



## THE INTERRELATIONSHIP OF EARLY COLONY DEVELOPMENT, MONTICULES, AND BRANCHES IN PALEOZOIC BRYOZOANS

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Mark Edward Podell

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#### ABSTRACT

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### THE INTERRELATIONSHIP OF EARLY COLONY DEVELOPMENT, MONTICULES, AND BRANCHES IN PALEOZOIC BRYOZOANS

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The early colony development of Ordovician trepostome bryozoan initially consists of a triangular stage, the protoecial cone, followed by a reversal of budding direction that produces a circular colony, the ancestrular disk, in which vestiges of the protoecial cone may be observed. Monticules, which are polymorphic clusters regularly positioned over colony surfaces, reproduce the structure of the zone of early development, including a replicate of the ancestrula, the monarchozooid. A second type of ancestrular replicate, the basilozooid, is found within the axial zones (endozones) of colony branches. A damaged colonly, in which several monticules were destroyed by borings, shows disruptions of normal growth patterns in the areas affected. Morphogenetic gradients are developed around both the ancestrula and monticules and within branch axes. The early development of a colony has substantial effects on all later stages of growth. Any regulatory activity carried out by the ancestrula could have been carried out by the ancestrular replicates at multiple locations in all stages of colony growth.

To Amy and my Parents

## ACKNOWLEDGEMENTS

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#### INTRODUCTION

The work of Cumings (1904; 1905; 1912) on early stages of colony growth firmly established the zoological affinities of the major Paleozoic bryozoan groups, many of which had previously been considered corals. This subject received no further attention, except for a brief reference by Borg (1965) in a posthumous publication, until the recent papers by Corneliussen and Perry (1973), Boardman and McKinney (1976), and McKinney (1977; 1978), who placed early colony development clearly within the context of the overall analytical and functional morphology of several genera. In addition, recently renewed interest in the documentation of the evolutionary patterns of paedomorphosis and recapitulation (Gould 1977) makes it necessary that complete development sequences be available for phylogenetic analysis. Furthermore the recognition of morphoregulatory variation in some graptolite lineages (Urbanek 1960; 1973), suggests the possiblity that bryozoans, which have analogous colony development, might display similar phylogenetic patterns. The common implication of all the above is that early colony development must not only be better known, but must be related both to later developmental stages and to phylogeny. This paper seeks to accomplish the first two of these three tasks.

Cuming's earlier papers (1904; 1905) compared the larval development and early astogeny of Recent bryozoans with those of the Paleozoic families Fenestellidae and Palescharidae. In his study of the early development of several genera (1912), he settled the issue of the systematic position of the Trepostomata. Borg (1965) briefly compared the early colony development of the Paleozoic genus Prasopora to that of modern cyclostomes. Corneliussen and Perry (1973) compared the initial region of the Silurian species Hallopora elegantula to that of the Ordovician H. dalei figured by Cumings. Boardman and McKinney (1976) provided a detailed comparison of the of the Paleozoic genus Rhombotrypa with that of Recent lichenoporid cyclostomes described by Harmer (1896) and Borg (1926; 1933). In addition, McKinney (1977a; 1977b; 1978) has incorporated early colony development into his overall studies of the functional morphology of Paleozoic lyre-shaped and paraboloid-based bryozoan colonies. This paper will provide additional details of early colonly development in a variety of Ordovician trepostomes, including scanning electron micrographs of important developmental stages, and will also attempt to show that the early developmental stages, in slightly modified form, are reproduced repeatedly in all later stages of colony growth.

Urbanek's work (1960; 1973; reviewed by Gould 1977), on morphogenetic gradients in graptolite colonies and their phylogentic modifications, provides an intriguing example of how the effects of a growth regulator, analogous to

auxins in plants, can be documented in the fossil record by means of "natural experiments" on damaged and regenerated colonies. This paper will illustrate an analogous situation in a damaged bryozoan colony in which normal growth patterns have been disrupted in the damaged area. In reference to Urbanek's work, however, Boardman and Cheetham (1973) thought it highly unlikely that a morphogenetic substance produced by the primary zooids of a bryozoan colony could be continuously diffused throughout all of colonly growth, primarily because of the limited size and apparently brief duration of a colony's initial region. The present study will illustrate, however, that the colony's founder zooid is regularly reproduced at multiple locations throughout all stages of colony growth, and that any morphogenetic activity carried out by the founder zooid was likewise reproduced by all of these secondary founders, or monarchic zooids.

Morphogenetic gradients in an Ordovician bryozoan colony were mapped by Anstey et al. (1976), who inferred from them the activity of a morphogentic substance analogous to that described by Urbanek. Similarly located physiologic gradients were measured in living cheilostome bryozoans by Bronstein (1939). In addition, Dzik (1975) believed that trends in cheilostome phylogeny reflected the modification of morphoregulatory substances. This study will illustrate the details, using scanning electron

microscopy, of the monarchic zooids found at the origin of morphogenetic gradients in later stages of the same colonies in which early development was also analyzed. Some preliminary details of this work have been presented in abstract and letter form by Anstey and Pachut (1977) and Anstey et al. (1978).

### MATERIALS AND METHODS

This study will emphasize the use of scanning electron microscopy (using an ISI Super III) to illustrate the details of all stages of colony development, based on both external colony surfaces and etched serial polished sections. Scanning electron micrographs provide better resolution of both skeletal wall structure and external morphology, especially of minute colonies, than that possible with light microscopy.

Specimen materials include 120 zoaria or brachiopod shells on which multiple zoaria were encrusted, of Middle and Late Ordovician age from Minnesota and the Ohio Valley respectively. All specimens were ultrasonically cleaned and "sputter" coated with gold prior to microscopy. Polished sections were briefly etched with formic acid (5-10 seconds). All micrographs were prepared at a standard beam orientation of 90 degrees to the microscope stage, thereby eliminating distortion due to foreshorting.

#### EARLY COLONY DEVELOPMENT

The growth of a stenolaemate bryozoan colony begins with the settlement of the founder zooid, the <u>ancestrula</u>. Initially the founder zooid grows parellel to the substrate, forming a tubular chamber constructed of external simple skeleton (Boardman and McKinney 1976) termed the <u>protoecium</u> (the zooid producing the protoecium is termed by Ryland (1970) the <u>proancestrula</u>). The proancestrula initially grows <u>distally</u> (along the substrate), but eventually turns upward (<u>anteriorly</u>) to become the ancestrula proper (orientation terminology from Gautier 1970). The protoecium may be separated from the ancestural by a slight constriction, as in the genus <u>Prasopora</u> (Cumings 1912), or by a diaphragm, as in the genus <u>Rhombotrypa</u> (Boardman and McKinney 1976). In most Ordovician trepostomes there is no demarcation between the two, as in the genus <u>Hallopora</u> (Pl. 1, fig. 4).

The external simple skeleton of the proancestrula appears to differ crystallographically from the skeleton of subsequently formed parts of the colony. In what are most likely trepostome protoecia encrusting on <u>Rafinesqunina</u> valves, the external surface of the skeleton consists of a fanlike cluster of proximally radiating elongate crystal units with sutured margins between crystals (Pl. 1, figs. 1-3; Pl. 2, fig. 1). As seen in etched sections, however (Pl. 1, figs. 4-6), the protoecial wall, although thinner, is constructed of multiple laminations identical to those in the wall of subsequently budded zooids.

#### EXPLANATION OF PLATE 1

- Fig. 1. Trepostome protoecium. Michigan State University, 220314-00024a. Scanning electorn micrograph, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 360.
- Fig. 2. Trepostome protoecium. Michigan State University, 220314-00024a. Enlargment of upper righthand portion of Fig. 1, rotated 90° to the left, illustrating elongate crystal units with sutured margins, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 2400.
- Fig. 3. Trepostome protoecia. Michigan State University, 220314-00024b. Scanning electron micrograph, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 180.
- Fig. 4. <u>Hallopora</u> sp. Michigan State University, 220314-00090. Scanning electron micrograph of a longitudinal section through the protoecium, ancestrula and associated thickened backwall, Madison, Indiana, Dillsboro Formation (Late Ordovician), X 200.
- Fig. 5. <u>Amplexopora</u> ? sp. Michigan State University, 220314-00027a. Scanning electron micrograph of a transverse section through the colony base illustrating the early stages of backbudding and skeletal wall structure, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 60.
- Fig. 6. Trepostome ancestrula. Michigan State University, 220314-00024c. Scanning electron micrograph of an etched and polished section through the protoecium, ancestrula, and primary zooid of the same colony as illustrated in Pl. 2 fig. 6 showing details of wall structure, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 400.

# PLATE 1



The first generation of additional zooids is produced by asexual budding from the distal side of the ancestrula near the substrate (Pl. 1, fig. 4). The <u>primary</u> zooids are those in contact with the distal wall of the ancestrula. <u>Rhombotrypa</u> has four primary zooids (Pl. 2, figs. 3, 5), whereas <u>Hallopora</u> (Pl. 5, fig. 2), <u>Amplexopora</u> ? (Pl. 1, fig. 5; Pl. 3, fig. 2), <u>Homotrypa</u> ? (text-fig. la; Pl. 3, figs. 3, 5), <u>Prasopora</u> (text-fig. 2), and 13 unidentifiable early colonies (Pl. 2, fig. 6; Pl. 3, figs. 1, 4) have three.

The second generation of zooids (secondary) buds distally from the primaries, and the third generation buds likewise from the secondaries, producing an initially triangular colony (Pl. 2, fig. 6) with the protoecium at its apex, termed the protoecial cone by Boardman and McKinney (1976). The shape of the protoecial cone is governed by the number of newly budded zooids produced per generation. Colonies with only a small increase in each generation form long isosceles triangles (Pl. 3, fig. 1), whereas an accelerated budding rate quickly enlarges the distal margin to produce subcircular colonies (Pl. 1, fig. 5). The latter type of development leads to the proximal displacement of the lateral sides of the growing margin, so that after only a few generations, zooids have filled in the region behind the ancestrula and form small circular colonies (Pl. 3, fig. 4). The proximal addition of later generation zooids that fill in the region behind the



TEXT-FIG. 1. Comparison of the ancestrula, monarchozooid, and basilozooid. A, An ancestrular cluster with the region of the protoecial flange (shaded), ancestrula (labeled A), primary zooids (labeled 1-3), secondary zooids (labeled a-d), and backbudded zooids (labeled e and f), enlarged from Pl.3, fig. 3. B, A monticule including the monarchozooid (labeled M), triangular central cluster of mesopores (shaded), and primary, secondary and backbudded zooids (labeled as in A), from Pl. 4, fig. 3. C, A branch axis (from Pl. 4, fig. 1, rotated 180°) including the basilozooid (labeled B) and the ring of zooids (shaded) that originated from it; this basilozooid is histologically continuous with the ancestrula; original primary and secondary zooids labeled as in A and B, all X 18.

ancestrula will be referred to below as <u>backbudding</u>. In the development of the protoecial cone, some taxa produce more buds on one side of the growing margin than the other, producing somewhat spiral protoecial cones that may be described as righthanded (Pl. 2, figs. 3, 4) or lefthanded colonies (Pl. 5, fig. 2).

At some early stage in the development of the protoecial cone, the proximal wall of the ancestrula and its laterally adjacent primary zooids becomes abnormally thickened, forming a V-shaped "flange" around the apex of the triangular colony (Pl. 2, fig. 6), the lateral ends of which extend as processes protruding from the colony margin (Pl. 2, fig. 5). The apical flange does not overlap the protoecuim, which still remains visable at this stage of development, projecting proximally form the center of the flange. After backbudding has filled in the space behind the ancestrula, the flange remains observable as a V-shaped region of thickened wall (text-fig. la; Pl. 3, figs. 3, 4) within the early colony, and its lateral edges may project into some zooecia (Pl. 2, fig. 5). This structure is particularly useful in identifying the ancestrula and the primary zooids in both early and somewhat later stages of colony growth (Pl. 3, figs, 2-5). This thickened wall region was observed in the early development of four trepostome genera by Cumings (1912) and in two additional genera by Boardman and McKinney (1976) and McKinney (1977b). Scanning electron micrographs of this thickened



TEXT-FIG. 2. Dominance effects in the early development of Prasopora conoidea Ulrich. Michigan State University 220323-00001. A, Transverse section cut at the colony base illustrating the radial disposition of cystiphragms and negative morphogenetic gradients centered on the ancestrula (shaded dark grey). Monarchozooids are shaded light grey, and zooids in which the cystiphragms point away from the ancestrula are colored solid black. B, Transverse section approximately 0.5 mm above the colony base showing the increase in the number of cystiphragms that have become reoriented around their respective monticules and the increase in the number of small zooids within the ancestrular and monticular clusters. C. Transverse section approximately 1.0 mm above the substrate showing the continuation of cystiphragm reorientation and the distal spread and enlargment of the clusters of small zooids. all X 18.

region viewed longitudinally (Pl. 2, fig. 2) and transversely (Pl. 2, figs, 4, 5) indicate that the small crystals making up the wall laminae change from a vertical orientation on its distalmargin to horizontal in the center to vertical again on its proximal margin, demonstrating that the wall laminae are folded over in a proximally developed flexure. Boardman and McKinney (1976) attributed an identical development (a double layer of external simple skeleton on the proximal flexure of the ancestrula) in <u>Rhombotrypa</u> to a proximal flexure of the external colony wall down to the substrate. The thickened flange and its lateral projections could have been of functional importance to the early colony, by creating turbulence in its wake and there by improving the filter-feeding ability of the early zooids.

Following the development of the protoecial flange, backbudding is accelerated at the expense of distal budding, so that the colonies become subcircular with the ancestrula centrally located (Pl. 3, figs. 2-5). This stage of development is termed herein the <u>ancestrular disk</u>. The loci and rates of subsequent budding determine the ultimate colony growth habit: peripheral budding produces sheetlike colonies (and variations thereof), whereas distal extension of the internal zooecia and internal budding produces the series mound to hemisphere to pillar to branching colony forms.

The development of morphogenetic gradients within the protoecial cone is variable. In both Rhombotrypa and

# EXPLANATION OF PLATE 2

- Fig. 1. Trepostome protoecium. Michigan State University, 220314-00024b. Enlargement of protoecium on left in Pl. 1, fig. 3, illustrating the radial orientation of crystal units, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 630.
- Fig. 2. <u>Hallopora</u> sp. Michigan State University, 220314-00090. Enlargement of thickened region on the left side of the ancestrula and protoecium of Pl. 1, fig. 4 (reversed image), illustrating wall structure within the protoecial flange, Madison, Indiana, Dillsboro Formation (Late Ordovician), X 1000.
- Figs. 3-5. Rhombotrypa sp. Michigan State University, 220314-00030. Versailles, Indiana, Dillsboro Formation (Late Ordovicain). 3, Scanning electron micrograph of a tangential section through the colony base showing a positive morphogenetic gradient, X 20. 4, Enlargement of initial region of fig. 3 displaying four primary zooids, ancestrula, and thickened wall, X 180. 5, Enlargement of lower right hand corner of fig. 4, illustrating the flange of the thickened wall protruding into the right hand most primary zooid, X 360.
- Fig. 6. Trepostome protoecial cone. Michigan State University, 220314-00024c. Scanning electron micrograph of early astogeny illustrating the external wall of the protoecium, thickened backwall, protruding flange, and primary zooids, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 100.

PLATE 2



Hallopora (Pl. 2, fig. 3; Pl. 5, fig. 2), the ancestrula is the smallest zooid in the early colony, and subsequent generations increase in size away from it, producing a positive morphogenetic gradient. In the earliest stage of Prasopora conoidea (text-fig. 2a), however, the ancestrula is the largest zooid, and subsequent generations decrease in size away from it, producing a negative morphogenetic gradient. Available data indicate, however, that all positive gradients disappear by the stage of the development of the ancestrular disk. All available ancestrular disks display either no obvious gradients (as in Rhombotrpya), or well developed negative gradients leading away from the ancestrula (as in most of the taxa studied). This suggests that some colonies experienced a developmental change from positive allometry in the protoecial cone to negative allometry in the ancestrular disk.

The dominance of the ancestrula within the ancestrular disk is illustrated by the orientation of cystiphragms in monticuliporid genera (Pl. 3, figs. 3, 5; text-fig. 2a). In addition to their radial development of morphogenetic gradients, the cystiphragms in each zooecium are radially aligned on the ancestrula. Identical radial alignment of cystiphragms is developed around the monticules of monticuliporids (Boardman and Utgaard 1966).

Furthermore, the ring of zooids immediately surrounding the ancestrula in many colonies becomes differentiated from the other zooids of the disk to form the first

- Fig. 1. Trepostome protoecial cone. Michigan State University, 220314-00046a. Scanning electron micrograph of a colony with a large number of distal zooids; protoecium is in the upper center of the micrograph, Madison, Indiana, Dillsboro Formation (Late Ordovician), X 75.
- Fig. 2 <u>Amplexopora</u> ? sp. Michigan State University, 220314-00027b. Scanning electron micrograph of the ancestrular disk with its centrally located ancestrula and protoecial flange, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 35.
- Figs 3, 5. Homotrypa sp. Versailles, Indiana, Dillsboro Formation (Late Ordovician). 3, Michigan State University 220314-00028a. Scanning electron micrograph of the ancestrular disk illustrating the ancestrula (distal to thickened wall area) surrounded by cystiphragms oriented towards it, X 35. 5, Michigan State University, 220314-0028b. Scanning electron micrograph of a ancestrular disk illustrating similar features to those in fig. 3, X 35.
- Fig. 4. Ancestrular disk. Michigan State University, 220314-00027c. Scanning electron micrograph illustrating the thickened wall around the ancestrula and negative morphogenetic gradient in peripherally spreading zooids, Versailles, Indiana, Dillsboro Formation (Late Ordovician), X 25.

PLATE 3



<u>monticule</u> (polymorphic cluster) of the early colony (textfig. 2b). Commonly the primary and secondary zooids of the protoecial cone (still observable because of the thickened wall area of the apical flange) become as large as the ancestrula, and many small newly budded zooids produced from the distal side of the ancestrula displace the large zooids away from the ancestrula, so that a ringlike structure is developed (text-fig. 2b, c). Most trepostome monticules include a central cluster of abnormally small zooids (Pl. 4, fig. 3, 4). With the appearance of the first monticule, early colony development is complete.

#### DEVELOPMENT OF MONTICULES

The second stage of colony development involves the differentiation of additional monticules as the colony grows peripherally. New monticules appear at regular distances from the ancestrular cluster (the original monticule) and from each other. In <u>Prasopora conoidea</u> (text-fig. 2a) new monticules arise at regular intervals of approximately one cm. The key developmental aspect of monticules is their nearly exact duplication of the ancestrular cluster, complete with a replicated ancestrula, primary and secondary zooids, and vestiges of the protoecial cone. In addition they display dominance effects over their region of the colony (which incorporates about 200 or so extramonticular autozooids) identical to the dominance of the ancestrula over the ancestrular disk. Large sheetlike

colonies (or the exozonal surfaces of monticulated colonies having other growth forms) are in fact simple aggregates of hexagonally arranged monticular subcolonies that each replicate the ancestrular disk. Because each subcolony is developed within the spatial constraints imposed by neighboring subcolonies, their boundaries cannot be circular like that of the ancestrular disk, but become nearly hexagonal (Anstey et al. 1976). The dominance effects displayed by monticules are shown by their location at the center of radially developed morphogenetic gradients within subcolonies and in certain taxa, radial alignment of cystiphragms or lunaria.

In the ancestrular cluster the backbudded zooids (e and f in text-fig. la) are separated from the ancestrula and the primary zooids (A, and l, 2 and 3) by the thickened wall region that remains from the apical flange of the protoecial cone, thus preserving the triangular structure of an earlier stage of development. In monticules the ancestrular replicate, the <u>monarchozooid</u> (Anstey and Pachut 1977; Anstey et al. 1978), is likewise at the apex of a triangular structure formed by the secondary zooids and central cluster of small zooids (textfig. lb; text-fig. 3; Pl. 4, figs. 3, 4), although in monticules there is no V-shaped region of thickened wall. In monticules, very small zooids (probably polymorphic) are budded from the distal side of the monarchozooid, and form a central cluster that is generally triangular

- Fig. 1. <u>Hallopora</u> sp. Michigan State University, 220314-00052. Scanning electron micrograph of a transverse section through a pillar shaped colony displaying an enlarged, centrally located basilozooid surrounded by several new zooids (rotated 180° from text-fig. lc), Madison, Indiana, Dillsboro Formation (Late Ordovician), X 40.
- Fig. 2. <u>Homotrypella hospitalis</u> (Nicholson). Michigan State University, 220314-00055. Scanning electron micrograph of a transverse section through a branch illustrating the centrally located enlarged basilozooid encircled by newly budded zooids, Madison Indiana, Dillsboro Formation (Late Ordovician), X 30.
- Fig. 3. <u>Hallopora</u> sp. Michigan State University, 220314-00019. Scanning electron micrograph of a monticular polymorphic cluster illustrating the monarchozooid (below central cluster of mesopores) and median primary zooid (above central cluster of mesopores), West Harrison, Indiana, Eden Shale (Late Ordovician), X 35.
- Fig. 4. <u>Peronopora</u> sp. Michigan State University, 220314-00017. Scanning electron micrograph of a monticule showing the monarchozooid (very bottom of micrograph) and the median primary zooid (center of micrograph at upper end of central cluster of mesopores), West Harrison, Indiana, Eden Shale (Late Ordovician), X 35.

## PLATE 4



in shape (shaded region in text-fig. 3). In the ancestrular cluster, the small zooids displace the primary zooids distally, as Cumings (1912) illustrated in Prasopora conoidea. In colonies with three primary zooids, the large zooid opposite the monarchozooid and separated from it by the small zooids in a monticule is a replicate of the median primary zooid of the early colony. The central cluster of small zooids commonly bifurcates around the median primary, thus forming a U-shaped structure on the distal side of the monticule and imparting to the monticule and additional element of bilateral symmetry. In many monticules the small central zooids increase in size from the monarchozooid to the median primary zooid (P1.5, figs. 1, 3) suggesting that continued budding within the monticule leads to the formation of a succession of median primaries, with the older ones displaced into the monticular border. This size gradient within the monticule itself duplicated the positive morphogenetic gradient observed in the protoecial cones of Hallopora and Rhombotrypa (Pl. 5, fig. 2; Pl. 2, fig. 3). In the genus Hallopora the median primary zooid of monticules is particularly distinctive because it is floored by a very shallow diaphragm (Pl. 4, fig. 3). In most taxa the large monticular polymorphic zooids form a complete ring around the central cluster of small zooids. The monarchozooid is usually located inside the outer ring of large polymorphs slightly into the small cluster of small zooids (text-fig. 1b),



TEXT-FIG. 3. Development of monticules in the early astogeny of <u>Prasopora concidea</u> Ulrich. Michigan State University, 22323-00001. A three dimensional reconstruction of the central portion of the colony base (approximately 1.5 mm high) form serial acetate peels illustrating the budding of small zooids (shaded light grey) from the ancestrula (shaded dark grey) and from two monarchozooids (shaded medium grey), Cannon Falls, <u>Minnesoa</u>, Decorah Shale (Middle Ordovician), X 18.

whereas the median primary zooid is usually well within the central cluster, and may be completely surrounded by small zooids. Outside the monticule the nonpolymorphic autozooids gradually decrease in size in a negative gradient extending from the monticular border to the subcolony boundary.

In the family Monticuliporidae cystiphragms are generally radially arranged around the monticules (Boardman and Utgaard 1966). In some genera the cystiphragms point towards the monticule, as in Prasopora, but in others away from it, as in Monticulipora. These arrangements suggest the developmental dominance of the monarchozooid over its own subcolony. Subcolony maps can be prepared by drawing their boundaries at the places where cystiphragms reverse their orientation. The dominance of the monarchozooid over these patterns is confirmed by observations of areas damaged by boring organisms in Prasopora simulatrix (textfig. 4). In undamaged subcolonies the radial alignment of the cystiphragms is well developed, but in the adjacent regions affected by the borings, no monticules are observable and the cystiphragms are randomly oriented. Presumably the loss of the monarchozooids to the borers resulted in a local absence of developmental regulation. This example provides additional confirmation of the hypothesis advanced elsewhere (Anstey et al. 1976, 1978; Pachut 1977) that bryozoan subcolonies were regulated by the diffusion of a morphogenetic substance released from the monarchozooid.



TEXT-FIG. 4. Subcolony development in <u>Prasopora simulatrix</u> Ulrich. Michigan State University, 220317-00009. Subcolony boundaries (solid white lines) based on the orientation of cystiphragms around individual monticular (black dots). The apparently irregular nature of the subcolony boundaries is an artifact caused by locally random orientation of cystiphragms within the boundary region. Where monarchozooids have been removed by borers (areas labedled B), cystiphragms are randomly oriented, Frankfort, Kentucky, "Trenton" Formation (Middle Ordovician), X 18.

The post-ancestrular disk development of Prasopora conoidea documents the transfer of local dominance from the ancestrula to the newly differentiated monarchozooids in the peripheral regions of the colony. Serial sections taken from the lowest level within the colony show that the cystiphragms are not initally radially aligned on their local monticules, but are all pointing towards the ancestrula. Higher sections show that the zooids nearest each monticule are the first to turn away from the ancestrula and towards the local monarchozooid, and that the realignment progresses as "waves" that spread radially from the monticular centers. At the height of 1mm above the substrate, all of the zooids have become incorporated into local subcolonies, each dominated by a monarchozooid and the only zooids still aligned with the ancestrula are those in its local subcolony (text-fig. 2c). This evidence strongly suggests that zooid alignment is regulated by a morphogenetic substance produced initially by the ancestrula and diffused outward into the colony. Subsequently newly differentiated monarchozooids begin to produce the same substance which gradually increases in concentration radially away from each, thereby spreading the zones of local dominance until the early colony is completely subdivided into such zones.

#### DEVELOPMENT OF BRANCHES

Cumings (1912) suggested that the development of colony branches could be related to that of monticules,

- Fig. 1. <u>Amplexopora</u> <u>septosa</u> (Ulrich). Indiana University, 8979-17005. Light micrograph of a tangential section through a monticule showing the monarchozooid (centrally located in lower half of micrograph) and enlargement in new zooids as they are displaced distally away from it, Miamitown, Ohio, Eden Shale (Late Ordovician), X 40.
- Fig. 2. <u>Hallopora</u> <u>dalei</u> (Milne-Edwards & Haime). Indiana University, 9106-23. Light micrograph of a transverse section through the colony base illustrating the positive morphogentic gradient radiating away from the centrally located ancestrula, near Guilford, Indiana, Dillsboro Formation (Late Ordovician), X 35.
- Fig. 3. <u>Heterotrypa ulrichi</u> (Nicholson). Indiana University, 8976-25007. Light micrograph of a tangential section through a monticule illustrating the distal spread and enlargement of new zooids from the monarchozooid, Miamitown, Ohio, Eden Shale (Late Ordovician), X 40.
- Fig. 4. <u>Hallopora nodulosa</u> (Nicholson). Indiana University, 8974-15005. Light micrograph of a transverse section through a branch showing the enlarged, centrally located basilozooid and negative morphogenetic gradient radiating away from it, Gallatin County, Kentucky, Eden Shale (Late Ordovician), X 35.
- Fig. 5. <u>Hallopora ramosa</u> (D'Orbigny). Indiana University, 9004-13. Light micrograph of a transverse section taken through a branch displaying the centrally located basilozooid and negative morphogenetic gradient radiating away from it, near Guilford, Indiana, Dillsboro Formation (Late Ordovician), X 35.
- Fig. 6 Eridotrypa simulatrix (Ulrich). Indiana University, 9135-14. Light micrograph of a transverse section cut through a branch illustrating centrally located, enlarged basilozooid, near Guilford, Indiana, Dillsboro Formation (Late Ordovician), X 35.

# PLATE 5



and Blake (1976) effectively illustrated the developmental interrelationship of branches and monticules in the genus Rhabdomeson. Branching colonies, however, commonly have two developmental zones: an inner (axial) zone of long, vertically oriented thin-walled undifferentiated zooecia, termed the endozone, and an outer (cortical) zone of short, thick-walled zooecia with a variety of intrazooecial and extrazooecial structures, the exozone. Even massive and hemispherical colonies may have cyclic repetitions of laminar growth zones that vary from endozonal to exozonal characteristics. Monticules are developed only within the exozone, and the regulation of exozonal characteristics is related to the morphogenetic gradients associated with monarchozooids. This study seeks to demonstrate that a second type of ancestrular replicate, the basilozooid (Anstey and Pachut 1977; Anstey et al. 1978) is found with in the axial zones of colony branches, and may be involved in the regulation of endozonal development.

After the stage of the ancestrular disk, some colonies grow upward from the substrate by vertical extension of the zooecial tubes instead of lateral extension of the colony by marginal budding. Such colonies initially become a hemispherical mound two or three mm high, which subsequently becomes attenuated into a pillar. The region of upward growth is centered on the ancestrula, which continues up the branch axis as a centrally located zooid (text-fig. 5). This zooid, the basilozooid, is histologically continuous with the ancestrula, is centered within the endozone, and exozonal differentiation occurs at uniform distances from it. In the genus <u>Hallopora</u> (text-fig. 5), new buds develop on all sides of the basilozooid, and gradually displace the original primary and secondary zooids outwards by newer buds so that the new buds collectively form an inverted axial cone centered on the basilozooid that expands in diameter up the branch (text-fig. lc, 5a).

A hemispherical colony of <u>Homotrypella hospitalis</u> (Pl. 4, fig. 2) produced a small pillarlike protuberance on the margin of the colony. Within this structure, which resembles an early stage in branch development, a large axial zooid is not only centrally located, but the cystiphragms of all the surrounding zooids are radially aligned with it.

Large axial zooids are present in the endozones of many Paleozoic branching colonies (Pl. 4, figs. 1, 2; Pl. 5, figs, 3-5), which are probably basilozooids. Unusually large axial zooids are also present in a number of post-Paleozoic cyclostomes (Nye 1976). In addition to large size, central or near central location, vertical continuity within the branch axis, and location at the origin of morphogenetic gradients in size, shape, zooecial structure, and budding, are general characteristics of basilozooids.

The processes leading to branch bifurcation are incompletely known, but new branches may arise from an expansion of the axial endozone and the differentiation of a second

TEXT-FIG. 5. Development of colony branches in the astogeny of Hallopora spp. longitudinal section reconstructed from serial acetate peels. A, Michigan State University 220314-00089. A colony branch illustrating the centrally located basilozooid (shaded dark grey), zooids originating directly from it (shaded light grey), and zooids originating from other parts of the endozone (shaded medium grey), West Harrison, Indiana, Eden Shale (Late Ordovician). B, Michigan State University, 220314-00052. Pillarlike colony illustrating the continuation of the ancestrula as a basilozooid (shaded dark grey), and budding of new zooids (shaded light grey) from the basilozooid. Transverse, sections B] and B\_ illustrate the basilozooid (dark grey) and buds originating from it (light grey) at two levels within the colony, Madison, Indiana, Dillsboro Formation, (Late Ordovician). C, Michigan State University, 220314-Longitudinal view of pillarlike colony with 00067. similar additions of new zooids to that of A and B. Transverse section  $C_1$  illustrates a very early stage in the budding of new zooids from the basilozooid, Miamitown, Ohio, Eden Shale, (Late Ordovician), all X 17.

TEXT-FIGURE 5



basilozooid, just as new monticules develop as a distance effect with respect to previous ones. A transverse section of <u>Leptotrypella pellucida</u> (not illustrated) has two separate basilozooids in an expanded endozone, suggesting that branch bifurcation is a result of the duplication of the axial monarch. Some branching and frondescent colonies have small warty protuberances capped by a monticule, suggesting that some branches may have developed directly from a monticule. Whether or not the development of a branch can cause absorption of previously exisiting exozonal skeleton is presently unkown. More complex developmental processes than those described above must have been involved in the growth of frondescent and anastomosing colonies.

#### CONCLUSIONS

Early colony development, as observed in Ordovician trepostome bryozoans, consists initially of distal budding from the ancestrula along the substrate, forming a flat triangular colony in which a positive morphogenetic gradient may be present. The completion of backbudding forms a circular colony, the ancestrular disk, characterized by negative morphogenetic gradients leading away from the ancestrula. Subsequent growth may be marginal, by means of budding along the substrate, and/or upward, by vertical extension of the colony center. Colony surfaces develop regularly positioned polymorphic clusters, or monticules, in which the monarchozooid replicates the ancestrula and maintains negative morphogenetic gradients to the margin of the monticular subcolony. Branch axes also contain an ancestrular replicate, the basilozooid, which may maintain morphogenetic gradients within the axial endozone. From these observations it may be concluded that the early development of a colony has a substantial effect on all later stages of colony growth. The common development of morphogenetic gradients originating from ancestrular replicates indicates that this phylum might well be a good one in which to investigate heterochronous patterns of evolution caused by variation in morphoregulatory factors.

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