic space were in that position at a particular stage of development. Comparison of figured autozooecia with others covered by a protective overgrowth in the same zoarium indicates that essentially the entire length of the auto-

zooecium is present as illustrated (Plate 5: figures 4, 5). In this species, at least, the autozooid was apparently skeletally complete with the development of a single funnel-cystiphragm, regardless of the nature and function of the soft parts therein.

Attempts to distinguish between possible remains of membranous structures and assumed skeletal structures in living chambers of Ordovician monticuliporids have not been convincing. Less direct criteria may be applied to delicate structures of questionable original composition where definite remains of membranes or organic composition are lacking. An obvious approach is a comparison of relative size and shape of fossilized structures found in assumed living chambers with membranous organs in the Recent cyclostomes studied. Unfortunately, this comparative evidence is confused because the major part of a terminal-vestibular membrane of a Recent cyclostome has the same general shape as a known skeletal cystiphragm or funnel-cystiphragm of an Ordovician monticuliporid. As skeletal cystiphragms become thinner and depart from paralleling the overlapping skeletal series, it becomes more difficult to distinguish them from more delicate funnel-cystiphragms, which in turn approach in appearance the most perfect of terminal-vestibular membranes. Comparison cannot be made with the Devonian Antarctic species because a structure that is membranous in it does not necessarily mean that a similarly shaped structure must have been membranous in an Ordovician species. Unfortunately, structures shaped like cystiphragms and diaphragms, that apparently were membranous in the Devonian Antarctic species, must be considered skeletal because of microstructure in most Ordovician species.

The only remains studied which might reasonably be considered membranous structures in Ordovician monticuliporids occur in the living chambers of two speciments of *Peronopora* (Plate 5: figures 4*c*, 5; Plate 11: figure 7, arrows). Most of the skeletal cystiphragms in the overlapping series are thick enough to show typical skeletal laminae and physical continuity outwardly into zooecial walls. Funnel-cystiphragms are generally clearly skeletal at their outer ends at least. The smallest funnels observed (Plate 5: figures 4*c*, 5) are axially centered at the outermost end of the autozooecial chambers and are encircled by funnel-cystiphragms. They show minutely thin, discontinuous walls that appear to be calcified and

little more than one lamina thick. These smallest funnels are so minute and fragile, however, that it seems unreasonable to rule out entirely a membranous origin for them.

There seem then to be two kinds of funnels preserved in the genus *Peronopora:* (1) the smallest funnels, either skeletal or membranous, encircled by (2) larger funnels, the skeletal funnel-cystiphragms that define the immediate living chamber (Figure 3). Comparison of the partly calcified funnels (Plate 5: figures 4*a, b*) and the apparently membranous funnel of *Peronopora* (Plate 11: figure 7), and the membranous Devonian Antarctic funnel (Plate 4: figure 1*a*), with the hornerid terminal-vestibular membrane (Plate 2: figure 4*b*), illustrates the confusion caused by similarity in shape of fossilized funnels and known terminal-vestibular membranes.

If the funnel-cystiphragms of *Peronopora* are skeletal at their outer ends at least, it seems necessary that they were grown by an inner epidermis lining the immediate living chamber that they define (Figure 3). The occurrence together of two sizes of funnels, the smaller-sized funnel within a rigid funnel-cystiphragm, does suggest rather convincingly that the absolute size of whatever soft parts might have been present, must have been small indeed; the funnel-cystiphragms thus further reduced the size of inferred functional soft parts relative to total zooecial diameter.

Skeletal cystiphragms of the largely Middle Ordovician genus *Prasopora* (Plates 6, 7) are generally thin-walled and microcrystalline rather than laminated, which further obscures the recognition of skeletal cystiphragms from possibly membranous funnels or funnel-cystiphragms. The overlapping series of thin cystiphragms is considered to be skeletal because of direct connection with zooecial walls that also are relatively thin and have an identical microstructure.

Funnel-cystiphragms occur in zoaria (Plate 6; Plate 7: figure 5*b*) of *Prasopora* from many different localities. They are microcrystalline and generally can be distinguished from skeletal cystiphragms by: (1) position within the tubular chamber enclosed by combinations of skeletal cystiphragms, diaphragms, and zooecial walls; (2) association with conspicuous fossilized brown deposits and impurities in the wider inner part of the flask; (3) generally thinner-walls (Plate 6: figures 1*a, d*); and (4) generally greater length parallel to the zooecial axis (Plate 6: figure 1*d*). In a few specimens of *Prasopora* there is some

confusion caused by cystiphragms in an apparently overlapping series that form a transition with funnel-cystiphragms to fashion a flask-shaped chamber (Plate 6: figure 2b; Plate 7: figure 6). This apparent transition tends to reinforce the hypothesis that funnel-cystiphragms are skeletal.

The funnel-cystiphragms of *Prasopora* are exceptional in showing multiple funnels in the neck region of a single flash-shaped chamber (Plate 6: figures 2b to 6). Funnel-cystiphragms can be double or can have as many as four funnels in connected series with varying degrees of regularity. Despite the apparently skeletal composition of the funnel-cystiphragms, the perfection of some of the funnel shapes (Plate 6: figures 3, 6) suggest comparison with terminal-vestibular membranes of Recent cyclostomes, especially with the doubled terminal-vestibular membrane of the Recent heteroporid (Plate 1: figure 5a).

In considering the hypothesis that the fossilized funnel-cystiphragms were terminal-vestibular membranes that were calcified during life, it is important that no Recent bryozoans are known in which that membrane is calcified and inflexible. In fact, the living animal as we know it requires a flexible terminal membrane for tentacle extension. Further, if the funnel-cystiphragms were portions of the terminal-vestibular membrane they would presumably be parts of the outer membrane and form part of the outer wall of the coelom. Structural continuity with autozooecial walls requires that funnel-cystiphragms were deposited on the inner wall of the coelom. Emplacement of a skeletal layer between the outer cuticle and depositing epidermis of multiple terminal-vestibular membranes of the presumed outer membrane (Figure 1) would produce closed coelomic compartments isolated from each other by essentially impervious skeletal walls within a single autozooid. Calcification of parts of the outer membrane within the autozooecium does not seem feasible.

DIAPHRAGMED TREPOSTOMES.—It is useful to examine funnel-cystiphragms in diaphragmed trepostome genera (informally here, genera that generally lack skeletal cystiphragms and have diaphragms as the prominent intrazooecial structure) in order to understand better the available evidence for the mode of growth of flask-shaped chambers and multiple funnel-cystiphragms. Some diaphragmed trepostome genera that develop basal skeletal diaphragms sequentially along zooecial length also display funnel- and flask-

shaped skeletal structures (Plates 8, 9) similar to those of monticuliporids in general shape and relationship to assumed living chamber and fossilized brown deposit (Cumings and Galloway 1915: pls. 10, 11). The similarity is so marked that there seems no reasonable question that they are analogous (see plate descriptions for details) to the funnel-cystiphragms and flask-shaped chambers found in monticuliporids. Shape of intrazooecial structures (Plate 8: figures 1–4) found in diaphragmed genera are virtually identical to those (Plate 6) of the monticuliporid genera studied. Two intact living chambers (Plate 8: figures 3, 4) protected by incrusting overgrowths have double and single funnel-cystiphragms in the same general position as those in the living chambers (Plate 5: figures 4, 5; Plate 6) of the monticuliporids. The shape of the funnel-cystiphragm of Plate 5, figure 4d, is identical to that of Plate 8, figure 7, including the skeletal layers apparently grown subsequently that sealed the necks of the flask-shaped chambers.

Thickened, laminated funnel-cystiphragms and associated zooecial linings (Plate 9, figures 3–6), found in the diaphragmed genera *Amplexopora* Ulrich, 1882 and *Heterotrypa* Nicholson, 1879 (Ordovician), and *Leptotrypella* Vinassa de Regny, 1920 (Devonian), readily reveal the relative time of development of funnel-cystiphragms. A reasonable question to ask in the interpretation of funnel-cystiphragms is whether the multiple funnels are more representative of the complete, functional autozooid than a single funnel in the same zoarium. Preservation of only the first of the several funnels that might have formed the complete animal is always a possibility but is difficult to evaluate by itself. Evidence that partially calcified funnel-cystiphragms must have been complete though partly membranous in life (Plate 9; figures 3, 6c) is the inward extension of funnel-cystiphragm shape by included brown deposits beyond the fossilized extent of the funnel-cystiphragm. If calcification or at least preservation of a structure is only partial, the possibility of total lack of preservation of a membranous structure has to be considered.

Study of the laminae of that part of the zooecial lining connected directly to each funnel-cystiphragm (Plate 9: figures 3–6) reveals a progressive superposition of zooecial lining of outer funnel-cystiphragms on inner ones, indicating the same time-sequential development along zooecial length for funnel-cystiphragms as is generally demonstrable for basal diaphragms

(Plate 8: figure 6a, superposition of diaphragms in mesopore to right is typical) and skeletal cystiphragms (Plate 5: figures 4, 5). (For an explanation of the use of skeletal microstructure see Boardman and Cheetham 1969:210.) The assumed position of the depositing epidermis and its general parallelism with skeletal laminae in Paleozoic trepostomes indicate that laminae represent approximate growth surfaces and that an inner funnel-cystiphragm had to be completed before an outer one started to grow. A significant time period between growth of succeeding funnel-cystiphragms can only be assumed if a segment of zooecial lining or wall laminae occurs between laminae connected to the funnel-cystiphragms. If there is no zooecial lining between connected zooecial linings (Plate 9: figures 4b, 6c for funnel-cystiphragms; Plate 5, figure 4d, for skeletal cystiphragms), no indication is available of time between the growth of succeeding intrazooecial structures. If, however, there is an observable thickness of zooecial lining or complete wall between associated linings of succeeding structures (Plate 9: figure 5 and possibly 6a), an unknown period of time can be assumed during which the intervening laminae were deposited. Uniformity of growth rate would be required to give relative time estimates proportional to intervening thickness.

Inner ends of flask-shaped chambers (Plate 9: figures 4a, 6a) or entire flask-shaped chambers (Plate 6: figure 6; Plate 9: figure 5) can form time sequences outwardly also. The younger living chamber protected by an incrusting overgrowth in Plate 9, figure 5, apparently overtook zooecial wall growth and had to build a thin wall outward from the funnel-diaphragm, emphasizing the skeletal nature of these thin walls and the need for a segment of skeletal living chamber outward from the funnel-cystiphragm.

In summary, therefore, an outer position for the same kind of structure along the axis of a zooecium generally means a later time of development. As applied to multiple funnel-cystiphragms, the inner one formed before the outer was started, rather than the simultaneous growth necessary if multiple funnel-cystiphragms were different parts of a functioning autozoid. This time-sequential relationship suggests that single funnels in complete living chambers under overgrowths represent that part of the complete animal for that stage of development rather than nonpreservation of a second funnel that was necessarily there in the living animal. Further, the double funnels of the

Devonian Antarctic species (Plate 1: figure 2; Plate 4: figures 2a, b) might well be membranous equivalents of skeletal funnel-cystiphragms, just as normally skeletal diaphragms and cystiphragms are membranous in that exceptionally preserved species. The funnels in Plate 1, figure 2, appear to be duplicates of the same structure, rather than separate structures in the same lophophore-gut complex as in Plate 1, figure 3a, of the preserved soft parts of the Recent cyclostome. It seems probable then that each funnel of multiple funnel-cystiphragms that is attached to a single flask-shaped chamber represents a stage in sequential ontogenetic development.

Reconstruction of Flask-Shaped Chambers

Evidence from specimens of *Peronopora* bearing on the partial reconstruction of an autozooid containing a funnel-cystiphragm and flask-shaped chamber (Figure 3) seems generally compatible with the present understanding of Recent cyclostomes. The interpretation assumes funnel-cystiphragms and skeletal walls of inner ends of the chambers in monticuliporid and diaphragmed genera to be part of the skeletal complex produced by the inner membrane. The enclosed space beind a funnel-cystiphragm would not have been coelomic, but would have been a skeletal space generally lacking impurities, similar in appearance at least to the space behind skeletal cystiphragms. The flask-shaped chamber with included brown deposits apparently contained all of the soft parts, and, if so, had to form the immediate living chamber of the zooid for that stage of development.

The reconstruction of a generalized monticuliporid (Figure 4) assumes a complete autozooid at the single funnel-cystiphragm stage of development. A tubular epidermis and coelomic connection would be necessary through the neck of the funnel-cystiphragm in order to calcify that structure and to connect the coelomic spaces at the inner and outer ends of the living chamber.

The outermost segment of calcified zooecial wall beyond the last-formed funnel-cystiphragm must have been deposited by an inner epidermis continuous with the one that deposited the earlier formed skeleton of the autozooid. In cyclostome Bryozoa, either single- or double-walled in the sense of Borg, a coelomic space overlies all growing skeletal areas. Presumably, therefore, an outer coelomic space of unknown shape and
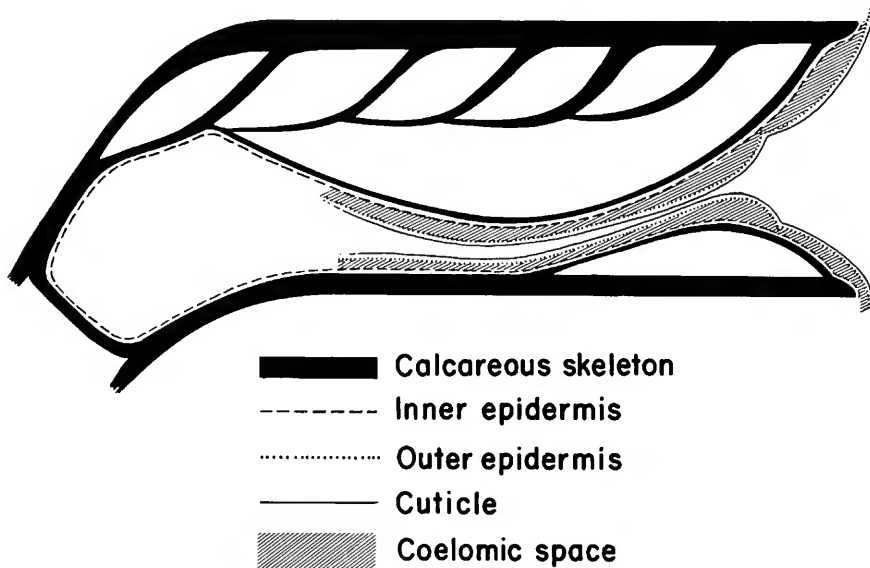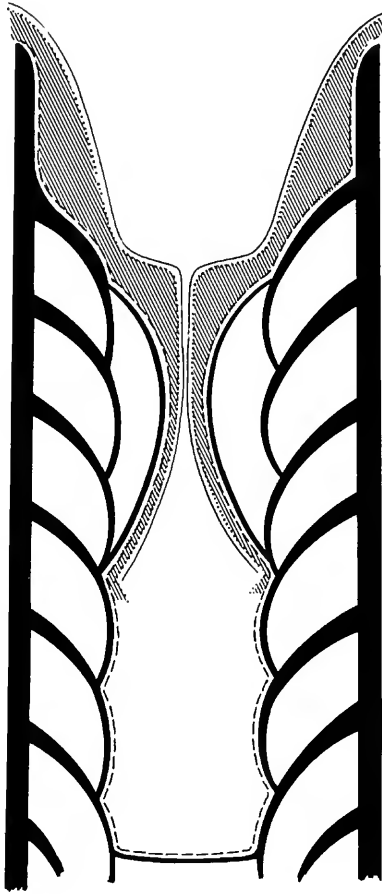
FIGURE 3.—Partial reconstruction of an autozooid of a monticuliporid (*Peronopora*) showing the skeleton, including overlapping skeletal cystiphragms, that line the distal side of the auto-zooecium, funnel-cystiphragm that forms the neck of a flask-shaped living chamber, and possibly soft, membranous funnels within funnel-cystiphragm inferred from questionable evidence (Plate 5: figures 4, 5) and mode of growth assumptions. Functional organs of flask-shaped chamber are unknown (see text).

size occurred between the depositing epidermis and the terminal-vestibular membrane of the monticulip-orid. It is biologically possible (for example in brachiopods) to have skeletal growth extending beyond coelomic spaces, but no evidence is known in Recent tubular Bryozoa suggesting such an arrangement.

The only evidence for an orifice depressed below the skeletal aperture and the configuration of the outer-most portion of the terminal-vestibular membrane shown in the reconstruction is the vague suggestion of depression in some figured specimens of *Peronopora* (Plate 5: figures 4c, 5), if the smallest funnels were originally membranous, and the Devonian Antarctic specimen (Plate 4: figures 1a, b) in which the edges of the assumed membrane are upturned. For mon-ticuliporids, a specimen (Plate 6: figure 5) that might have significance shows a shallow cystiphragm extend-ing outward from a funnel to what could have been the growing end of the zooecium as would be antici-pated by a terminal-vestibular membrane. The relative time relationships of the structures and extent of zooecial wall in this poorly preserved specimen are unknown, and it seems unlikely that the cystiphragm grown by the inner membrane paralleled the outer terminal membrane after the zooecial wall was estab-

lished. In several specimens an outer funnel has a more fragile appearance than the inner funnel-cystiphragm (Plate 7: figure 5a) suggesting that it may be part of a terminal-vestibular membrane, but these are most likely skeletal structures.

The reconstruction (Figure 5) of a generalized Ordovician monticuliporid at the double funnel-cystiphragm stage of development shows two funnel-cystiphragms, enclosing an elongated segment of coelomic cavity. In the absence of other evidence, and assuming parallelism between soft and hard parts, a membranous connection is drawn at the junction of the funnel-cystiphragms similar to that of the doubled terminal-vestibular membrane (Plate 1: figure 5a) that produces coelomic partitioning.

Mode of Growth of Trepostome Autozooecia

The application of the double-walled concepts of Borg's cyclostome work to trepostome skeletal mor-phology and the inferred relative time of formation of trepostome skeletal structures, as discussed above, suggests a generalized and hypothetical mode of out-ward growth for trepostome autozooecia. One of the critical questions which should be explained by a
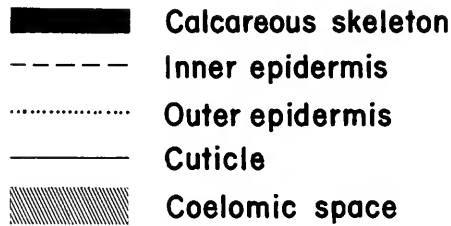
Calcareous skeleton
Inner epidermis
Outer epidermis
Cuticle
Coelomic space

FIGURE 4.—Partial reconstruction of an autozooid of a monticuliporid (*Prasopora*) showing the skeleton, including overlapping skeletal cystiphragms that encircle the living chamber, a funnel-cystiphragm that forms the neck of a smaller flask-shaped living chamber (Plate 1: figure 1*a;* Plate 6: figures 1, 2*a*), and soft parts that are inferred from mode of growth assumptions only. The reconstruction shows autozooid in a single-funnel stage of development. Functional organs of flask-shaped chamber are unknown (see text).

FIGURE 5.—Partial reconstruction similar to that of Figure 4 except in a later, two-funnel stage of development (Plate 1: figure 1*b*; Plate 6: figures 2*d*, 3, 4).

growth hypothesis is the spacing and inferred relative time relationships of skeletal diaphragms along an autozooecium, assuming that some if not all of the diaphragms provided floors for living chambers.

The concepts applied to trepostomes here are those used throughout this paper and include: (1) the assumption that all skeletal structures were grown by an inner membrane comparable to that in Recent cyclostomes (membrane described in Borg 1926:196), and (2) the assumption that a separate outer membrane was the source of most of the membranous

organs that occupied the autozooecium (Borg 1926: 322–334).

In diaphragmed trepostomes in which laminae can be traced adequately, the laminae of basal diaphragms are generally continuous with a zooecial lining that extends outward far enough to line the greater part of the living chamber (Plate 8: figure 4; Plate 9: figures 3–6). If basal diaphragms are too thin, it is more difficult to follow laminae along the wall (Plate 8: figure 2) but commonly these few diaphragm laminae seem to attach to the surface of the previously formed wall and extend outwardly for indeterminable distances along the zooecium. The general impression is that the laminae of a basal diaphragm extend outward along the zooecial wall to form at least a partial lining of the living chamber.

An obvious exception to this generalization can be seen in a diaphragm (Plate 8: figure 4) covering the living chamber under an overgrowth in *Heterotrypa* sp. At the junction with the zooecial wall the laminae of this diaphragm certainly would have been incorporated immediately within the parallel series of cortex laminae if outward growth of the zooecium had not been halted. The outward extension of this diaphragm would not have been as the lining of the living chamber but as a part of the adjacent cortex. Subsequent growth of the zooecial wall would necessarily have started without a chamber adequate to holding feeding organs. The infrequent preservation of most of a living chamber with protected funnel-cystiphragms and fossilized brown deposits well below the surface of a zoarium without benefit of overgrowth might well depend on the development of a diaphragm that begins near the aperture as a cover, rather than at the base of an established living chamber. The diaphragm above the abandoned living chamber of the heterotrypid (Plate 8: figure 2) joins the cortex and intersects the boundary immediately, followed by continued growth of the zooecial wall, thus preserving most of that chamber.

In diaphragmed species of trepostomes it is most common for the distance between successive diaphragms in the exozone of an autozooecium to be considerably less than the length of the living chamber at the outer end of the autozooecium. For example, the average distance between successive diaphragms in the figured specimen of *Heterotrypa* (Plate 8: figure 4) is less than the width of the zooecial chamber and the length of the living chamber is slightly more than three zooecial chamber widths. Assuming that consecutive

diaphragms functioned as living chamber floors, and that succeeding living chambers were approximately the same length, it follows that a newly developed living chamber occupied the outer portion of the last living chamber in the sequence.

To attempt an explanation of the mode of growth of autozooecia that have overlapping living chambers, it seems necessary to assume that: (1) during or between the formation of successive basal diaphragms the autozooecial wall was extended at its outer end by a distance equal to that between those diaphragms, and (2) the establishment of a new living chamber in a new position resulted from some interruption in the existence of the soft parts connected to the outer membrane.

In Bryozoa, the most likely interruption in the existence of soft parts is the periodic degeneration and regeneration of organs attached to the outer membrane (Borg 1926: 463). The one-to-one relationship of fossilized brown deposit to diaphragm (Plate 7: figure 4) suggests a degeneration state with a brown body remnant for each basal diaphragm developed, in this zoarium at least (Cumings and Galloway 1915: 353, 354). If similar to the process reported for Recent cyclostomes, the regeneration of membranous organs took place from the outer membrane inwardly. For each new regeneration cycle, however, the outer membrane would have been displaced outwardly by the amount of the zooecial wall growth accomplished by the inner membrane during the period of degeneration of the membranous organs. Assuming the organs to be approximately similar in dimension from one cycle to the next, the inner ends of the organs would not extend as far inwardly as they did in the preceding cycle. The outer position of the new basal diaphragm then apparently would be controlled by the new outer position of the membranous organs.

Lateral Structures and Cyclic Growth

Skeletal structures that were positioned along the sides of functioning living chambers should generally be recognizable in well-preserved specimens. Relative time and positional relationships are determined by evidence such as the superposition of laminae as discussed above, inclusion of small structures such as spines in zooecial lining associated with a basal diaphragm, and the relative position of intersection of laminae from the structure in question with the zooecial boundary. This

intersection marks the position of the skeletal aperture during the growth of the connected lateral structure.

MURAL SPINES.—The recurved mural spines in a Silurian halloporid (Plate 8: figure 6a) can be interpreted as lateral structures because laminae of the outermost spine of the three just above the funnel-cystiphragm seems to continue outwardly into the wall and as best can be determined (not shown in the figure) intersect the zooecial boundary within approximately one zooecial width along the wall. This should mean that the spine was formed at a time when the outer end of the zooecium was a zooecial width beyond, placing the spine in a lateral position in a living chamber that was nearly two zooecial widths long.

The arrangement of these spines in ten or more orderly longitudinal rows (Plate 8: figures 5, 6b) suggests that they had some regular relationship to the morphology of the autozooid. The laminae from the funnel-cystiphragm (Plate 8: figure 6a) lap up on the first spine of the three, indicating that that spine was present when the funnel-cystiphragm was formed. In Recent cyclostome autozooids the eight ligaments that hold the membranous sac, tentacle sheath, and vestibular membrane in place (Figure 1) are in approximately that position. Perhaps the spines of the halloporid were ligament attachment points, and outward growth of the membranous sac established progressively younger, closely spaced attachment points. The relative size and inward inclination of the Recent heteroporid ligament (Plate 2: figure 3b) are comparable to the halloporid spines.

The spacing of spines on the right-hand zooecial wall of the specimen illustrated (Plate 8: figure 6a) is comparable to the spacing of thickened diaphrams in the adjacent mesopore farther to the right. In the several thin sections examined of this species, the spacing of the two structures seems to be similar. The apparent correlation is between different structures of two different polymorphs, however, suggesting that both structures might have responded to some colony-wide control.

The time relationships of spines and mesopore diaphragms are not straight across the intervening zooecial-mesopore wall. The diaphragms are distributed throughout the length of the mesopore, nearly to its outer end. The short distance between diaphragm and aperture is reflected in the short longitiudinal interval required by diaphragm laminae to enter the mesopore wall and intersect the zooecial-mesopore boundary.

The mesopore diaphragm formed at the time that the outermost spine shown in the figure was formed is in a position just short of a zooecial width outward from that spine. This diaphragm is connected to wall laminae intersecting the zooecial-mesopore boundary opposite the zooecial laminae connected to the spine, indicating that the spine and diaphragm were formed at the same time.

Not all mural spines in trepostomes have a recognizably orderly arrangement, constant shape, or the same relative position in living chambers. Devonian leptotrypellid spines (Plate 8: figure 9; Plate 9: figure 4) are irregularly shaped, are concentrated around the bottom or inner end of the assumed living chamber, and are outside the flask-shaped chamber of the funnel-cystiphragms. If they did have an attachment function, it was probably to a different structure than that of the Silurian halloporid spines. Their position suggests that they might have been part of the lophophore retraction mechanism.

CYSTIPHRAGMS.—Skeletal cystiphragms of monticuliporids are lateral in position along the living chamber, and some species have an approximate one-to-one correlation and microstructural connection between cystiphragms of autozooecia and diaphragms of intervening mesopores (Plate 11: figures 5, 7). The laminae of the outermost mesopore diaphragms are in juxtaposition at the zooecial-mesopore boundary with the laminae of the outermost cystiphragms, indicating coeval growth of the two structures and giving them the appearance of structural units across the boundary. The cystiphragm generally diverges from the zooecial wall opposite the next to last mesopore diaphragm in this specimen, however, so the time of development correlation again is not directly across a zooecial-mesopore wall, but is determined by juxtaposition of connected laminae at intervening boundaries.

In most species of *Prasopora*, as many as four mesopore diaphragms occur most commonly opposite the interval between succeeding cystiphragms in adjacent autozooecia (Plate 5: figure 3), suggesting differing cycles between these polymorphs. Autozooecial diaphragms and cystiphragms, however, have very nearly the same spacing between the rare flask-shaped chambers.

In monticuliporids, correlation of cystiphragms among adjacent autozooecia based on spacing and size variation is commonly demonstrable; also of dia-

phragms among adjacent autozooecia, and of diaphragms in neighboring mesopores. The wide expression of cyclic growth suggests interzooidal coordination of the kind that can be expected from colony-wide inner and outer membranes.

The irregular shape and spacing of cystiphragms typical of some species of *Prasopora* (Ross 1967: pl. 49, figs. 1, 3, 4), in contrast, makes correlated cyclic growth difficult to recognize, if it exists at all. An unusual example of cyclic growth, however, produced sinuous living chambers (Plate 11: figure 6) formed by modified cystiphragms that project from alternate sides of the autozooecium like shelves, rather that being circular collars ringing the zooecial cavity. The interzooecial correlation of cystiphragm placement shown in the figure is typical of the species (Ross 1967: pl. 49, figs. 8, 10).

HEMIPHRAGMS.—Several Ordovician genera of trepostomes developed lateral skeletal structures in living chambers that have been called hemiphragms. Hemiphragms are shelf-like transverse extensions of the zooecial wall that arise alternately from proximal and distal sides of the zooecium and extend part of the way across the chamber (Plate 10: figures 1–3; Plate 11: figures 1, 2). The free edge of the hemiphragm is generally straight or only slightly curved. Microstructure of the hemiphragms indicates that calcification took place from both sides (Plate 10: figure 1) probably by a simple infold of the inner depositing epidermis.

The function of these transverse shelves in possibly feeding or reproductive autozooids is obscure. The sinuous living chamber produced is comparable in shape to that of the prasoporinid discussed above (Plate 11: figure 6).

The apertural configuration of a living chamber in thick-walled specimens (Plate 11: figure 2) caused by the outwardly decreasing wall thickness produces a marked funnel shape to the chamber without the development of any intrazooecial structures such as cystiphragms. A few curved skeletal partitions suggest that intrazooecial funnels were also developed (Plate 10: figures 2a, b). The position and length of regularly shaped fossilized brown deposits (Plate 10: figures 1–3) in shapes reasonable for feeding or reproductive bodies suggest that the soft parts bent around the projecting hemiphragms in living position.

In the Middle Ordovician species of *Hemiphragma* Ulrich, 1895, that contain mesopores, diaphragms

appear to be reasonably well correlated across several adjacent mesopores (Plate 11: figures 1, 2). Laminae from a hemiphragm form a structural unit that includes the intervening zooecial-mesopore wall and one or more mesopore diaphragms. Basal diaphragms are rare in the genus. A few plates extend from hemiphragm to wall to complete the partitioning of the living chamber and they probably acted as basal structures.

MONILAE AND RING SEPTA.—During the later Paleozoic, stenoporid trepostomes commonly developed extreme annular thickenings in autozooecial walls which have the appearance of a string of beads in longitudinal section (Plate 10: figures 4–7; Plate 11: figure 3). These beads or monilae are interzooecially aligned, forming layers of monilae generally parallel to zoarial growth surfaces (Plate 11: figure 3).

Transversely oriented, centrally perforated skeletal partitions were developed in a few Middle and Late Paleozoic genera (Plate 11: figure 4). In some species these partitions, called perforated diaphragms, or more recently, ring septa (Gautier 1970:5) occur together with monilae in autozooecial walls (Plate 10: figures 4, 5, 7; Plate 11: figure 3). Monilae and ring septa have recently been described in detail relative to autozooecial living chambers (Gautier 1970). Study of the National Museum of Natural History collections added little to those observations.

Ring septa were secreted from outer surfaces or unequally from both outer and inner surfaces, to judge from the laminated microstructure in section (Gautier 1970: pl. 1, figs. 1, 2). The outermost septum was positioned just inside the autozooecial aperture in the living chamber (Plate 11: figure 4). If present, outermost basal diaphragms and plates that covered foramina in ring septa and apparently acted as living-chamber floors are generally located two to three ring septa inward from the aperture (Gautier 1970:10); their position indicates general living-chamber length and maximum length possible for enclosed soft parts. Some species have ring septa but lack basal diaphragms or plates, giving no direct indication of living-chamber length.

Light brown, translucent, membranous-appearing material commonly is scattered within autozooecia in well-preserved Late Paleozoic Bryozoa. In a few specimens containing ring septa, the membranes are tubular and run through the foramina of one or more ring septa suggesting living position of membranous organs

(Plate 10: figures 4, 5a and McKinney 1969: pl. 50, figs. 2, 3, 5). Cuffey (1967:53) figures and reports skeletal intrazooecial tubes that pass through foramina of ring septa. These might well be the skeletal counterparts of the membranous tubes, much as funnel-cystiphragms might be skeletal counterparts of parallel segments of inner membrane. This analogy is questionable, however, until more information is available regarding the position, time of formation, and microstructure of the tube relative to the ring septum and living chamber.

The same relative size of membranous tubular structure occurs in a species lacking the restriction of ring septa (Plate 10: figure 6). Perhaps the elongate, cylindrical shape characterized the membranous organs of the Late Paleozoic stenoporids with or without ring septa. One funnel-shaped skeletal structure seen in a stenoporid (Plate 10: figure 7) is most likely a continuation of a skeletal layer that is draped across several adjacent zooecia shown in the figure (arrows) and not analogous with funnel-cystiphragms.

Almost as common as the occurrence of the brown membranous material in later Paleozoic trepostomes is the passing of an unbroken fragment of the membrane from one autozooecial cavity into an adjacent one (Plate 10: figure 5b). The membrane passes through the wall with an indistinct indication of a break, or no apparent break or pore. This raises some question about the basic nature of the membranous material as a product of a single autozooid and needs further investigation.

The cyclic layering of monilae parallel to the zoarial growth surface is commonly correlated with the positioning of ring septa. The correlation can be either one-to-one (Plate 11: figure 3) or one ring septum to several monilae. Ring septa are most commonly positioned on the inner sides of the monilae or in the intervening thin-walled intervals, but position can vary in adjacent autozooecia in some specimens (Plate 11: figure 3).

A structure descriptively comparable to a ring septum was reported by Robertson (1903:138, pl. 14, fig. 26; 1910: pl. 18) in Recent specimens of the cyclostome genus Crisia Lamouroux, 1812. A single structure shaped like a ring septum occurs near the inner end of enlarged ovicells, scattered among the autozooids in minor numbers, and at one stage the septum supports the large embryo. Also reported is a chitinous or membranous tube centered on the foramen

of the septum and extending inward from the septum to the bottom of the living chamber.

Descriptively, the combination of a ring septum and membranous tube in both later Paleozoic stenoporids and a Recent cyclostome suggests comparison. Functionally, however, multiple ring septa in stenoporid trepostome autozooecia where they must have been involved with feeding organs make comparison with single reproductive structures difficult. The chitinous tube in Crisia apparently surrounds large numbers of cells but no recognizable organs.

CYSTOIDAL DIAPHRAGMS AND LUNARIA.—Intrazooecial structures that appear to be partly basal and partly lateral are the curved cystoidal diaphragms in an undescribed Ordovician cystiporatid (Plate 9: figures 1, 2). The diaphragm provides a living chamber greatly restricted in cross-sectional area at the inner end, a different shape than others considered above. Similarly shaped cystoidal diaphragms and living chambers occur in a few Middle Devonian atactotechid trepostomes (Boardman 1960: pl. 20).

In the Ordovician cystoporatid illustrated, the inner end of the living chamber, filled with reddish-brown granules, is on the proximal side of the autozooecium and rests in the notch of the lunarium of the autozooecial wall. The granules or brown deposit might represent any kind of organic accumulation and does not necessarily indicate the position of the lophophore relative to the lunarium at the outer end of the autozooecium.

In a Recent lichenoporid (Plate 2: figures 1, 2) the lophophore is on the proximal side of the autozooecium. Some lichenoporids show a well-developed lunarium (Utgaard 1968:1034–1035), also on the proximal side, suggesting that the lophophore rests on the lunarial deposit. Unfortunately, a difference in microstructure between lunarium and the remainder of the zooecial wall—generally required to recognize a lunarium—was not discernable in the specimens of Plate 2, so a direct relationship was not observed.

SUMMARY OF CYCLIC GROWTH.—To summarize possible inferences based on the cyclic development of lateral structures: hemiphragms, some skeletal cystiphragms, cystoidal diaphragms, funnel-cystiphragms where they occur in cycles, and ring septa are perhaps more comparable in frequency with basal diaphragms of autozooecia. That frequency in the cycle suggests that these structures might have been expressions in different stocks of degeneration and regeneration. Lat-

eral structures in autozooecia, such as the mural spines described in the halloporid and skeletal cystiphragms that have a one-to-one relationship with mesopore diaphragms, and perhaps some monilae in later Paleozoic forms, express a more frequent change such as might be involved with an increase in length of the soft organs during a single regeneration. The lack of cavity space in strongly tabulated mesopores typical of earlier Paleozoic trepostomes suggests that mesopores did not include growth-determining autozooidal organs. If they did not, tabulated mesopores could provide a direct measure of the most frequent colony-wide growth cycles without zooidal modification. Correlation of the same kind of structure interzooecially and correlation of autozooecial structures with mesopore diaphragms, especially by structural skeletal units that cross zooecial boundaries, suggest some dependence of growth of the autozooid on colony-wide controls, such as might be provided by inner and outer membranes with coelomic space between.

Because the study of zooids separately and together in restricted portions of colonies suggests that growth cycles are interzooidal in expression, it should be possible to relate apparent growth cycles of the zooids to those of the entire colony. Published studies of indications of cyclic growth over major portions of colonies are few. Studies by Borg (1933:299–306; 314–316) on Recent cyclostome species and Gautier (1970:fig. 7) on Late Paleozoic trepostomes of the genus *Tabulipora* suggest that more episodes of cyclic growth are indicated in axial endozones of ramose forms than are recorded in proximally adjacent exozones. A study by Malecki (1968:figs. 7, 8, 11) on Permian species of *Tabulipora* indicates more generally a one-to-one correlation between abandoned growing tips in the thin-walled axial region and a layer of monilae with attached ring septa proximally along the sides of the branch. Variations in cyclic correlation between zooids and the entire colony can certainly be anticipated and probably were due to more than one factor. There is good evidence that zooids in basal segments of some trepostome colonies reached a maximum ontogenetic development and either stopped growing a skeleton or died out entirely (Cuffey 1967:67; Boardman 1960:39, fig. 14). Attempts to correlate cycles would have significance only in the distal portions of ramose zoaria that were growing at the time of death of the colony.

Functional Morphology

It is assumed that trepostomes are tubular Bryozoa, that all fossil tubular Byrozoa had protrusible lophophores as part of their food-gathering structures, and that these structures were housed in the consistently present autozooecia. In trepostomes, the only available zooecia for housing these organs other than the autozooecia are mesopores, exilapores, polymorphic zooecia in monticules, and possibly some acanthopores. None of these structures is present in all species so that the primary food-gathering role for them is not feasible. In addition, acanthopores, even if some had cores containing tissue rather than skeletal material, and mesopores that are tabulated virtually to the aperture, do not provide space enough to accommodate feeding organs. Exilapores could have contained elongated bodies and might be dimorphic autozooecia, but they would appear to have been undersized for feeding purposes when compared with living cyclostomes. Monticules (small clusters scattered fairly evenly through most trepostome zoaria of zooecia different in size and/or morphology from autozooecia) generally have some polymorphs that are larger than surrounding autozooecia and could have housed feeding organs. No significant evidence is available from this study of widespread differences in the nature of soft parts in these larger polymorphs nor is there any evidence that feeding organs might have been limited to the larger polymorphs which are few in number relative to autozooecia.

Funnel-shaped, membranous structures that open outwardly and more or less span the living chamber in tubular Byrozoa are observed in Recent species to be associated with protrusible lophophores and are inferred in fossils to indicate the presence of protrusible lophophores. Funnel-shaped structures observed to date in living cyclostomes are membranous and are formed in the retracted position by terminal vestibular membranes or by tissues in the region of the sphincter muscle at the juncture between the membranous sac and the vestibular membrane. Doubled funnels, one invaginating the other, are known in living cyclostomes from a combination of terminal-vestibular membrane and sphincter muscle in the retracted position (Plate 1: figures 3a, b), or in a single known occurrence of a doubled terminal-vestibular membrane (Plate 1: figure 5a).

The funnel-shaped structure in the Devonian Antarctic specimen (Plate 4: figures 1a, b) is interpreted

as membranous and inferred to indicate the presence of a protrusible lophophore in a feeding autozooid during life (Figure 6). The two levels of membranous connections between the suggested terminal-vestibular membrane and the zooecial wall observed in the Devonian specimen do not seem to be represented in Recent cyclostomes by analogous structures. The evidence that the funnel-shaped structure and connections were membranes seems convincing, however, and the perfection of the shape of the funnel suggests only minor distortion from the living shape. Perhaps the membranous connections are a part of the mechanism that was necessary to achieve a depression of the orifice below the skeletal aperture and, therefore, are not needed in Recent cyclostomes in which the orifice is above the aperture.

In the Devonian Antarctic species, the consistently shorter segments in the autozooecia that contain cystiphragm- and diaphragm-shaped structures and brown deposits (Plate 1: figure 2; Plate 4: figures 2a, b, d, e, 3) suggest zooidal units of different function than the longer unit inferred above to be feeding in function. The structures in these shorter segments seem to be morphologically comparable to the flask-shaped chambers of other early Paleozoic trepostomes, even though the cystiphragms and diaphragms were apparently membranous in the Devonian species.

In the great majority of flask-shaped chambers in Paleozoic trepostomes, funnel-cystiphragms are of skeletal microstructure and are inferred to have been shaped by subparallel depositional epidermis of the inner membrane. The presence of a retractable lophophore does not seem to be precluded by an inflexible skeletal funnel, as a considerable coelomic volume is possible within the living chamber outward from the funnel-cystiphragm. Room for passage of membranous structures through the neck of a funnel-cystiphragm, however, is considerably restricted.

The shape of skeletal funnels is either so generalized within the phylum that functionally different combinations of organs could have been counterparts to the funnels with little functional significance reflected in the skeletal shape, or subparallelism of organs is indicated and membranous counterparts were also funnel-shaped, suggesting a retractable lophophore. Both possibilities seem to be reasonable working hypotheses.

The occurrence of fossilized brown deposits is considered to indicate the presence of organic material during the life of the colony. Brown deposits are pre-

dictable in early Paleozoic trepostomes in three positions in autozooecia: (1) in the last-formed living chambers under an intrazoarial overgrowth; (2) in minute, hollow, skeletal spheres attached to living chambers; and (3) in flask-shaped chambers bounded by a combination of basal diaphragms and funnel-cystiphragms (Cumings and Galloway 1915: 350–353). The presence of brown deposits correlated with basal diaphragms (Plate 7: figure 4) and cystoidal diaphragms (Plate 9: figures 1, 2) is rare and is inferred to reflect degenerated brown bodies in the cyclic growth of the autozooids.

In intrazoarial overgrowths, it is assumed either that overgrowths developed from neighboring autozooids within the colony to continue outward growth in regions where zooids had met accidental death, or that overgrowths themselves caused sudden death of the covered zooids. Either way, these covered living chambers commonly contain brown deposits in species that generally do not contain them elsewhere in the zoarium. The presence of fossilized brown deposits then suggests sudden death of the zooid and immediate covering of the living chamber to preserve chemically an indication of some part of the soft tissue. There seems to be no evidence that covering of the living chambers by overgrowths took place only when the covered autozooids were in the degenerated stage, so it is inferred that the autozooids could have been either in the degenerated or functional phase of the cycle at the time of death.

Small, hollow, spherical bodies of laminated skeletal material occur commonly in living chambers of autozooecia in a few Devonian and Carboniferous genera of trepostomes. The spheres or cysts generally are filled with brown deposits and are fastened to zooecial walls or diaphragms (Boardman 1960: pl. 9, fig. 1d, pl. 10, fig. 4; Dunaeva 1968: fig. 1). Spheres occur in the same zoaria with flask-shaped chambers in *Leptotrypella furcata* (Plate 8: figure 7) and *L. polita* (Plate 8: figures 9a, b; Plate 9: figures 4a, b). It has been suggested that these spherical bodies look like the eggs (Dunaeva 1968:62) of some cheilostomes. The skeletal walls of the sphere, however, suggest that they are encysted foreign bodies or perhaps even encysted brown bodies.

Brown deposits in flask-shaped chambers probably indicate the presence of soft parts during life that were preserved because of restriction of oxidation of inclosed tissues by the skeletal necks of the chambers,

FIGURE 6.—Reconstruction of the hypothetical feeding organs of *Leptotrypella? praecox* Boardman, from the Lower Devonian of the Ohio Range, Antarctica. The known parts above and below the break midway along the tentacles are based on the suggested relationships of structures seen in two autozooecia (Plate 4: figures 1*a, b,* above) and (Plate 3: figure 6*b,* below). The unknown parts are patterned after generalized cyclostome morphology. The fossil specimens show no indication of a sphincter muscle or junction between tentacle sheath and membranous sac, and, in fact, direct evidence that the membrane around the assumed gut region is actually a membranous sac rather than the gut itself is lacking. Note the general similarity of outline shape, however, to the gut region of the hornerid (Plate 2: figure 4*a*).
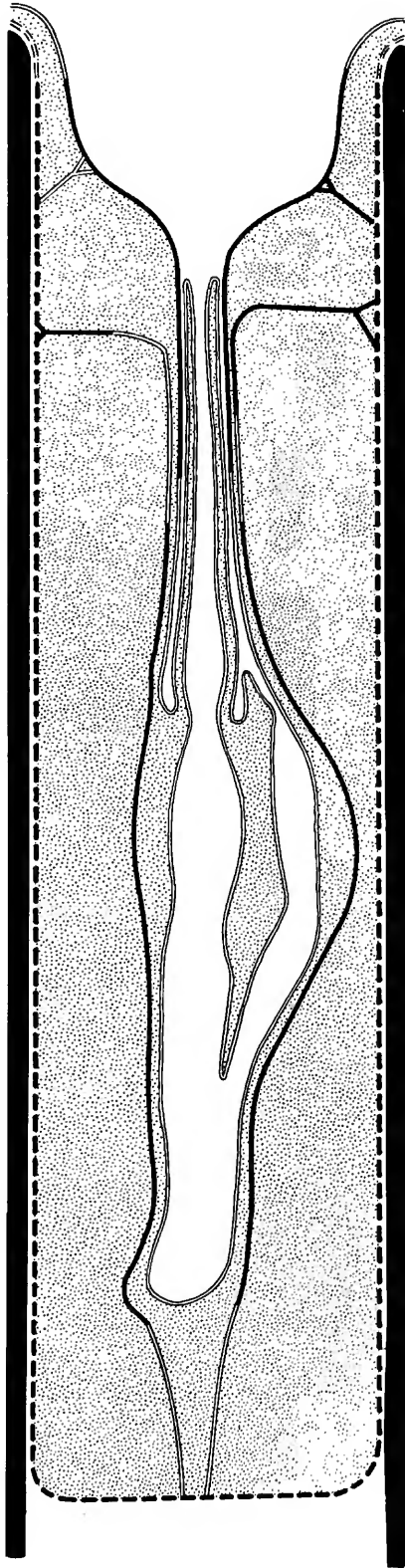
KNOWN

COELOMIC SPACE

CALCAREOUS SKELETON

- - - - - - - INNER EPIDERMIS

———————— OUTER MEMBRANE

UNKNOWN
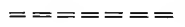
======= INNER EPIDERMIS

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by a capping diaphragm, or by a combination of the two. Flask-shaped chambers occur in relatively few early Paleozoic trepostomes, and, where they do occur, they can be scattered without apparent pattern (Plate 11: figure 6), concentrated in narrow zones paralleling or at the zoarial surface (Plate 7: figure 7), or more or less evenly distributed through the zoarium (Plate 7: figure 5b). Normal cyclic growth occurred between flask-shaped chambers in an autozooid generally without brown deposits, whether it was expressed by sequentially grown diaphragms, cystiphragms, or hemiphragms.

The actual distribution of flask-shaped chambers in the living colonies would certainly be important to functional interpretation if it could be known. Either the real chamber distribution is approximated in the fossils, or the structure was more common but not often preserved. It is conceivable that the organs that occupied a flask-shaped chamber were the customary organs for the autozooid and that just occasionally by an environmental accident, for example, the immediate living chamber was calcified, or, if regularly calcified, the chamber was not resorbed. The presence of cyclic distributional patterns of the chambers in a few species and the overwhelming numbers of species for which flask-shaped chambers have not been recognized argue against accidental preservation of a commonly occurring structure. It is assumed here that the general nature of the distribution of skeletal flask-shaped chambers is approximated in the fossil record.

In early Paleozoic monticuliporids (Plates 5, 6) and diaphragmed trepostomes (Plates 8, 9), therefore, flask-shaped chambers apparently were not abundant enough to reflect or support food-gathering organs. It seems most significant, further, that the number of tentacles that could have been extruded through many of the funnel-cystiphragm necks, assumed to be skeletal and inflexible, must have been greatly restricted. The cross-sectional size of lichenoporid tentacles (Plate 2: figure 2, ×150) is much greater than the neck sizes of monticuliporids (Plate 5: figures 4, 5, ×150; Plate 6, ×100). Not more than two or three lichenoporid tentacles could have passed through the necks in some of the heterotrypids (Plate 8: figures 1–4, ×100). The cyclostome "necks" that look so similar (Plate 1: figures 3a, b) are membranous and expand to allow the tentacles to pass through (Plate 1: figure 5d).

Further, if the sequence of development has been worked out accurately, and, if earlier formed funnel-cystiphragms were not entirely membranous or resorbed during the ontogeny of the peronoporid autozooecium (Figure 3; Plate 5: figure 4d), the development and function of the funnel-cystiphragm was limited to the last episode in the life of that autozooecium. The function of food gathering does not seem likely on such a restricted schedule.

With so little actually known and so much that is necessarily inference and speculation, it seems most reasonable to relate support or reflection of food-gathering organs to skeletal structures that are characteristic of the autozooecia of a species, rather than to those that are exceptional. Basal diaphragms, skeletal cystiphragms, cystoidal diaphragms, hemiphragms, ring septa, and perhaps annular thickenings in zooecial walls, have the constancy of distribution in autozooecia of species in which they occur to suggest that these structures influenced the shape of the living chambers that housed the feeding organs.

The model in Figure 1 was made at the beginning of the study when the flask-shaped chamber of a diaphragmed trepostome looked as if it reflected the shape of enclosed feeding organs. The cystiphragms in that diaphragmed trepostome are now interpreted to be analogous to funnel-cystiphragms in monticuliporids and the preferred hypothesis suggests that something other than feeding organs was housed in the flask-shaped type of living chamber. In a diaphragmed trepostome, the presently preferred model for a feeding autozooid would lack the cystiphragms and resulting constriction in the soft parts. In a monticuliporid, the inferred living chamber for feeding organs includes the consistently present skeletal cystiphragms but not the inner funnel-cystiphragms. The living chamber that contained the feeding organs of a monticuliporid model would then be cylindrical in shape inwardly and would expand outwardly beyond the last-formed cystiphragm into a short funnel- or bell-shaped outermost section.

Remaining suggestions for the function of flask-shaped chambers include use as a chamber for degenerated remains of soft parts (the brown bodies of Recent species and the hypothesis referred by Cumings and Galloway 1915:354), use as a living chamber for a zooid like a single-tentacled nanozooid of unknown function, or use as a chamber involved in some manner with sexual reproduction. The growth of skeletal structures specifically to house brown bodies or other waste products has not been recognized in living

Bryozoa. The subsequent growth of funnel-cystiphragms to form multiple funnels from the same chamber suggests that, whatever the function, it was carried on by living tissue subject to cyclic growth. It seems virtually impossible to emplace more than one brown body from more than one degenerative-regenerative cycle in a flask-shaped chamber.

A nanozooid (Borg 1926:232–239) is a polymorph in the cyclostome genus *Diplosolen* Canu, 1918, that is considerably smaller than the feeding autozooids. The length and diameter are reported to be approximately one third those of adjacent feeding autozooids. Nanozooids have their zooecia dispersed among the larger autozooids and have a single tentacle. They have body walls, membranous sacs, and muscular systems comparable to feeding autozooecia, but no feeding or reproductive organs or other indication of function. The single tentacle apparently can be protruded so that a nanozooid can be considered a dimorphic autozooid. Little evidence other than reduced size seems available to suggest comparison with flask-shaped chambers in Paleozoic forms, especially because nanozooids have their own zooecia and an unknown function.

The flask-shaped chamber in early Paleozoic monticuliporids and diaphragmed trepostomes seems best explained as a part of the mechanism of sexual reproduction. The flask-shaped chamber could possibly represent a brood chamber for larval development, or could have contained a male or female stage that alternated with feeding stages in autozooid ontogeny. The scattered or cyclic distribution of the chambers is more generally comparable to that of reproductive bodies than to that of feeding bodies in Recent species. A sexual zooid provides a functional rather than a degenerated body to support subsequent growth of multiple funnel-cystiphragms from a single chamber and specialized skeletal structures are commonly grown in Recent Bryozoa for brooding or sexual organs.

The apparent lack of flask-shaped chambers in Recent species and the wide variation in skeletal morphology that supports sexual organs makes any interpretation of specific sexual function difficult. The only comparison of flask-shaped chambers with zooids in Recent species that seems to have merit is with the male autozooids reported in a few cheilostome species that have a reduced number of tentacles relative to adjacent feeding autozooids. A lophophore with few tentacles seems to be consistent with the shape and constriction of the funnel-cystiphragms of the flask-shaped chambers (Figures 3–5). In cheilostomes some male autozooids are reported to show no zooecial difference (Gordon 1968: fig. 1) and some are zooecially dimorphic compared with feeding autozooids (Cook 1968: fig. 3).

If the flask-shaped chambers in Paleozoic species contained functioning organs, those organs and their skeleton constituted a zooid, that is, a member or unit of a colony consisting of body wall enclosing a coelom that is connected by body walls to other members of the colony. If the chambers were parts of zooids, therefore, those zooids, regardless of function, were polymorphic with the zooids of the consistently present and less restrictive chambers that alternated with the flask-shaped chambers in the same autozooecia and that occurred in other autozooecia throughout the zoarium. It follows that at least two different kinds of zooids were contained in a single zooecium at different ontogenetic stages of development and that intrazooecial polymorphism, therefore, occurred in these trepostome species. The ability of the zooid to regenerate functional organs provides a reasonable mechanism for emplacement of different kinds of zooids in a zooecium at different times.

An alternation of feeding and male reproductive zooids in the same living chamber, each with its own orifice, the smaller male orifice inside the larger, has been reported in a cheilostome species (Rogick 1956: 183, pl. 1. figs. 3, 6). Regeneration of the male sexual stage following the asexual or feeding stage was subsequently reported in the same species (Powell 1967: 249). This sequence would be similar to that hypothesized for the Paleozoic peronoporid (Figure 3; Plate 5: figures 4, 5). Flask-shaped chambers in Paleozoic trepostomes are interpreted to have been the living chambers of intrazooecial polymorphs which might have functioned as sexual autozooids.

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PLATES

PLATE 1

Prasopora grayae Nicholson and Etheridge, 1877. H. A. Nicholson collection, Royal Scottish Museum 1967–66–406; Craighead Limestone (Ordovician) near Girvan, Scotland.

  1a. Longitudinal section of segment of autozooecium, ×100, overlapping series of skeletal cystiphragms that leave smaller central living chamber occupied by funnel-cystiphragms and flask-shaped structure filled with the customary reddish-brown particles of fossilized brown deposit. Small funnel at bottom of figure is apparently from earlier growth cycle. Direction of growth is upward.

  1b. Longitudinal section from same colony, ×100, outer funnel-cystiphragm somewhat out of plane of section and inner funnel-cystiphragm continuing downward into flask-shaped chamber.

Leptotrypella? praecox Boardman, 1965. Horlick Formation (Lower Devonian), Ohio Range, Antarctica.

  2. Longitudinal thick section of autozooecium of paratype USNM 167678, ×100, after treating with hydrochloric acid, showing a pair of nearly identical funnels, apparently the outer (upper) one is invaginated by the inner one.

HETEROPORID CYCLOSTOME. Recent specimen from Vancouver Island, British Columbia, British Museum (Natural History).

  3a. Longitudinal view of whole mount of segment of preserved autozooid, ×100, showing funnel shape of the terminal-vestibular membrane invaginated by dark mass of cells around the sphincter muscles. Outer ends of tentacles are enclosed in membranous sac in dark mass at bottom of figure. Lateral ligament attachments do not show in specimen but are necessarily at level on specimen just below lower margin of figure.

  3b. Similar portion of another autozooid from same colony, ×100.

  4. Longitudinal view of whole mount of preserved soft parts removed from zooecium, ×100, showing sphincter muscle mass above, membranous sac housing tentacles below, and short ligaments projecting laterally from sac (arrow).

HETEROPORID CYCLOSTOME. Recent specimen from Pacific Area, British Museum (Natural History).

  5a. Longitudinal thin section of outer segment of autozooid, ×150, showing delicate, doubled, terminal-vestibular membrane opening outward to left in figure. Structure apparently consisted of two funnel-shaped membranes if outermost one (arrows) was intact.

  5b. Longitudinal thin section of segment of autozooid, ×150, showing ends of tentacles pulled back to level A of lateral ligaments and the dark U-shaped mass of cells of the sphincter muscle (level B) in a closed position. The terminal-vestibular membrane is missing and the base of the tentacles is at the bottom of the figure. Note the cells in the smaller polymorphs on either side of the autozooid.

  5c. Longitudinal section of autozooid, ×150, showing ends of tentacles between lateral ligaments and sphincter muscles (level B). Note the membrane of the tentacular sheath passing upward through opening in sphincter muscle and appearing to continue as the vestibular membrane. Outward from the tentacular sheath is the membrane and associated cells of the outer end of the membranous sac, stretching from the ligaments to the sphincter muscles, just as Borg indicated as in Figure 1. The membranous sac extends inward and surrounds the elongated gut in the lower left corner of the figure. Note that laminated zooecial lining stained more darkly than the cortex suggesting higher organic content of lining.

  5d. Longitudinal thin section of segment of autozooid, ×150, showing tentacles projecting outward past lateral ligaments (at level A) and through sphincter muscle (at level B) greatly modifying shape of the profile of that muscle. Note double membranes of the tentacular sheath and membranous sac visible inward from lateral ligaments.

PLATE 1

1a

1b

2

3a

5a

3b

4

5b

5c

5d
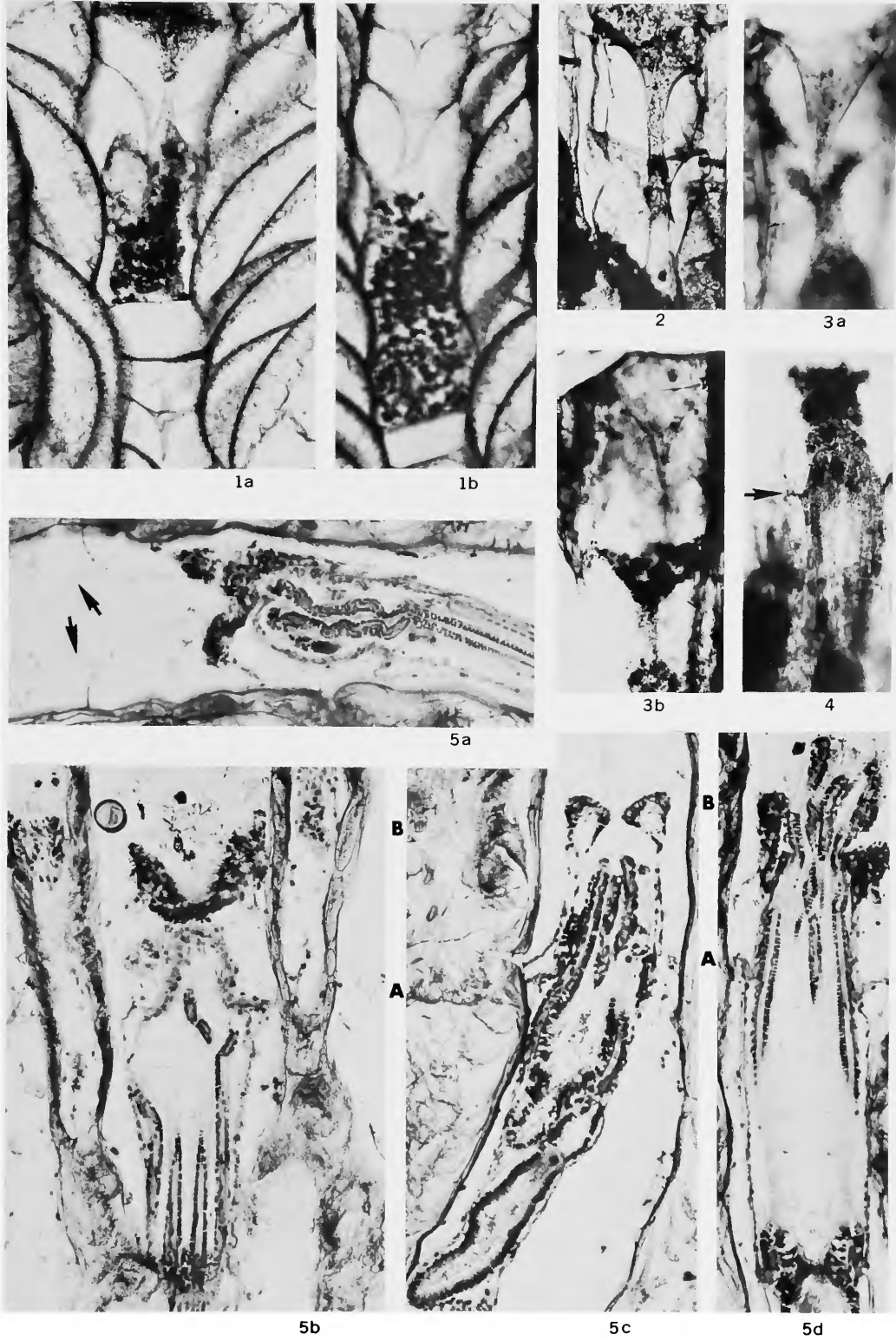
PLATE 2

All illustrations are ×150

LICHENOPORID CYCLOSTOME. Recent specimen from Galapagos Islands, British Museum (Natural History).

1. Longitudinal section of autozooids, in middle one showing cone-shaped terminal-vestibular membrane, small sphincter muscle mass, and membranous sac (arrow) seen on proximal side of zooid at ligament level (proximal side and center of colony to right in figure). Short, thick parallel structures at base of tentacles are retractor muscles; ovoid structure lateral to muscles is part of gut. Large irregular sac-shaped structures on distal sides of zooids (left in figure) are male sex organs.

2. Longitudinal section of autozooids showing level of lateral ligaments attaching membranous sac to zooecia (arrows). Note male sex organs absent but membranous sacs retain proximal position. Insert is of tangential section of two autozooids showing cross section of radially arranged tentacles on proximal sides of zooids (upward in insert is toward center of colony); distal sides occupied by sex organs.

HETEROPORID CYCLOSTOME. Recent specimen from the Pacific area, same colony as Plate 1, figure 5.

3a. Longitudinal thin section of preserved autozooid showing base of tentacles (right side of figure), two portions of gut, and male sex organ (left side of figure), all enclosed by thin membranous sac.

3b. Longitudinal thin section directly through lateral ligament (arrow) showing both tentacular sheath and membranous sac connected directly to ligament from both directions (outward direction to right in figure). Ends of tentacles are just outward from ligament.

HORNERID CYCLOSTOME. Recent specimen from Arctic Ocean, British Museum (Natural History).

4a. Longitudinal thin section of different segments of preserved autozooids. Zooid opening to right lacks terminal-vestibular membrane and sphincter muscle cells are apparently somewhat deteriorated. Lateral ligaments, tentacle sheath, membranous sac, tentacles withdrawn well below ligament level, and gut are well preserved. Note relatively broad exozone of skeleton, laminated throughout, and position of lateral ligaments outward from sharp zooecial bend (arrow) toward surface of colony. Middle autozooid in figure shows inner end of gut and four brown body masses. Autozooid at left shows undifferentiated brown body material at innermost end of long autozooecium. Total length of autozooecium can be as much as five times that of functional lophophore and gut at outer end.

4b. Longitudinal thin section of another fragment from same colony showing terminal-vestibular membrane and dark mass of the sphincter muscle intact. Note narrow exozone indicating younger ontogenetic stage of development. Lateral ligaments are attached well inward from zooecial bend (arrow), suggesting that functional soft parts retain fairly constant relative dimensions from skeletal apertures regardless of stage of development. Note outer membrane on outer skeletal surface above and below aperture. Nonlaminated appearance of zooecial wall to left in figure caused by breaking loose of skeletal material in sectioning process.

PLATE 2
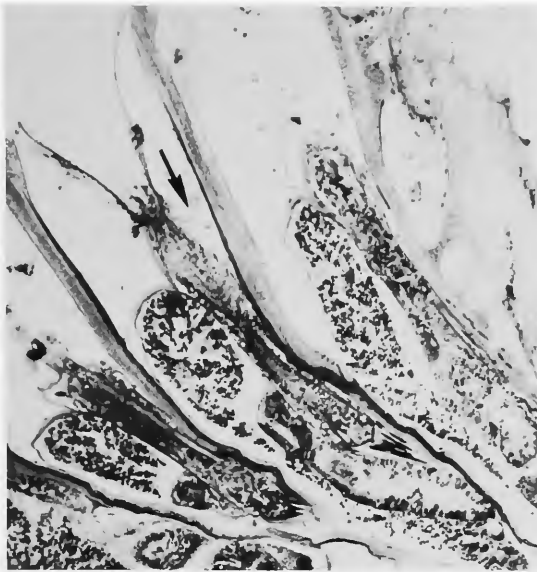
1

2

3a

3b

4a

4b
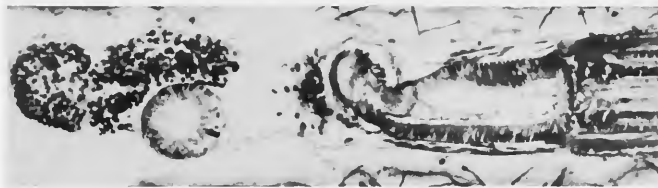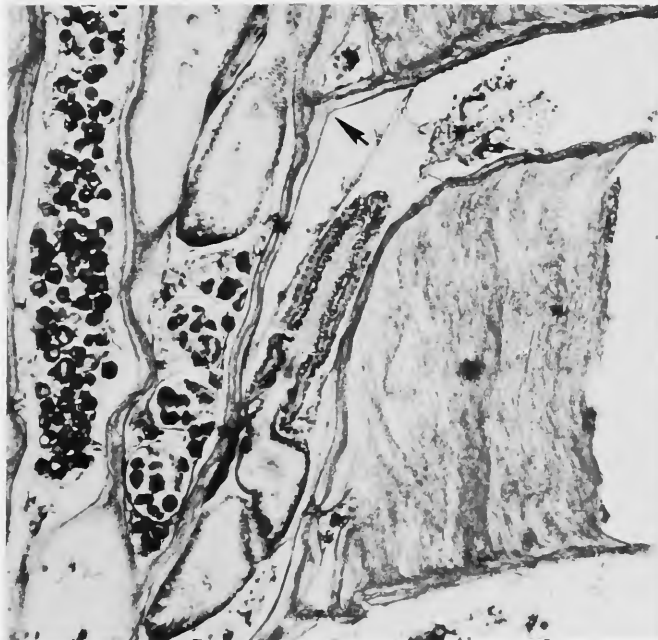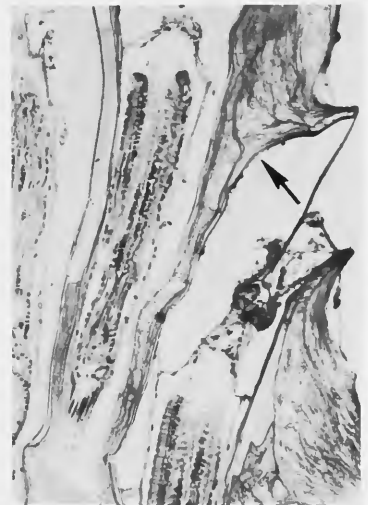
PLATE 3

Lᴵᴄʜᴇɴᴏᴘᴏʀɪᴅ ᴄʏᴄʟᴏꜱᴛᴏᴍᴇ. Recent specimens from Galapagos Islands, British Museum (Natural History).

1. External basal view of small colony, ×50, showing large, circular basal disc of ancestrula (arrow) and ancestrula curving in two planes to left and upward away from basal disc.
2. Longitudinal section near margin of colony, ×150, showing simple laminated basal skeletal layer of colony (arrow) that is a direct extension of basal disc of ancestrula to left in figure. Laminae of basal layer dip to left opposite growth direction requiring edgewise distal growth of laminae, similar to basal skeletal layers in many trepostomes. The compound internal walls that apparently arise by epidermal infolding from the basal skeletal layer are all granular-to-microcrystalline in texture.
3. Basal thin section similar in orientation to colony in Figure 1 cut just above ancestrular disc to show budding pattern, ×100. Ancestrula (arrow) curves to left and contains what appear to be normal functional parts of a feeding autozooid.
4. Longitudinal section, ×300, through basal disc and proximal portion of ancestrula. The laminated floor of disc is broken and displaced upward. In lower right corner of figure basal laminated layer continues distally to right beyond notch (arrow) to margin of colony that is similar to portion shown in Plate 3, figure 2. In lower left, laminated layer of disc turns sharply to upper right corner of figure, then turns back on itself to form basal layer for the discordant part of colony corresponding to that portion growing downward toward bottom of Plate 3, figure 3. Colony then is essentially as diagrammed (Figure 2) after Borg, with the basal skeletal layer in this species laminated and all internal compound walls that budded by infolding from basal layer microcrystalline.

Disporella separata Osburn, 1953. Recent cyclostome from South Caronodos Island, Baja, California, Mexico; collected by William C. Banta. USNM 167679.

5. Longitudinal thin section, ×300, showing a stained membrane lining zooecial wall (arrow). Several sections from colony showed lophophore and gut structures degenerated or greatly reduced with membranes across apertures of most autozooids.

Leptotrypella? praecox Boardman, 1965. Horlick Formation (Lower Devonian), Ohio Range, Antarctica.

6a. Longitudinal section, ×100, of holotype USNM 144807, showing well-formed structure filled with iron oxide grains, apparently inward from funnel, suggesting shape of gut and reproductive organs as in Recent cyclostomes.
6b. Longitudinal section from same colony showing similar structure, ×100.

PLATE 3
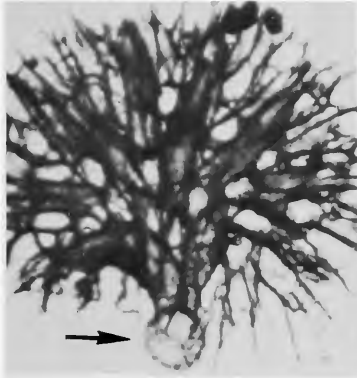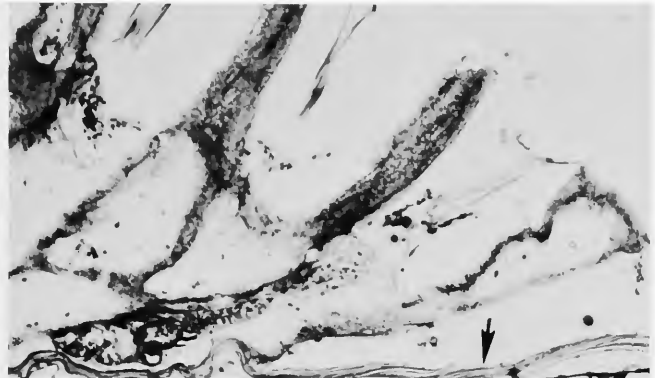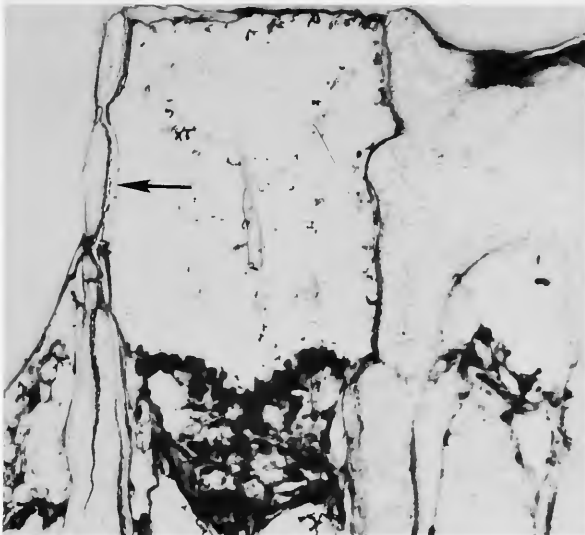
PLATE 4

Leptotrypella? praecox Boardman, 1965.   Horlick Formation (Lower Devonian), Ohio Range, Antarctica.

1*a*. Longitudinal section of holotype USNM 144807, ×100, funnel at top of figure leading downward to dark mass (arrow) thought to be part of lophophore and gut complex. Below is thin, tubular membrane leading down to membranous diaphragm just above dark mass at bottom of figure.

1*b*. Longitudinal section of same funnel, ×200, showing apparent attachment of funnel to zooecial wall on right side just below dark, circular foreign body, and below that at neck level in funnel a transverse membrane (arrows) similarly attached to zooecial wall and running short distance down neck on right side.

1*c*. Longitudinal section of apparent funnel and neck of another autozooid, ×100.

2*a*. Longitudinal section from paratype USNM 167680, ×100, poorly preserved pair of funnels in upper third of figure leading downward to well-preserved segment of body. Note remnant of membranous cystiphragm (arrow) and thickened membrane adjacent to skeleton and lining living chamber.

2*b*. Longitudinal section from same colony, ×100, showing funnels attached to inner membrane of zooecial wall, the outer one above with a collapsed neck apparently invaginated by inner one. Membranous cystiphragms to left lead down to diaphragm that apparently marks bottom of living chamber.

2*c*. Longitudinal section, ×200, complete membranous linings in chambers partitioned by membranous diaphragms presumably below functional gut. Diaphragms analyzed by electron probe.

2*d*. Longitudinal section, ×100, single funnel leading downward to tubular neck. Again cystiphragms lead to diaphragm presumably at bottom of living chamber.

2*e*. Longitudinal section, ×100, single funnel centered just out of the plane of section at neck and a complex of lateral membranous cystiphragms. Transverse line on either side of presumed gut connecting to autozooecial wall to right is crack in calcite.

2*f*. Section of closed chamber, ×400, membranous chamber lining displays microstructure of cell size but apparently not cell appearance.

3. Longitudinal section of paratype USNM 144809, ×100, showing single funnel above and gut below with usual membranous cystiphragm and diaphragm at base of living chamber.

PLATE 4
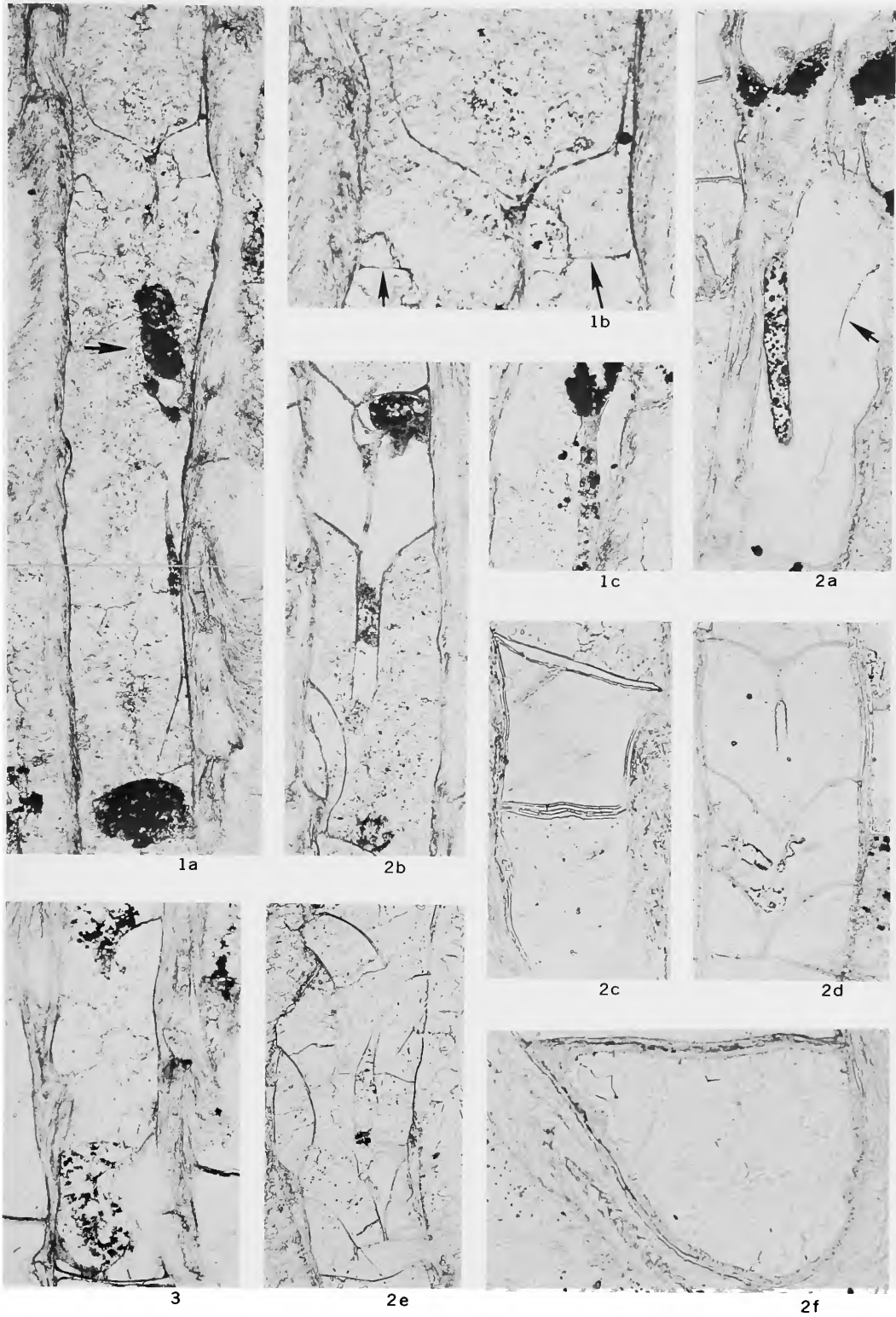
PLATE 5

Gortanipora sp.   Maquoketa Shale Group (Upper Ordovician), Wilmington, Illinois.
    1. Longitudinal section, USNM 167681, ×100, shows fringed margin (arrow) of incomplete cystiphragm due to lateral position of cystiphragm in the living chamber.

Gortanipora cylindrica (Bassler, 1903).   Whitewater Formation (uppermost Upper Ordovician), Richmond, Indiana.
    2. Longitudinal section of syntype USNM 41758, ×100, incomplete cystiphragms with fringed margins (arrow) in usual position on distal side of autozooecium. These cystiphragms suggest the smaller fringed heterophragms in Devonian genera such as *Trachtoechus* Duncan, 1939, and *Eridocampylus* Duncan, 1939.

Prasopora orientalis Ulrich, 1893.   Trenton Group (Middle Ordovician), Trenton Falls, New York.
    3. Longitudinal section of syntype USNM 44054, ×50, living chamber under an overgrowth containing fossilized brown deposits. Closely tabulated mesopore to right.

Peronopora sp.   Southgate Formation, Eden Group (Upper Ordovician), railroad cut at Bald Knob, Cincinnati, Ohio.
    4a. Longitudinal section USNM 167682, ×150, living chamber with funnel-cystiphragm plugged with pyrite. Funnel-cystiphragm has skeletal wall that thins to membranous appearance inward (to left) and the inner part of the flask-shaped chamber is indicated primarily by concentration of impurities. Note thinning of skeletal cystiphragms inwardly.
    4b. Longitudinal section from same zoarium, ×150, funnel-shaped structure that appears membranous (arrow) except for short, very thin segment joining the autozooecial wall at the upper right that is apparently calcified.
    4c. Longitudinal section of another autozooecium, ×150, showing funnel-cystiphragm that encircles the living chamber and inside that skeletal structure a smaller, more strongly curved funnel (arrow) that appears minimally calcified.
    4d. Longitudinal section of another autozooecium, ×150, showing strongly calcified funnel-cystiphragm thinning inwardly. Skeletal cap (arrow) at neck of funnel-cystiphragm is subsequent growth.

Corryville-Arnheim Formations (Upper Ordovician), railroad cut 4 miles east of Weisburg, Indiana.
    5. Longitudinal section USNM 167683, ×150, living chamber containing large, encircling funnel-cystiphragm which in turn contains more strongly curved, smaller funnel and cystose structures (arrow) that appear minimally calcified.

PLATE 5
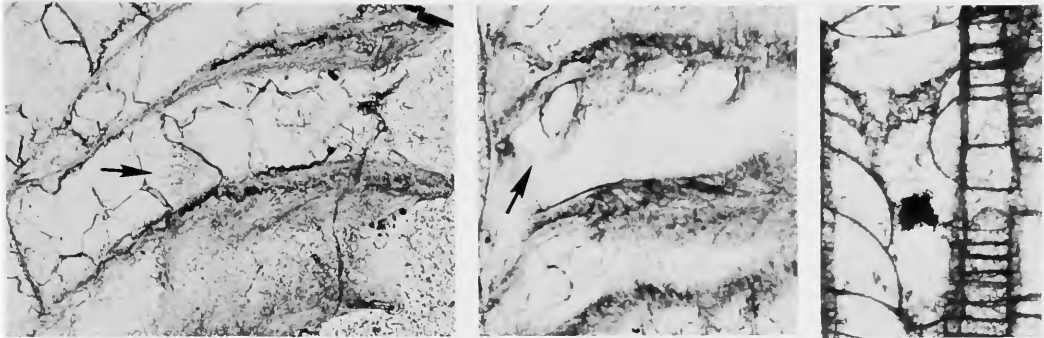
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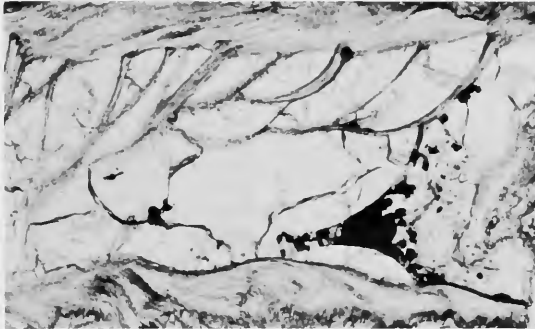
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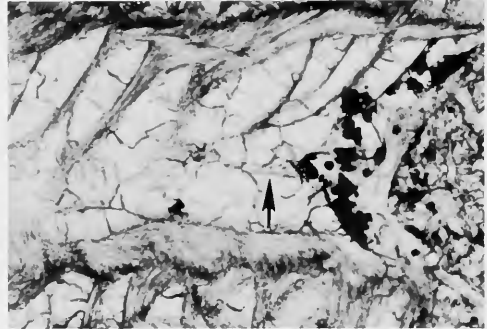
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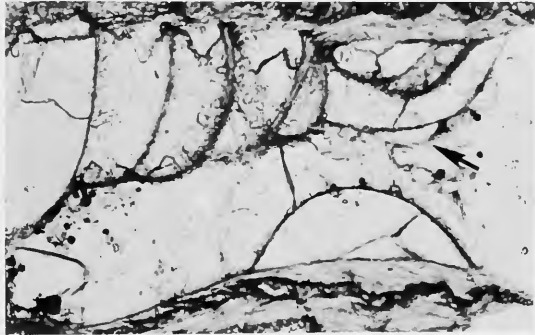
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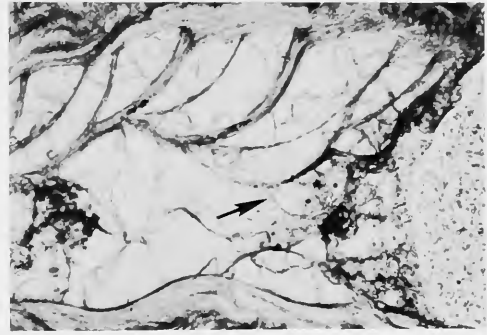
4c

4d

PLATE 6

Prasopora grayae Nicholson and Etheridge, 1877.   H. A. Nicholson collection, Royal Scottish Museum 1967–66–406; Craighead Limestone (Ordovician) near Girvan, Scotland.

    1*a*.   Longitudinal thick section, ×100, showing thinness of single funnel-cystiphragm wall relative to overlapping skeletal cystiphragms surrounding the living chamber. The dark granules in the flask-shaped chamber are the fossilized brown deposits of Cumings and Galloway, and are bright reddish brown in color; similar deposits show in all figures on plate.

    1*b*–1*d*.   Longitudinal sections from same zoarium, ×100, showing abandoned living chambers well down in autozooecia at the single funnel-cystiphragm stage of development.

Prasopora simulatrix Ulrich, 1886.   Trenton Group (Middle Ordovocian), Trenton Falls, New York.

    2*a*–2*d*.   Longitudinal sections from same zoarium, USNM 167684, ×100, showing single and multiple funnel-cystiphragm stages of development. Note the difficulty of distinguishing skeletal cystiphragms and funnel-cystiphragms in 2*b*. There are two vertical rows of overlapping cystiphragms on the right and only one on the left with little difference in shape and thickness.

    3.   Longitudinal section, USNM 167685, ×100, autozooecium with perfectly symmetrical double funnel-cystiphragms.

Trenton Group (Middle Ordovician), Belleville, Canada.

    4.   Longitudinal section, USNM 167686, ×100, showing a flask-shaped chamber at the double funnel-cystiphragm stage of development.

Trenton Group (Middle Ordovician), Kirkfield, Canada.

    5.   Longitudinal section, USNM 167687, ×100, showing flattened cystiphragm (arrow) at top left of figure just above funnel-cystiphragm that would parallel approximately the simplest configuration of a terminal membrane approaching the skeletal aperture (see Figure 4).

Trenton Group (Middle Ordovician), Canada.

    6.   Longitudinal section, USNM 167688, ×100, single autozooecium with two cycles of flask-shaped chamber development. Notice a single diaphragm dividing chambers.

PLATE 6
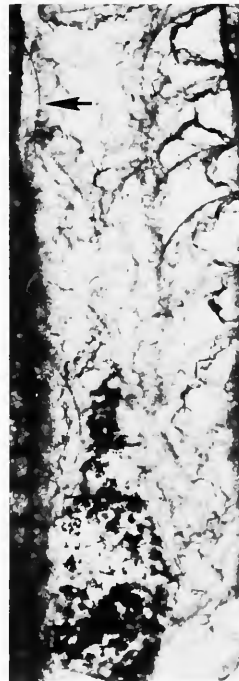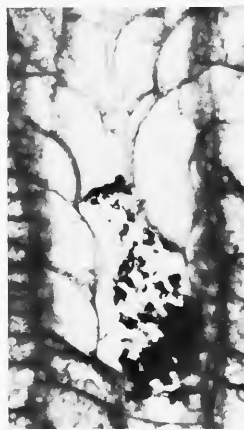
PLATE 7

Orbignyella sp.   Bellevue member of the McMillan Formation (Upper Ordovician), Cincinnati, Ohio.

   1.   Transverse section of USNM 167689, ×50, showing region of zoarium that was apparently injured during the life of the colony and partly filled in with cystiphragms.

Prasopora simulatrix Ulrich, 1886.   Trenton Group (Middle Ordovician), West Covington, Kentucky.

   2.   Longitudinal section of USNM 167690, ×100, showing change in direction of auto-zooecial wall growth (arrow) and the spanning of that change by the outer of two funnel-cystiphragms.

Prasopora contigua Ulrich, 1886.   Upper Ordovician, River Quarries, Covington, Kentucky.

   3.   Longitudinal section of USNM 167691, ×100, showing a flask-shaped chamber spanning a change in direction of growth of autozooecial wall (arrow).

Trachytoechus sp.   Petoskey Limestone Formation (Middle Devonian), Petoskey, Michigan.

   4.   Longitudinal section, USNM 37518, ×30, showing fossilized brown deposit with each basal diaphragm.

Prasopora grayae Nicholson and Etheridge, 1877.   (Same specimen as figured on Plates 1 and 6.)

   5a.   Longitudinal section, ×100, showing a funnel-shaped structure (arrow), almost membranous in appearance, above a flask-shaped chamber.

   5b.   Longitudinal section, ×30, showing more or less evenly cyclic distribution of flask-shaped chambers in zoarium.

Prasopora simulatrix Ulrich, 1886.

Trenton Group (Middle Ordovician) Trenton Falls, New York.

   6.   Longitudinal section, USNM 167684, ×100, showing complex of funnel cystiphragms that apparently developed without outward displacement.

Trenton Group (Middle Ordovician), Escanaba River, Michigan.

   7.   Longitudinal section, USNM 167692, ×30, showing concentration of brown deposits and imperfectly shaped chambers at level of zooecial wall thickening.

PLATE 7
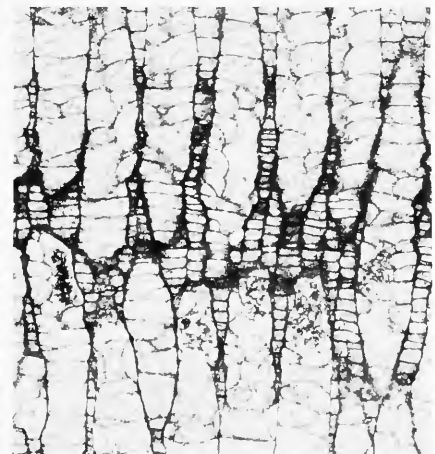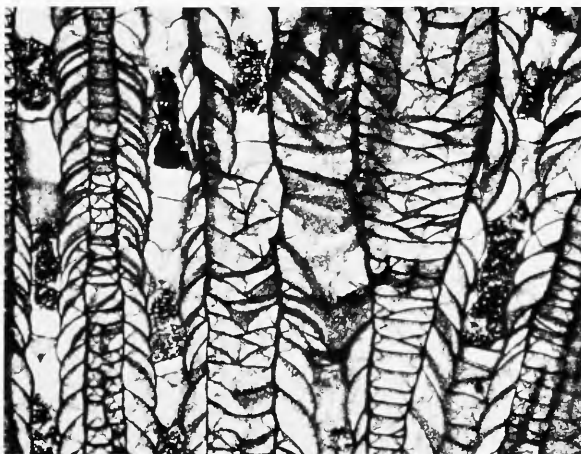
PLATE 8

Heterotrypa sp.
Upper Ordovician, Cincinnati, Ohio.
  1.   Longitudinal section, USNM 167693, ×100, showing double funnel-cystiphragms in a diaphragmed trepostome. Note fossilized brown deposit in opening of inner funnel. Apparently the entire flask-shaped chamber moved outward with the development of the second funnel-cystiphragm.
Corryville Member of the McMillan Formation (Upper Ordovician), Ohio.
  2.   Longitudinal section, USNM 167694, ×100, showing a flask-shaped chamber with a capping diaphragm.
Economy Member of the Eden Group (Upper Ordovician), Cincinnati, Ohio.
  3.   Longitudinal section, USNM 167695, ×100, living chamber under protective overgrowth in a double funnel-cystiphragm stage of development.
Economy Member of the Eden Group (Upper Ordovician), West Covington, Kentucky.
  4.   Longitudinal section, USNM 167696, ×100, living chamber under protective overgrowth plus a capping diaphragm in a single funnel-cystiphragm stage of development.

Hallopora sp.   Waldron Formation (Middle Silurian), Nashville, Tennessee.
  5.   Tangential section, USNM 167697, ×30, showing mural spines in zooecial walls.
  6*a.*   Longitudinal section, USNM 167698, ×100, showing funnel-cystiphragm and sequence of recurved mural spines. Closely spaced diaphragms to right are in mesopore.
  6*b.*   Longitudinal section of same zoarium, ×100, mural spines are cut transversely showing their alignment parallel to axis of autozooecium.

Leptotrypella furcata (Hall 1877).   Windom Member of the Moscow Shale (Middle Devonian), Menteth Creek, New York.
  7.   Longitudinal section, USNM 133901, ×100, flask-shaped chamber filled with debris and capped at neck by subsequent skeletal growth. Compare with flask-shaped chamber shown in Plate 5, figure 4*d*.

Trachytoechus variacellus (Hall, 1883).   Centerfield Limestone Member of the Ludlowville Formation (Middle Devonian), Cayuga Lake, New York.
  8.   Longitudinal section, USNM 133874, ×100, single flask-shaped chamber filled with debris.

Leptotrypella polita Boardman, 1960.   Kashong Member of the Moscow Shale (Middle Devonian), Kashong Creek, Seneca Lake, New York.
  9*a.*   Longitudinal section of holotype, USNM 133913, ×100, flask-shaped chamber filled with brown deposit. Note mural spines projecting from right side of autozooecial wall.
  9*b.*   Longitudinal section from same zoarium, ×100, flask-shaped chamber at double funnel-cystiphragm stage of development. Mural spines are consistently in this position throughout the zoarium.
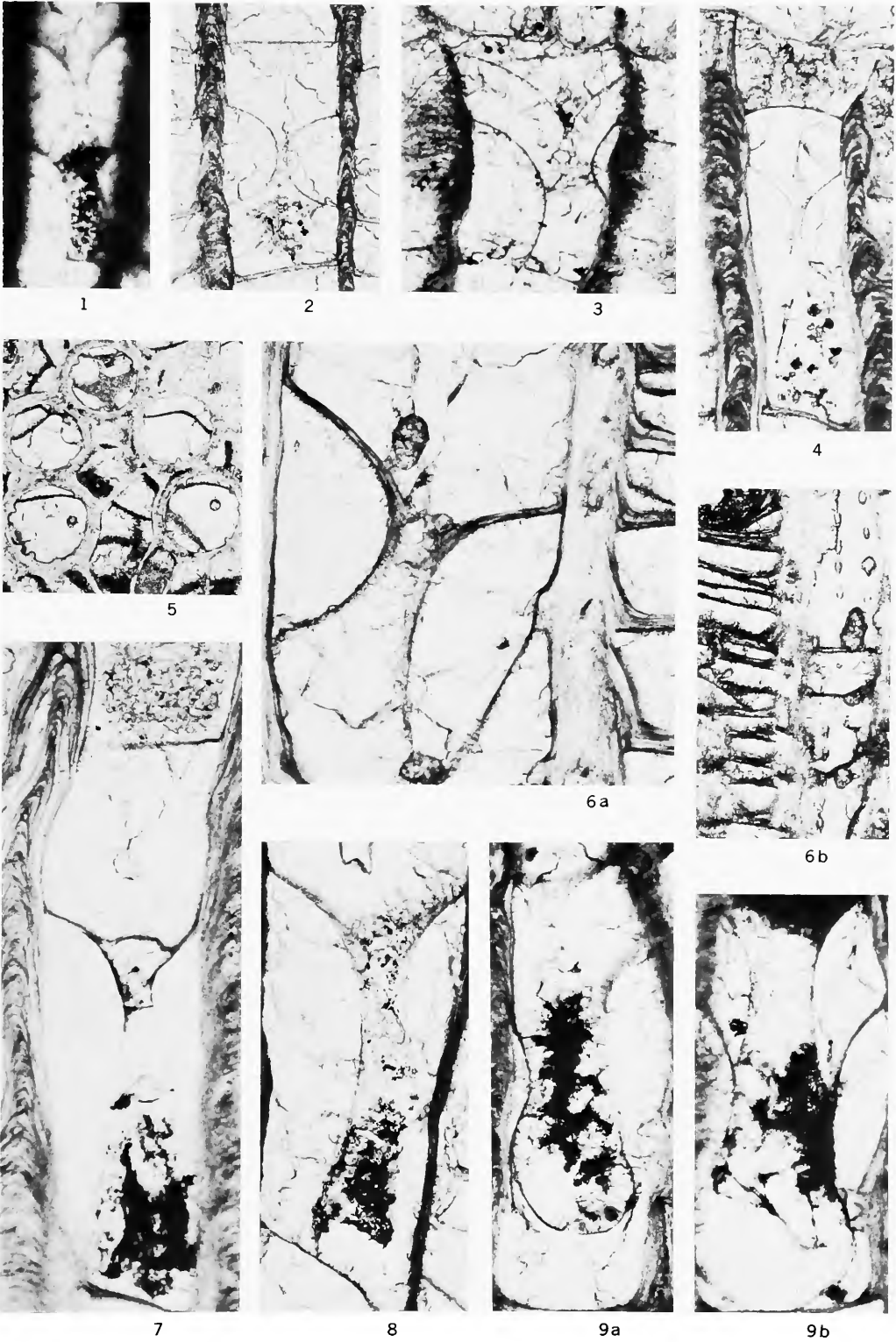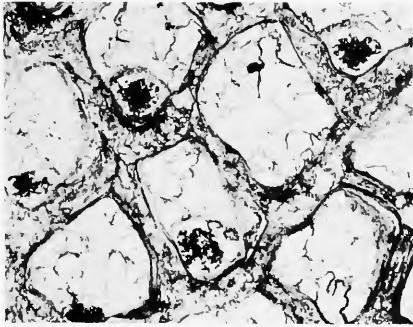
PLATE 8

PLATE 9

UNDESCRIBED FISTULIPORID. Tulip Creek Formation (Middle Ordovician), Arbuckle Mountains, Oklahoma.

  1*a*. Tangential section, USNM 167699, ×50, showing position of inner end of living chamber and inclosed brown deposit relative to lunarial notch on proximal side of autozooecium.

  1*b*. Longitudinal section of same specimen, ×50, showing living chambers defined by cystoidal diaphragms. Brown deposits are concentrated in inner narrow ends of chambers.

  2. Longitudinal section, USNM 167700, ×50, showing extent of entire living chamber under a protecting overgrowth to left.

Amplexopora robusta Ulrich 1883. Bellevue Member of the McMillan Formation (Upper Ordovician), Cincinnati, Ohio.

  3. Transverse section of syntype, USNM 43640, ×100, showing living chambers shaped by extreme thickening of zooecial lining rather than cystiphragms. Note that flask-shaped chamber is sharply defined inwardly only by distribution of brown deposits.

  6*a*. Transverse section of syntype, USNM 167701, ×100, showing four levels of sequential flask-shaped development; the lowest level at bottom of figure is shaped by thickened zooecial lining, the next level by a combination of diaphragm and funnel-cystiphragm growth, the third level by thin and obscure outer ends of a funnel-cystiphragm (arrows), and the last level at the top of figure is indicated by a thickened portion of a funnel-cystiphragm or centrally perforated capping diaphragm.

  6*b*. Transverse section from same zoarium, ×100, showing flask-shaped chamber at bottom and partial funnel-cystiphragm near top that was developed subsequently.

  6*c*. Transverse section, ×100, showing incomplete sequential funnel-cystiphragms and the shape of the flask-shaped chamber indicated by position of brown deposit only.

Leptotrypella polita Boardman, 1960. Kashong Member of the Moscow Shale (Middle Devonian), Kashong Creek, Seneca Lake, New York.

  4*a*. Longitudinal section of holotype, USNM 133913, ×100, showing sequential shifting of floor of flask-shaped chambers.

  4*b*. Longitudinal section, ×100, from same zoarium showing double funnel-cystiphragm stage and mural cyst, abnormally thickened and filled with brown deposit, in position normally occupied by spine.
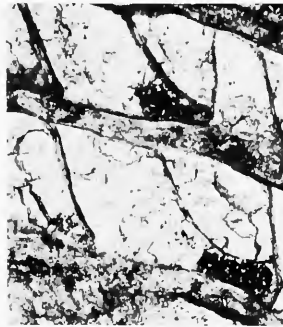
Heterotrypa sp. Economy Member of the Eden Group (Upper Ordovician), West Covington, Kentucky.

  5. Longitudinal section, USNM 167696, ×100, two successive flask-shaped chambers, outer of which shows extension of thin calcified chamber lining (arrow) beyond the normal autozooecial wall under a protective overgrowth.
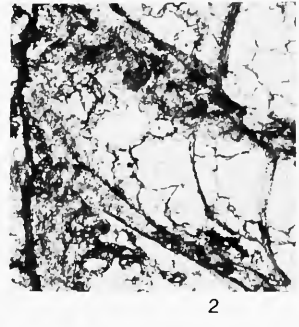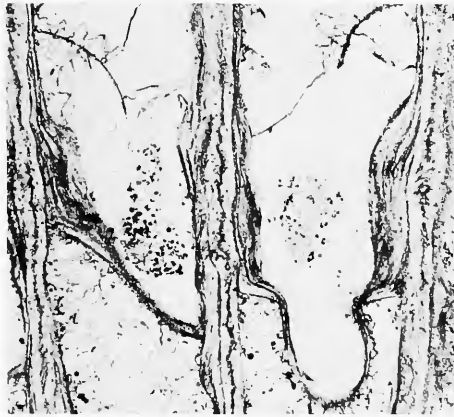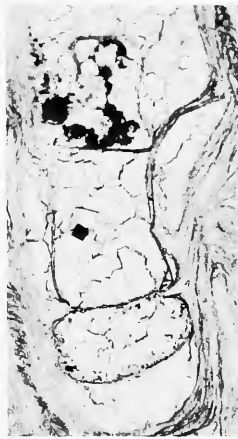
PLATE 9

1a

1b

2

3

4a

4b

5

6a

6b

6c

PLATE 10

Hemiphragma sp. Fernvale Formation (Upper Ordovician), Pulaski, Tennessee.
1. Longitudinal section, USNM 167702, ×100, flask-shaped concentration of brown deposit bending around shelf-like hemiphragms. Note skeletal diaphragm linking lowest hemiphragm to autozooecial wall, and the doubled microstructure of the hemiphragms indicating calcification from both outer and inner sides.

Arnheim Shale (Upper Ordovician), Clifton, Tennessee.
2a. Longitudinal section, USNM 167703, ×100, flask-shaped concentration of brown deposit resting on hemiphragm at inner end and extended outward by curved skeletal partition at outer end.
2b. Longitudinal section, ×100, showing a funnel-shaped skeletal structure attached to outer end of brown deposit.

Maquoketa Shale Group (Upper Ordovician), Wilmington, Illinois.
3. Longitudinal section, USNM 167704, ×100, showing concentration of brown deposit maintaining nearly perfect flask shape even though indented by two hemiphragms.

Tabulipora ramosa (Ulrich, 1890).
Glen Dean Limestone (Upper Mississippian), Glen Dean, Kentucky.
4. Longitudinal section, USNM 167705, ×100, reddish-brown membranous tube in cross section passing through foramen of ring septum.

Glen Dean Limestone (Upper Mississippian), Falls of the Rough, Grayson County, Kentucky.
5a. Longitudinal section, USNM 167706, ×100, membranous tube passing through foramina of ring septa.
5b. Longitudinal section, ×100, showing membranous material crossing through zooecial walls of three adjacent autozooecia.
5c. Longitudinal section, ×100, long segment of membrane passing outward from endozone into exozone of a single autozooecium.

*Stenodiscus* sp. Pennsylvanian?, Santa Fe, New Mexico.
6. Longitudinal section, USNM 167707, ×100, showing membranous tube in specimen lacking ring septa. Laminated oval masses of zooecial wall are monilae.

Tabulipora sp. Lower Carboniferous, River Indigo, Timan, Arkhangelsk, U.S.S.R.
7. Longitudinal section, USNM 167708, ×30, showing funnel-shaped structure in upper right of figure that appears to be part of a continuous skeletal layer (arrows) draped across adjacent autozooecia at that level in the exozone and not comparable with a funnel-cystiphragm. Note monilae show correlation in spacing even with interruption in growth suggested by interzooecial skeletal layer.
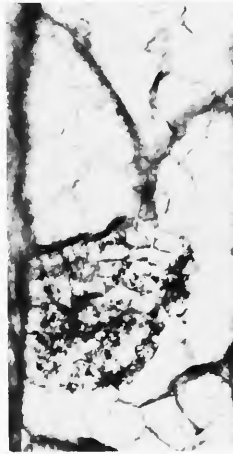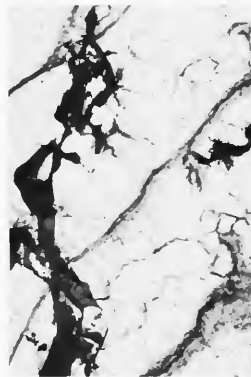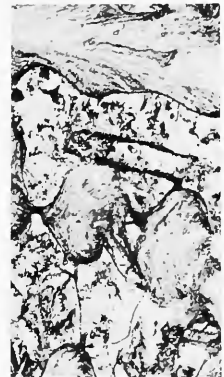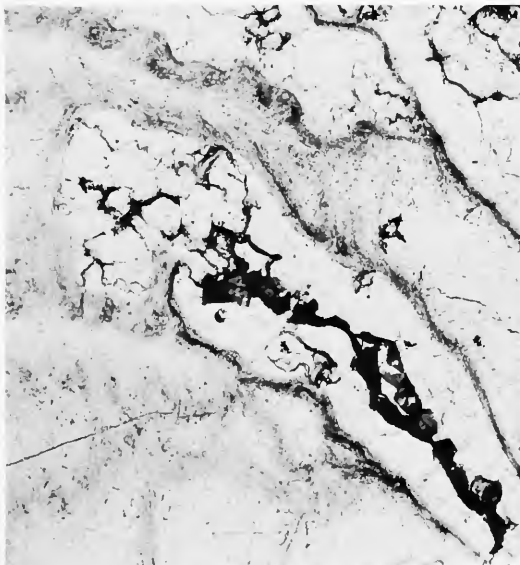
PLATE 10
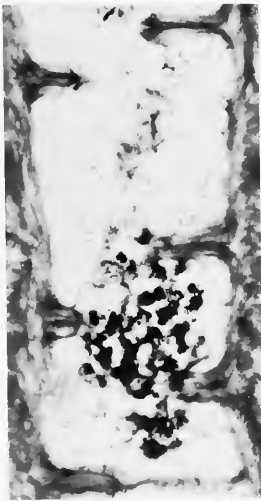
1

2 a

2 b

3

4

5 a

5 b

6

5 c

7

PLATE 11

Hemiphragma sp. Bromide Formation (Middle Ordovician), Spring Creek, Arbuckle Mountains, Oklahoma.

1. Longitudinal section, USNM 167709, ×100. show'ng laminae of tabular hemiphragms in autozooecia extending along zooecial wall for interval of two to three diaphragms in adjacent closely tabulated mesopore below. Note that all mesopore diaphragms with laminae abutting at zooecial-mesopore boundary with those from a hemiphragm-wall unit are outward in position (to right) from that hemiphragm.

2. Longitudinal section, USNM 167710, ×50, showing living chamber protected by overgrowth on left. Notice the similar spacing of diaphragms across the several adjacent mesopores on either side of the autozooecium. The long tube or rod-appearing structures deflecting laminae to the left are acanthopores.

Tabulipora sp. Lower Carboniferous, River Indigo, Timan, Arkhangelsk, U.S.S.R.

3. Longitudinal section, USNM 167708, ×30, showing interzooecial spacing correlation of monilae in autozooecial walls. Note different positions of ring septa relative to monilae in adjacent autozooecia.

Tabulipora ramosa (Ulrich, 1890). Glen Dean Limestone (Upper Mississippian), Sloans Valley, Kentucky.

4. Longitudinal section, USNM 167711, ×50, showing outward extent of living chambers containing ring septa under protective overgrowth.

Peronopora sp.

Upper Ordovician, West Covington, Kentucky.

5. Longitudinal section USNM 167712, ×100, showing correlation of spacing of skeletal cystiphragms in autozooecia and diaphragms in intervening mesopore.

Southgate Formation, Eden Group (Upper Ordovician), railroad cut at Bald Knob, Cincinnati, Ohio.

7. Longitudinal section, USNM 167682, ×100, showing microstructural relationships of cystiphragm wall-mesopore diaphragm structural units. The vague inner funnel (arrow) in the living chamber of the autozooid lowest in the figure is similar in shape and size to those in Plate 5, figures 4*a* and 4*b*, but appears completely uncalcified.

Prasoporina selwyni (Nicholson, 1879). Prosser Formation (Middle Ordovician), Escanaba River, Michigan.

6. Longitudinal section, USNM 167713, ×50, showing shelf-like skeletal cystiphragms that produce sinuous living chambers. Closely tabulated, narrow tubes are mesopores. Note brown deposits in flask-shaped chamber in lower right and in sinuous chambers in uppper left.
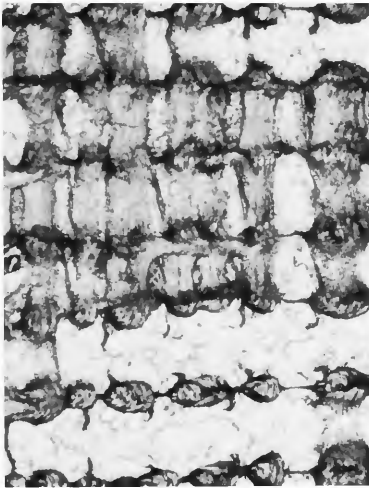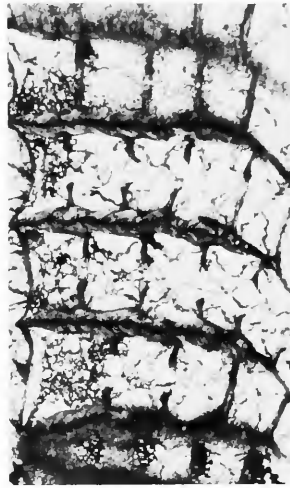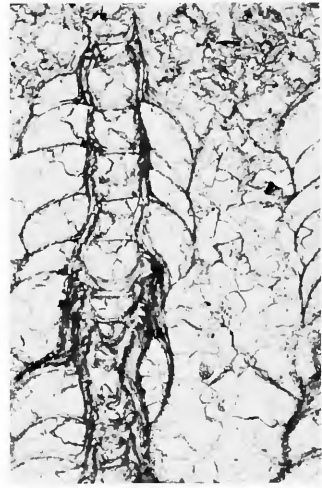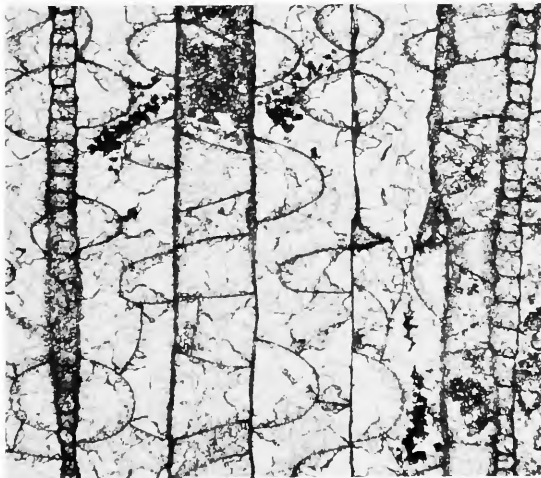
PLATE 11
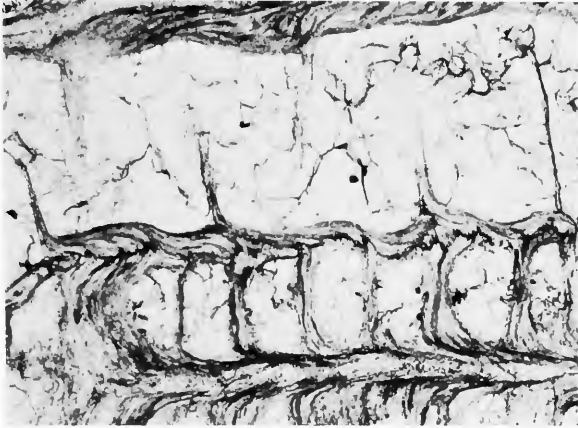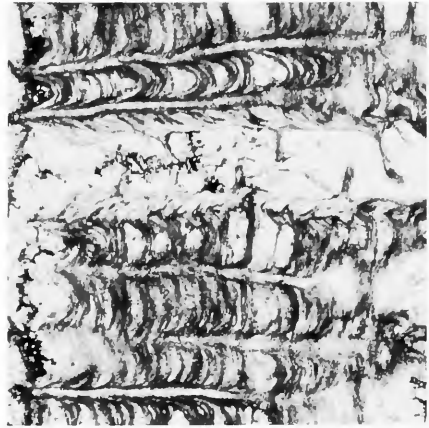
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