# Morphology, Anatomy, and Systematics of the Cinctiporidae, New Family (Bryozoa: Stenolaemata)

RICHARD S. BOARDMAN
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and
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SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 70

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## ABSTRACT

Boardman, Richard S., Frank K. McKinney, and Paul D. Taylor. Morphology, Anatomy, and Systematics of the Cinctiporidae, New Family (Bryozoa: Stenolaemata). *Smithsonian Contributions to Paleobiology*, number 70, 81 pages, 137 figures, 1992.—The study of thin sections, peels, and SEM micrographs of skeletons, and sections of skeletons and soft parts together, has revealed new morphology and anatomy resulting in new growth and functional interpretations in a new stenolaemate family, the Cinctiporidae. Cinctiporids are found primarily in the New Zealand region and range from upper Cretaceous to Recent. In contrast to the present classification of stenolaemates, the family includes eight species grouped into two free-walled genera, one fixed-walled genus, and one mixed free-/fixed-walled genus. This unconventional family is inferred to be monophyletic based upon a number of shared character states, zones of astogenetic change with fixed, free, and fixed/free apertures, and zones of repetition with both fixed- and free-walled zooids. These taxa are described using both external and internal skeletal morphology and soft part anatomy. Zooids of cinctiporids are typically several times larger than those of other stenolaemates, facilitating detailed observations.

In dendroid growth habits, growth rates of zooids are greatest in endozones at growing tips of branches, and in cinctiporids skeletal and fully regenerated polypide sizes are roughly proportional. Growth rates decrease greatly as young zooids reach exozones by saltation in a series of polypide cycles. In exozones, attachment organs become fixed in position, some in attachment scars in skeletal linings, resulting in regenerated polypides being fixed in position in subsequent cycles. During regenerating phases of any single cycle, polypides grow inward from attachment organs, ingesting and eliminating as they grow. Retractor muscles must function, therefore, and must slide their skeletal connections inward also as polypides increase in length. In early phases of a regeneration the developing polypides ingest and eliminate from within their living chambers. Elimination within living chambers is apparently facilited by faecal pellets passing out through the atrium and vestibule. The funiculus of stenolaemates generally ends blindly against skeletal walls preventing connection to neighboring zooids by that means as in gymnolaemates. A large funicular muscle or muscles aids in retracting polypides of the cinctiporids.

Skeletal walls calcified from one side necessarily form against pre-existing membranes. Exterior skeletal walls in stenolaemates calcify against outer cuticles, preserving the shapes of the cuticles as they are calcified, explaining growth undulations on frontal walls and intimate contacts that basal colony walls make with substrates.



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# Morphology, Anatomy, and Systematics of the Cinctiporidae, New Family (Bryozoa: Stenolaemata)

*Richard S. Boardman*
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*and*
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## Introduction

The new family Cinctiporidae belongs to the class Stenolaemata, one of the three classes of Bryozoa and the only class that is entirely marine. The oldest known member of the family is a species from the Maastrichtian of South Africa. The remainder of the family occurs in the Oligocene to Pleistocene of New Zealand and today two species grow profusely on adjacent continental shelves of New Zealand. The type genus of the Cinctiporidae is *Cinctipora* Hutton, 1873. The type species of *Cinctipora* is *C. elegans* Hutton, 1873, primarily a free-walled species that first appears in the Pliocene and today lives at depths of 12 to possibly 192 meters surrounding the South Island of New Zealand (Figure 1). In all, the family includes four genera and eight species. Two of the genera are free-walled, one genus is fixed-walled, and one is a free-/fixed-walled combination.

A coordinated study of both skeleton and organs of the family Cinctiporidae demonstrates what can be learned of the biology of stenolaemates and how this information can be applied to the systematics of stenolaemates. The family is ideal because it is relatively available and its zooids are unusually large, in fact gigantic, in comparison with other stenolaemates so that its parts are readily observed. Both free- and fixed-walled species are included in the family because of a number of similarities in skeleton and organs, and because of a mixture of free- and fixed-walled zooids in some colonies.

Stenolaemates (and all other Bryozoa) are triploblastic coelomates with an histologically complex set of internal organs and a wide diversity of anatomies (see Borg, 1926; Nielsen, 1970; Nielsen and Pedersen, 1979; Boardman, 1983:88–93; Boardman and McKinney, 1985; McKinney and Boardman, 1985; Schäfer, 1985). Consistent with soft part complexity, the internal morphology and microstructure of stenolaemate skeletons of all ages have long been known to be widely variable among taxa (for some post-Paleozoic examples see Brood, 1972; Nye, 1976; Harmelin, 1976; McKinney, 1977).

Nevertheless, relatively little is known about either the organs of living stenolaemates or the skeletal interiors of post-Triassic taxa, and most of these species continue to be described and classified using only the relatively few characters evident on colony exteriors. Taxonomists classifying other animals of comparable complexity and employing modern taxonomic procedures generally apply many more than the few readily available characters that have been used for stenolaemates. Current taxonomic procedures (for bryozoans, Blake and Snyder, 1987; Cheetham and Hayek, 1988) all begin with observations of many characters in order to identify those that vary enough to suggest different taxa. The more characters and character states considered and the larger the number of faunas and potential taxa studied, the more adequate the data for phylogenetic classification.

Observations of living colonies of *C. elegans* (P.D.T.) and other species (F.K.M. and Marjorie J. McKinney) were carried

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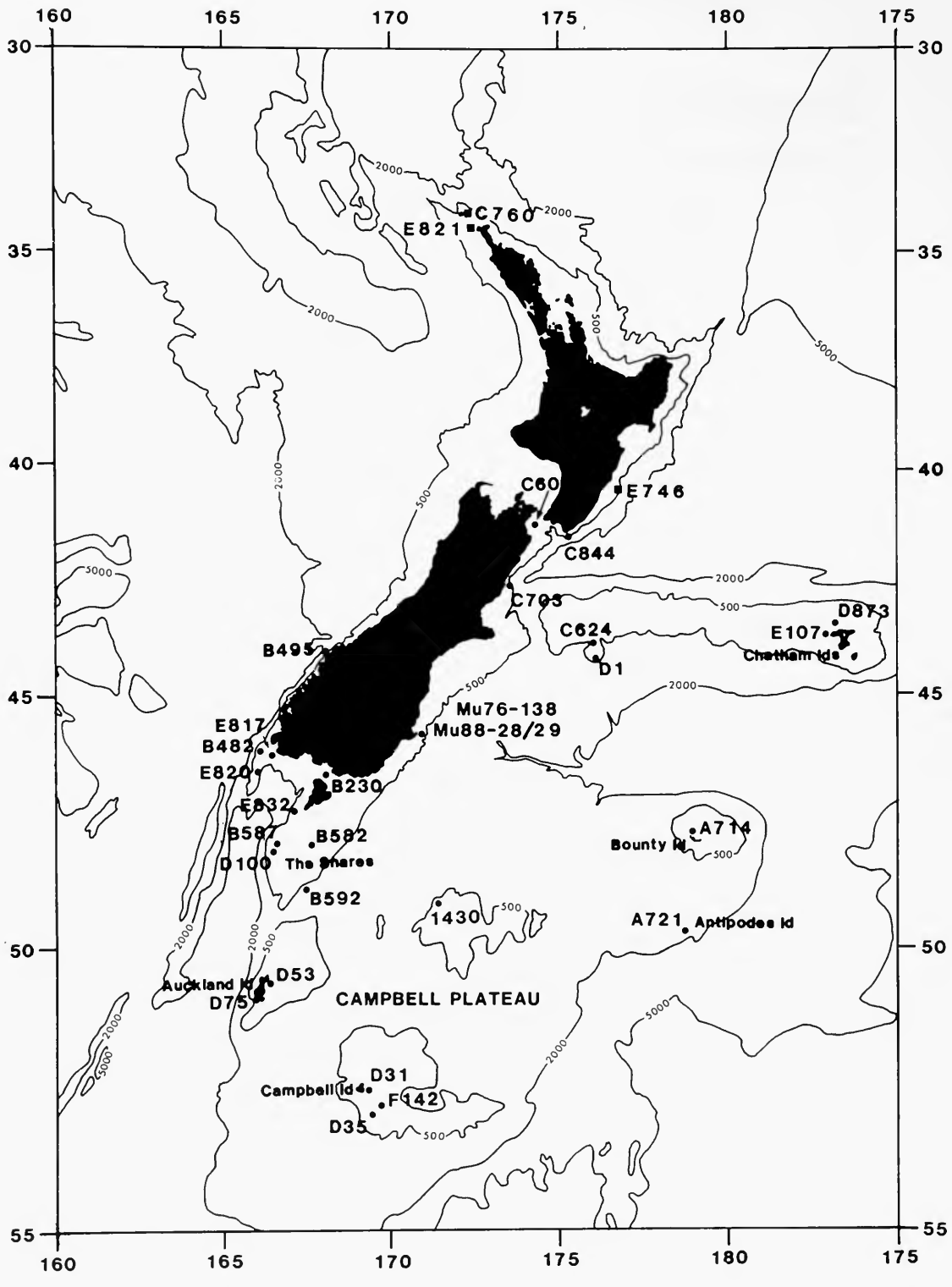


FIGURE 1.—Collecting stations for living cinctiporids. All are New Zealand Oceanographic Institute (NZOI) stations except for Mu76-138 and Mu88-28/29 of the Portobello Marine Laboratory, University of Otago, and 1430 of USARP, the University of Southern California Eltanin Program. Localities for *Cinctipora elegans* are circular dots, those for *Attinopora zealandica* are squares.

out to check interpretations (R.S.B.) and the significance of measurements made from Recent and fossil colonies (F.K.M.). This paper utilizes peels, thin sections and scanning electron microscopy of skeletons, including uncoated specimens (Taylor, 1986), and sections of both skeletons and soft parts together (Nye et al., 1972). The colony growth habit, external and internal skeletal morphology and microstructure, and some of the organ anatomy of the zooids are included in the taxonomic descriptions. Some of the observed and interpreted functions presented here may be helpful in future work on phylogenies and classification.

The inclusion in this study of fossil species, also from New Zealand (mainly collected by P.D.T.), demonstrates the application of detailed information from living species to the biologic understanding and taxonomic description of related fossils.

For the convenience of readers an appendix is added that is a literature review of the soft parts of stenolaemates. The general terminology and concepts of stenolaemates used here are found in the revised edition of Volume G of the Treatise on Invertebrate Paleontology (Boardman, 1983:49–137).

This empirical approach to modes of growth and functions through the study of a single family, even though supplemented by observations of living species of other families, can only suggest answers to some of the many questions concerning stenolaemates. The morphology and anatomy of other taxa vary widely, promising differing modes of growth and other functions. In-depth observations of living colonies of many taxa and studies of their histology, ultrastructure, and physiology are necessary to obtain a working understanding of the life processes and classification of the Stenolaemata.

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We are indebted to Marjorie J. McKinney for long hours observing living colonies and the preparation of thin sections and peels for the taxonomic section of the paper. Richard N. Abbot (Appalachian State University) advised us on crystallographic axis orientation. The opportunity for the McKinneys to observe living cyclostomes during a Yugoslav Council of Academies exchange program was made possible by a combination of grants from the National Geographic Society and the U.S. National Academy of Sciences.

Susan Barnes and Chris Jones (Department of Mineralogy, The Natural History Museum, London) assisted with SEM, and Gordon Cressey of the same department determined crystallographic axes of calcite crystallites in the walls of *C. elegans*. Several scientists gave generously of their time and expertise during the tenure of a University of Otago William Evans Visiting Fellowship awarded to P.D.T. that is gratefully acknowledged. They include Daphne Lee and Doug Campbell (Department of Geology, University of Otago), Dave McKinnon (Department of Geology, University of Canterbury), and Dennis Gordon (New Zealand Oceanographic Institute, Wellington (NZOI)) who provided guidance and help during geological fieldwork; and John Jillett, Keith Probert, Chris Spiers, and Clive Heseltine (Portobello Marine Laboratory, University of Otago) for arranging trawls on the Otago Shelf and for providing laboratory facilities. Loans of specimens from New Zealand were made possible through the kindness of Dennis Gordon (NZOI), Alan Beu and Ian Keyes (New Zealand Geological Survey, Lower Hutt (NZGS)), Daphne Lee (University of Otago), and Phil Powell (Oxford University Museum).

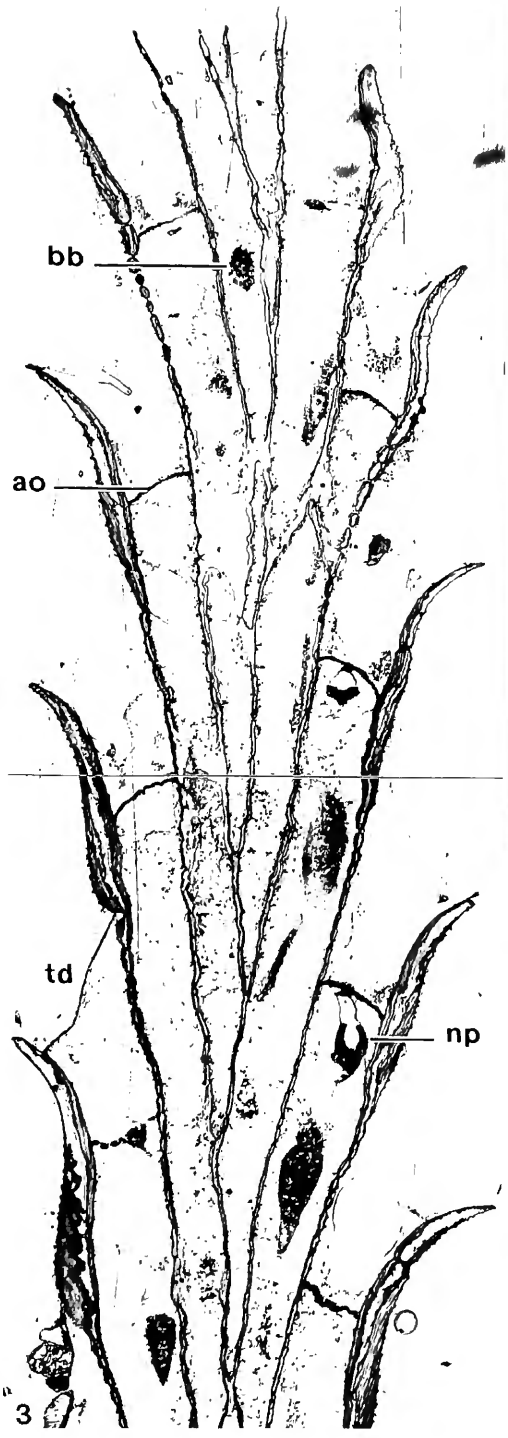
## Morphology and Anatomy of *Cinctipora elegans*

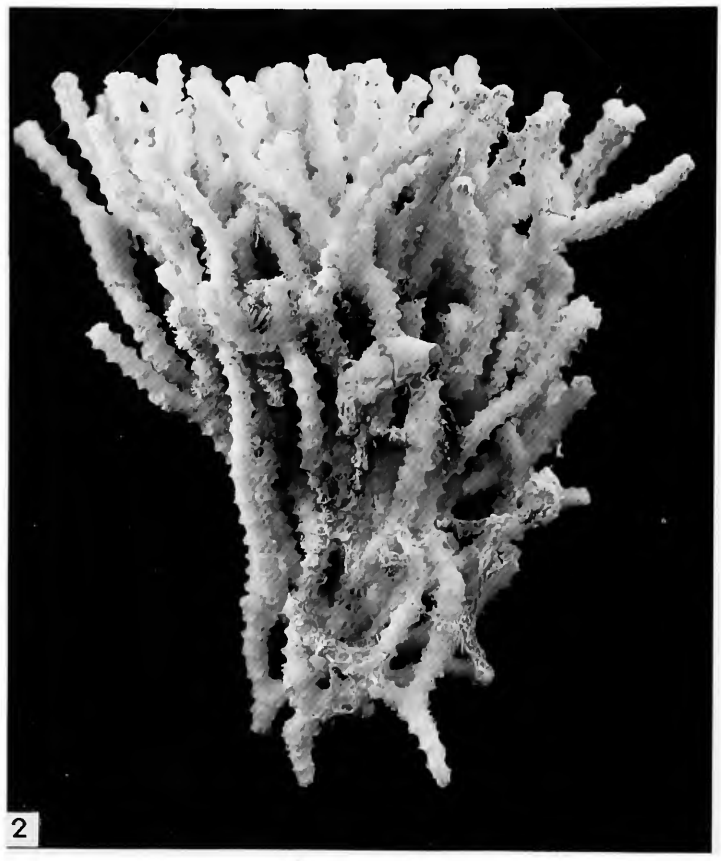
### Zone of Astogenetic Repetition

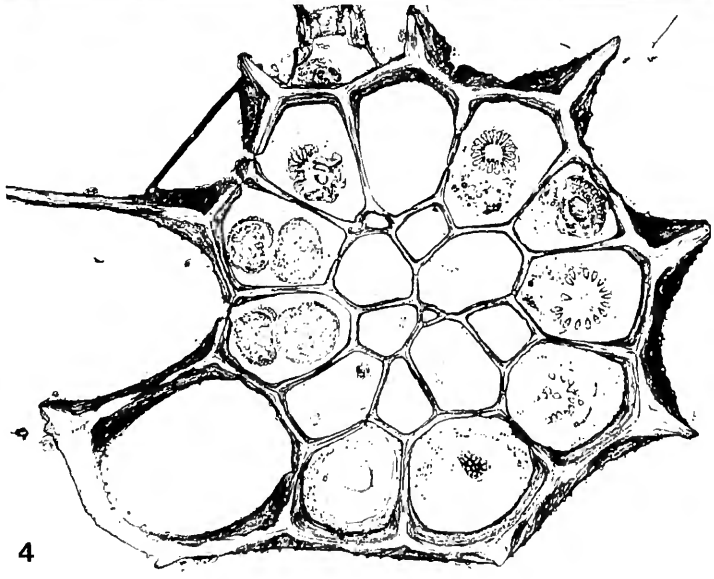
MORPHOLOGY.—In the zone of astogenetic repetition colonies of *Cinctipora elegans* form bushes of bifurcating branches (Figure 2). Within a colony the branches are cylindrical and subequal in diameter. They are formed by large, monomorphic zooids that are arranged either spirally (Figures 3, 4) or annularly about an imaginary axis. The distal ends of branches are pale pink caused by the presence of actively feeding zooids. Proximal to the pink zones, branches are relatively white, apertures of the zooids are covered by calcified terminal diaphragms, polypides are absent, surfaces are variably fouled by encrusting organisms, and zooids are dormant.

Within any single colony of *C. elegans* the zooidal pattern ranges from annular to spiral. This is achieved through variation in the spiral pitch angle. A pitch angle of zero degrees produces an annular arrangment. In most colonies, small pitch angles produce partial spirals in which each spiral of zooids is interrupted by an offset or dislocation of zooid apertures in order to start the next spiral. These offsets generally appear on the same side of the branch (Figure 6*a*). Steeper pitch angles produce complete, uninterrupted spirals.

Zooids of *C. elegans* are typically free-walled initially and intersect colony surfaces at low angles (Figure 3) permitting interior vertical walls of zooids to extend distally beyond living chambers and functional apertures to form exozones of thickened skeletal shields that are visible externally (Figures 5, 6*b*). The shields are longitudinally elongate, subrectangular, and concave outwardly. They are pierced by a few scattered communication pores and most have a minutely pustulose




FIGURES 2–4.—*Cinctipora elegans*. 2, Bleached colony, BMNH 1989.10.20.1 from Otago Shelf (×1.75). 3,4, sta Mu76-138; 3, USNM 250076, longitudinal section of branch of degenerated zooids, developing brown body (bb), flattened attachment organ (ao), calcified terminal diaphragm (td), newly regenerating polypide (np) (×30); 4, Transverse section with spiral arrangement of zooids, USNM 454183 (×50).

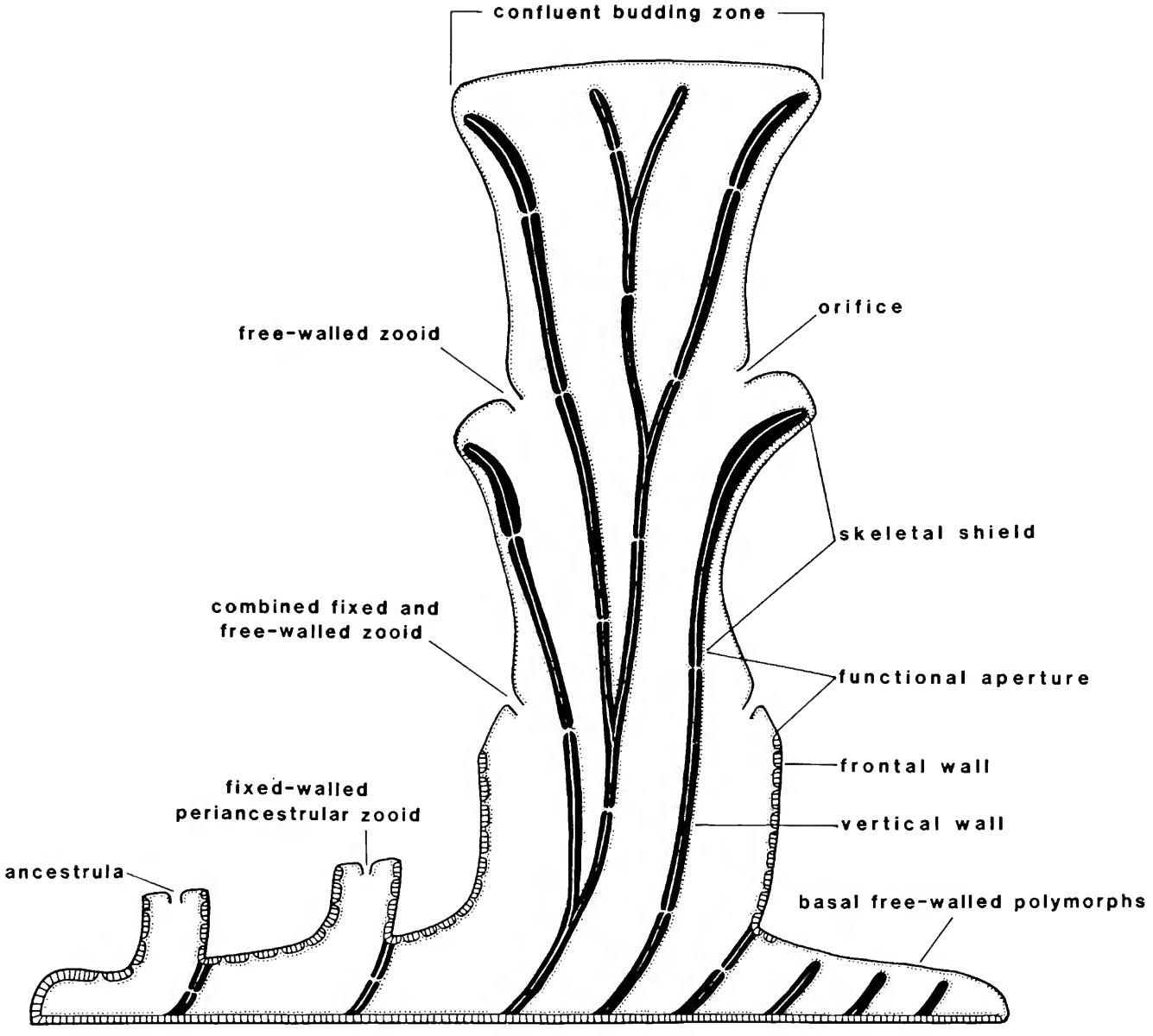
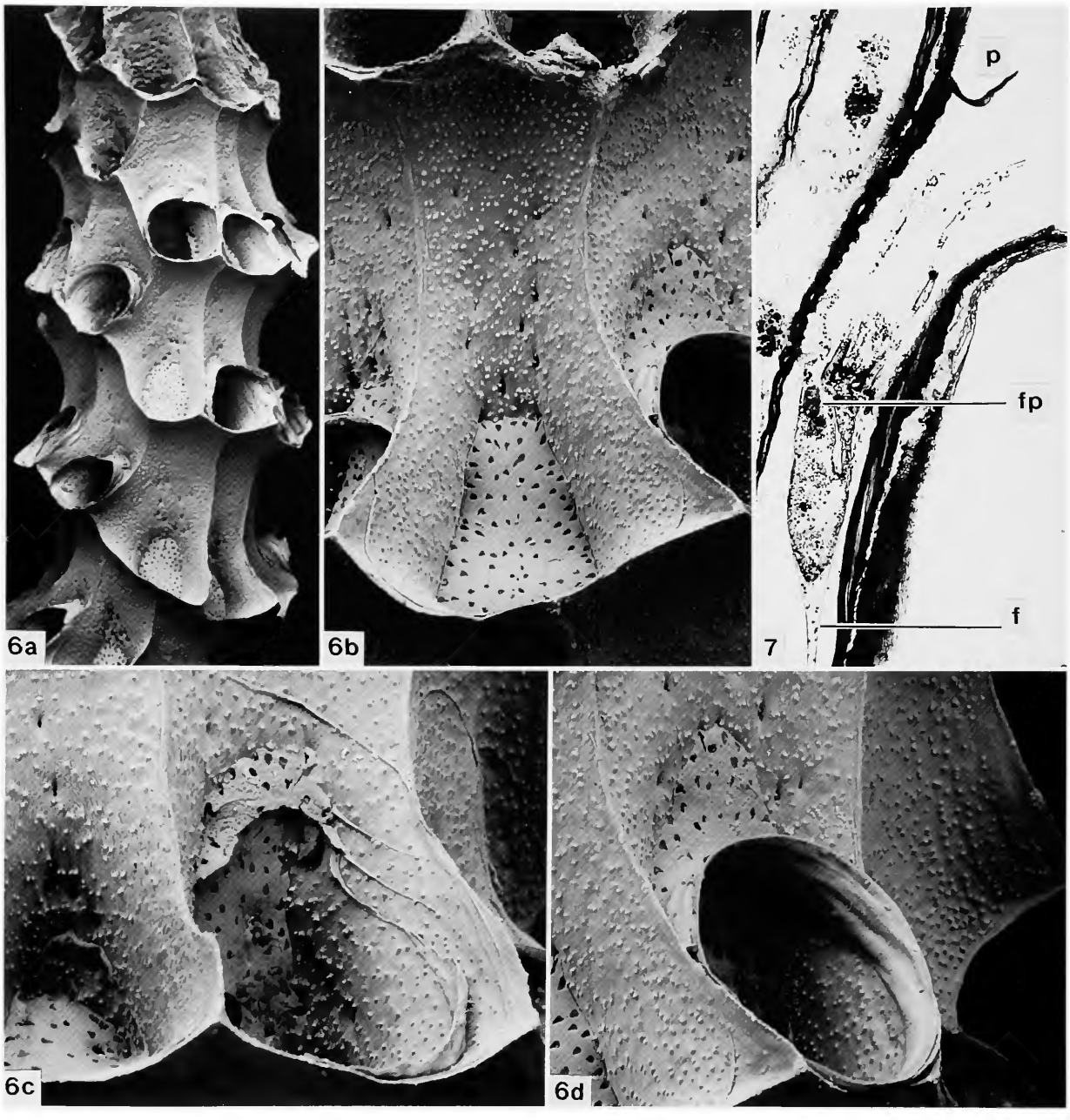



FIGURE 5.—Primary zone of astogenetic change of *Cinctipora elegans*. Calcified exterior walls indicated by pattern of transverse lines, calcified interior walls black.

surface of a kind that necessarily grows under a covering epidermis and body cavity. Shields terminate laterally and distally as ridges at zooidal boundaries. The lateral boundaries generally parallel branch axes and are commonly aligned with the midlines of zooids of adjacent whorls or annular rings.

The great majority of skeletal apertures of stenolaemates are terminal and at zooidal boundaries. The cross-sectional sizes and shapes of apertures and exozonal living chambers are comparable. In *C. elegans*, the skeletal shields enlarge terminal zooidal boundaries well beyond the dimensions of living chamber cross-sections. As a result, functional apertures of zooids are subterminal, located at the bases of the shields in the approximate positions of terminal diaphragms (Figures 5, 6). Therefore, unlike most stenolaemates, orificial membranes of *C. elegans*, by definition, do not extend across entire skeletal apertures to zooidal boundaries but cover only the functional




FIGURES 6, 7.—*Cinctipora elegans*. 6, BMNH 1989.10.20.2, NZOI sta E107: *a*, spiral arrangement of zooids with offsets, some with emergent peristomes (×20); *b*, skeletal shield with terminal diaphragm (×64); *c*, interrupted growth of 3 emergent peristomes, oldest above, terminal diaphragms inside (×86); *d*, completed peristome (×80). 7, Longitudinal section of regenerating, partly protracted polypide with peristome (p), faecal pellet (fp), funiculus (f), USNM 454184 from edge of Otago Shelf off Otago Peninsula (×50).

apertures at the bases of skeletal shields.

Zooids are free-walled in earliest ontogenetic stages at distal ends of branches. Exterior-walled peristomes develop in later stages of the pink zones in most zooids of some colonies and are sporadic to lacking in others (Figures 6–8). The late development of peristomes transforms zooids from free-walled to fixed-walled at their functional apertures. Zooids lacking peristomes remain free-walled.

The peristomes of *C. elegans* have exterior walls and an unexpected morphology (Figures 6–8). In fixed-walled steno-

laemates peristomes are exterior-walled and are skeletal extensions of frontal walls. Frontal walls are exterior walls that begin growth from the ends of vertical interior walls at zooidal boundaries. The exterior walls of the peristomes of *C. elegans*, however, grow without the support of frontal walls in much the same manner as terminal diaphragms, that is, they emerge as extensions of late-forming skeletal linings just inward from the ends of vertical walls at functional apertures (Figure 7). These peristomes are here termed emergent peristomes. Emergent peristomes display growth stages, starting with the first indications of skeletal growth on skeletal shields (Figure 6*c*), and ending with complete encirclement of apertures by thin exterior walls that transform the free-walled zooids into fixed-walled zooids (Figure 8).

The emergent peristomes of *C. elegans* seem too superficial to indicate polymorphism of their zooids and no essential differences have been noted in the feeding organs of those zooids (Figure 7). Zooids with peristomes occur singly or in apparently randomly located clusters. Emergent peristomes are interpreted here as products of later feeding stages responding to some unidentified microenvironmental stimulus that results in more tightly defined functional apertures. Besides the cinctiporids, the only other known occurrences of peristomes of comparable structure are in all feeding zooids of a species identified as *Heteropora? pacifica* Borg (Boardman, 1983, fig. 34).

Terminal diaphragms of zooids seal living chambers from the surrounding environment (Figure 6*b*). In *C. elegans*, terminal diaphragms are exterior, thickly calcified walls that occur just inside of functional apertures and emergent peristomes (Figure 6*a–c*). They contain scattered pseudopores and their presence is interpreted to mean that their zooids have become dormant.

In some zooids, depressed attachment scars are arranged in a transverse ring (Figure 9*a–c*) inward from the functional aperture on skeletal surfaces of living chambers. These scars apparently develop in thickening vertical walls at points of prolonged contact with the ligaments of attachment organs (Figure 10). The pustulose surfaces of skeletal shields extend inward to the attachment scar rings on axial and lateral sides of living-chamber walls. Inward from the rings the skeletal walls are smoothly laminated and some have faint longitudinal grooves (Figure 9*d,e*).

In some colonies of *C. elegans* the attachment scars were not found (Figure 11). In other colonies, the attachment scars occur in some zooids and not in others and the pustules extend inward from the attachment ligament level (Figure 12). Apparently the attachment scars can range within the species from lacking, to faint, to deeply inset.

Communication pores are closely concentrated in axial walls of zooids, from just behind apertures down to the attachment level (Figure 13). Below the attachment level communication pores are more scattered, either in transverse rings, in longitudinal rows, or without apparent pattern.

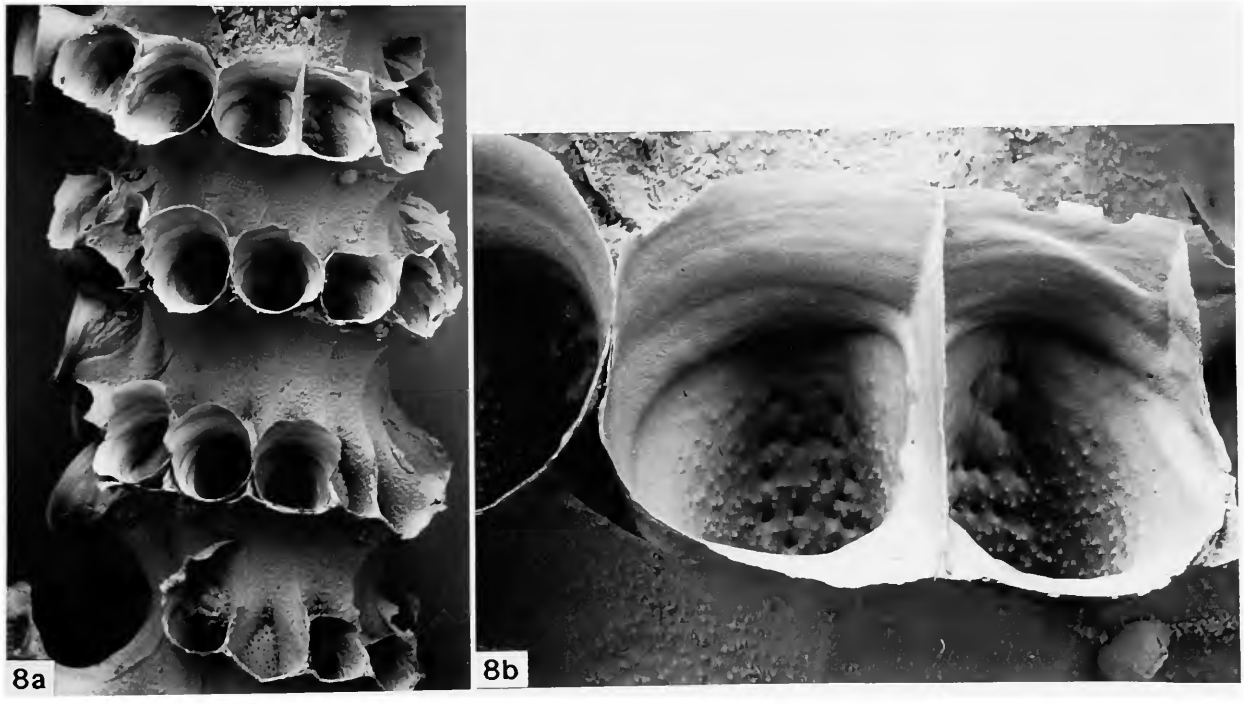



FIGURE 8.—Emergent peristomes of *Cinctipora elegans*. 8, Fully extended peristomes, NZOI sta E107: *a* (×19); *b* (×84).

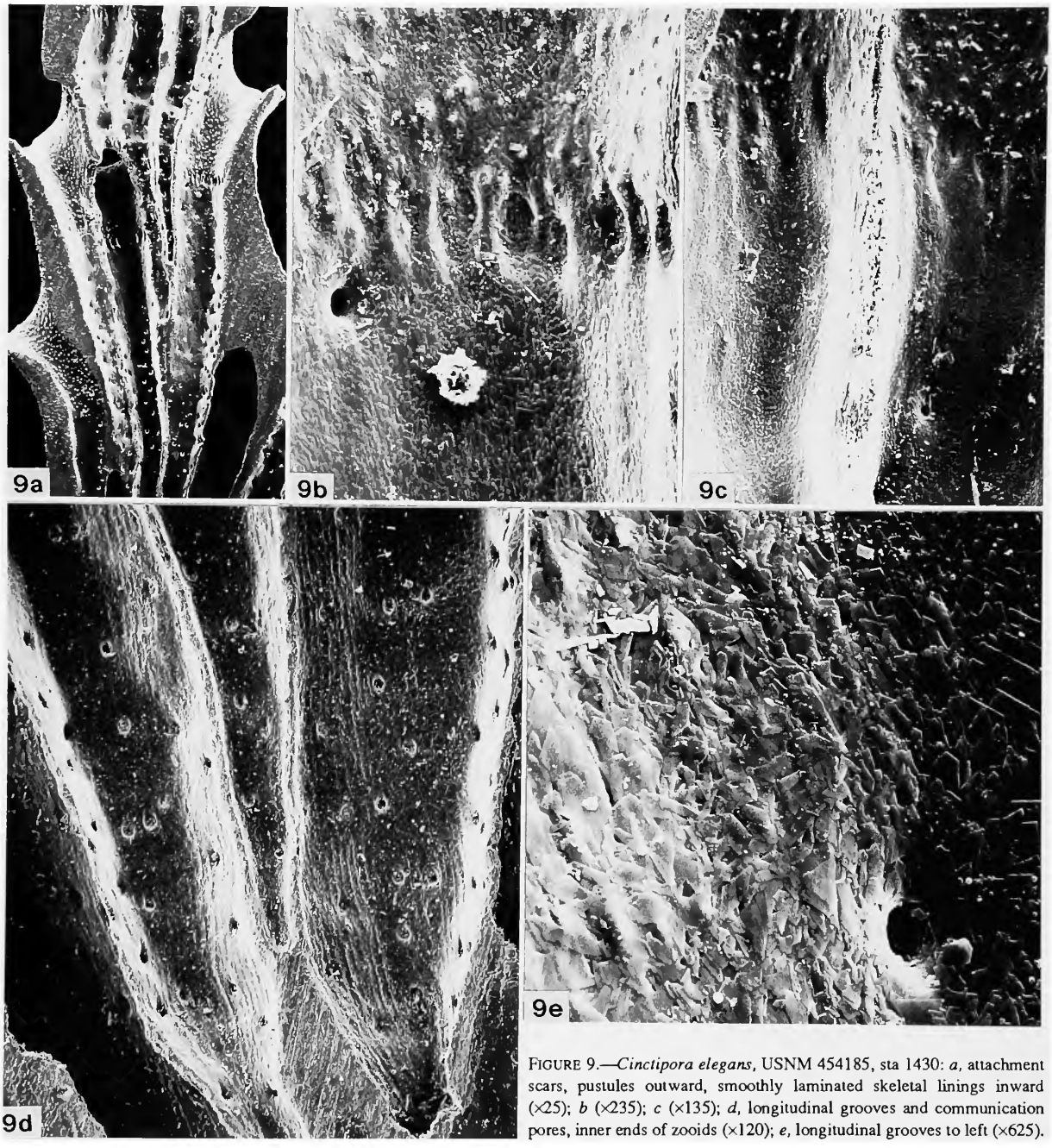



FIGURE 9.—*Cinctipora elegans*, USNM 454185, sta 1430: *a*, attachment scars, pustules outward, smoothly laminated skeletal linings inward (×25); *b* (×235); *c* (×135); *d*, longitudinal grooves and communication pores, inner ends of zooids (×120); *e*, longitudinal grooves to left (×625).

ANATOMY.—(For a literature review of the soft parts of other stenolaemates see "Appendix.") The attachment organ in *C. elegans* (Figures 10, 14–18) is strongly thickened, and in the retracted position in fully functioning zooids it has a truncated conical shape. The organ is attached to the zooidal skeleton by 24 robust, closely and evenly spaced ligaments (Figure 16), which are inset into the skeletal attachment scars (Figure 9*a–c*) in some zooids. The outer circular edge of the attachment organ is connected to the outer edge (in the retracted position) of the cylindrical atrial sphincter muscle (Figures 10, 14, 15, 17). The membranous vestibular wall is loosely attached to the flattened top of the attachment organ, extends unattached through the cylinder of the sphincter muscle, and terminates at the inner end of the sphincter muscle (Figures 15, 17, 18) where the outer end of the tentacle sheath is also attached. The tentacle sheath attachment filaments (Figure 10) stretch the tentacle sheath subparallel to the configuration of the attachment organ (Figures 15, 17).

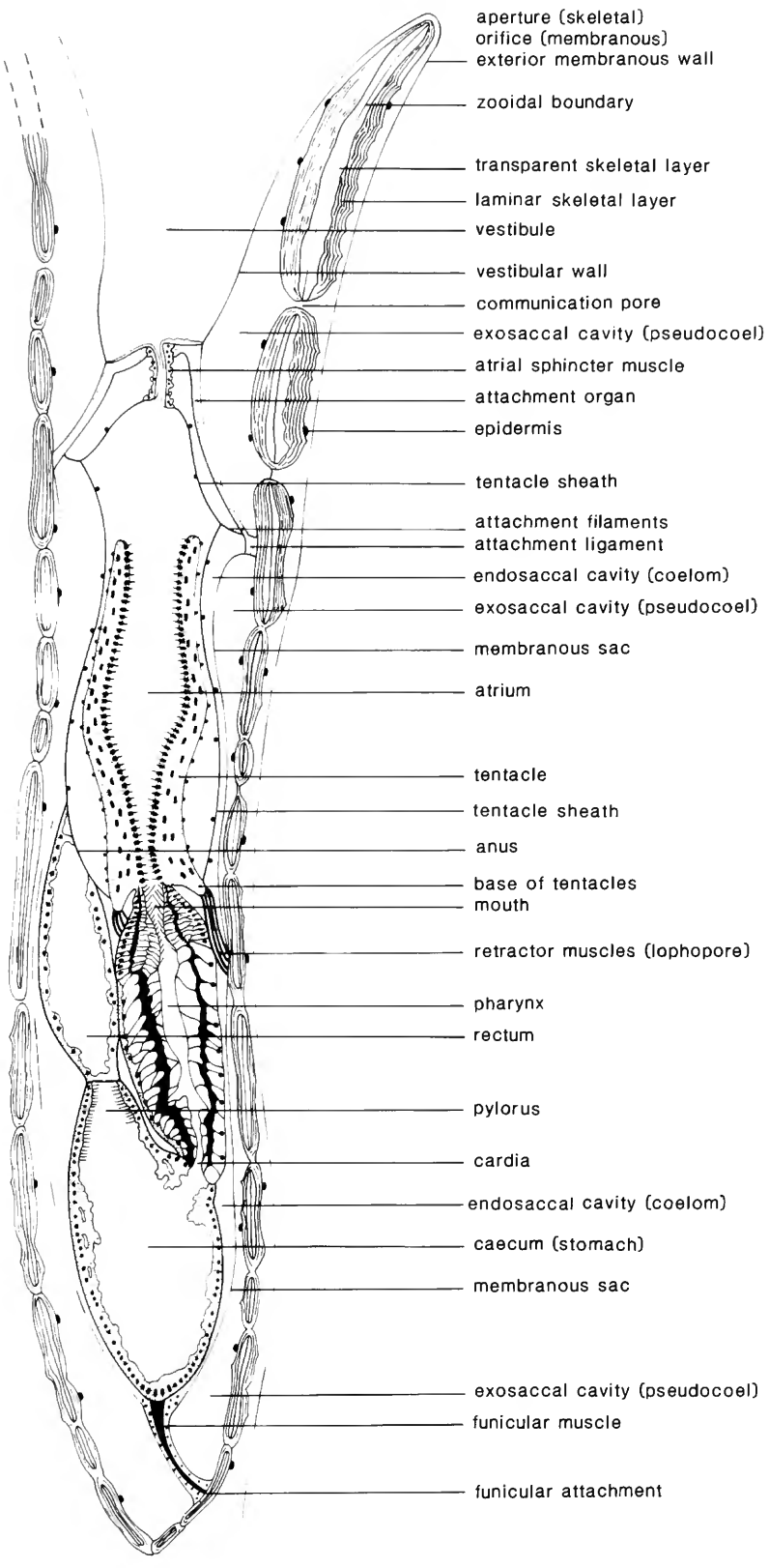
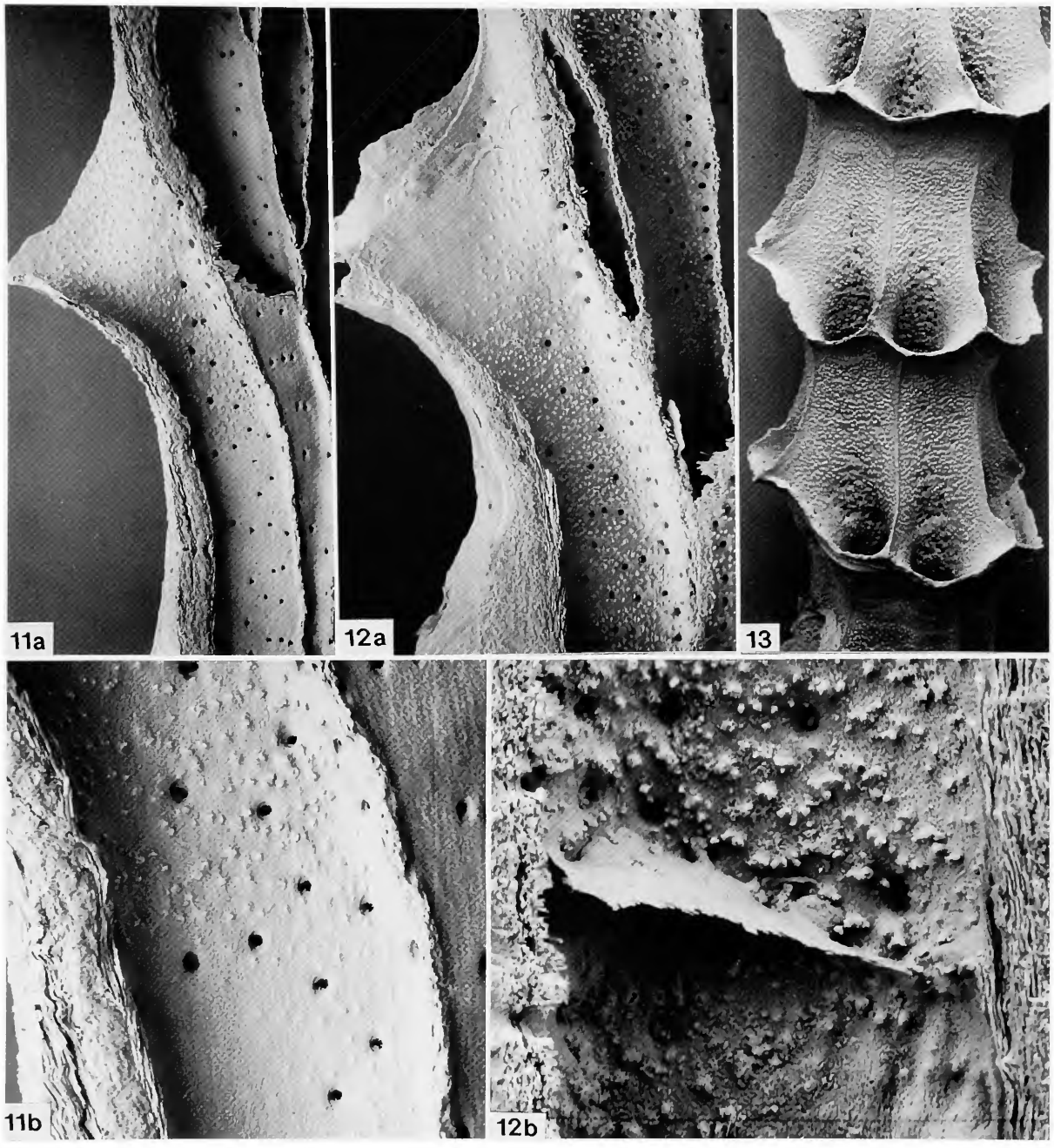
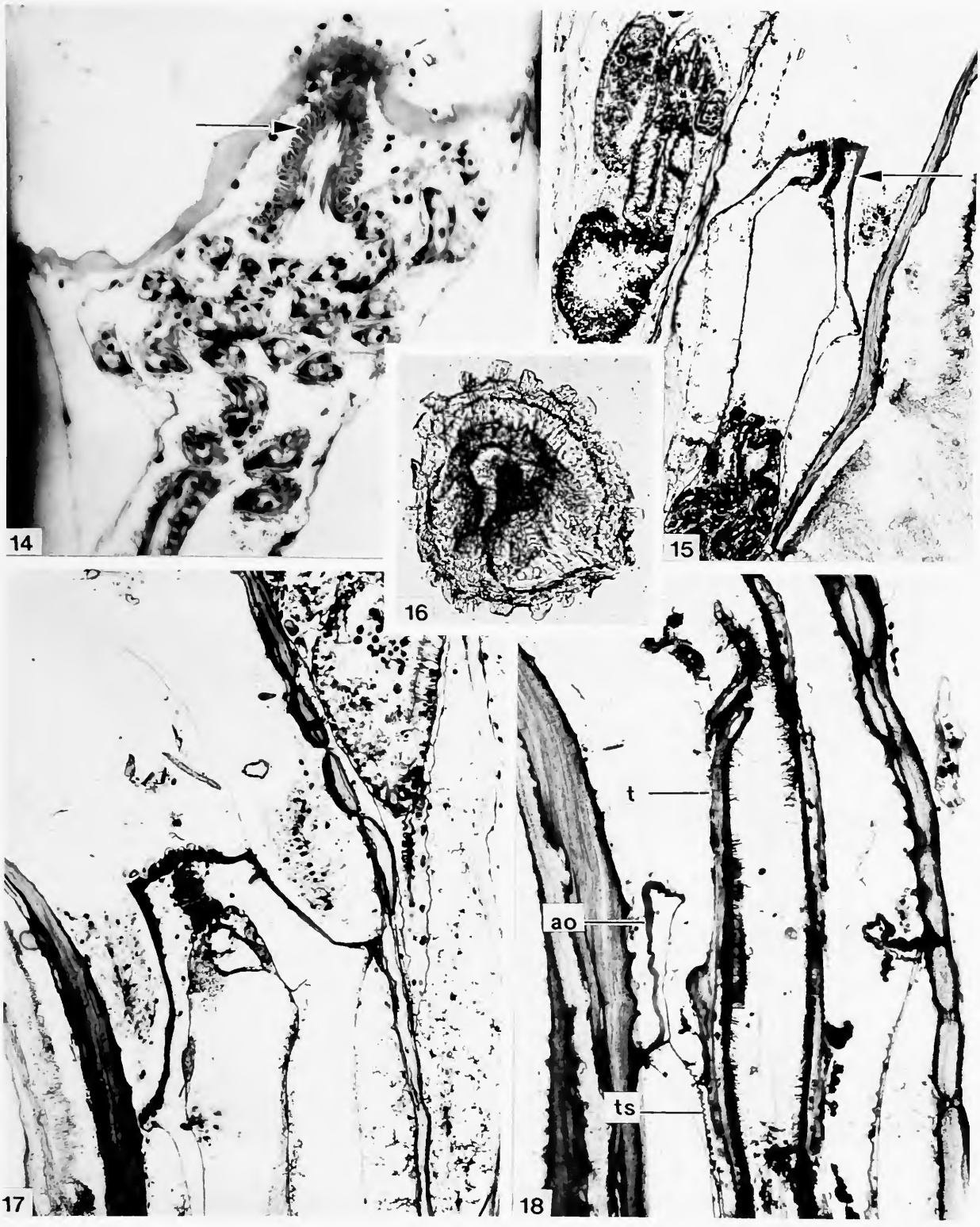



FIGURE 10.—Longitudinal section of retracted feeding zooid of *Cinctipora elegans*.




FIGURES 11–13.—*Cinctipora elegans*. 11, NZOI sta E820: *a*, zooidal skeleton lacking attachment scars (×60); *b* (×203). 12, NZOI sta E107: *a*, attachment scars lacking, pustules throughout living chambers (×64); *b*, attachment scars below calcified diaphragm with pustules in both directions from scars. Diaphragm may be calcified attachment organ (×254). 13, Concentration of communication pores on axial walls of zooids at and below functional apertures, NZOI sta E820 (×28).

The contracted atrial sphincter muscle closes off the atrium from the vestibule (Figure 10). As the tentacles are protruded the sphincter muscle relaxes and the attachment organ is pushed aside (Figures 7, 18). In the relaxed position the vestibular wall can be seen to extend down to the inner end of the sphincter muscle where it joins the outer end of the tentacle sheath (Figure 18). Therefore, the sphincter muscle is protected from the surrounding environment by the ectodermal vestibular wall. The sphincter muscle is also seen to be connected directly to the membranous sac and attachment organ, both considered




FIGURES 14–18.—Attachment organs of *Cinctipora elegans*. 14, Cells of atrial sphincter muscle (arrow) and randomly cut tentacles, USNM 454186 off Otago Heads (×300). 15, Normal shape of attachment organ (arrow) and retracted tentacle sheath, alimentary canal of adjacent zooid, upper left, USNM 250076, sta Mu76-138 (×100). 16, Isolated attachment organ with 24 ligaments, USNM 250077, sta Mu76-138 (×150). 17, Normal shape of retracted attachment organ on left, funiculus and funicular muscle on right, USNM 250064, sta Mu76-138 (×150). 18, Tentacles with cilia (t) partly protruded past collapsed attachment organ (ao), vestibular wall connected to inner end of relaxed atrial sphincter muscle and outer end of crenulated tentacle sheath (ts), USNM 454184, from edge of Otago Shelf off Otago Peninsula (×150).

to be mesodermal by Nielsen and Pedersen (1979:76). These connections suggest that the atrial sphincter muscle could be mesodermal in origin (Borg, 1926:212) rather than ectodermal as indicated by Nielsen and Pedersen (1979:83). Detailed histological work is necessary to solve the problem.

The lophophore and digestive tract of *C. elegans* are robust, occupying half or more of the cross-sectional area of a living chamber at the level of the gut. The 16 tentacles of each zooid are ciliated laterally (Figures 19–21). Cilia are lacking along the frontal midline as reported by Nielsen (1987:232). The mouth and outer end of the pharynx are densely ciliated; cells of the remainder of the pharynx are large, inflated, and unciliated (Figure 22). The cardia is merely an opening to the caecum. Gizzards are not included in the digestive tract. The cilia of the pylorus cells are densely packed and are shorter than those of the pharynx. The pylorus wall can constrict, apparently to close off the pylorus from the rectum. The anus is on the axial side of the living chamber and is located in the tentacle sheath near the base of the fully retracted tentacles.

The attachments of retractor muscles (Figures 23–26) encircle the base of the lophophore. The other ends of the retractor muscles insert into skeletal surfaces of the living chamber in three clusters in the form of an inverted triangle on the side opposite to the anus (Figure 26). Muscles from the anal side of the lophophore wrap around either side of the pharynx to insert at the two corners at the base of the triangle, and muscles on the near side insert directly at the apex of the triangle. No retractor muscles are attached to the cardia.

The funiculus (Figures 27–29) contains robust retractor muscles that attach to the caecum and to the skeletal wall of the living chamber so that in the retracted position the caecum is pulled inward. In a few zooids within some colonies, however, the caecum is not pulled toward the end of the living chamber but is recurved outward just below the pylorus, indicating that the funicular muscle is not functioning (Figure 27). The funiculus is most commonly attached to solid skeletal wall, not over a communication pore, so that communication with adjacent zooids through the funiculus generally is not possible.

## Primary Zone of Astogenetic Change

The primary zone of astogenetic change of *C. elegans* (Figures 5, 30, 31) reveals unexpected mixtures of free- and fixed-walled morphologies. As in all stenolaemates, the basal disc of the ancestrula must begin with a skeleton of exterior walls that is fixed-walled initially. In the few free-walled species in which ancestrulae have been studied, ancestrulae in later growth stages become free-walled in accordance with the other zooids of the colonies.

In *C. elegans*, however, the ancestrula remains fixed-walled and outside of the main part of the colony. The walls of the ancestrula are exterior with the exception of the patch of interior wall between the body cavities of the ancestrula and succeeding zooids. The exterior wall contains pustules in its laminar skeletal lining and is pierced by scattered pseudopores that are more numerous near the periphery of the basal disc. The ancestrula can be followed by another fixed-walled zooid (periancestrular bud) having exterior walls. Both the ancestrula and the periancestrula can give rise to as many as three erect branches in ways not well understood because of lack of specimens with zones of change (Figure 31).

Zooids of the first erect whorl of a branch of *C. elegans* have apertures that are a combination of fixed- and free-walled, another unexpected morphology not seen before in stenolaemates (Figure 5). An exterior frontal wall grows up to the proximal side of the aperture, causing the orificial wall to be attached there. Distally, an interior skeletal shield is formed and the orificial wall is unattached, making the distal part of the aperture free-walled. Zooids of the second whorl are totally free-walled and similar to the zooids of the remainder of the colony, ending the zone of change.

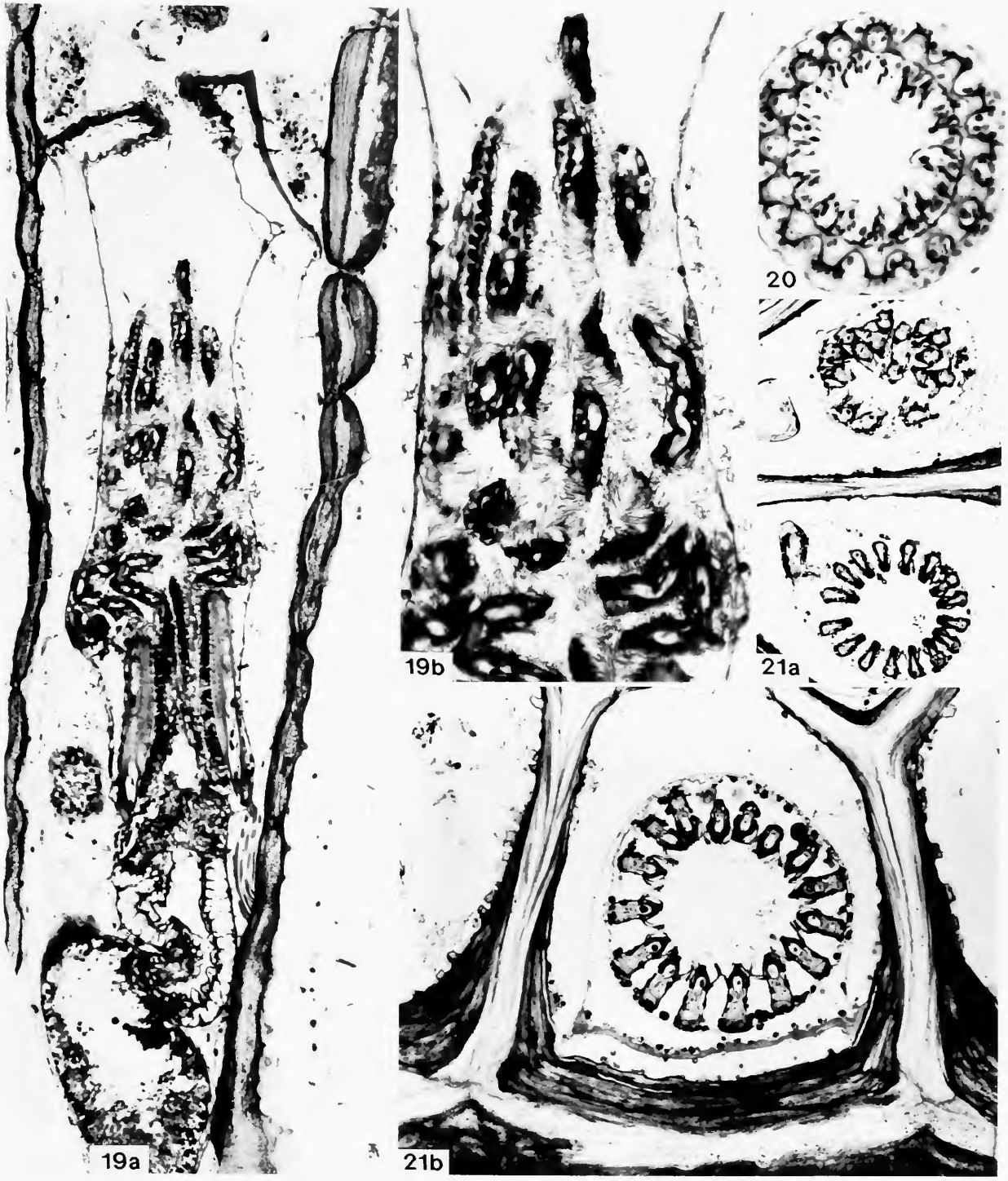
Free-walled supporting and space-filling polymorphs, which have variable shapes and sizes in cross-section, irregularly encrust the lower portions of the zone of change. The largest polymorphs generally have pustulose interior walls and some have terminal diaphragms; some of the smallest lack both.

## Rejuvenations

Proximal Rejuvenations.—The reversal of growth direction proximal to broken ends of branches of *C. elegans* is a form of intracolony rejuvenation of growth (Figures 32, 33). The new growth starts from the parent colony as a secondary zone of astogenetic change that lacks an ancestrula. The secondary growth has a whorl of erect zooids similar to the first whorl of erect zooids in a primary zone of astogenetic change, that is, the apertures of the erect zooids are fixed proximally by frontal walls and free distally at the bases of skeletal shields.

The basal attachment complex of a proximal rejuvenation includes small encrusting polymorphs (Figure 32) that are covered by an exterior skeletal wall. The covering wall is connected to the exterior frontal walls of the zooids of the first erect whorl. The encrusting polymorphs are comparable to the smaller polymorphs in primary zones of change (Figures 30, 31). Growth lines of the exterior wall covering the polymorphs indicate a complex pattern of growth directions that finally connects covering walls of the polymorphs with the parent colony.

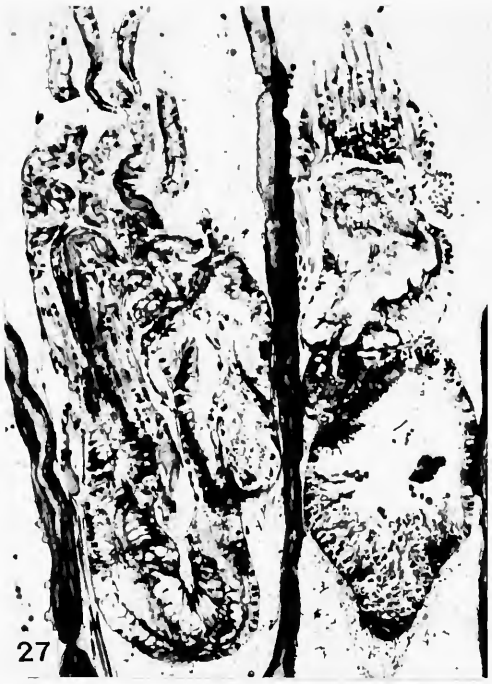
In colonies of most free-walled taxa, the outermost cuticular layer of the exterior basal wall of a rejuvenation is laid down on the encrusted surface. In proximal rejuvenations of *C. elegans*, the equivalents of those basal walls are the exterior basal encrusting walls of the small supporting polymorphs (Figure




FIGURES 19-21.—Tentacles of *Cinctipora elegans*. 19, Longitudinal sections, USNM 250065, sta Mu76-138: *a*, fully regenerated polypide in retracted position, basal portion of tentacles stiffened in orderly arrangement, outer ends relaxed (×150); *b*, relaxed tentacles showing cilia (×300). 20, Transverse section at base of tentacles, USNM 454187, off Otago Heads (×300). 21, Transverse sections showing differences in cross-sectional shapes of tentacles at different levels, USNM 454184, edge of shelf off Otago Peninsula: *a* (×150); *b* (×200).

FIGURE 22.—Digestive tract of *Cinctipora elegans,* longitudinal sections, including base of tentacles, mouth, pharynx with ciliated cells at outer end, cardia, outer ends of caecum (stomach), cilated pylorus, USNM 250065, sta Mu76-138 (×300): *a,* empty rectum; *b,* rectum with faecal pellet.

FIGURES 23–26.—Retractor muscles of *Cinctipora elegans*, all from sta Mu76-138 except for figure 24. 23, Transverse section with pharynxes above encircled by retractor muscles, stomachs below, USNM 454183 (×150). 24, USNM 454187 off Otago Heads: *a*, longitudinal section, cluster of muscles bending around pharynx cut transversely (×300); *b*, longitudinal section, muscles attached to base of lophophore and skeletal wall (×150). 25, Longitudinal section, muscles attached to base of lophophore and skeletal wall (left), constriction between pylorus and rectum with faecal pellet (right), USNM 250065 (×300). 26, Longitudinal section, muscle clusters in inverted triangle, third cluster partly shown at bottom edge of figure (left), atrial sphincter muscle partly relaxed, faecal pellet entering atrium from anus (zooid to right), USNM 454188 (×150).



FIGURES 27–29.—Funiculus in longitudinal sections of *Cinctipora elegans*. 27, Polypide doubled up, apparently lacking attached funiculus (left), funiculus attached (right), USNM 454188, sta Mu76-138 (×150). 28, Inner ends of caecae in regenerating colony, each with funiculus and funicular muscle, USNM 454184, edge of continental shelf off Otago Peninsula (×100). 29, Funiculus and funicular muscle in fully regenerated colony, USNM 250064, sta Mu76-138 (×150).

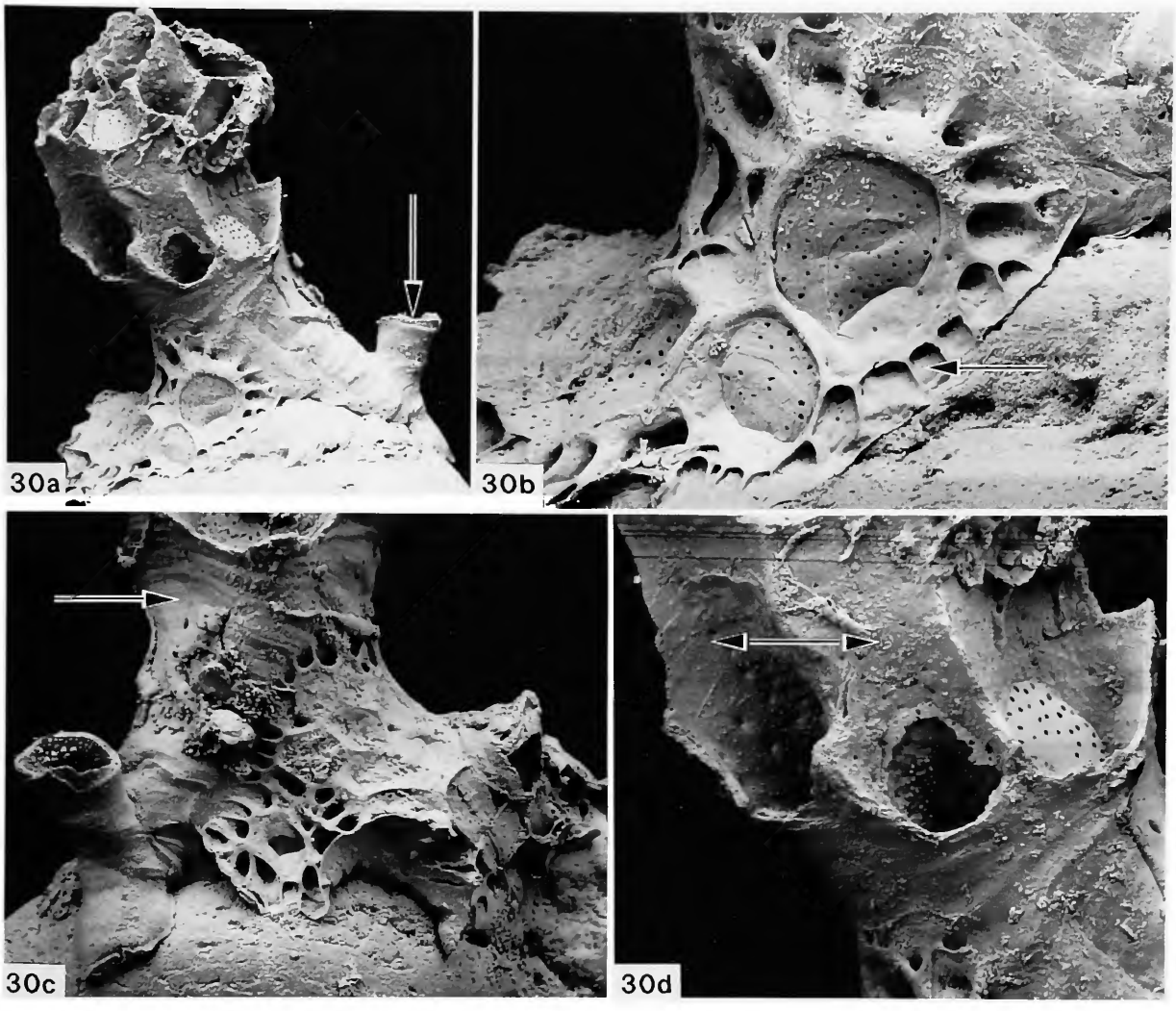



FIGURE 30.—Primary zone of astogenetic change of *Cinctipora elegans*, BMNH 1989.10.20.3, sta Mu88-29: *a*, ancestrula (arrow) (×19); *b*, small supporting polymorphs (arrow) surrounding large polymorphs with terminal diaphragms, both free-walled (×65); *c*, ancestrula left front, exterior frontal walls of first erect whorl (arrow) (×29); *d*, interior skeletal shields of first erect whorl of fixed-free zooids (arrow) (×46).

32*c*). The exterior covering walls of the polymorphs and the frontal walls of the first erect whorls of a secondary zone of change in *C. elegans* are lacking in other studied free-walled stenolaemates and are unexpected discoveries in this species.

Proximal rejuvenations are instructive because presumably the rejuvenated zone of change originates by mitotic growth from a supporting branch of the parent colony. Most zooids in proximal broken ends of supporting branches have terminal diaphragms and thus are dormant. The mitotic growth from dormant zooids indicates they retain a functional cuticle, epidermis, and body cavity and are totipotent for some period of time after having ceased to feed.

FRONTAL REJUVENATIONS.—A frontal rejuvenation produces a secondary branch that projects at a high angle from the supporting branch of the parent colony (Figures 34–36). Normal branch bifurcations of the colony growth habit originate within endozones. A frontal rejuvenation forms within an exozone through the aperture of a connecting zooid from the supporting branch (Figures 34, 36*b*). These rejuvenations also begin as secondary zones of astogenetic change (Figures 34–36). Some of these develop with an irregular growth of basal polymorphs (Figure 34) that can be partly covered by exterior skeletal walls typical of proximal rejuvenations (Figure 36*a*).

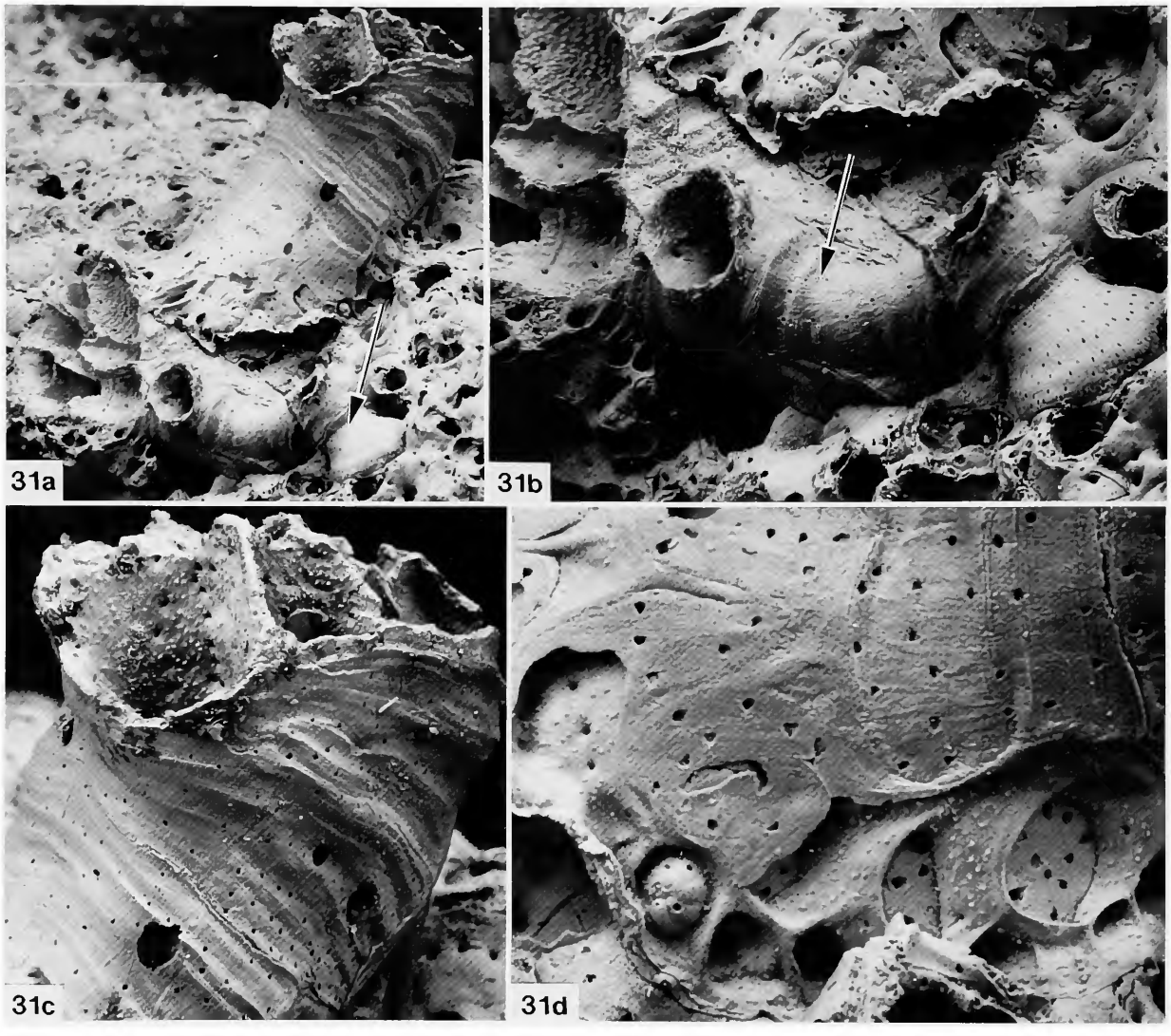



FIGURE 31.—Primary zone of astogenetic change of *Cinctipora elegans*, encrusting cheilostome *Celleporina*, BMNH 1989.10.20.4, Otago Shelf: *a*, ancestrula (arrow), periancestrula and two whorls that would have been at the base of two colony branches, both fractured (×25); *b*, broken ancestrula and periancestrula (arrow) (×58); *c*, broken exterior frontal walls of erect whorl with pseudopores (×63); *d*, small supporting polymorphs surrounding larger polymorphs with terminal diaphragms, both free-walled, exterior walls above (×128).

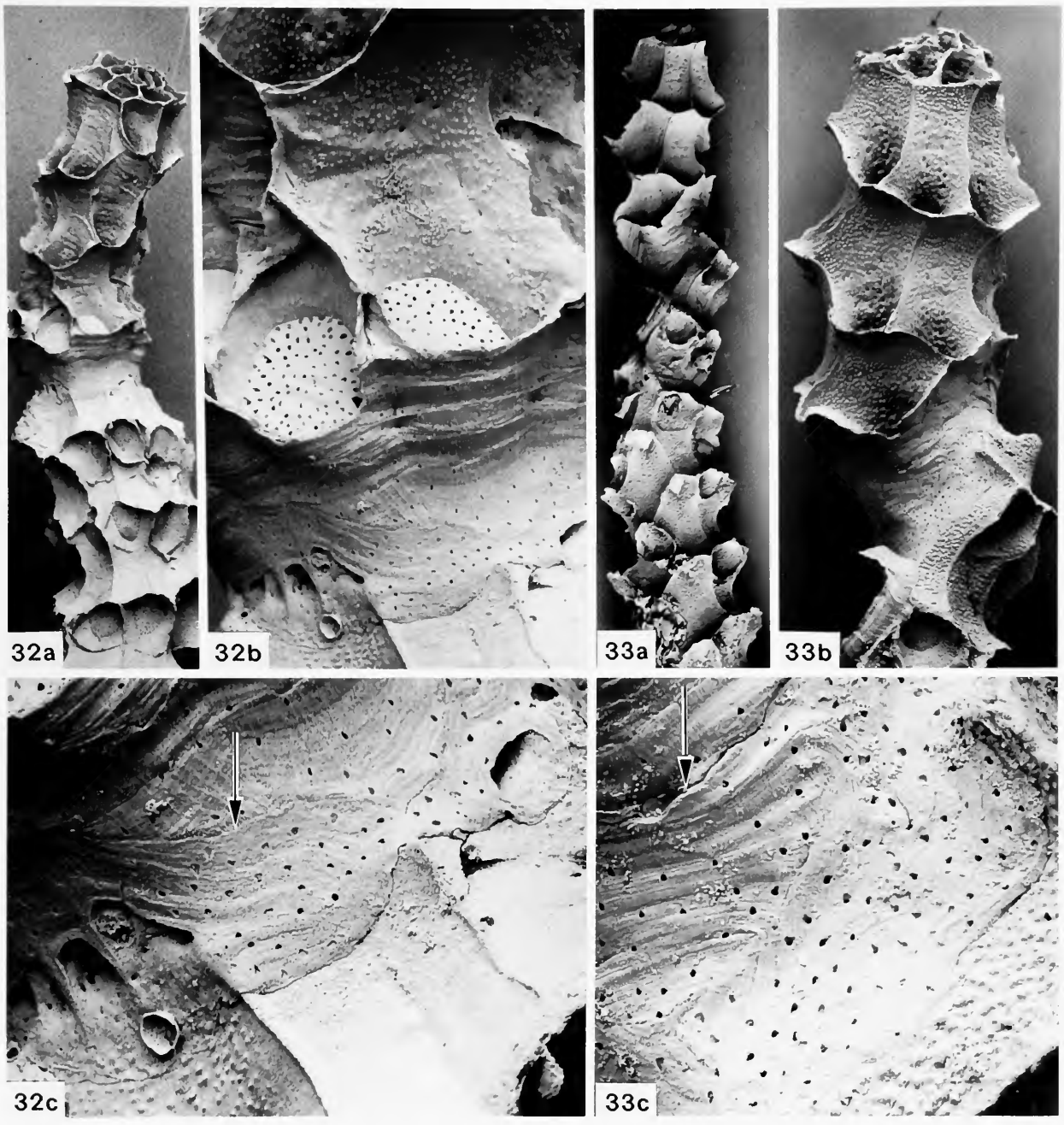
## Cinctiporid Skeleton

### VERTICAL WALLS

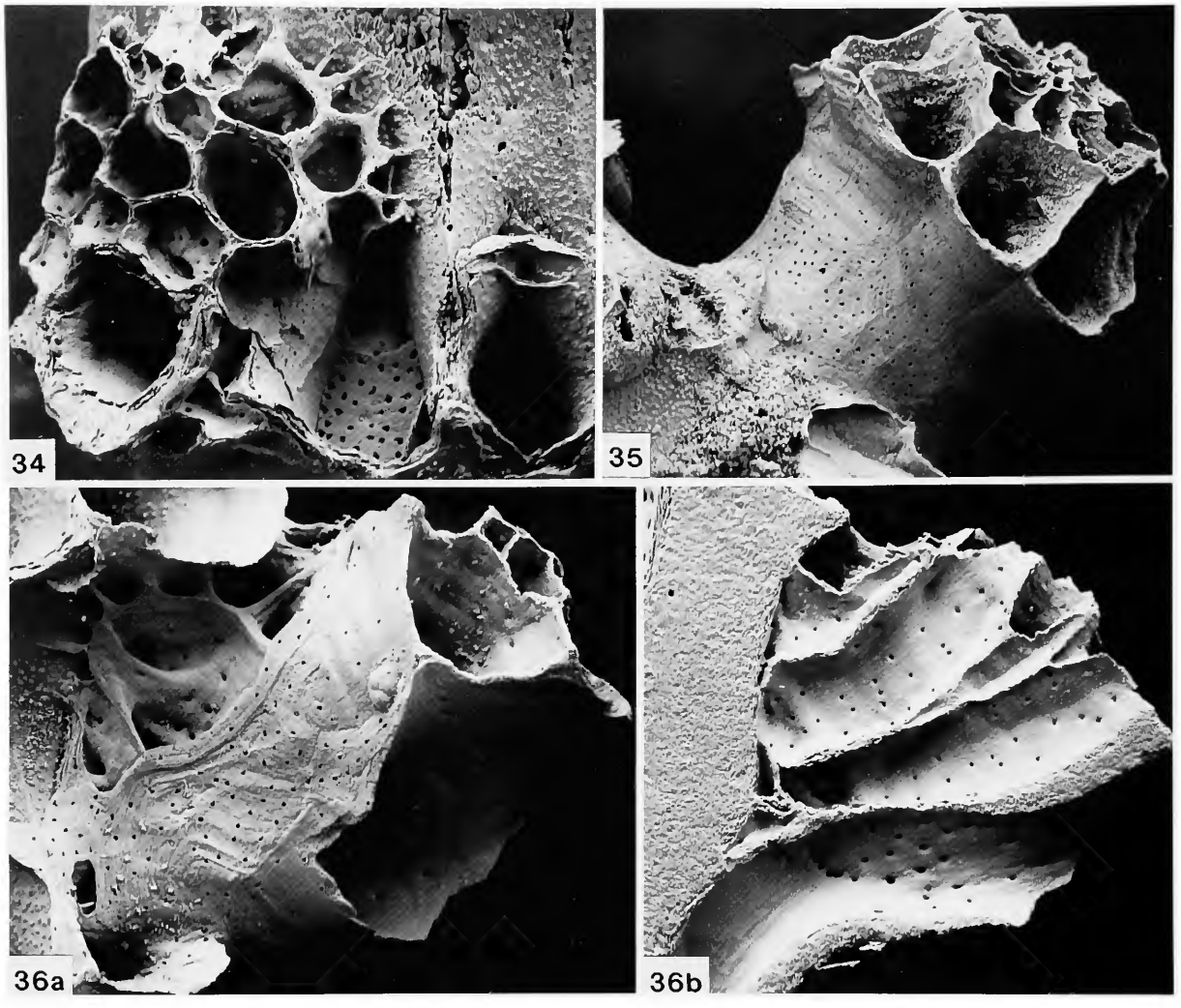
In stenolaemates, vertical walls are interior and compound. They originate at growing margins of colonies, either from exterior basal or reverse skeletal walls of colonies, interior median walls of bifoliate colonies, or other vertical walls of older zooids. Adjacent zooids contribute half of each compound wall and together determine its direction of growth.

In the exozones of free-walled cinctiporids, skeletal shields are outwardly concave because they develop in conjunction with endozonal walls of two axially adjacent younger zooids and their lateral boundaries extend outward as ridges (Figure 4).

Vertical walls of cinctiporid zooids are constructed of two differing layers, or zones, of calcareous crystals. The layer grown initially is adjacent to the zooidal boundary; therefore, it is the outer skeletal layer of a zooid. It is referred to here as the transparent layer. The second layer develops closely behind the




FIGURES 32, 33.—Proximal rejuvenations in *Cinctipora elegans*. 32, NZOI sta D53: *a*, primary branch below oriented downward, rejuvenated branch above growing upward (×12); *b*, secondary zone of astogenetic change growing upward (×53); *c*, exterior frontal walls of rejuvenated first erect zooids above, boundary (arrow) with exterior skeletal wall partly covering basal encrusting polymorphs below (×93). 33, NZOI sta E832: *a*, primary branch below oriented downward, rejuvenated branch above growing upward (×9); *b*, rejuvenated branch growing upward (×20); *c*, exterior frontal wall of rejuvenated first erect zooid above, boundary (arrow) with exterior basal wall below (×103).




FIGURES 34–36.—Frontal rejuvenations in *Cinctipora elegans*. 34, Early development of frontal rejuvenation showing large connecting zooid originating from supporting colony and connected, free-walled polymorphs, NZOI sta C844 (×51). 35, A second frontal rejuvenation from NZOI sta C844 started by a secondary zone of change (×35). 36, NZOI sta E832 (×47): *a*, frontal rejuvenation of secondary zone of change supported by encrusting polymorphs partly covered by a basal exterior skeletal wall; *b*, longitudinal section of same rejuvenation showing connecting zooid from supporting colony below.

first at growing edges of walls so that it lines the living chamber. It is here called the laminar layer. The skeletal wall of a neighboring zooid includes similar transparent and laminar layers (Figures 37–39) so that the layers of immediately adjacent zooids fuse in a mirror image about the intervening zooidal boundary.

The transparent layer of the vertical wall in both endozone and exozone is made of long fibrous crystals deposited closely parallel to zooidal boundaries with their long dimensions approximately at right angles to the zooidal growth direction (Figures 40, 42*a*,*b*). The crystals are well-ordered in arrangement. In longitudinal thin sections the crystals are generally cut at right angles to their length and those regions appear transparent in plane light (Figure 39*a*). In transverse sections crystal lengths generally parallel the plane of the section and their fibrous shapes appear vague (Figures 37, 38*a*). In areas of a section where the orientation is intermediate the fibrous shapes generally cannot be seen (Figure 38*b*).

In transverse sections (Figures 37, 38*a*) the fibrous crystals either parallel zooidal boundaries or form elongate chevrons

FIGURES 37–39.—*Cinctipora elegans*. 37, Transverse section showing beaded appearance of zooidal boundaries (arrow), and transparent and laminar layers, also part of attachment organ and its ligaments attached to skeletal wall, USNM 250064, sta Mu76-138 (×150). 38, USNM 454189, sta 1430: *a*, transverse section of exozone (×150); *b*, transverse section showing pustules in laminar layer (×100); *c*, same section under cross-polarized light. 39, USNM 454190, sta 1430: *a*, longitudinal section of shield showing pustules on outer side (right) of shield only (×100); *b*, same section under cross-polarized light.

that intersect the boundaries at slight angles. The chevron appearance can be reversed in direction in the same wall. This occurs when crystals either converge or diverge slightly from the planes of the zooidal boundaries.

The crystallographic C-axes of the fibrous crystals of the transparent layer are perpendicular to crystal length. In addition, the C-axes approximately parallel each other and are parallel to the zooidal growth direction. Therefore, in transverse sections C-axes are approximately perpendicular to the planes of the sections in endozones and much of the transparent layer is black to dimly gray in cross-polarized light throughout complete rotation of a section (Figure 38*c* is nearly transverse). Fewer crystals remain at extinction in the exozones because of the angular divergence of the growth direction of the zooids from branch axes.

In longitudinal thin sections crystals of transparent layers are cut at right angles to their length and their C-axes generally are parallel to the section. As a result, in longitudinal sections under cross-polarized light the transparent layer of a rotating section goes to extinction four times as a section is rotated 360 degrees (Figure 39*b*).

The second layer, the laminar skeletal layer, lines zooidal chambers throughout their length (Figures 37–42). In endozones it is characterized by flattened crystals of irregular size and shape (Figure 41). In the exozone the crystals are lath-shaped and orderly in arrangement (Figure 42*c,d*). Growth lines on the crystals indicate that they grow by edgewise growth in the direction of local skeletal growth (Figure 42*c,d;* Boardman and Cheetham, 1969:212).

In all section orientations, the laminar layer appears finely laminated in both plane and polarized light. The majority of the fine laminations generally parallel living chamber surfaces and are not immediately related to positions of zooidal boundaries. The endozone-exozone transition of the vertical walls is marked by a thickening of the transparent layer and generally a much greater outward thickening of the laminar layer (Figures 37, 38).

Some disorderliness of arrangement of the flattened crystals of the laminar layer is caused by the formation of pustules. Sections show that pustules once started are maintained as the laminar zone increases in thickness (Figures 38, 39). Apparently crystals continue to pile on top of the pustules as growth continues (Figure 42*c,d*).

Zooidal boundaries are marked by a thin layer of crystals of irregular shape and orientation (Figures 40*c*, 42*a,b*). In transverse thin sections and plane light at lower magnifications this boundary layer appears as a single linear series of irregular masses that are translucent and light brown in color (Figures 37, 38*a*). In longitudinal sections the crystals appear to be an unbroken line of the same color. Examination of broken surfaces of zooidal walls using the SEM and peels of etched sections under high magnifications through a light microscope, indicate that the "organic-rich partitions" reported by Boardman (1983:66) are merely the narrow zone of irregular crystals reported here.

## Exterior Skeletal Walls

Frontal Walls.—Frontal walls are exterior skeletal walls that extend from edges of vertical walls to terminal apertures that support orificial walls. Thus, frontal walls form the outermost skeletal wall of most fixed-walled colonies (Figure 43*a*).

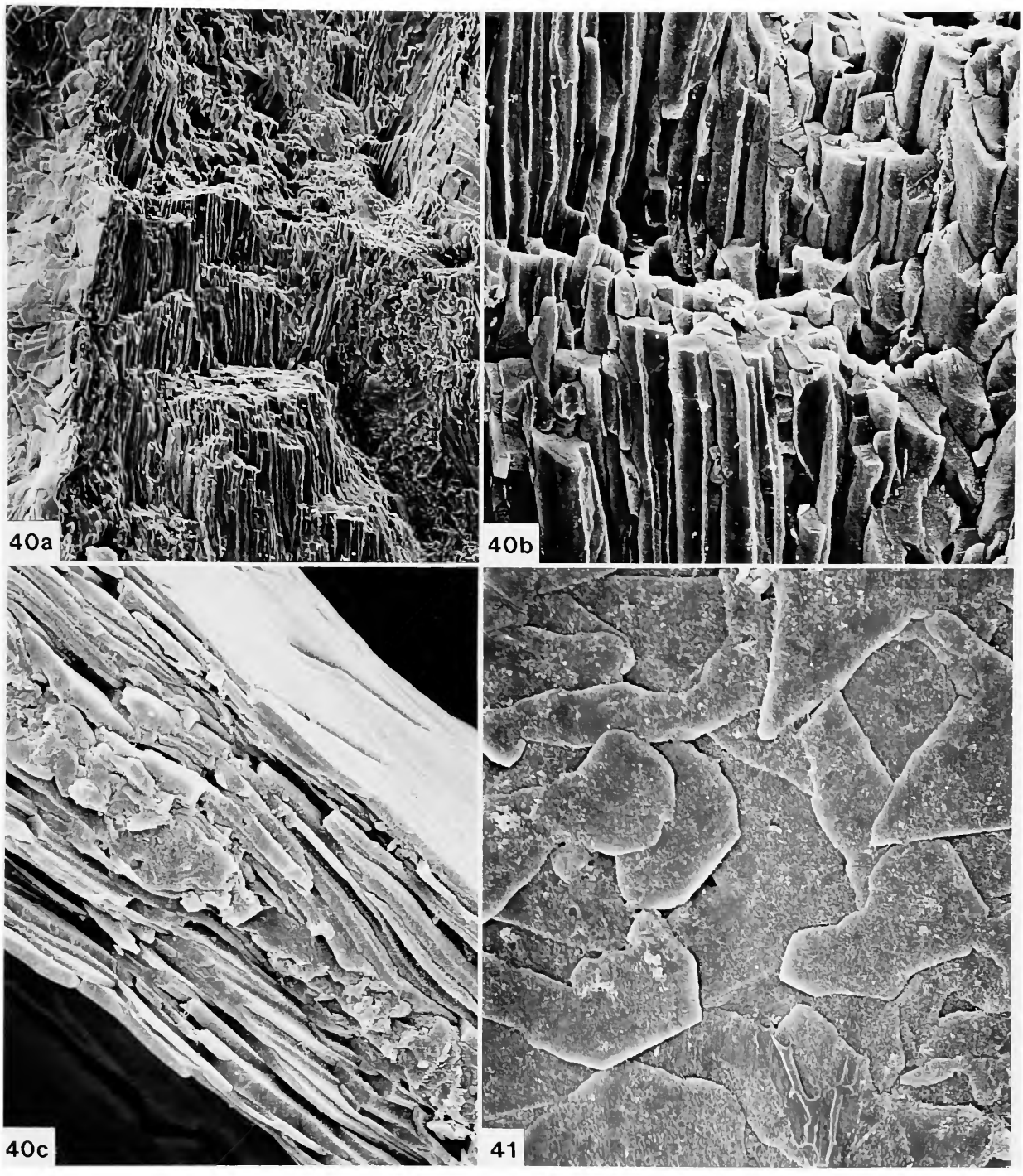
All exterior skeletal walls are simple, that is, calcified from one (inner) side. They require an outer cuticle to serve as a locus for crystal deposition and to provide direction (Boardman, 1983, fig. 34,1d). The direction reflects the shape of the cuticle as it is calcified. In cinctiporids, apparently the outer cuticles of frontal walls are somewhat inflated and undulated, resulting in the outward convexity and transverse undulations of the frontal walls as seen externally (Figures 43, 46).

The discontinuous linear undulations in frontal walls of the cinctiporids encircle branches approximately at right angles to branch axes. In frontal walls with normal growth, the wall undulations parallel growing edges of the walls at the growing tips so that the undulations act as approximate growth lines. A membranous exterior wall generally caps a growing branch tip symmetrically and apparently controls the growth of the interior vertical walls that partition the space in the confluent budding zone under the cap (Figure 5). The vertical walls, in turn, support the growth of the frontal walls (Figures 44, 46), also controlled by the membranous cap. The membranous cap is a colonial rather than a zooidal structure. Therefore, the growing edges of the skeletal walls are controlled by the colony so that many transverse undulations in frontal walls cross zooidal boundaries.

The frontal walls of cinctiporids contain scattered pseudopores that externally are sharply defined. Many are pointed. The points are generally oriented in the direction of growth of the frontal wall, at right angles to the wall undulations (Figure 43*b*). In fixed-walled species of cinctiporids, the transparent and laminar skeletal layers of a vertical wall of a single zooid continue unbroken into its frontal wall. The transparent layer, therefore, is adjacent to the outer cuticle in the frontal wall and the laminar layer continues to line the zooidal cavity (Figures 44, 45).

In most fixed-walled stenolaemates the attachment organ of a polypide is attached to its vertical wall on the axial side and its frontal wall on the outer side. Because of the continuity of skeletal layers from vertical to frontal walls, zooidal organs of fixed-wall cinctiporids are provided with a uniform laminar lining around the full perimeter of a living chamber (Figures 45, 47). This uniformity can be especially significant for organs that have direct skeletal connections such as attachment ligaments and retractor muscles.

Mural pores (wall pores including both communication




FIGURES 40, 41.—Vertical walls of *Cinctipora elegans*, sta Mu88-29. 40, BMNH 1989.10.20.6: *a*, fractured skeletal shield showing fibrous crystals of transparent layer, inner surface of shield with flattened crystals of laminar layer to left (×1000); *b*, same fibrous crystals (×5000); *c*, broken edge of compound endozonal wall with small irregular crystals of zooidal boundary, fibrous crystals on either side and flattened crystals of laminar lining (×5000). 41, Flattened, irregularly shaped and oriented crystals of laminar layer of endozonal wall, BMNH 1989.10.20.7 (×5000).

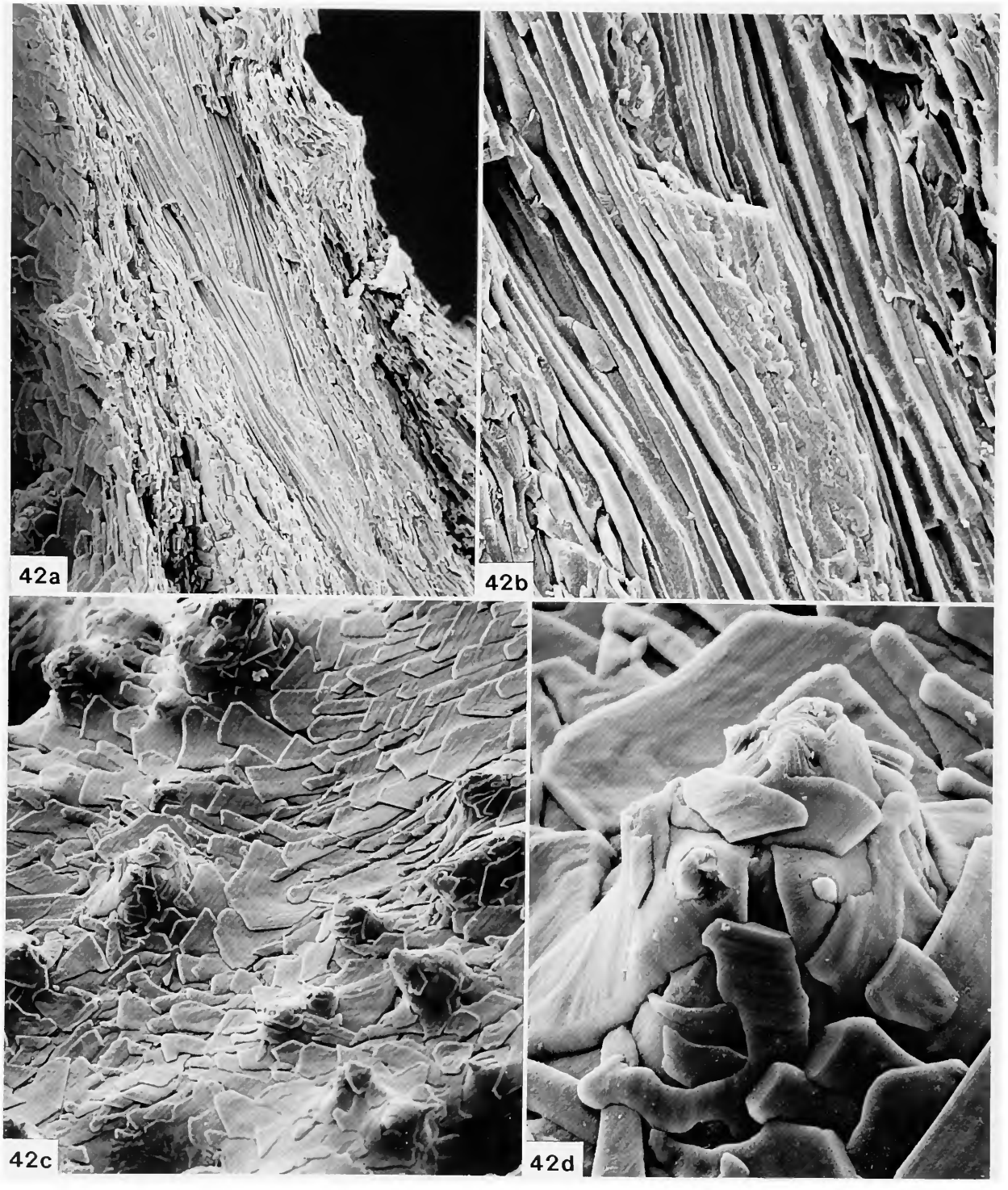
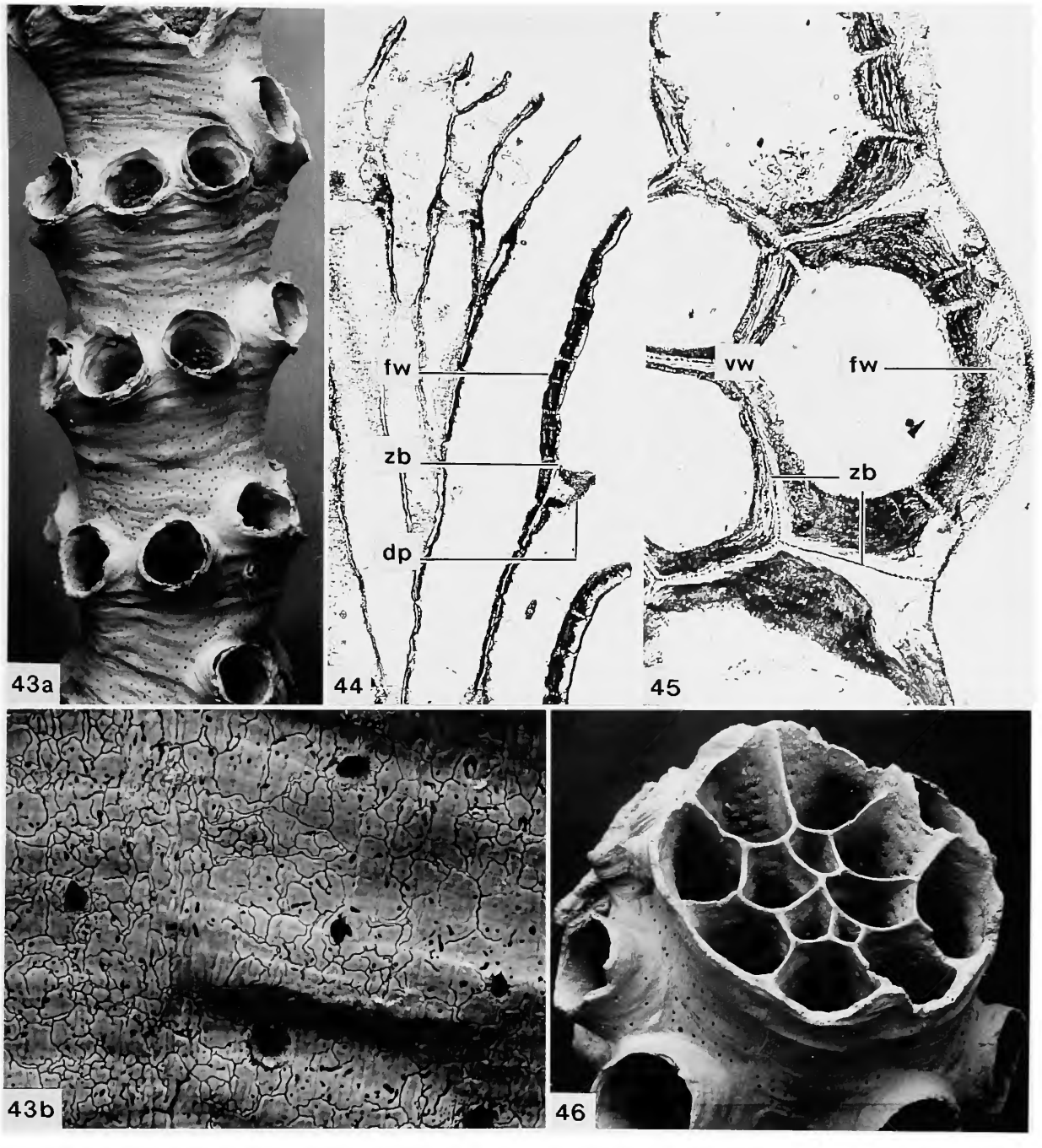
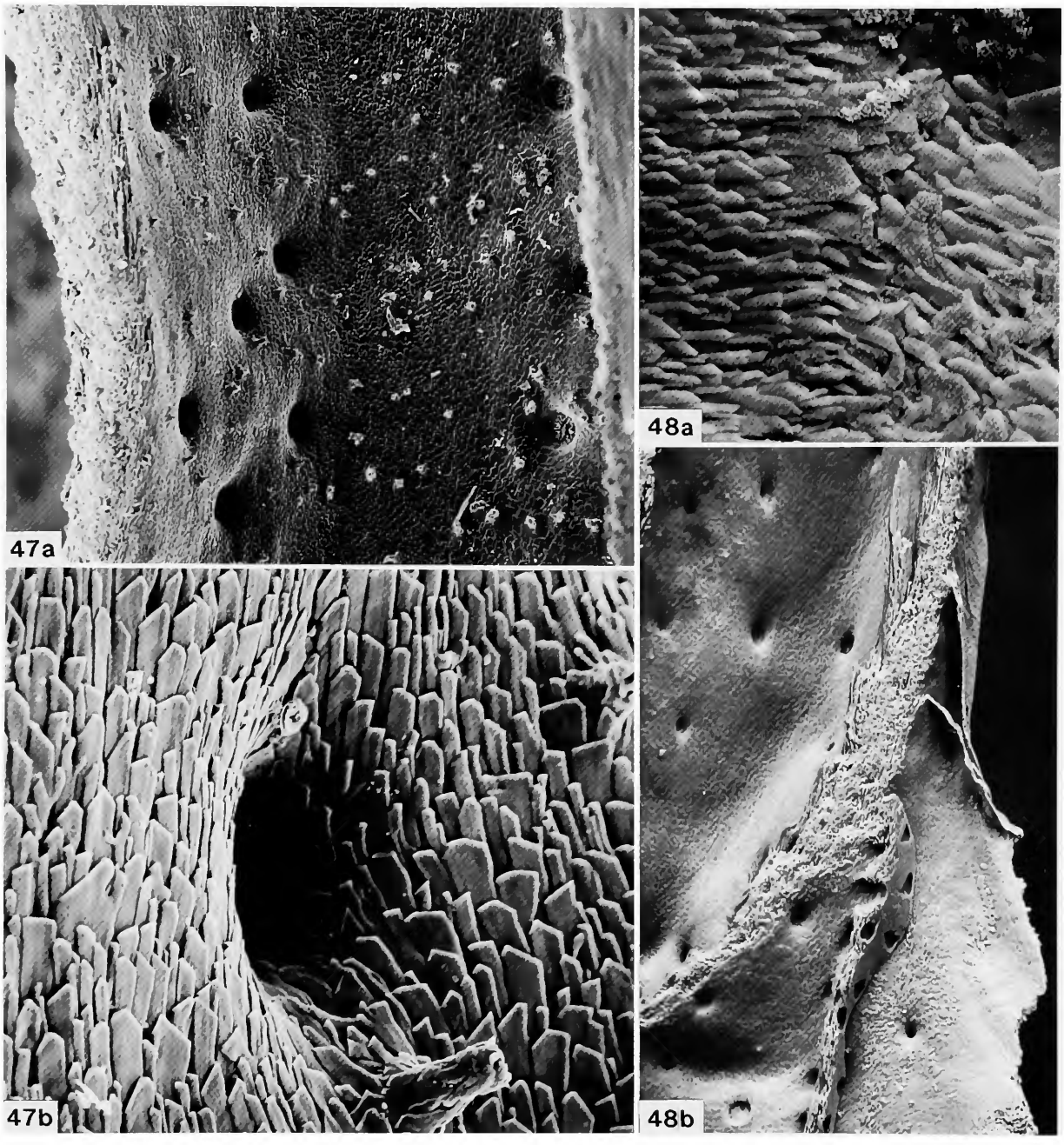



FIGURE 42.—Exozonal vertical walls of *Cinctipora elegans*, BMNH 1989.10.20.6, sta Mu88-29: *a*, broken edge of exozonal wall of skeletal shield with zooidal boundary in middle of compound wall, long fibrous crystals of transparent layer, and smaller crystals with pustules of laminar layer (×1200); *b*, same (×5000); *c*, outer surface of skeletal shield with typical flattened crystal of laminar zone well oriented between pustules (×1200); *d*, same showing single pustule and growth outlines on crystals (×5000).




FIGURES 43–46.—Frontal walls of *Attinopora zealandica*. 43, NZOI sta E746: *a*, branch showing frontal walls with transverse undulations crossing poorly defined zooidal boundaries, scattered pseudopores, and terminal apertures with concentrations of communication pores visible through them, low peristomes, some with emergent peristomes added (×18); *b*, relatively smooth exterior of frontal walls with cuticle removed, some pointed pseudopores (growth direction upward), and zooidal boundary vertical through middle (×320). 44, Longitudinal section showing growing tip with vertical walls of endozone at surface and the last frontal wall (fw) to be grown, distal peristome (dp), and zooidal boundary (zb) at skeletal surface, NZOI sta E281 (×40). 45, Transverse section showing vertical walls of endozone (vw), frontal wall (fw) of exozone, and zooidal boundaries (zb), NZOI sta E281 (×100). 46, Broken end of branch with endozonal walls forming polygonal living chambers within outer ring of frontal walls, NZOI sta C760 (×40).




FIGURES 47, 48.—47, *Attinopora zealandica*, NZOI sta C760: *a*, inner surface of laminar layer of vertical wall to right with communication pores with radial spines, and frontal wall to left with pseudopores lacking radial spines (×250); *b*, inner surface of laminar layer of frontal wall with pustule and pseudopore (×2000). 48, *Cinctipora elegans*, NZOI sta C624: *a*, inner surface of emergent peristome showing some disorderliness in orientaton of crystals of laminar layer (×950); *b*, longitudinal section showing two emergent peristomes bending away from vertical wall above and thicker terminal diaphragm below (×169).

pores and pseudopores) have a differential impact on organs located between vertical and frontal walls. Because of their external position, pseudopores of frontal walls (Tavener-Smith and Williams, 1972:125; Nielsen and Pedersen, 1979:66) do not have the potential for interzooidal transfer of nutrients that communication pores of interior vertical walls have (Figure 47).

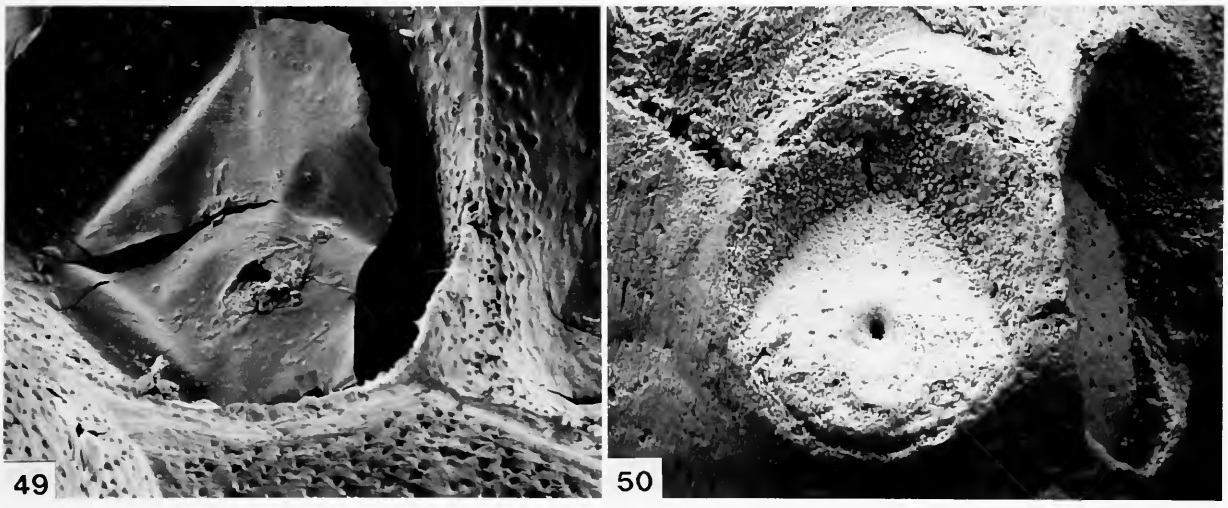
EMERGENT PERISTOMES.—Emergent peristomes are extremely thin and irregularly shaped exterior walls (Figures 6–8). They originate from late-forming laminar layers of a supporting vertical-wall lining. Growth begins at a functional aperture (Figures 7, 48*b*), and the emergent peristome subsequently bends sharply outward and acquires an outer cuticle. Crystals of inner surfaces of peristomes are comparable to those of laminar layers of vertical walls in exozones except for some disorderliness of orientation (Figure 48*a*). Pseudopores similar to those of frontal walls form in basal regions of peristomes but are lacking outwardly. Externally, peristome walls are smoother than frontal walls because undulations are much finer or lacking.

TERMINAL DIAPHRAGMS.—In post-Triassic stenolaemates, terminal diaphragms are exterior skeletal walls formed by calcification on inner sides of membranous diaphragms or orificial walls. In zooids of cinctiporids, terminal diaphragms are formed on the inner surfaces of orificial walls. Terminal diaphragms are generally just inside of emergent peristomes (Figure 48*b*) and are the last of the exterior skeletal walls of zooids to form as they become dormant.

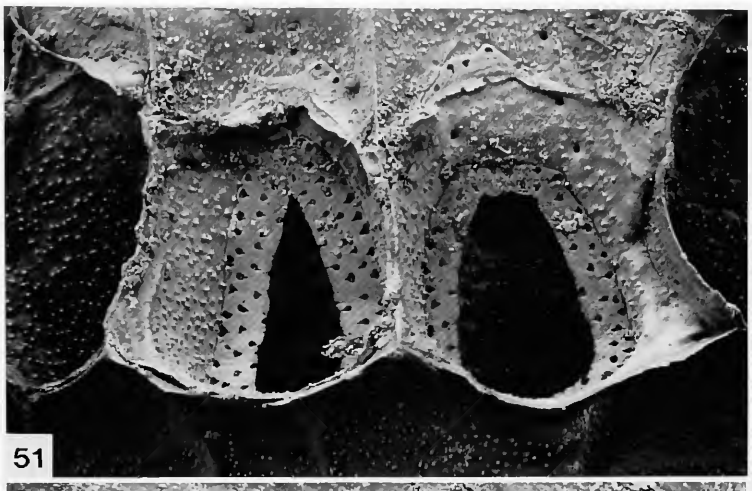
Rarely, the calcification of a membranous orificial wall to form a terminal diaphragm results in the retention of the functional shape of the wall and its orifice (Figures 49, 50). These structures were first reported and interpreted in Jurassic specimens (Walter and Powell, 1973; Boardman and McKinney, 1976:69). Exceptional examples are figured by Pitt and Taylor (1990) in Cretaceous meliceritids.

Calcification of terminal diaphragms in cinctiporids proceeds from late-growing laminae of vertical walls (Figures 48*b*, 52) toward diaphragm centers (Figure 51). Terminal diaphragms also have pseudopores that are pointed on external surfaces and their points are oriented centripetally, consistent with that growth direction. The cuticle of the membrane undergoing calcification remains on the outer surface of the skeletal diaphragm and covers the external ends of the pseudopores (Figure 53). The smoothness of the cuticle is reflected on the external mineralized surface of the diaphragm (Figure 54). The internal surfaces of diaphragms have crystals like those of the laminar layers of vertical walls in exozones and emergent peristomes (Figure 55). The flexibility of the cuticle before calcification is demonstrated by terminal diaphragms that are modified by adhering foreign particles (Figure 52).

We generally have considered that terminal diaphragms result in irreversable dormancy in *Cinctipora*. However, resorption of terminal diaphragms has been reported in the genus *Crisia*, so revival of dormant zooids cannot be ruled out in cinctiporids (Harmer, 1891:142).




FIGURES 49, 50.—49, Membranous orificial wall with outer end of vestibule in center of zooid of *Cinctipora elegans*, BMNH 1989.10.20.8, sta Mu88-29 (×100). 50, Fossil terminal diaphragm, calcified orificial wall, and outer end of vestibule that retained their functional shapes, from holotype of *Semicinctipora amplexus*, NZGS BZ 156, McDonald Limestone, McDonald Quarry, North Otago (×80).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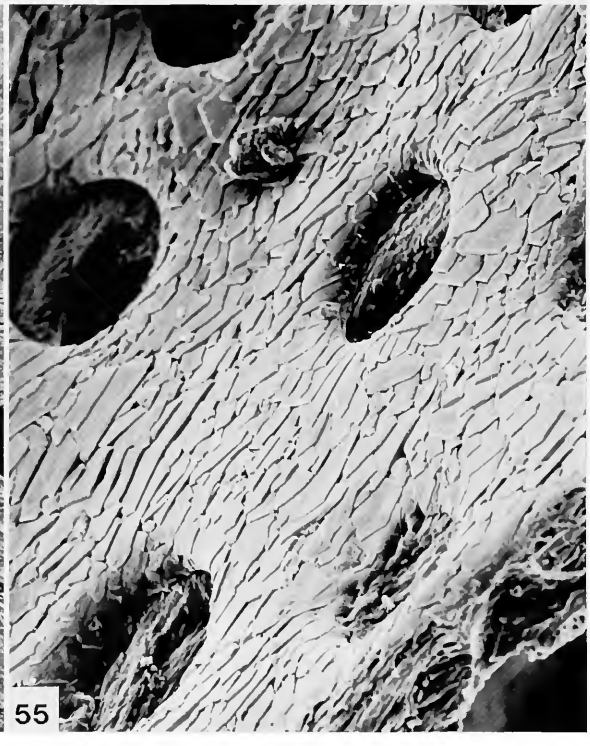
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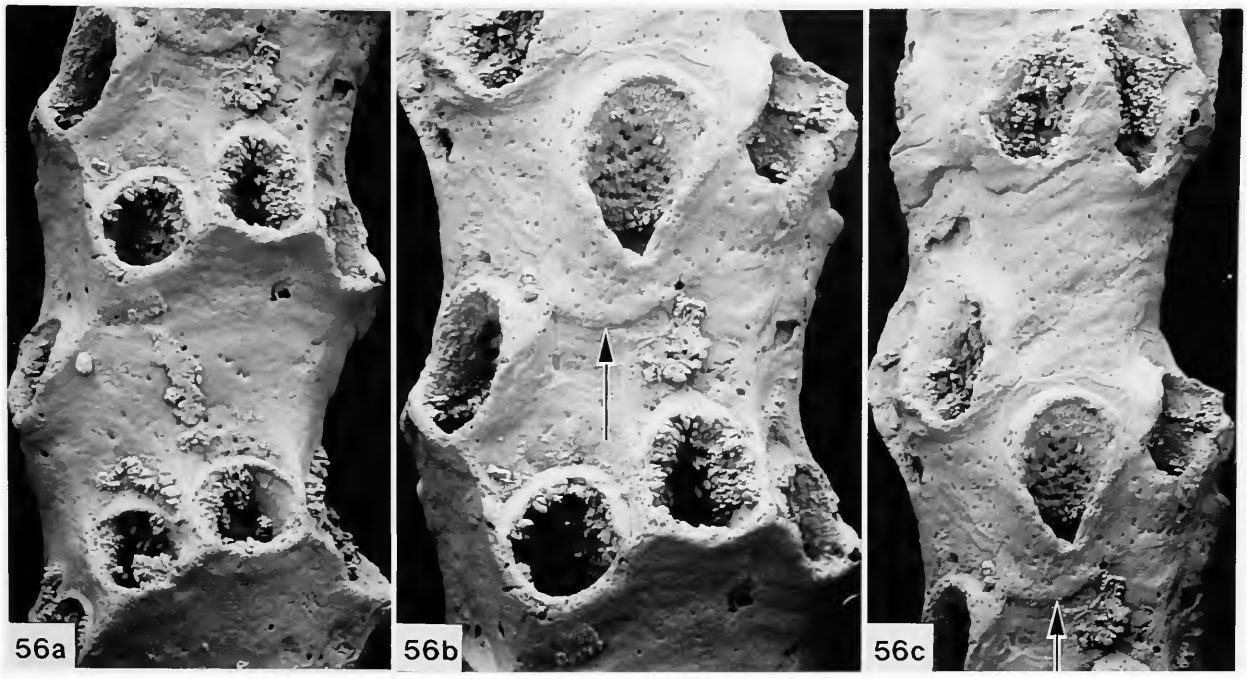



FIGURE 56.—*Cinctipora elegans*, BMNH D58647, Pliocene from Pitt Island of the Chatham Islands: *a*, most of the proximal end of branch showing skeletal shields (×35); *b*, middle of branch, zooids below with skeletal shields, zooids above with frontal walls, boundary between the two regions (arrow) (×42); c, distal end of branch with frontal walls, boundary between regions (arrow) (×35).

## PLASTICITY OF SKELETAL GROWTH

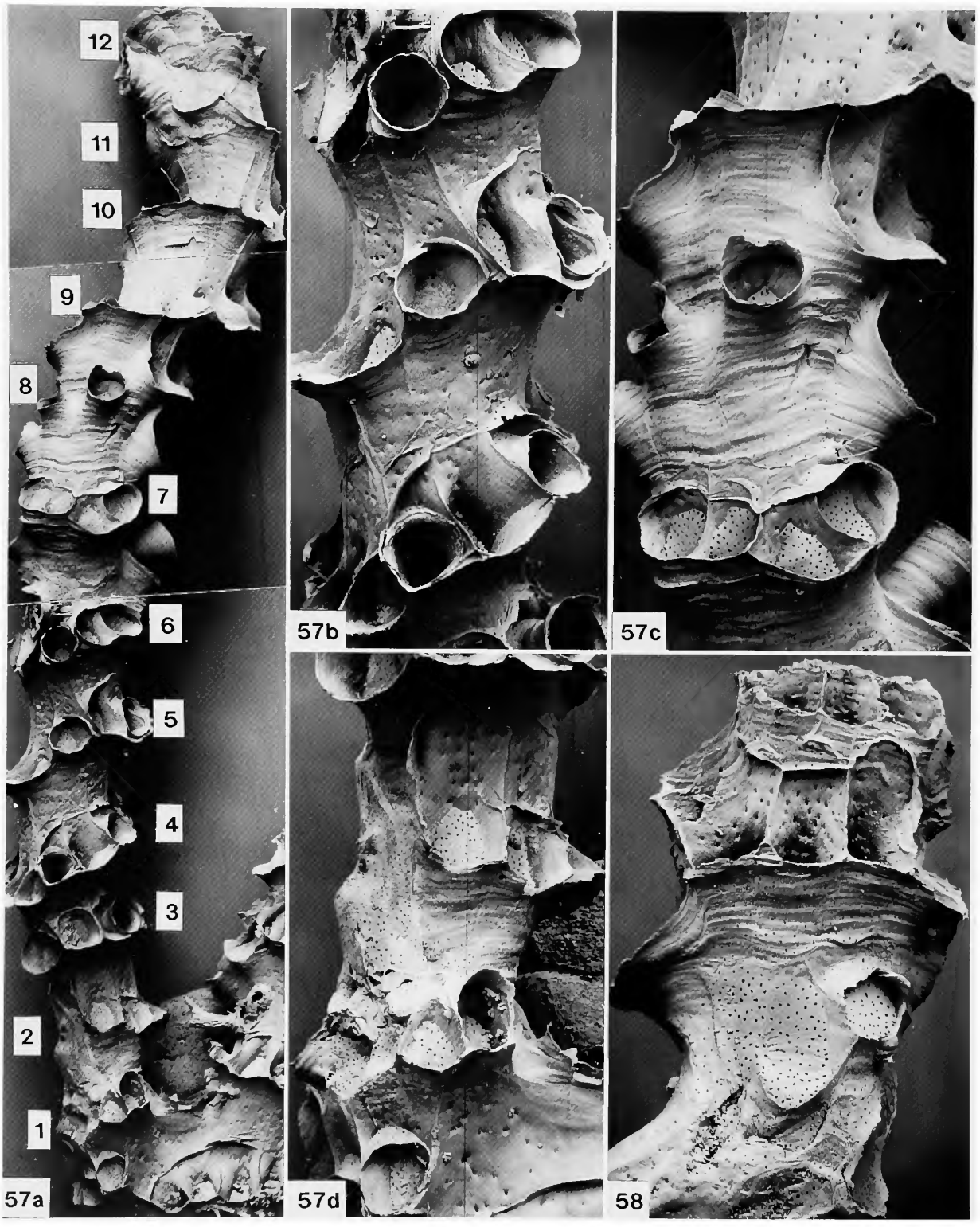
Three cinctiporid colonies are unique in our collections for revealing microenvironmental variation so extreme that it has caused a re-evaluation of the fixed- and free-walled characters in the phylogeny and taxonomy of the cinctiporids (see "Systematics" section below). Some zooids of the three colonies have interior skeletal shields and others have exterior frontal walls resulting in both free- and fixed-walled apertures in a colony, a combination not previously reported within the zone of repetition of a stenolaemate colony (Figures 56–58).

Within branching colonies of most stenolaemates, endozones determine the arrangement of zooids and their apertures at colony surfaces. The morphology of both endozones and exozones is established at the growing tips of the branches. Within the branches of the three unusual colonies the endozones have the spiral arrangement of zooids normal for the species. The unexpected variations in body walls occur in the exozones as growth proceeds from whorl to whorl.

One colony with both free- and fixed-walled apertures is represented by a single branch of *C. elegans* from the Pliocene of the Chatham Islands (Figure 56). The branch begins proximally with free apertures and skeletal shields. Distally the branch changes abruptly to fixed apertures and frontal walls. Apparently, the colony had the genotype for both types of exozones and underwent a microenvironmental change to develop the frontal walls.

The other two unusual colonies are Recent specimens of *C. elegans* from a station just west of the Chatham Islands. Disregarding emergent peristomes that form subsequently below growing tips of branches, the zooids of whorls 3 to 5 and

FIGURES 51–55 (opposite page).—Terminal diaphragms of *Cinctipora elegans*. 51, Partially formed terminal diaphragms and emergent peristomes, BMNH 1989.10.20.2, from Otago Shelf (×69). 52, Longitudinal section with terminal diaphragm connected to late-forming laminar layer of zooidal wall, foreign particle bent cuticle before calcification, USNM 250065, sta Mu76-138 (×50). 53, External view of terminal diaphragm and pseudopores covered with cuticle, BMNH 1989.10.20.8, sta Mu88-29 (×700). 54, Outer side of terminal diaphragm with cuticle removed, pointed pseudopores and joints between plates toward center of diaphragm, BMNH 1989.10.20.10, sta Mu88-29 (×700). 55, Inside surface of terminal diaphragm with crystals of laminar layer, BMNH 1989.10.20.9, sta Mu88-29 (×1200).




FIGURES 57, 58.—*Cinctipora elegans*, NZOI sta C624. *57a*, Branch with complex development of both interior skeletal shields and exterior frontal walls, numbers are whorl numbers used in text discussions (×12); *57b*, whorls 3–6, mostly skeletal shields (×26); *57c*, whorls 7–9, mostly frontal walls (×26); *57d*, whorls 1–3, both skeletal shields and frontal walls (×26). 58, Short branch with complex development of skeletal shields and frontal walls (×28).

10 (Figure 57*a,b,d*) (in the more complex and interesting of the two colonies) developed skeletal shields proximally and distally from their apertures and, before the growth of any emergent peristomes, were free-walled (Figure 59, whorls A, F). The zooids of whorls 1 and 6 (Figure 57*b,d*) were formed with apertures having skeletal shields and free orificial walls proximally and frontal walls and fixed orificial walls distally (Figure 59, whorl B). Some zooids of whorl 8 (Figure 57*c*) developed frontal walls both proximally and distally and were fixed-walled (Figure 59, whorls C, D). Zooids of whorls 2 and 7 (Figure 57*c,d*), and some zooids of whorls 8 and 9 (Figure 57*c*) have frontal walls and fixed apertures proximally and skeletal shields and free apertures distally (Figure 59, whorl E).

Only a small branch of the second Recent colony is available (Figure 58) and it has an alternation of proximal frontal walls followed by distal shields to produce fixed-free apertures (Figure 59, whorl E). Before reaching the apertures of the next whorl distally some of the shields support an expansion of exterior skeletal wall on their surfaces (see discussion of exterior ridges below). Another interpretation of this short branch is as a distal rejuvenation of an injured or possibly broken branch and therefore the alternation of frontal wall to skeletal shield is the beginning of a secondary zone of astogenetic change characteristic of rejuvenations in *C. elegans*.

In cinctiporids, the outer skeletal wall distal to the aperture of a zooid is the wall proximal to the aperture of the zooid in the next younger whorl. Therefore, the proximal walls of zooids in a whorl, whether they are interior skeletal shields or exterior frontal walls, are generally determined at the distal sides of the apertures of the zooids of the next older whorl. The distal sides of the apertures of a whorl are determined at the growing tip of a branch as exozonal growth begins. For example, the proximal side of aperture B (Figure 59) was determined by the distal side of aperture A. If the distal side of A had been fixed and a frontal wall grown, zooid B would have been like zooids C and D. If the distal side of D had been free and and a skeletal shield grown, zooid E would have been like zooids A and F.

As a result of this dependent relationship of zooids in adjacent whorls, it is evident that zooid B can be produced in a sequence of A to C and zooid E can be produced in a sequence of D to F. Zooids B and E can also be produced in adjacent whorls (Figure 57*a,d*, whorls 1 and 2) by alternating the growth of skeletal shields and frontal walls on distal sides of apertures from whorl to whorl.

The distal side of an aperture also determines whether that aperture is terminal or subterminal in cinctiporids. Subterminal apertures formed in zooids A, E, and F (Figure 59) because their axial vertical walls grew distally as skeletal shields, taking their zooidal boundaries distally past their functional apertures to the proximal sides of the next younger apertures. Terminal apertures formed in zooids B, C, and D because growth of their axial vertical walls was terminated at the distal sides of their apertures by junctions with outer cuticles to form the short,

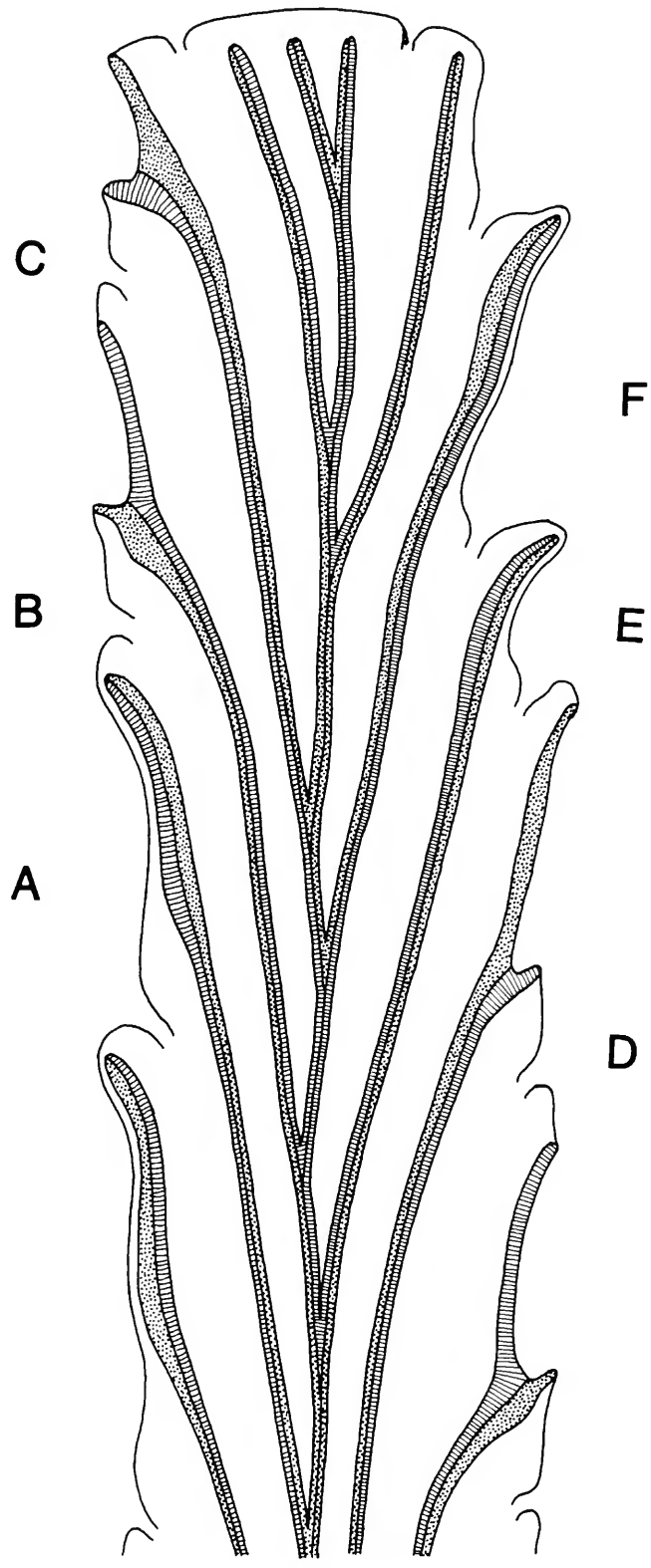



FIGURE 59.—Different combinations of skeletal shields and frontal walls at lettered apertures of specimen in Figure 57.

exterior-walled peristomes.

We can only assume that either extrinsic or intrinsic microenvironmental conditions control the development of interior skeletal shields and exterior frontal walls within the genotype of this single colony (Figure 57). The most evident factor in this interchangeability is the apparent ease with which outer cuticles can alternate from membranous exterior walls opposite interior skeletons to direct contact with exterior skeletal walls and back again. Empirically, contact of zooidal boundaries of vertical walls with outer cuticle produces an exterior frontal wall distally and lack of contact permits the vertical walls of endozones to continue distal growth as skeletal shields. This change can even occur laterally within a single whorl (whorls 2 and 8, Figure 57*c,d*), suggesting zooidal rather than colony control of distal walls in those relatively few zooids as exozones begin to develop at growing tips of branches.

A major variation of shield-frontal wall alternation occurs in the fossil species *Semicinctipora annulata* (Figures 60, 61). The alternation apparently occurs in all zooids of the species, indicating genetic rather than microenvironmental control of expression. Zooid apertures are arranged annularly. Externally they have curved and broadly convex distal margins, and straighter and relatively sharp proximal margins when unbroken. In longitudinal sections distal margins are seen to be free-walled and proximal margins are fixed-walled (Figure 61). The changeover from interior to exterior skeletal walls occurs approximately midway between whorls. The changeover apparently was accomplished by the zooidal boundaries in the compound interior walls intersecting the exterior cuticle to terminate the distal skeletal growth of the proximal zooids. Skeletal growth continued distally as simple exterior walls (frontal walls) of the next younger zooids to form their attached proximal apertures. The contact between zooidal boundaries of compound interior walls and exterior cuticle midway between whorls terminated vertical wall growth just as it does in the formation of frontal walls at apertures.

Returning to the larger colony of *C. elegans* with outer-wall alternations (Figure 57), changes from skeletal shields to frontal walls occur between the apertures of whorls 7 and 8 (Figures 57*c*, 62*a*), and 10 and 11 (Figures 57*a*, 62*b*). These changes require the cuticle of the membranous walls over the shields to change distally to a contiguous cuticle covering the frontal walls. Sections of *S. annulata* (Figure 61) indicate how these changes are made. If frontal wall undulations are indeed time indicators, these changes are not made simultaneously around the branches.

It seems likely that a change from frontal wall to shield can not be made in a distal direction between whorls. This change would require the cuticle to become loosened from the frontal-wall skeleton and the growth of the outer side of a compound wall initiated. We have not found that sequence.

Structures other than outer skeletal walls further demonstrate the versatility of skeletal growth of cinctiporids. In addition to the scattered emergent peristomes discussed above, thin, irregularly shaped ridges of skeleton originate from thin layers of interior laminar skeleton of skeletal shield (Figures 57*b*, 58, 62*a*). These thin layers of interior skeletal walls presumably lack contiguous cuticles until they bend outward at high angles from originating walls to become exterior skeletal walls. Apparently, the cuticle of the membranous exterior walls covering the interior skeletal walls can be readily incorporated onto the exterior skeleton of peristomes and smaller irregular patches wherever needed.

The contiguous cuticle and the lack of a depositing epidermis on outer surfaces of exterior frontal walls presumably keep patches of interior skeleton from originating there.

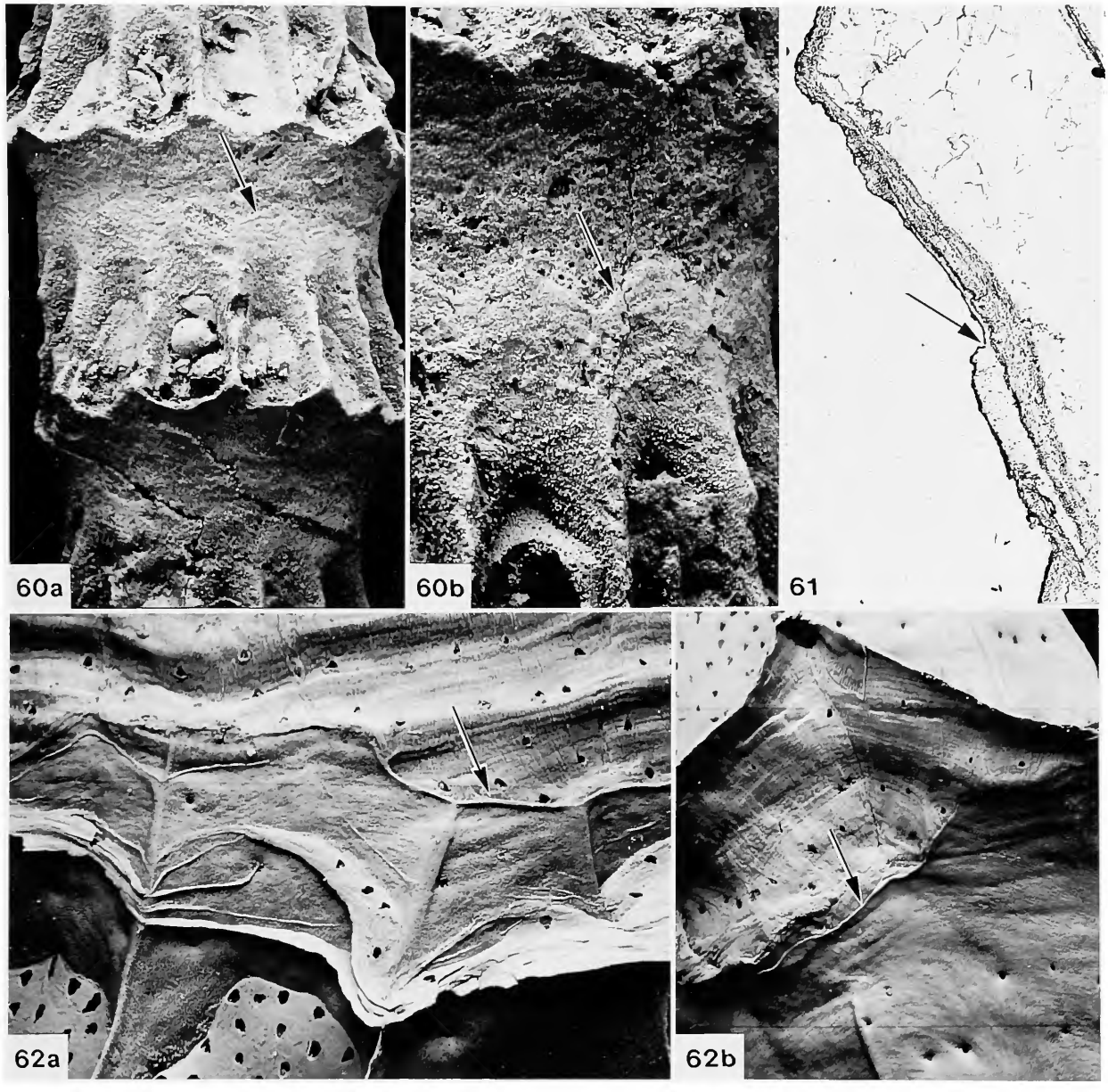
## Growth of *Cinctipora elegans*

### Polypide Growth and Cycles

Some ontogenetic variation has always been assumed for stenolaemate soft parts, but they have not been studied or illustrated in detail. Further, the relationship of ontogeny and polypide cycles (degeneration-regeneration cycles) to the growth of soft parts has never been studied in stenolaemates. Detailed histological studies of the initial budding of stenolaemate polypides have been published (Borg, 1923; 1926: 319–334; Nielsen, 1970), but subsequent ontogeny of polypides has only been mentioned (Silén and Harmelin, 1974; Boardman and McKinney, 1985:38; McKinney and Boardman, 1985:202; McKinney, 1988; McKinney and Jackson, 1989). Study of the growth of soft parts in stenolaemates is long overdue and is essential to improving our basic understanding of the skeletal features of the class.

The polypide cycle in Bryozoa has been interpreted as a reaction to adverse environments, to embryogenesis, or as a form of excretion. Gordon (1977) interpreted the cycle as a rejuvenation that extends the life span of the zooid and colony. Polypide recycling in stenolatemates seems to be essential to the mode of growth of tubular skeletons that are much longer than enclosed polypides (Boardman, 1971:18; 1983:78–81). With each regenerating phase of the cycle, new polypides are established in new outward positions from their immediate predecessors to permit continued outward lengthening of zooidal walls. Lengthing by recycling occurs in both endozones and exozones in many stenolaemates.

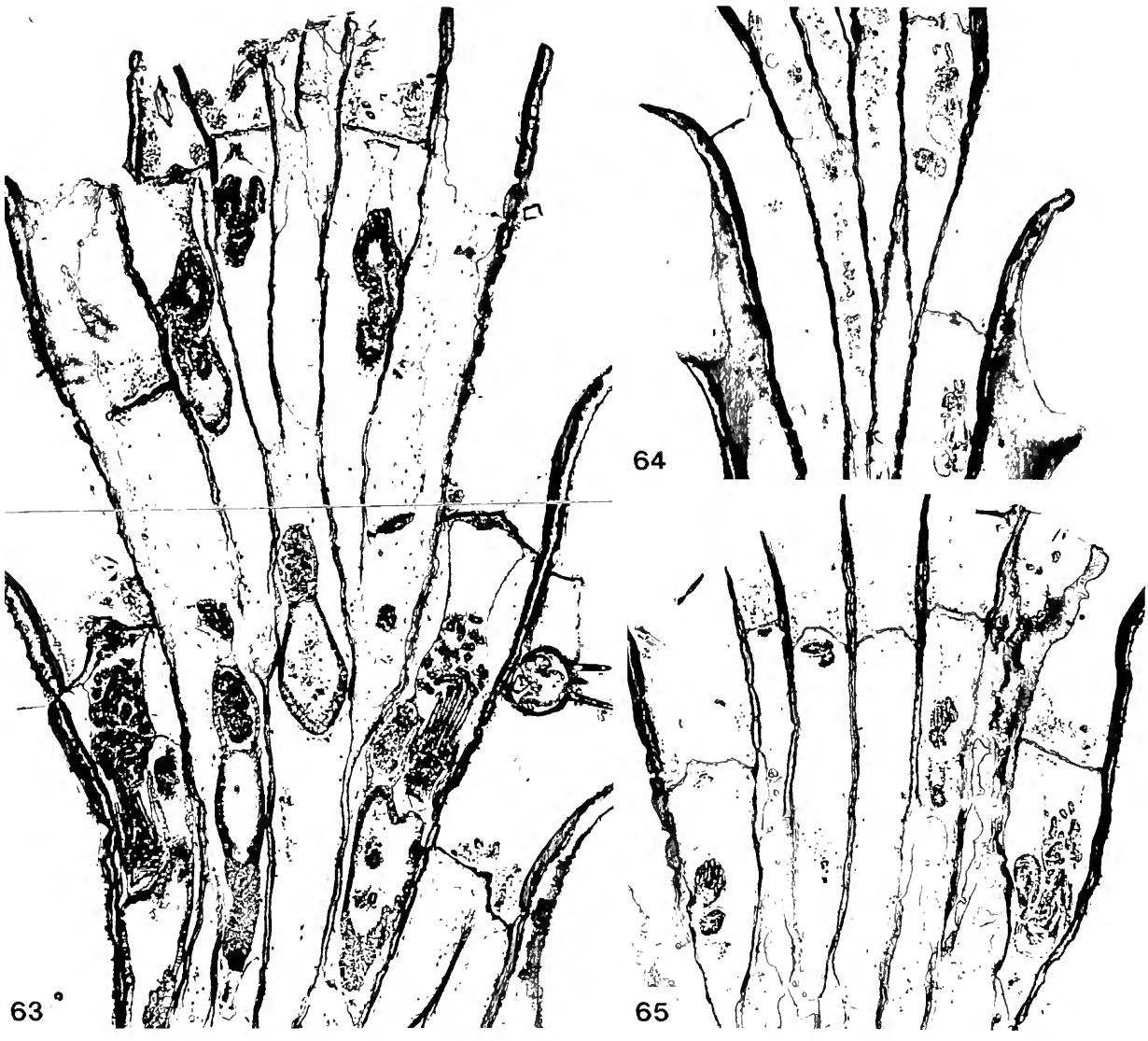
Polypide cycles are assumed for *C. elegans* because of the presence of single brown bodies in some zooids and the size relationships of polypides in functioning zooids. The fully regenerated state of the cycle is assumed for branches of *C. elegans* that display maximum ranges of ontogenetic sizes of polypides (Figure 63). The smallest polypides are in the youngest zooids located axially in the endozones at growing tips of branches. The largest polypides are attained by zooids in permanent lateral positions in the third or fourth whorls. Proximally, fully regenerated polypides are slightly smaller and




FIGURES 60–62.—60, 61, *Semicinctipora annulata*, Lower Miocene, Forest Hill Limestone, Forest Hill Quarry. 60, NZGS BZ 154 (holotype): *a*, branch showing typical external shape of zooids, boundary between vertical wall and frontal wall midway between whorls (arrow) (×30); *b*, frontal wall with pseudopores above boundary (arrow) with vertical wall below (×75). 61, BMNH D59305, longitudinal section showing vertical wall with thickened transparent layer followed distally (arrow) by frontal wall with thin outer transparent layer and laminar layer of skeletal lining (×100). 62, *Cinctipora elegans*, NZOI sta C624: *a*, two terminal diaphragms below of whorl 7 of branch in Figure 57, proximal parts of skeletal shield with ridges of thin exterior wall, followed by (arrow) frontal wall that continues to the next aperture of whorl 8 above (×119); *b*, change from skeletal shield to frontal wall (arrow) just below aperture of whorl 11 (×79).

the pink zone of active zooids generally extends for only about 8 whorls, approximately 10 mm, below growing tips. Below this pink zone the zooids are dormant; their apertures are covered by calcified terminal diaphragms forming a necromass.

The degenerated state of the cycle is assumed for zooids of *C. elegans* that lack lophophores and alimentary canals but are




FIGURES 63–65.—*Cinctipora elegans*, all longitudinal sections. 63, Fully regenerated growing region showing maximum ontogenetic size variation of polypides, undersized polypides have attached retractor muscles, USNM 250065, sta Mu76-138 (×50). 64, Colony in regenerating stage with uniformly undersized polypides with attached retractor muscles in permanent exozonal positions, USNM 454191, off Otago Heads (×30). 65, Regenerating colony with axial zooids of growing tip with attachment organs in temporary position but lacking polypides, undersized polypides to extreme right and left with attached retractor muscles, polypide to extreme right doubled up apparently with unattached funicular muscle, USNM 454192, sta Mu76-138 (×50).

not dormant, that is, zooids that also lack thickly calcified terminal diaphragms. Flattened attachment organs apparently are retained in exozonal zooids from cycle to cycle (Figure 3). A brown body is found in many of these zooids. Brown bodies do not accumulate in living chambers as they do in many other stenolaemates, so most of them apparently are eliminated or absorbed before the fully regenerated state is reached.

Colonies are assumed to be in various stages of regeneration of the cycle when polypides of the older zooids having fully developed exozones in functioning ends of branches are either uniformly or unevenly undersized (Figures 64, 65).

No colony sectioned for this study was completely degenerated. One colony with a branch of mostly degenerated zooids (Figure 3) also had another branch of functioning zooids down through the fourth whorl (Figure 15). In the fifth and sixth whorls the polypides were progressively more degenerated.

Proximally from the sixth whorl, the zooids were generally dormant with calcified terminal diaphragms and single brown bodies. Apparently, colonies can have branches at different stages of the polypide cycle. This colony also suggests that the final degeneration of polypides is a preliminary step to the formation of calcified terminal diaphragms and resulting zooid dormancy.

Using these criteria to recognize the stages of polypide cycles, branches from eight sectioned colonies were inferred to have zooids fully regenerated. Four of these were collected in March on the Otago Shelf off the Otago Heads, three from station Mu76-138 in October (one of these also had the degenerated branch), and the eighth from the edge of the continental shelf off the Otago Peninsula, date unknown. Of the 11 colonies that have both degenerated and regenerating polypides in varying proportions, eight were collected in January from station 1430, two from station Mu76-138 in October, and one from the Otago Shelf off the Otago Heads in March. These few colonies seem to show no seasonal pattern to polypide cycles in the species.

## Polypide Growth and Attachment Organs

The positions of retracted polypides within enclosing skeletons is determined in most stenolaemates primarily by attachment organs. In zooids of *Cinctipora elegans*, the retracted positions of polypides are fixed permanently, relative to enclosing skeletons, near the beginning of the exozone. The fixed position is indicated by the formation of a single ring of attachment scars formed by ligaments inset into the skeletal lining of the vertical walls of zooids of some colonies. Inward from attachment rings the vertical walls are smooth and laminar, outwardly they are pustulose and laminar (Figure 9*a–c*). Ligaments of an attachment organ in this position apparently remain in the scars of the ring in the skeletal wall from cycle to cycle as the laminar lining thickens around the ligaments. Apparently, two kinds of depositing epidermis produce the smooth and pustulose microstructures in the laminar layers of vertical walls and these layers remain fixed in place on either side of the ring of attachment scars as thickening of the laminar layers proceeds.

In exozonal zooids proximal to growing tips of *C. elegans*, polypide regeneration growth necessarily starts from the flattened attachment organs (Figure 3) and extends inward. This is because every lophophore and alimentary canal, no matter what regenerating size, is fastened to an attachment organ.

Undersized polypides in studied sections, including those of younger endozonal zooids or regenerating exozonal zooids, can be seen to have lophophore retractor muscles attached to skeletons (Figures 63–67). Also, many reveal attached funicular muscles and faecal pellets in digestive tracts (Figure 66). Zooids in one narcotized colony in an early regenerating stage display the partial ability of undersized polypides to protrude lophophores with faecal pellets in rectums (Figure 7). Some of the smallest regenerating polypides have attached lophophore retractor muscles but their tentacles are perhaps too short to have begun feeding (Figures 65, 67). Therefore, during their inward regenerative growth from attachment organs, fully formed but still undersized polypides have functioning musculature and alimentary canals that permit them to ingest and presumably to supply at least some of their own nutrients. The smallest fully formed polypides apparently started ingesting while their mouths and tentacle crowns were well within living chambers when fully protracted (Figure 69).

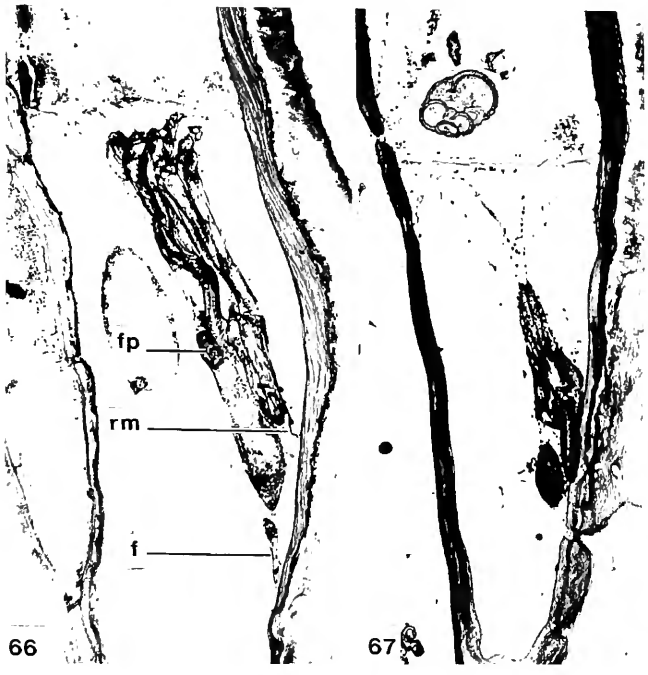
We assume here that in order to attain full size in exozonal zooids a polypide of *C. elegans* has to undergo continuous growth inward from its attachment organ within one regenerating phase. In order to grow that much in a single phase, polypides must shift attachment points of lophophore retractor muscles and funicular muscles inward along skeletal surfaces.

Nielsen and Pedersen (1979, fig. 22) illustrate a thickened filamentous basement membrane of the membranous sac and a thin epithelial cell between the end of a retractor muscle and its skeleton in the genus *Crisia*. The muscle, the two layers of tissue, and the organic matrix of the calcified wall are all held together by hemidesmosomes. Perhaps the migration of muscle insertions called for in cinctiporids and probably occurring in many other stenolaemates with attachment organs compares to the shifting of adductor muscles and their scars during the growth of a clam shell.

The gradual shifting of the skeletal attachment of funicular muscles inward during a single regenerating growth cycle of a polypide, and the observation that only two of the insertions seen in section are directed toward communication pores indicates that the funiculus does not act as a means of interzooidal communication. If indeed the shifting is gradual during growth the insertion will most commonly be over skeleton rather than over the widely and irregularly spaced communication pores. Insertion over a communication pore therefore would be fortuitous and it is unlikely that the funiculus is a means of communication between zooids in *C. elegans*.

A search for markings on inner surfaces of skeletal walls reveals longitudinal grooves that can completely line living chambers from inner ends to attachment ligaments (Figure 9*d,e*). Thus, they are too broadly distributed to have been caused either by sliding muscle insertions or attachment ligaments and are not understood.

Zooids that lack visible attachment scars (Figures 11, 12*a*) apparently do not signify a different mode of growth for regenerating polypides. Some colonies have zooids both with and without visible scars (Figure 12). It seems unlikely that two different modes of growth of feeding polypides occur in the same colony or species. Also, the length of exozone shields is not longer for zooids lacking attachment scars than for those that have them, suggesting that attachment organs remain in a fixed position at bases of exozones regardless of the formation of scars. Measurements indicate that the vertical walls forming




FIGURES 66-67.—Undersized polypides of *Cinctipora elegans*, all longitudinal sections. 66, Undersized polypide in exozone of regenerating colony with faecal pellet (fp), attached retractor muscles (rm), and funiculus (f), USNM 454193, sta 1430 (reduced to ×79 for publication). 67, Undersized polypide in exozone of regenerating colony with attached retractor muscles, perhaps too undeveloped to ingest, USNM 454194, sta 1430 (reduced to ×79 for publication).

skeletal shields in functioning zooids continue to increase in thickness in exozones (Figure 70). Perhaps, however, zooids that lack scars were not functional long enough or deposited laminar tissue fast enough near the bases of shields to build up deposits around attachment ligaments. No explanation is suggested for polypide growth in zooids that develop pustules in the laminar layer well below the expected attachment level (Figure 12*a*).

## BRANCH GROWTH AND ZOOIDAL GROWTH RATES

Growth of elongated branches in colonies of stenolaemates requires that endozones of zooids grow parallel to branch axes at faster rates than exozones grow laterally. Branching habits in cinctiporids primarily are produced by four factors: (1) faster growth rates in endozones than in exozones, (2) attachment organs establishing permanent positions in exozones, (3) zooids intersecting colony surfaces at low angles, and (4) early dormancy of zooids and the resulting cessation of growth of exozones.

The two different growth rates, one endozonal and the other exozonal, involve both skeleton and soft parts in *C. elegans*.

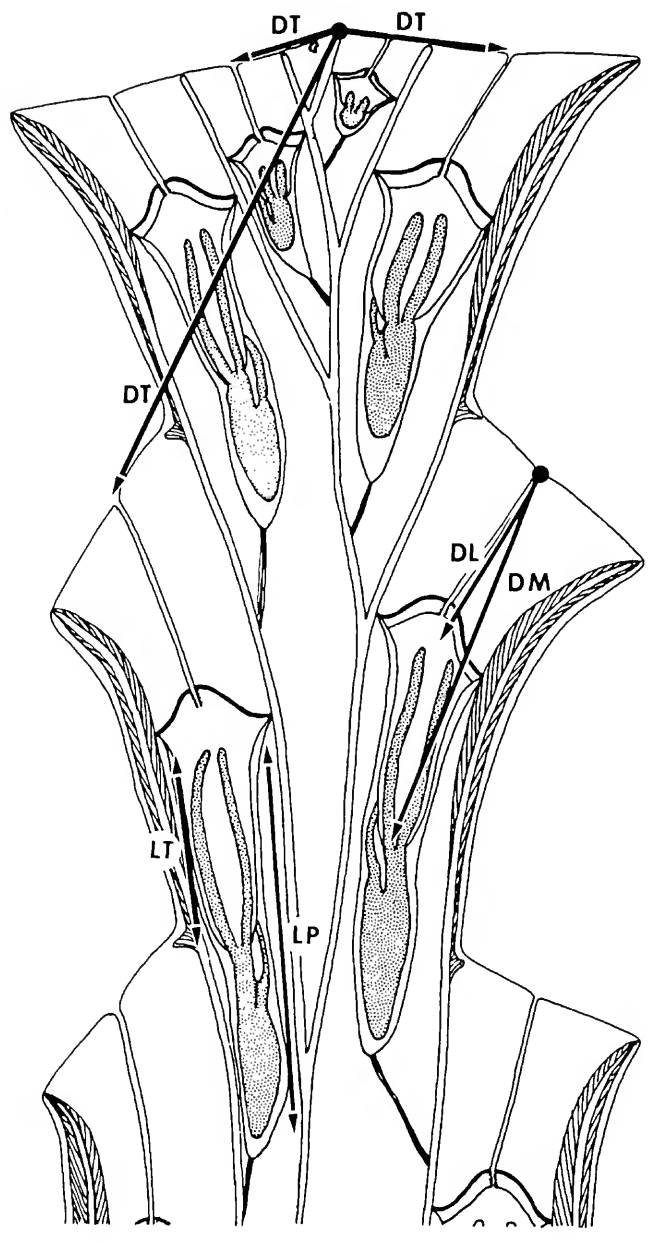



FIGURE 68.—Measurements of organs, longitudinal view. Key: DT = distance from growing tip of branch to center of functional aperture, LT = length of tentacles, LP = length of polypide, DL = depth to ligament attachment, DM = depth to mouth, DM − DL = length of tentacle sheath. Relative positions of polypides in chambers and shelf on distal sides of apertures not correct.

The change in growth rate from the faster growing endozones to the slower growing exozones (boundary indicated by the dotted band in Figures 70-77) begins approximately 0.8 mm from the branch tip (linear distance DT, Figure 68) as living chambers develop their full diameters (Figure 72) and vertical walls begin to thicken to form skeletal shields (Figure 70). The

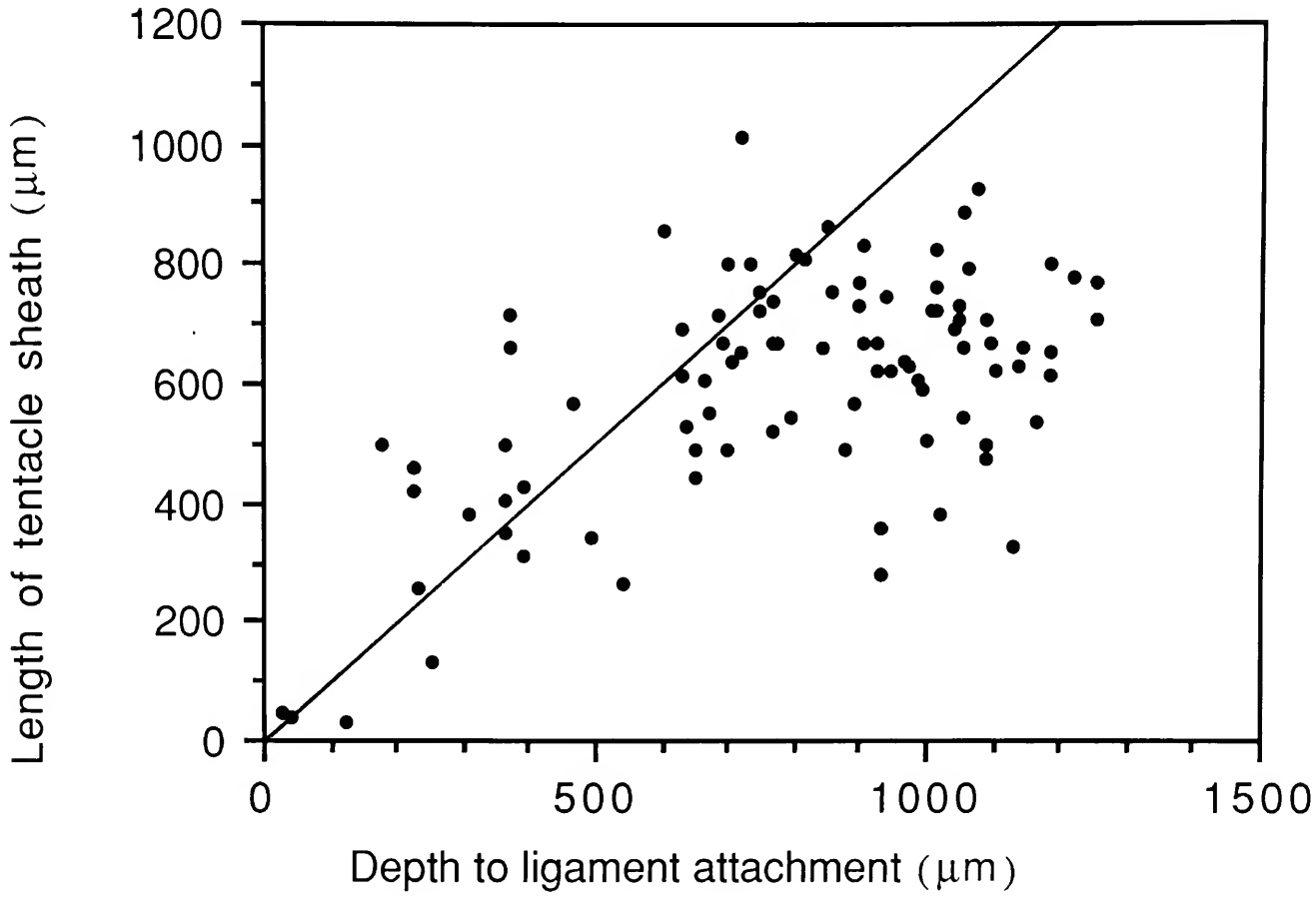



FIGURE 69.—Scatter diagram of length of tentacle sheath against depth of ligament attachment in *Cinctipora elegans*. Diagonal line plots equal length and depth measurements. Only those zooids with points above line can protrude lophophores fully if tentacle sheath does not stretch.

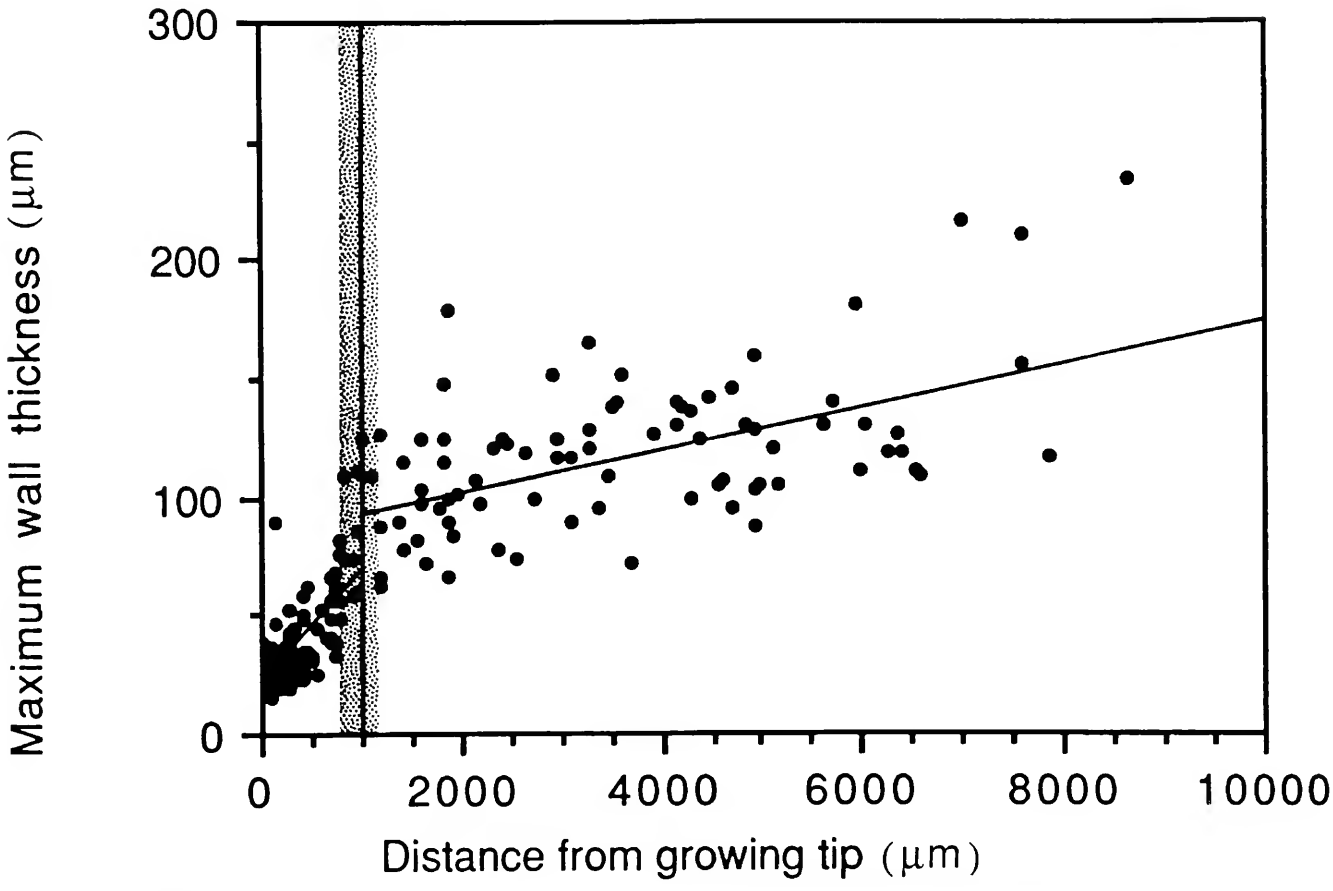
establishment of living chambers with exozonal dimensions is followed at approximately 1 mm from the branch tip by polypides that, when fully regenerated, attain full size and fixed positions in living chambers for the first time (Figures 73, 74). In *C. elegans* the change from endozonal to exozonal growth generally occurs somewhere in the third whorl below branch tips.

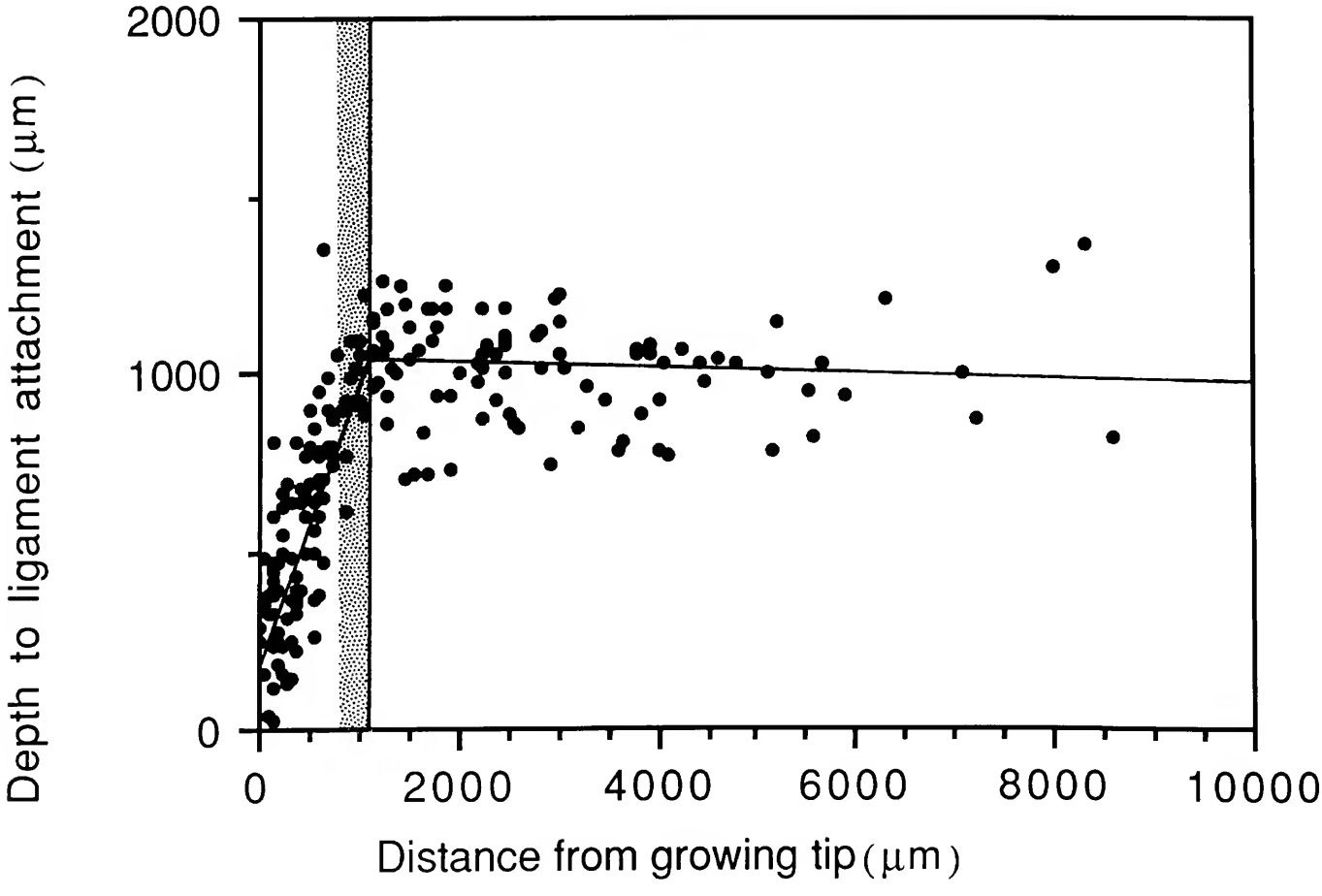
Polypides have their maximum length within the most distal 2 mm of exozonal growth (1000–3000 μm from growing tips in Figure 73); this is also the region of greatest absolute tentacle length (Figure 74). Presumably, therefore, this is the region of greatest nutritional intake.

Polypides of intermediate length, however, have the longest tentacles in proportion to their overall length (Figure 75). Of these, it is the polypides of intermediate length within 1 mm of growing tips, within exposed endozones, that have proportionally the very longest tentacles (above 70% in Figure 76). Presumably, fully regenerated zooids having the proportionally longest tentacles are the most robust, that is, capable of providing nutrients for the highest growth rates. These tentacles are concentrated in the most distal few whorls of growing tips where endozonal growth rates of both skeletons and soft parts must be the most rapid in order to produce branching colonies.

In addition to supporting the growth habit requirement that endozones grow faster than exozones in *C. elegans*, the correlated growth rates of both skeletons and polypides in endozones also explain why fully regenerated polypides in endozones are roughly proportional in size to their skeletons.

The change in skeletal growth rates depicted in the graphs must be generally true for branching colonies of radially arranged zooids in fossil and Recent stenolaemates. The proportional growth rates of soft parts and skeleton in *C. elegans* also suggests that proportional hard-soft growth has occurred in other dendroid stenolaemates (McKinney and Boardman, 1985; McKinney, 1988; and personal observations). Other zooidal patterns provide different ontogenetic


Maximum wall thickness (μm)
300
200
100
0
0
2000
4000
6000
8000
10000
Distance from growing tip (μm)


Depth to ligament attachment (μm)
2000
1000
0
0
2000
4000
6000
8000
10000
Distance from growing tip (μm)

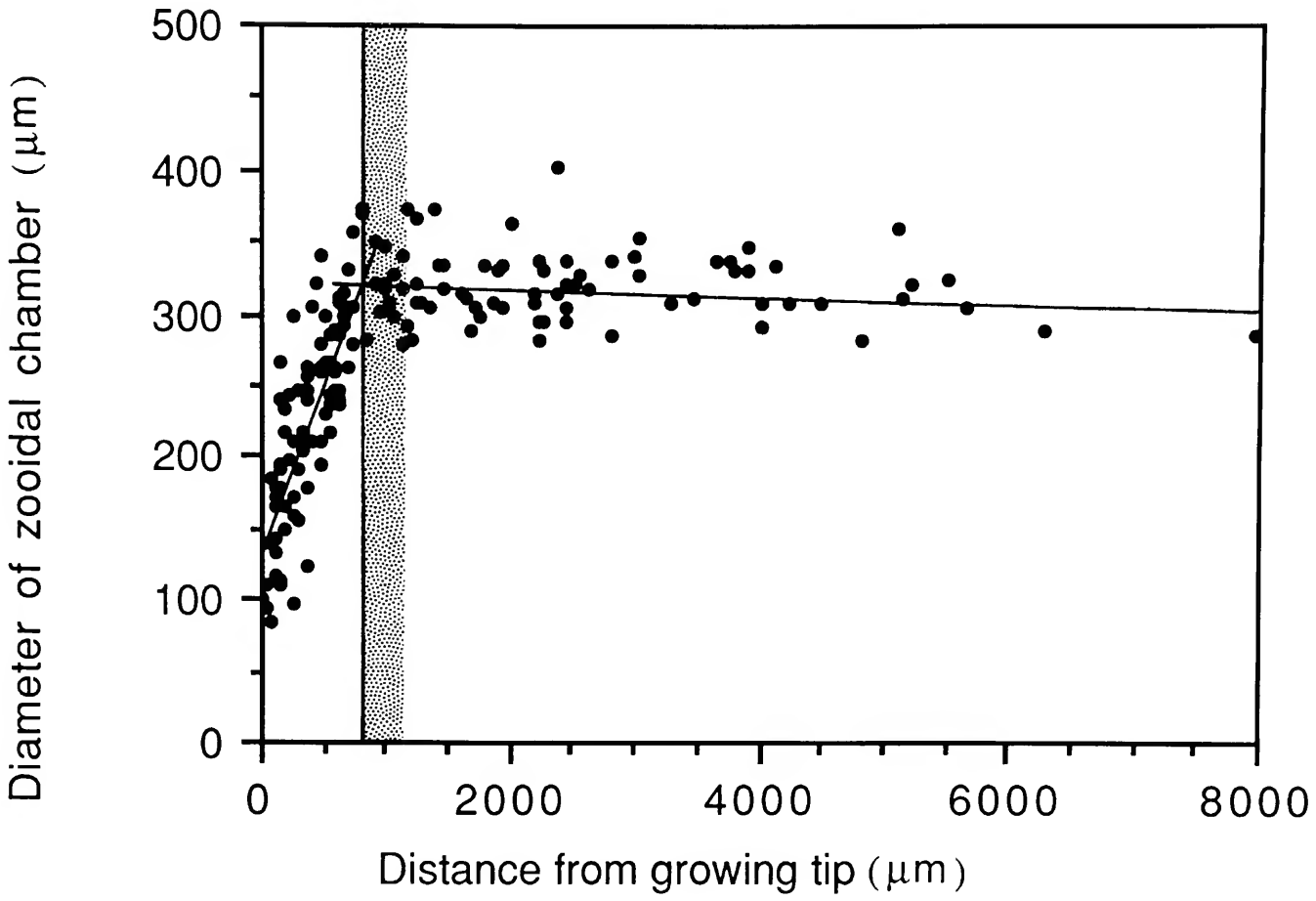



FIGURE 72.—Scatter diagram of diameter of zooidal chamber at attachment ligaments against distance from growing tip in *Cinctipora elegans*. Distance direct from center of tip to center of functional skeletal aperture. Vertical line indicates general distance from branch tips to youngest zooids with full-size chamber diameters; stippled band indicates approximate distances of the several growth rate changes. Endozonal regression from branch tips is Y = 137 μm + 0.244X, r = 0.775. After reaching full-size, chamber diameters curve levels off to Y = 326 μm − 2.36 × $10X^{-3}$, r = 0.144.

FIGURE 70 (opposite page, upper).—Scatter diagram of maximum wall thickness against distance from growing tip in *Cinctipora elegans*. Distance direct from center of tip to outer edge of wall being measured. Vertical line indicates general distance from branch tips of youngest exozones; stippled band indicates approximate distances of the several growth rate changes. Endozonal regression from branch tips is Y = 22.3 μm + 0.0456X, r = 0.728. Exozonal walls thicken proximally at slower rate, Y = 85.3 μm + 0.00932X, r = 0.546. Specimens for this and subsequent scatter diagrams are from sta USC 1430, Mu76-138, stations off Otago Heads, and edge of continental shelf off Otago.

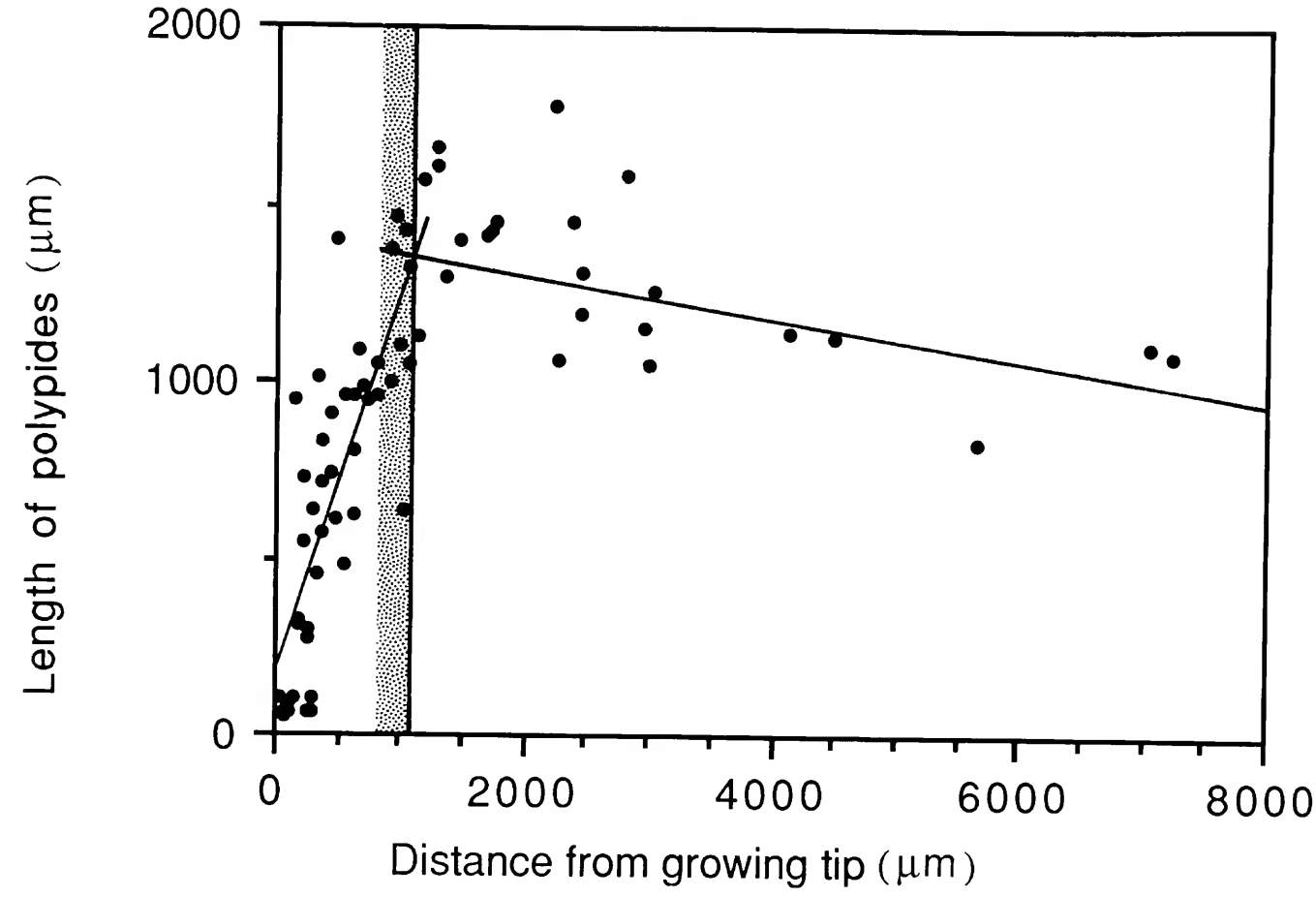
FIGURE 71 (opposite page, lower).—Scatter diagram of depth of ligament attachment against distance from growing tip in *Cinctipora elegans*. Distance direct from center of tip to center of functional skeletal aperture; depth also from center of functional skeletal aperture. Vertical line indicates general distance from branch tips to youngest zooids with permanent positions of ligament attachments; stippled band indicates approximate distances of the several growth rate changes. Endozonal regression from branch tips is Y = 213.4 μm + 0.782X, r = 0.727. After reaching fixed positions, curve levels to Y = 1031 μm − 8.06 × $10X^{-3}$, r = 0.105.

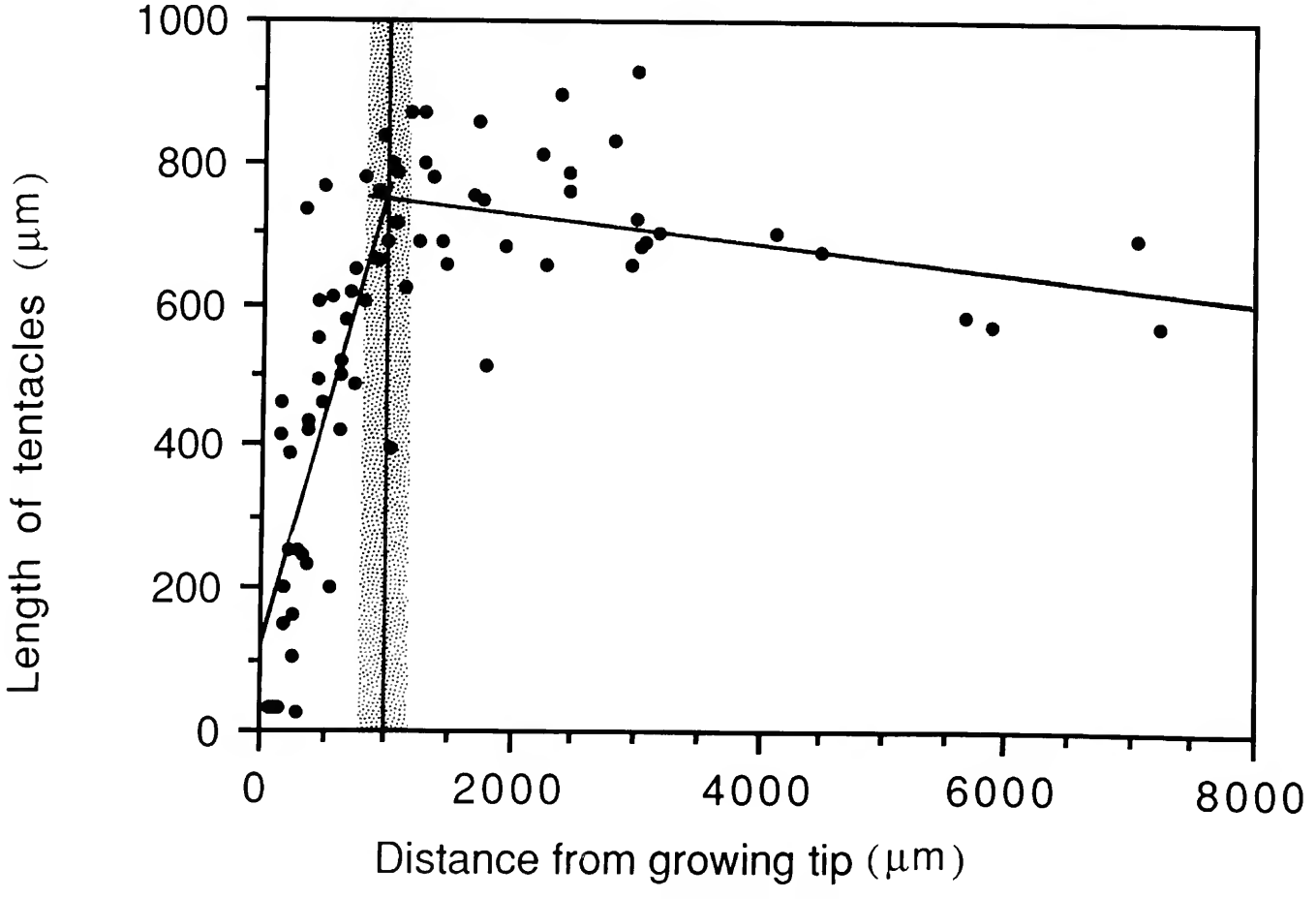
patterns across growing tips of branches (Key, 1990), but more rapid endozonal than exozonal growth rates seem to be a general rule.

## BRANCH GROWTH AND POLYPIDE CYCLES

Understanding the mode of growth of soft parts of the youngest zooids in endozones of growing branches of *C. elegans* is complicated by the polypide cycles characteristic of the phylum. In the youngest endozonal zooids at growing tips of colonies (Figures 63, 65), polypides and their attachment organs necessarily must move outward from branch axes as their enclosing skeletons grow until they reach permanent lateral positions in newly developed exozones.

As the zooids shift in position and increase in size, do their polypides and attachment organs grow and shift gradually and continuously within a single regenerating phase, or do they do


2000
1000
0
Length of polypides (μm)
0
2000
4000
6000
8000
Distance from growing tip (μm)


1000
800
600
400
200
0
Length of tentacles (μm)
0
2000
4000
6000
8000
Distance from growing tip (μm)

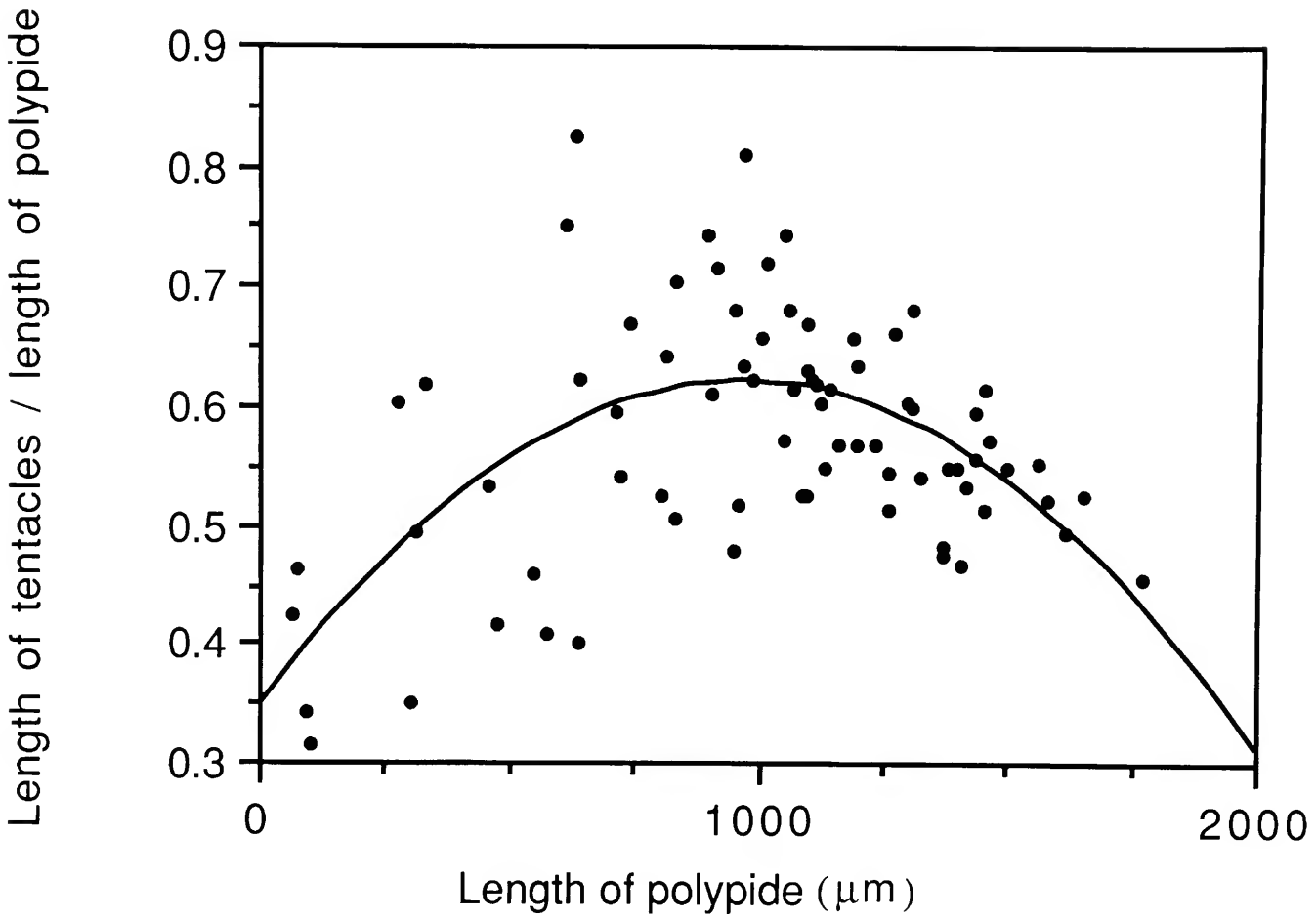



FIGURE 75.—Scatter diagram of length of tentacles/length of feeding organs against length of feeding organs in *Cinctipora elegans*. Note that feeding organs of intermediate length have proportionally the longest tentacles (Y = 403 μm + 0.512X − 2.79 × 10X, r = 0.500).

FIGURE 73 (opposite page, upper).—Scatter diagram of length of feeding organs in fully regenerated colonies against distance from growing tip in *Cinctipora elegans*. Distance direct from center of tip to center of functional skeletal aperture. Vertical line indicates general distance from branch tips to youngest zooids with full-size feeding organs; stippled band indicates approximate distances of the several growth rate changes. Endozonal regression from branch tips is Y = 133.4 μm + 1.110X, r = 0.753. After reaching full-size, feeding organs curve levels off to Y = 1436 μm − 0.059X, r = 0.446.

FIGURE 74 (opposite page, lower).—Scatter diagram of length of tentacles in fully regenerated colonies against distance from growing tip in *Cinctipora elegans*. Distance direct from center of tip to center of functional skeletal aperture. Vertical line indicates general distance from branch tips to youngest zooids with full-size tentacles; stippled band indicates approximate distances of the several growth rate changes. Endozonal regression from branch tips is Y = 115.2 μm + 0.674X, r = 0.750. After reaching full-size, tentacles curve levels off to Y = 770.7 μm − 0.0208X, r = 0.327.

so in a number of polypide cycle saltations in which the positions of their attachment organs and polypides shift outward with each regeneration until permanent positions in exozones are reached?

If growth and shifting of polypides from axial to exozonal positions take place gradually within one regenerating phase, only one polypide would be involved per zooid. As a result, all axial zooids of any significant size would have proportionally sized polypides fastened to attachment organs and brown bodies would be absent in their living chambers. In colonies in degenerated or regenerating phases, however, some of the longer endozonally located zooids contain only a flattened attachment organ in the living chamber (Figure 65). Other endozonal zooids contain a brown body but lack an attachment organ (Figure 3). These combinations indicate that endozonal

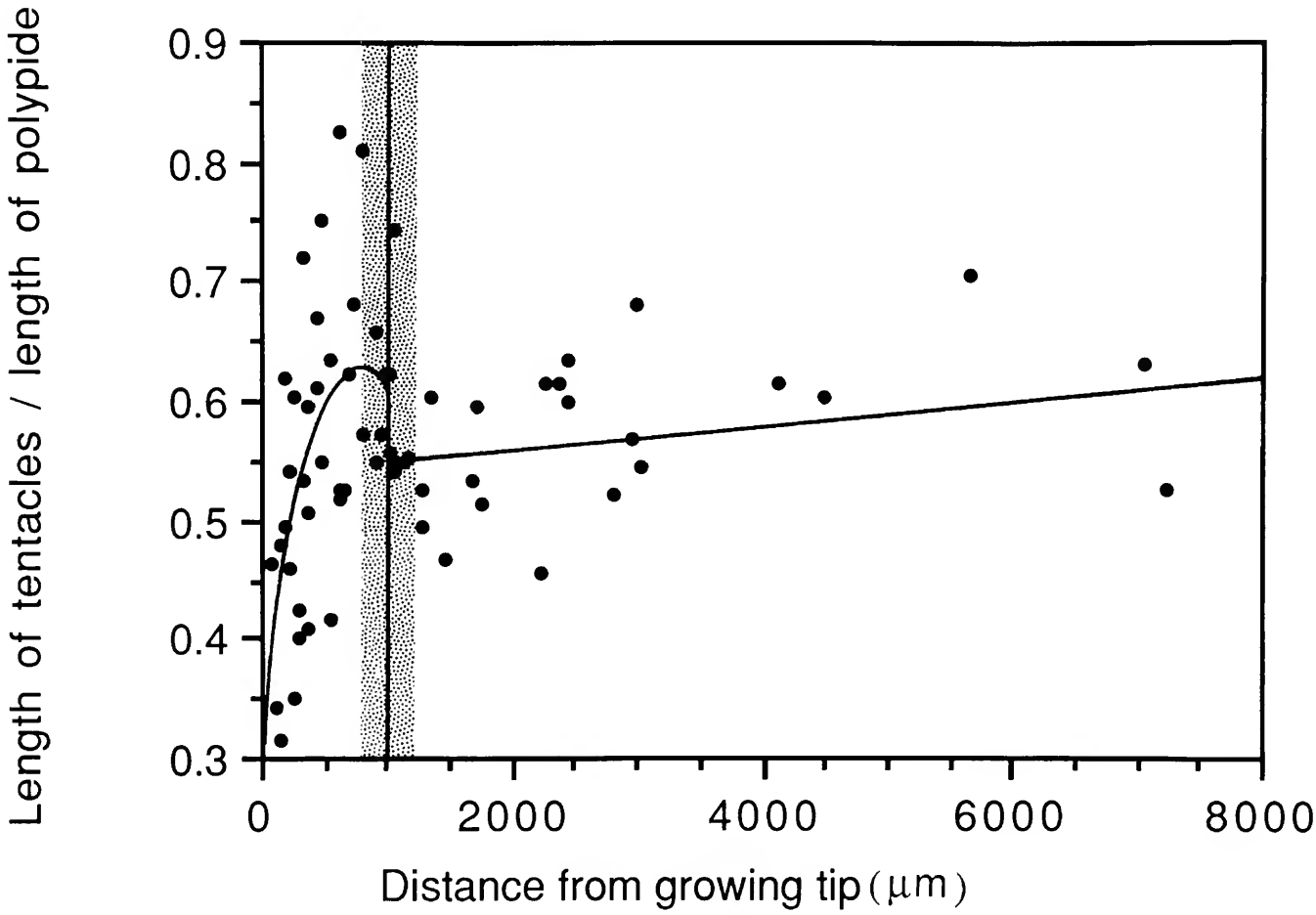



FIGURE 76.—Scatter diagram of length of tentacles/length of feeding organs against distance from growing tip in *Cinctipora elegans*. Distance direct from center of tip to center of functional skeletal aperture; vertical line indicates approximate distance from center of branch tips to youngest zooids with full-size tentacles. Endozonal regression across ends of branches is $Y = 0.350 + 7.47 \times 10X - 4.95 \times 10X$, $r = 0.578$. Curve beginning 1 mm proximal to branch tips is $Y = 0.556 + 8.92 \times 10X$, $r = 0.229$ and is not significantly different from zero slope ($P = 0.127$).

zooids undergo cycles. The lack of an attachment organ in some indicates at least one previous degeneration in which both the polypide and the attachment organ are lost. Apparently, a new attachment organ and polypide must be regenerated in a more outward position for the zooid to continue its growth to the exozone.

In summary, young axial polypides and their attachment organs in *C. elegans* apparently shift positions and grow to progressively larger sizes in progressively longer skeletons through a series of polypide cycles until full polypide and skeletal size are established in permanent exozonal positions. At this point, attachment organs are retained and remain in fixed positions as polypides cycle. The endozonal growth is accomplished at a more rapid rate than exozonal growth, thereby producing an elongate branching growth habit (Figures 70–77). The fixed positions of polypides in zooids that cease lengthening in exozones and the dormant condition of zooids in just a few whorls below growing tips produce branches of subequal diameters throughout a colony.

## RECOGNITION OF POLYPIDE CYCLES

How prevalent are polypide cycles among stenolaemates and is it possible to infer those cycles in colonies preserved in spirit? One obvious indication of cycles in preserved stenolaemates is the existence of two coexisting cycles in the same colony, that is, a degenerated zone separating two functioning zones of zooids, or the reverse, a functioning zone between two degenerated zones. Another obvious indication of cycles in a species is the retention of brown bodies in living chambers of

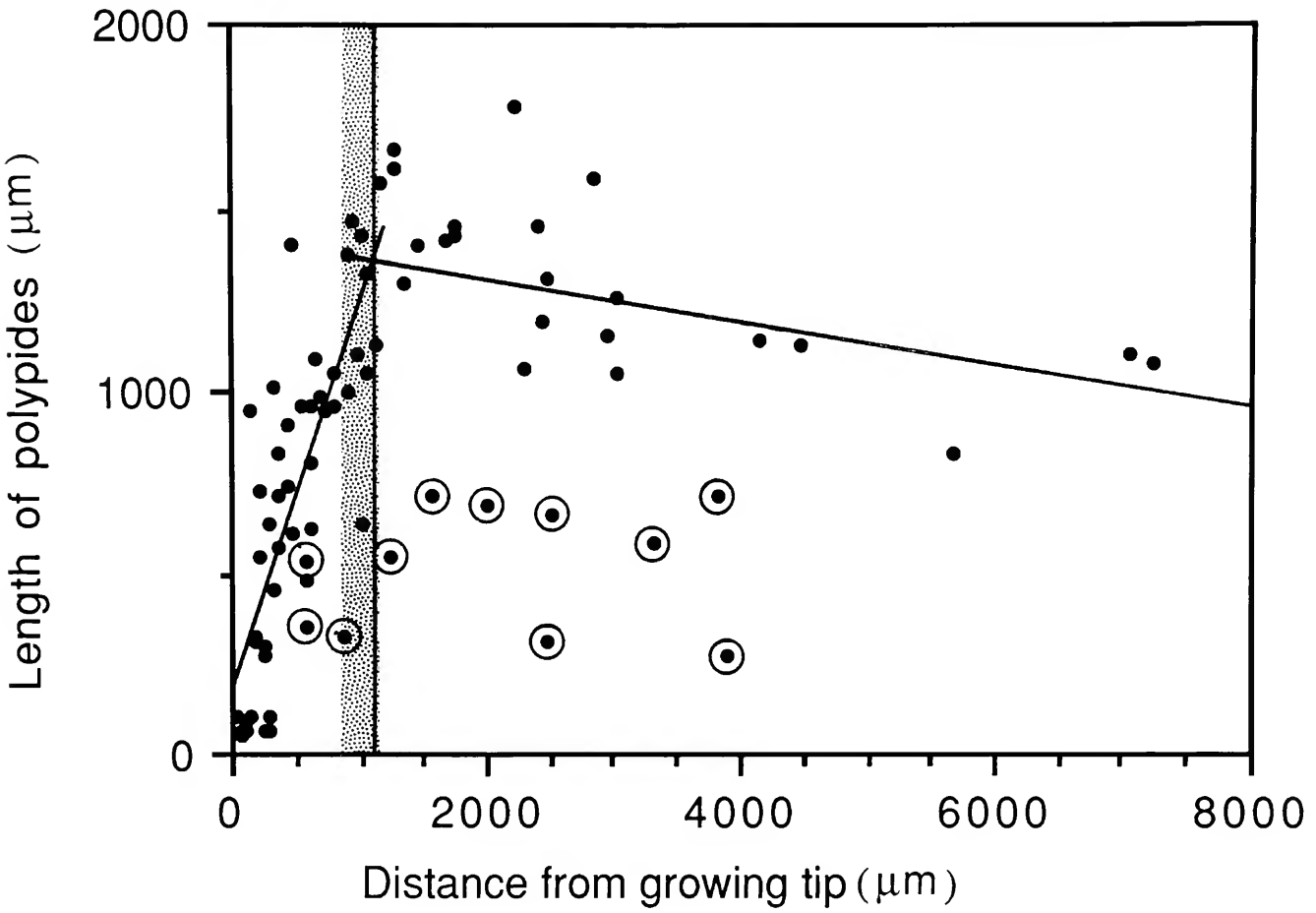



FIGURE 77.—Scatter diagram of length of feeding organs in both regenerated (solid dots) and regenerating (circled dots) colonies against distance from growing tip in *Cinctipora elegans*. Distance direct from center of tip to center of functional skeletal aperture.

zooids. In *C. elegans*, however, not enough zooids remain functional in ends of branches for two cycles to occur and although brown bodies can be found, they do not accumulate from cycle to cycle and are not seen in all sections.

Is it possible to recognize polypide cycles without finding either brown bodies or more than one cycle? Assuming no polypide cycles in a species, a zooid would have the same polypide throughout its growth and its functional life. This suggests that in all actively growing regions of a colony, polypides should be approximately proportional in size to their skeletons, as Figures 63, 73, and 74 indicate for fully regenerated zooids.

Lack of cycles should also mean that zooids having empty living chambers (Figure 3) have completed their growth and their polypides have been resorbed, either prematurely in the endozone, or at the end of a completed growth cycle in the exozone. The exozonal zooids presumably would be approaching a dormant stage that is protected by calcified terminal diaphragms, thus ending the single polypide growth cycle of a zooid.

The hypothesis for single polypide growth, however, does not account for the colonies that have zooids with undersized polypides in full-sized skeletons (Figures 64, 66, 67, 77). Our evidence, taken from fully regenerated zooids, so far suggests that fully regenerated polypides and their enclosing skeletons are proportional in size (Figures 70–74). This should be true also for single polypide growth.

Polypides either of uniform or different undersizes in full-sized skeletons apparently require an interruption in growth. In bryozoans that interruption is most likely a polypide cycle. Therefore, neighboring polypides of the same or different undersizes in full-sized skeletons apparently are indications in themselves that a species undergoes polypide cycles.

## Functional Morphology

### Lophophore Protrusion and Feeding

The basic mechanics of lophophore protrusion in stenolaemates were not understood until annular muscles were discovered in the membranous sacs of *Crisia eburnia* and the function explained by Nielsen and Pedersen (1979:79) (also see review by Taylor, 1981:235). They report that the annular muscles of the membranous sac apparently contract sequentially from the base of the sac outward, squeezing the alimentary canal and lophophore out toward the zooidal aperture. All retractor muscles and the atrial sphincter muscle relax and stretch as the polypide moves outward (Figures 7, 18, 78).

The protrusion of the alimentary canal and lophophore apparently results in the transfer of some body fluid from the outer spaces of the exosaccal cavity (Figure 10), through the gaps between attachment ligaments of the attachment organ, and into inner exosaccal spaces. As the base of a lophophore is pushed past the attachment organ the tentacle sheath is compressed and wrinkles as it turns inside out (Figures 18, 78). Only alimentary canals, tentacle sheaths, and lophophores are protruded. Membranous sacs, attachment organs, atrial sphincter muscles, and reproductive bodies remain in place.

In most stenolaemates, including *Cinctipora elegans*, the protruded organs are anchored by ligaments of attachment organs. The extent of protrusion apparently is limited by the cumulative lengths of the tentacle sheath attachment membranes and inverted tentacle sheaths. The tentacle sheath is longer than the depth to ligament attachment below the functioning aperture in only 23% of the zooids measured (Figure 69). The mouths of the remaining zooids, therefore, cannot protrude outward to or beyond functional skeletal apertures, so they must remain within living chambers unless the tentacle sheaths and attachment membranes can stretch. For example, several zooids with depth of ligament attachment exceeding 800 μm have tentacle sheaths less than 500 μm long, generating just under a 300 μm shortfall in length for the base of the lophophore and mouth to clear the aperture.

Laboratory observations of feeding zooids of *C. elegans* indicated that slightly less than half of the length of the tentacle crown protruded past the skeletal aperture, with the base of the lophophore and the mouth remaining well within the living chamber. The ends of the tentacles remained within their zooidal boundaries and were fairly straight except at their tips because the angle of spread of the crown was limited by the diameter of the functional aperture. However, one zooid in a growing tip was observed to extend its tentacles fully past the aperture. In addition, a colored slide of a colony in its natural environment shows tentacles well extended out from shields at angles indicated by enclosing emergent peristomes (Figures 6–8). Perhaps these are examples of attachment membranes and tentacle sheaths actually stretching.

During feeding in the laboratory, large particles were rejected by inward flicking of individual tentacles or by expulsion through the top of the tentacle crown without any significant movement of the tentacles. Ciliary reversals, or perhaps pharyngeal contractions, could be involved in expulsions. Retraction of individual tentacle crowns occurred rapidly at the slightest stimulation without any indication of a colony-wide response.

The restricted feeding positions of tentacle crowns in the laboratory suggest that mouths can remain well within living chambers during normal feeding, especially for undersized zooids.

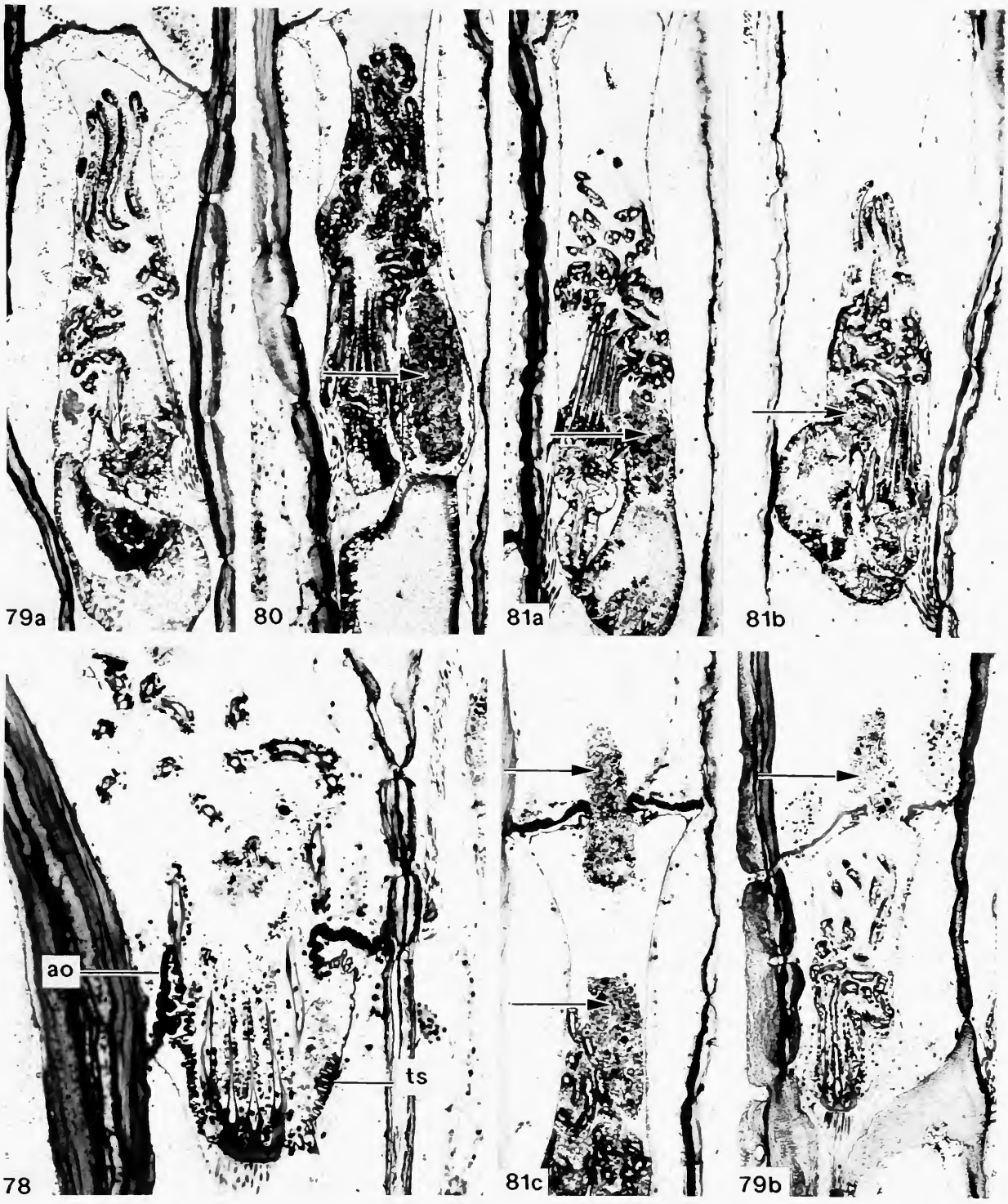
### Elimination

It has been generally assumed that bryozoans eliminate faecal pellets through the anus and tentacle sheath directly into open water while the lophophore is protruded and the tentacle sheath, therefore, is turned inside out. Observations of feeding stenolaemates in the laboratory and in the natural environment indicate, however, that most species protrude tentacle crowns just far enough for the crowns to open clear of skeletal apertures at best, but not far enough for the anus to clear the living chamber.

In stenolaemates in the retracted position, the anus opens into the atrium through the tentacle sheath at varying distances outward from the mouth (Figure 22). Sections of *C. elegans* (Figures 79–81) indicate that faecal pellets pass through the anus and into the atrium while the lophophore is retracted or retracting (Figure 81*a,b*). Pellets then pass from the atrium, past the atrial sphincter muscle (Figure 81*c*), and into the vestibule (Figure 79*b*). Elimination then could be completed by protrusion of tentacles, pushing pellets out through the vestibule and functional aperture into open water.

We (FKM) have observed tentacle crowns extended in feeding positions for two species of *Tubulipora* and one species each of *Crisia* and *Exidmonea* (all fixed-walled species). Their tentacle crowns just clear skeletal apertures at outer ends of peristomes. Mouths were level with apertures when tentacles were fully protruded, and anuses were not seen to clear living chambers. Food particles were milled by cilia in the pharynx and pylorus as they passed through the gut. Faecal pellets were formed in the rectum and remained at the anus for a few to many minutes. Pellets passed through the anus and into the atrium as a polypide retracted rapidly. Thus, a pellet was in the atrium with the tentacles retracted, as in Figure 81*c*. Once in the atrium, pellets generally slid between the tentacles within the lophophore or were manipulated there by jerky motions of the polypide. A few pellets remained in a lateral position outside the lophophore but within the atrium. As the tentacles protruded, pellets were pushed out past the relaxed atrial sphincter muscle and the vestibule from the middle third of the tentacle length and released as the tentacle crown opened. Once in open water pellets either were fanned away or were ejected further by reversal of cilia.

These observations of living stenolaemates correspond with




FIGURES 78–81.—*Cinctipora elegans* from sta Mu76-138, all longitudinal sections (all ×100 except for 78). 78, Base of lophophore just inward from relaxed atrial sphincter muscle and attachment organ (ao), tentacle sheath compressed and crenulated just before being turned inside out (ts), USNM 250064 (×150). 79, USNM 454192: *a*, polypide with empty rectum; *b*, polypide with faecal pellet (arrow) being pushed out of atrium into vestibule as tentacles start to protrude. 80, Faecal pellet (arrow) in rectum, USNM 250065. 81, USNM 454188: *a*, faecal pellet (arrow) entering atrium from rectum; *b*, faecal pellet (arrow) midway between rectum and atrium; *c*, one faecal pellet in atrium and another (arrows) caught in atrial sphincter muscle.

the positions of pellets found in *C. elegans* (Figures 79–81). Perhaps the passage of pellets out through the atrium and vestibule is necessary for undersized polypides that must function within living chambers. In addition, a detailed study of faecal pellets of three species of marine Bryozoa, two ctenostomes, and a cheilostome, reported that 65% of all faecal pellets produced were eliminated during either the protrusion or retraction of lophophores (Best and Thorpe, 1987:17–24). These faecal pellets, therefore, also were eliminated through the atrium and vestibule even though their lophophores protracted well beyond living chambers. Presumably, the other 35% were eliminated while the tentacle crowns were fully protracted so that some bryozoans apparently can eliminate faecal pellets both ways.

## Communication Pores

Communication (interzooidal) pores (Figures 8*b*, 13, 82–84) occur in vertical walls in all of the Recent stenolaemate species we have studied. The pores were interpreted by Borg (1926:199) to be open communication pores connecting zooids physiologically. It is probable that the pore openings of the skeleton are formed by the obstruction of special cells on each side of a zooidal boundary, and together they prevent calcification (pers. comm., Claus Nielsen, 1990; Figure 83*a*). Once a communciation pore is functioning the special cells could regulate the transfer of nutrients but not allow free passage of fluids (pers. comm., D.P. Gordon, 1989). These cells have been seen in place in our sections, but only rarely, suggesting that their absence could be a problem of preservation in our slides. Nielsen and Pedersen (1979:72) indicate that in *Crisia eburnea* the more distal pores are open and the basal pore in each zooid has radial spines and is closed by a single epithelial cell.

In *C. elegans* some pores apparently are without skeletal obstructions (Figure 82). Many other communication pores in *C. elegans* (Figures 83*b*, 84) and in many other Recent stenolaemates have radial spines (Brood, 1972:45, 64; 1976:381). These spines would seem to have little effect on the transfer of nutrients among zooids.

Indirect evidence seems to require that communication pores actually are a means of nutrient transfer among zooids. In post-Triassic stenolaemates, polymorphs (Boardman, 1983, figs. 49.5, 49.6, 49.9) and brood chambers (Boardman, 1983, figs. 52, 61.1) occur that never develop feeding organs. In many species brood chambers and nonfeeding polymorphs are linked with feeding zooids only via communication pores. The transfer of nutrients through the pores from feeding zooids seems necessary.

Another widespread example of interzooidal transfer of nutrients is the calcification of inner sides of diaphragms that are terminal to living chambers of feeding zooids and polymorphs (Figures 3, 51–55; Boardman, 1983, figs. 42.5, 42.6). Calcification of these terminal diaphragms occurs on inner sides of membranous diaphragms or collapsed orificial walls after feeding organs have degenerated and a zooid is no longer contributing to its own nutrition.

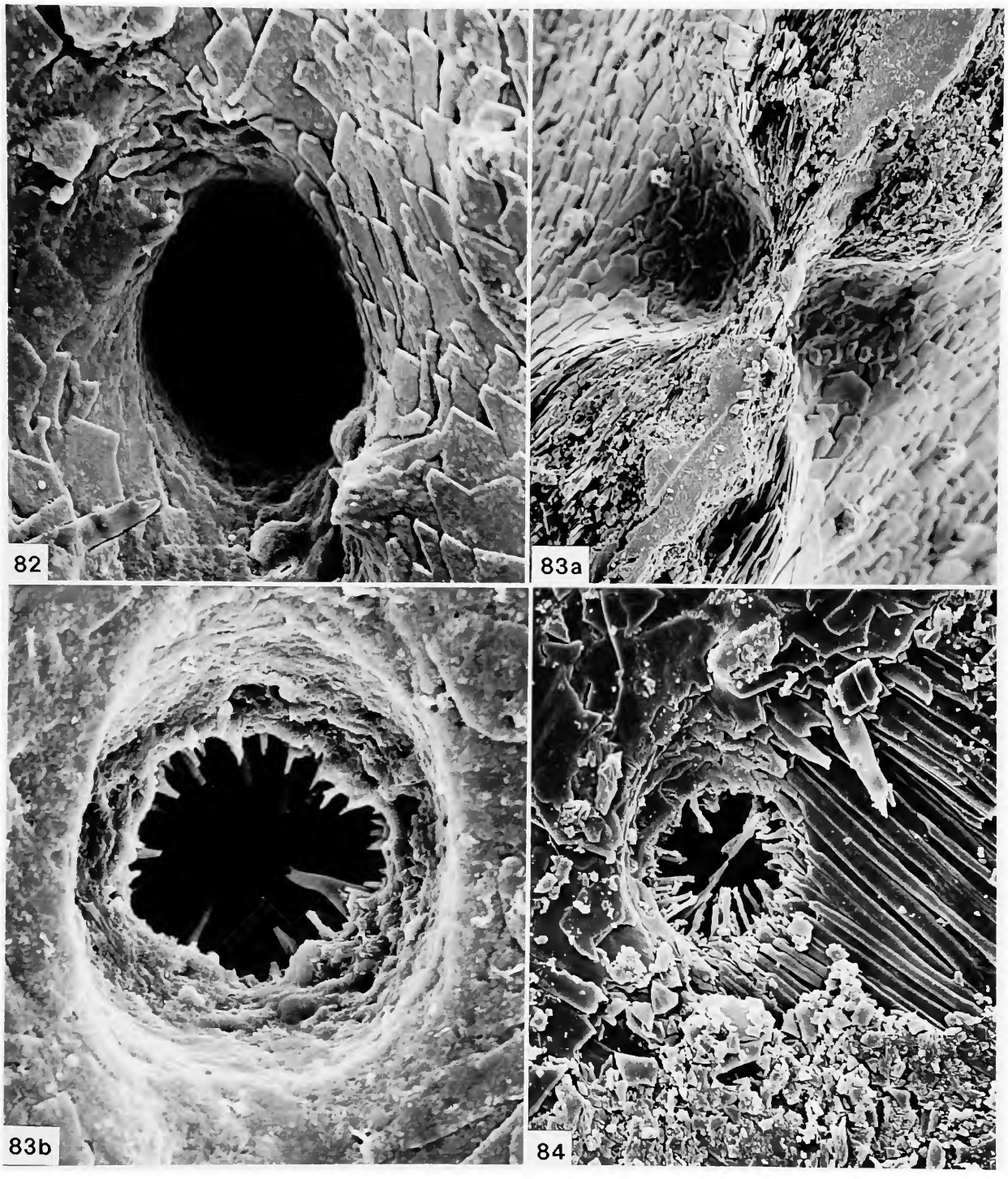
With few exceptions, Paleozoic stenolaemates lacked communication pores and calcification occurred only on outer surfaces of zooidal walls, including cystiphragms and basal and terminal diaphragms. In these taxa, colony-wide distribution of nutrients apparently could occur only through confluent outer body cavities (Figure 5). The only exceptions known in Paleozoic free-walled taxa are a few species that had gaps in calcification of vertical walls and therefore were able to exchange nutrients and develop diaphragms calcified on inner surfaces of membranes (Utgaard, 1983:333).

A concentration of communication pores occurs in axial sides of vertical walls at the level of functional apertures in free- and fixed-walled cinctiporids, both fossil and Recent (Figures 8*b*, 13). Similar concentrations also have been observed in Cretaceous meliceritidids. Within that taxonomic, temporal, and geographic range, more discoveries of taxa with these pore concentrations can be expected. Unfortunately, published figures of stenolaemates generally are not magnified highly enough to show communication pores at apertures so that a literature search proved unhelpful.

The functional significance of concentrations of pores provides for interesting speculation. It seems reasonable to infer that the concentrations indicate positions of greatest exchange of nutrients and other metabolites between adjacent zooids. A zooid in one whorl of *C. elegans* generally has common walls with two younger zooids in the next whorl distally (Figures 4, 37, 38*a*). In fully regenerated zooids (Figure 63) the concentrations of pores in axial walls of the oldest zooids begin at attachment levels and extend outward opposite their vestibular regions. In immediately adjacent younger zooids, on the opposite sides of shared vertical walls, those same concentrations of pores are opposite digestive tracts or atrial regions.

In exozones having regenerating undersized polypides (Figure 64), the concentration of pores still begins at the attachment level of the older zooid. In the two younger zooids, the smaller polypides have little or no overlap with the pores or the vestibular region of the older zooid. The longer the polypides become with each regeneration, the more overlap they develop.

The youngest zooids in the first one or two whorls at the growing tips of *C. elegans* have not developed that part of the skeletal wall that contains the concentrated pores, so exchange through communication pores from the next older zooids is available to them only through the scattered pores of the endozone. Nutritional contributions from older feeding zooids would seem to be an advantage before new zooids develop enough to contribute to their own nourishment. In both free-and fixed-walled colonies, nutrients from older zooids presumably are available to newly developing polypides through the




FIGURES 82–84.—Communication pores of *Cinctipora elegans*. 82, Apparently an open communication pore in thick skeletal shield, BMNH 1989.10.20.8, sta Mu88-29 (×2000). 83, BMNH 1989.10.20.7, sta Mu88-29 (×1200): *a*, offcentered section, communication pore showing concavities presumably formed by presence of special cells during calcification; *b*, communication pores partly closed by radial spines. 84, Exfoliated wall from necromass showing fiberous crystals of transparent zone and radial spines of communication pore, BMNH 1989.10.20.11, sta Mu88-29 (×2190).

confluent budding zones at growing tips in addition to the few connecting communication pores (Figures 5, 44).

The nutritional needs in other parts of a colony are a matter for more speculation. It would seem that actively feeding zooids in exozones are equally self supporting whether they are regenerating or fully regenerated, thereby maintaining an interzooidal balance. It seems necessary, however, that these relatively few feeding zooids in *C. elegans* produce stored nutrients for their own earliest nonfeeding stage during their next regeneration. Theoretically, this could be accomplished in *C. elegans* either through communication pores or through confluent outer body cavities before emergent peristomes are developed. Proximally, the feeding zooids must supply the nutrients for growth of terminal diaphragms as the zooids become dormant and for branch rejuvenations described above (Figures 32, 33).

## Systematics

Deducing phylogenetic and taxonomic relationships both within the new family Cinctiporidae and between cinctiporids and other stenolaemates is severely hampered by the nearly complete lack of knowledge of the internal morphology and anatomy of post-Paleozoic stenolaemate bryozoans. The general lack of investigation of interiors of Recent stenolaemates in published literature necessarily means that the phylogenetic and taxonomic values of features of organs and interiors of skeletons are largely unknown. Early attempts at establishing these values, necessarily based on observations of inadequate numbers of taxa, will undoubtedly be subject to major modifications in subsequent studies as the taxonomic base is enlarged.

The seminal work of Borg (1926) provides a starting point in many areas of stenolaemate biology and paleobiology, especially his recognition of two fundamentally different skeletal organizations in modern stenolaemates. These were referred to by Borg as single-walled and double-walled, and nowadays are termed fixed-walled and free-walled as used throughout this paper. The fixed- and free-walled organization can be distinguished externally in most taxa. The fixed- and free-walled dichotomy appears to have significance at high taxonomic levels throughout most of the class Stenolaemata. All suborders of post-Triassic stenolaemates as presently diagnosed contain taxa that are either fixed- or free-walled; the Tubuliporina and Articulata are defined as exclusively fixed-walled; the Cerioporina, Cancellata, and Rectangulata are defined as exclusively free-walled.

The new family Cinctiporidae is unique in the stenolaemate classification in containing a mixture of free- and fixed-walled organizations. Two of the included genera are primarily free-walled, one genus is fixed-walled, and one has fixed/free apertures produced by a combination of frontal walls and skeletal shields.

This unexpected mixture of free- and fixed-walled genera in a family inferred to be monophyletic challenges present ideas of stenolaemate phylogeny and taxonomy that are based on a clear-cut separation of free- and fixed-walled forms because the mixture indicates a minimum of evolutionary transition from one to the other. The mixture also complicates assignment of the Cinctiporidae to existing suborders that are defined as either free- or fixed-walled.

Another major challenge in establishing the family is inferring the taxonomic values of soft parts. As a starting point, some characters in the taxonomic descriptions below are taken from those organs that are interpreted to be directly involved with the growth or functions of skeletal features considered to be of taxonomic value. Based on the more completely described taxa of all ages, more is known about the internal skeletal features of stenolaemates as taxonomic characters than soft parts of Recent taxa. In addition, readily observed characters of organs that can be seen to vary from taxon to taxon are included. For example, enough is known about the number of tentacles to include a generalized statement of this character within a genus and a precise count within one of its species. Enough is also known about outer attachment organs to know that there are many different arrangements that surely have taxonomic value so they are included here in taxonomic descriptions (Boardman, 1983, figs. 39–49).

Consistent with past experiences with skeletal taxonomic characters, most quantitative details are considered to be significant at the species level, leaving most qualitative attributes at generic and suprageneric levels. Also, study of the fossil specimens of the cinctiporid genera from different time intervals beginning with the latest Cretaceous help to distinguish between skeletal characters that separate species and those critical at generic and suprageneric levels.

## Procedures

Collections of cinctiporids from each locality sampled in New Zealand and the surrounding shelf were examined and assigned to population samples based on outer skeletal walls (exterior frontal walls, interior skeletal shields, or combinations). A standard set of measurements (Figures 68, 85) was made for several specimens from each population sample, excepting a few of the numerous Recent population samples. Exterior measurements were made with a Wild M-8 microscope fitted with an ocular micrometer. For measurements of internal features, including both skeletal and soft parts where present, specimens were embedded in epoxy under vacuum (Nye et al., 1972), then cut, polished, etched, and acetate peels prepared (Merida and Boardman, 1967). An image of each peel was projected onto a Houston Instruments Hipad digatizing board on which a series of linear measurements were made. Where possible, 10 measurements of each external and internal feature were made per specimen. Thin sections were prepared of selected specimens, primarily for microstructural determination of skeleton, examination and measurement of soft parts in Recent specimens, and photography.

It is not possible with presently available techniques to

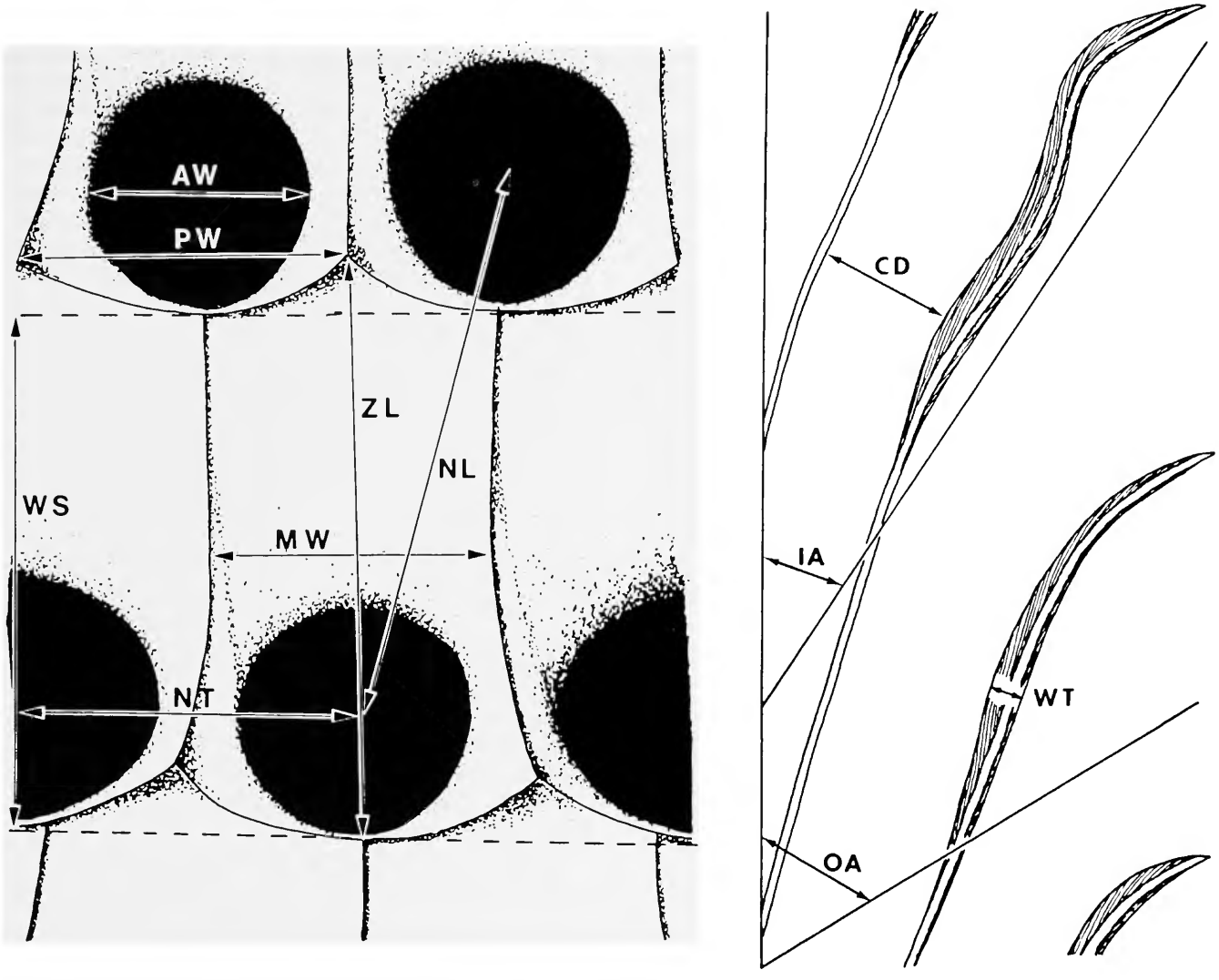



FIGURE 85.—Measurements of skeletal morphology, exterior view on left, longitudinal section on right. Key: AW = aperture width, CD = chamber diameter, IA = angle between inner exozone and branch axis, MW = minimum zooidal width, NL = nearest neighbor longitudinally, NT = nearest neighbor transversely, OA = angle between outer exozone and branch axis, PW = proximal zooidal width, WS = whorl spacing, WT = wall thickness in exozone, ZL = zooidal length.

determine all features of size for each zooid because internal features must be measured from acetate peels, thin sections, or ground or broken surfaces that pass through a specimen in single planes, necessarily missing many features. Therefore, only averages of measurements for colony fragments, rather than measurements of individual zooids, were recorded into a data matrix for statistical manipulation.

Discriminant analysis was performed on the data set at various levels of inclusion of specimens, using Statistical Package for the Social Sciences (SPSSX) (Norusis, 1985). This procedure tests distinctiveness of previously determined groups by calculating compound characteristics (discriminant functions) of each group, then comparing the features of each individual with those of each of the various groups and assigning the individuals to the group to which their features are most similar, next-most-similar, and so on. If each group is uniquely different from the others and contains members with sufficiently similar features, all individuals will be reassigned to the original group to which they belong.

In working with the cinctiporids, population samples were used as the original groups, and individual specimens characterized by their means constituted the members of the groups. Success of reassignment to original groups was typically 100% per population sample but was as low as 80% whether all cinctiporids or only those of a single outer-wall type constituted the data set. However, all of the occasional misassignments

were between two population samples that previously had been qualitatively determined to be the same species. This determination was subsequently supported by cluster analysis. In all cases of initial misassignment, the next-most-similar group was the original. The occasional mixing between population samples within species suggests that the inherent species characteristics may be expressed so narrowly that they prevail over minor, local ecophenotypic or temporal variation expressed among populations.

The most heavily weighted, measured features that constitute the first discriminant function within discriminant analysis of a single outer-wall type (exterior frontal walls, interior skeletal shields, or combinations) were used as the basis of unweighted pair group cluster analyses using SPSS for determination of species. The original, qualitatively determined species groupings, were upheld by the cluster analyses. The cluster analyses commonly mixed the sequence of addition of specimens from among population samples, which had been qualitatively assigned to a single species, and kept the clusters distinct until the final linkages.

Not including the Maastrichtian *Cinctipora* sp. (which is highly distinctive in size), the clustering procedures, based on the features identified as most discriminating, indicate that there are included in this study three free-walled species, *Cinctipora elegans* Hutton, *C. elongata,* new species, and *Cylindropora areolata* Tenison-Woods; two fixed-walled species, *Attinopora zealandica* (Mantell) and *A. campbelli,* new species; and two mixed-walled species, *Semicinctipora amplexus,* new species and *S. annulata,* new species.

### ABBREVIATIONS

The following abbreviations are used in occurrence and registration data: BMNH, Natural History Museum, London (formerly British Museum (Natural History)); OUM, Oxford University Museum; NZGS, New Zealand Geological Survey; UOGD, University of Otago Geology Department, Dunedin, New Zealand; USNM, collections of the former United States National Museum, now in the National Museum of Natural History, Washington, D.C.

## CINCTIPORIDAE, new family

TYPE GENUS.—*Cinctipora* Hutton, 1873.

DEFINITION.—Colonies dendroid, generally bushy, branches cylindrical, bifurcating, few anastomosing, generally slender, subequal in diameter throughout colonies. Zooids typically in annular or spiral arrangements about imaginary branch axes, few rhombic in some specimens. Apertures of adjacent annular rings widely spaced, spiral whorls widely to closely spaced in different genera. Apertures most commonly centered on lateral edges of zooids of adjacent spiral whorls or annular rings, few aligned longitudinally. Zooids functional in only few annular rings or whorls at growing ends of branches, remainder dormant, covered by calcified terminal diaphragms. Brood chambers unknown.

Zooids monomorphic in zones of astogenetic repetition, large to gigantic in most species, at low to moderate angles at colony surfaces. Outer skeletal walls of branches in free-walled colonies with skeletal shields, in fixed-walled colonies with frontal walls and short peristomes, or in combined free-/fixed-walled colonies with thickened shields transformed to frontal walls between apertures of adjacent rings or whorls. Communication pores closely spaced in axial walls of zooids at apertures in most genera. Emergent peristomes in some species. Below growing tips of branches exozone widths approximately constant producing no measurable ontogenetic variation in skeletons in most genera.

In thin section, zooidal boundaries of interior vertical walls narrow, well defined, translucent, actually crystals of irregular shape and orientation. Adjacent skeletal layer nearly transparent, actually fibrous crystals closely parallel to zooidal boundaries with long dimensions perpendicular to zooidal growth direction. Skeletal lining of zooidal chambers finely laminated as seen in all orientations, actually layers of lath-shape crystals that form pustules variously positioned in living chambers of most species.

Attachment organs, where known, strongly thickened, truncated cone-shape in retracted position, up to 24 closely and evenly spaced ligaments. Outer edge of attachment organ connected to outer edge of cylindrical sphincter muscle. Vestibular wall loosely attached to flattened top of attachment organ, and through cylinder of sphincter muscle, connects to inner edge of sphincter muscle where outer edge of tentacle sheath also attached.

Polypides robust, filling more than half living chamber diameters. Tentacles as many as 17 per zooid, two lateral bands of motor cilia only. Anus on axial side of zooid, retractor muscles inserted into skeleton on opposite side. During degenerated stage attachment organs intact, flattened, in fixed position in exozonal zooids. Brown bodies not accumulated.

REMARKS.—The combination of free- and fixed-walled organizations in the same family was first suggested to us by the enormous size of the zooids of the genera, unknown in other stenolaemates, and their apparent geographic restriction to New Zealand. The transitional nature of combined fixed/free apertures of zooids in the zone of change of *Cinctipora elegans,* the three transitional colonies of that species having both free-and fixed-walled zooids in the zone of repetition, and the new genus *Semicinctipora* with combined fixed/free apertures indicate that a monophyletic family that includes both free- and fixed-walled genera is possible. The remaining evidence for the family grouping is based on shared character states, including: similar skeletal-wall microstructure and ultrastructure; comparable soft part anatomy in both living species, one of them free-and one fixed-walled; similar arrangements of zooids in dendroid branches; scattered emergent peristomes in some species, even though they seem functionally superfluous in fixed-walled forms; pustules in skeletal linings of zooids of

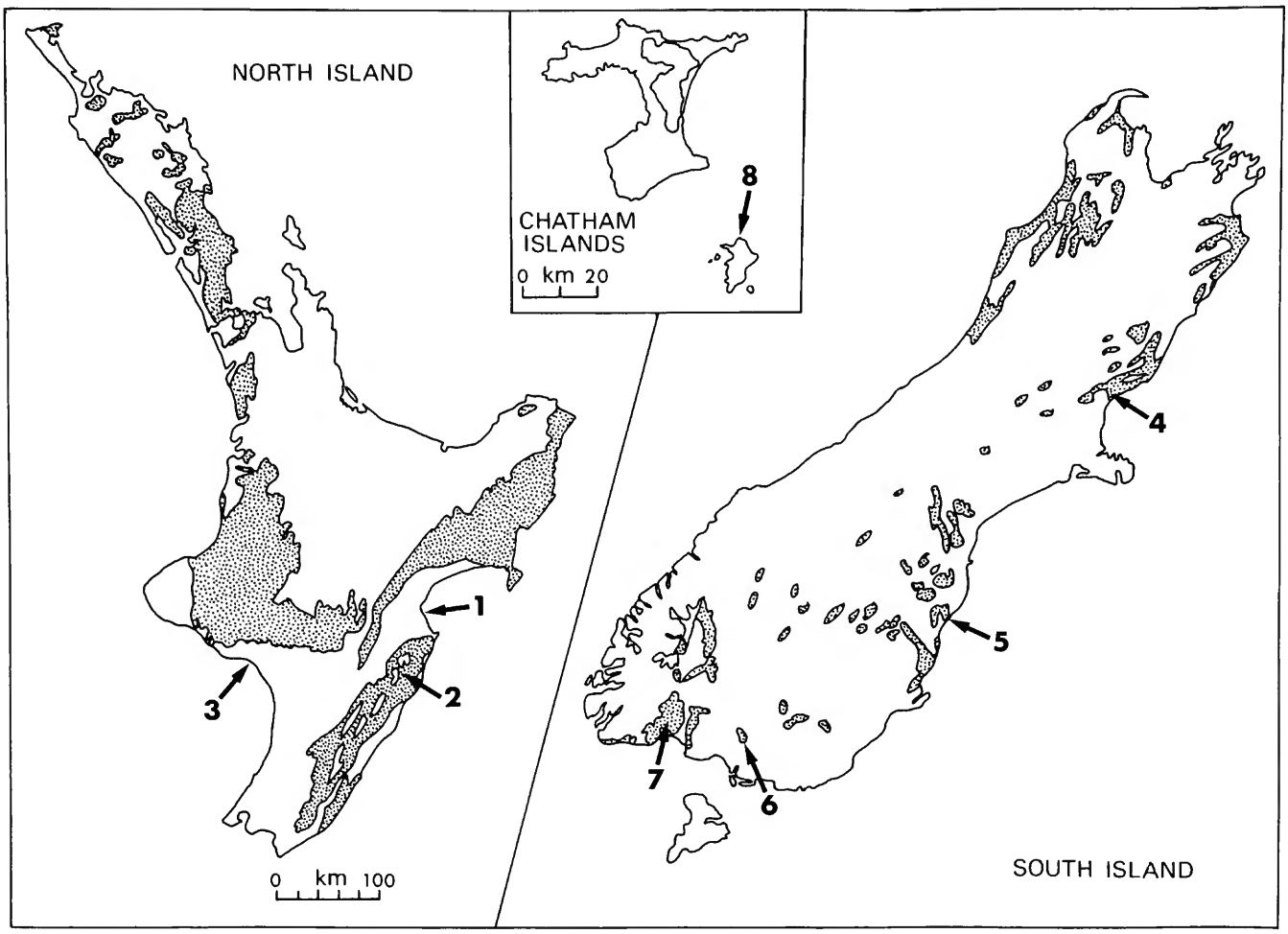



FIGURE 86.—Localities for fossil cinctiporids in New Zealand. Tertiary outcrops in the North and South Islands are stippled. Key: 1, Pleistocene (?Nukumaruan, ?Petane Limestone), Petane, Hawkes Bay (*Cinctipora elegans*); 2, Pliocene (Mangapanian, Te Aute Limestone), Hatuma Quarry, Waipukurau, Hawkes Bay (*Cylindropora areolata*); 3, Pleistocene (?Castlecliffian, ?Tainui Shell Bed), Shakespeare Cliff, Wanganui (*C. elegans, Attinopora zealandica*); 4, Miocene (Otaian, Claremont Limestone), Onepunga, Waipara, North Canterbury (*Attinopora campbelli*); 5, Oligocene (Whaingaroan, McDonald Limestone), Oamaru, North Otago (*Semicinctipora amplexus, A. campbelli*); 6, Miocene (Otaian-Altonian, Forest Hill Limestone), Winton area, Southland (*Cinctipora elongata, Semicinctipora annulata, A. campbelli*); 7, Miocene (Altonian, Clifden Limestone, Clifden Suspension Bridge, Southland (*C. elongata, A. campbelli*); 8, Pliocene (Opoitian-Mangapanian, Whenuataru Tuff), Moutapu Point, Pitt Island, Chatham Islands (*C. elongata, C. elegans*).

most species; the apparent absence of brood chambers and polymorphic zooids of any kind throughout zones of repetition; and communication pores closely spaced in axial walls opposite apertures in three of the four genera. These transitional and shared characteristics together have resulted in our inference that the taxa described below belong to a monophyletic family, the Cinctiporidae.

RANGE.—Maastrichtian of South Africa; Oligocene-Recent, New Zealand (Figure 86).

## PHYLOGENY OF THE CINCTIPORIDAE

The mixture of fixed- and free-walled characteristics found in the Cinctiporidae not only has wide implications for stenolaemate phylogeny in general but also presents difficulties when reconstructing the phylogeny of the cinctiporids themselves. The problem is one of polarity. The origin of the Cinctiporidae from either a fixed- or a free-walled ancestor seems possible. Plausible outgroups of each kind can be

suggested and until more is known about stenolaemate morphology and phylogeny a preferred outgroup is not indicated here. Therefore, two alternative phylogenies are presented for the cinctiporids, one with a free-walled and the other with a fixed-walled origin and outgroup. Each phylogeny is illustrated by means of a cladogram specifying character state transformations, and by an evolutionary tree that incorporates data on stratigraphic distribution (Figures 87, 90). Details of character state transformations at each node are supplied with the cladogram and will not be repeated in the text.

PHYLOGENY 1 (Free-walled Origin).—This phylogeny (Figure 87) infers that the Cinctiporidae evolved from a free-walled ancestor and therefore that free-walled organization as seen in *Cinctipora* is primitive for the family. A plausible free-walled outgroup for the Cinctiporidae is provided by *Filicea*, a late Cretaceous and Paleocene genus (Figure 88), which like *Cinctipora* has zooids with skeletal shields. Furthermore, the skeletal shields of *Filicea* resemble those of *Cinctipora* in possessing a concentration of communication pores at their bases. Microstructure of the vertical walls of the type species,

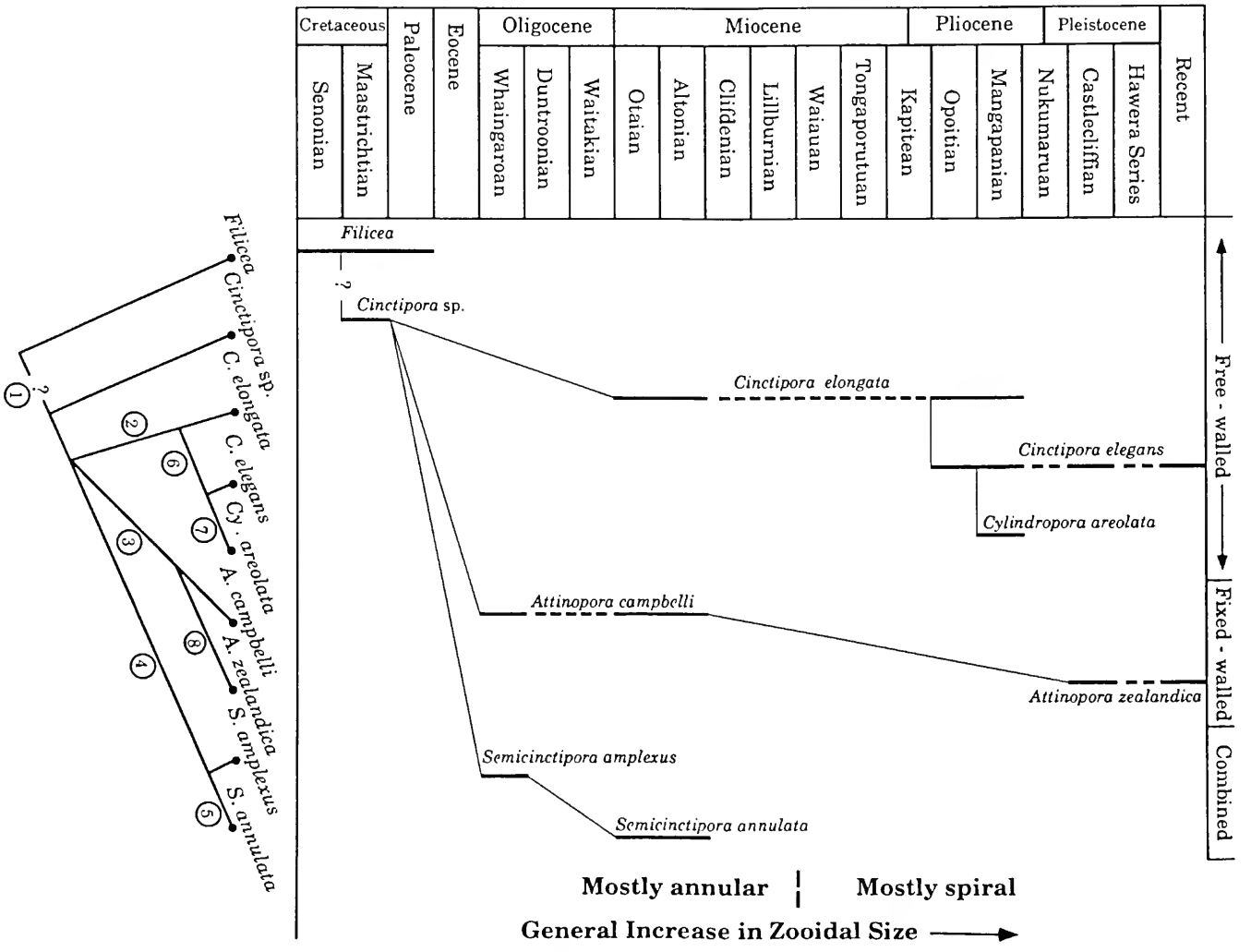
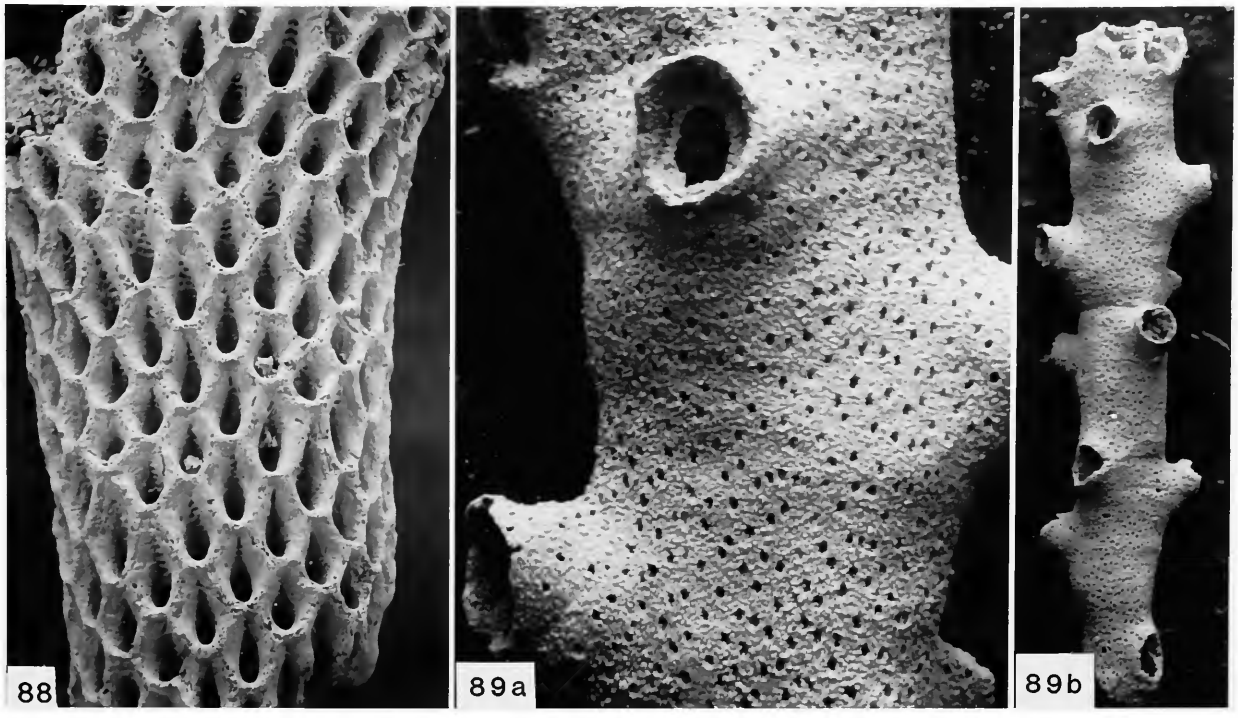



FIGURE 87.—Phylogenetic relationships of the Cinctiporidae starting with the free-walled genus *Filicea* as the outgroup; the phylogenetic tree above correlates with cladogram below. Numbered character-state transformations at nodes of the cladogram as follows: node 1, change from rhombic to annular zooidal arrangement about imaginary axis, increase in length of skeletal shields, possible loss of gonozooids; node 2, increase in zooidal and colonial dimensions; node 3, change to fixed-walled species; node 4, change to combined free-/fixed-walled species; node 5, increase in zooidal and colonial dimensions; node 6, decrease in skeletal shield length:width ratios, increase in spiral whorl development; node 7, change to larger branch diameters because of more zooids and some ontogenetic gradient in exozones, more closely spaced whorls; node 8, increase in zooidal and colonial dimensions.




FIGURES 88, 89.—Outgroups. 88, *Filicea subcompressa*, free-walled colony with clustered communication pores at bases of short skeletal shields, BMNH D58182 from the Santonian, Craie de Villedien, France (×26). 89, "*Entalophora*" sp., fixed-walled colony with pseudopores in frontal walls, BMNH D44600 from Coniacian Chalk, Chatham, Kent: *a* (×115); *b* (×30).

*F. regularis* d'Orbigny from the Santonian, is similar to that of the Cinctiporidae (McKinney 1975, pl. 4: fig. 4). Although gonozooids have been described from some species identified as *Filicea* (Voigt, 1973) they are unknown from others (E. Voigt, pers. comm. to P.D.T., 1990) as in the cinctiporids.

Morphologic differences between *Filicea* and the cinctiporids include zooidal arrangement and size. Zooidal budding in the type species of *Filicea* occurs around a bundle of axial zooids within endozones (McKinney, 1975), whereas budding in cinctiporids does not appear to involve axial zooids. The endozonal budding of *Filicea* results in a rhombic arrangement of zooids in exozones, in contrast to the annular to spiral arrangment typical of the cinctiporids. However, because the presence of single or multiple axial zooids is at best a generic character within other stenolaemate families (e.g., Rhabdomesidae; Blake, 1976, 1983), this difference is not considered crucial. There is other evidence as well for considerable plasticity in the stenolaemate endozone. For example, several genera of Paleozoic trepostomes, identified by their relatively constant exozones, are inferred to have convergently evolved 4-sided zooids in their endozones (Boardman and McKinney, 1976). Also, the zooids of *Filicea* are considerably smaller than the gigantic zooids of most cinctiporids, but are comparable in size to those of the oldest known member of the family, *Cinctipora* sp. A trend evident within the Cinctiporidae toward larger sized zooids if projected back in time suggests that any Cretaceous ancestors of the family would have possessed smaller zooids, typical of other stenolaemates.

The oldest known member of the Cinctiporidae is a poorly known species designated here as *Cinctipora* sp. from the Maastrichtian of Need's Camp in South Africa (Figures 103, 104). It is morphologically comparable to the other two species of the genus except that its zooidal and colonial dimensions are much smaller, as expected in older ancestors. It seems reasonable, therefore, to identify this South African species as the sister group of the New Zealand cinctiporids in this phylogeny, in spite of its geographic separation.

Phylogeny 1 clusters the four species of free-walled cinctiporids (*Cinctipora* sp., *C. elongata*, *C. elegans*, and *Cylindropora areolata*, Figures 91–111) as the primitive subgroup of cinctiporids. The fixed-walled genus *Attinopora* with its two species (*A. campbelli* and *A. zealandica*, Figures 43–47, 125–137) and the mixed free-/fixed-walled genus *Semicinctipora* with its two species (*S. annulata* and *S. amplexus*, Figures 112–124) are inferred to be two advanced subgroups, each subgroup evolving directly from *Cinctipora* sp. It would appear that *Semicinctipora* with its mixed free- and fixed-walled species might be an evolutionary intermediate

between the free- and the fixed-walled genera. The three transitional colonies of *Cinctipora elegans* having both free-and fixed-walled zooids, however, imply that no mixed-walled intermediate was needed to evolve from free- to fixed-walled species. Further, the prominent clusters of communication pores in axial zooid walls at aperture levels in the species of *Cinctipora* and *Attinopora* are lacking in *Semicinctipora*, suggesting that *Semicinctipora* is not intermediate between the other two genera but evolved directly from *Cinctipora* sp.

Simple application of zooidal development criteria for determining character polarity favors Phylogeny 1 because frontal exterior walls develop later than interior vertical walls in zooidal ontogeny in stenolaemates, and therefore it would be expected to be a phylogenetically advanced feature among cinctiporids.

PHYLOGENY 2 (Fixed-walled Origin).—This phylogeny (Figure 90) infers that the Cinctiporidae evolved from a fixed-walled ancestor and therefore that fixed-walled organization as seen in *Attinopora* is primitive for the family. A plausable fixed-walled outgroup for the Cinctiporidae is provided by several taxa traditionally placed in the Tubuliporina by Taylor and Larwood (1990:209–233). More particularly, dendroid tubuliporines are suggested of the kind often assigned to *Entalophora* or *Spiropora* but seemingly without a valid generic name (Figure 89). They differ from true *Entalophora* (see Walter, 1970:85–89) and *Spiropora* (see Voigt and Flor, 1970:39–61) in lacking gonozooids. The zooids of "*Entalophora*" (Figure 89) are comparable in size to the relatively small zooids of *Filicea*, the outgroup of phylogeny 1, and to the oldest cinctiporid, *Cinctipora* sp., the free-walled species from the Upper Cretaceous. They also have suitably short peristomes. Examples of such dendroid tubuliporines are numerous in the Upper Cretaceous chalks of NW Europe (e.g., Taylor, 1987:36), and apparently occur also in the Cenozoic of Australia (e.g., "*Spiropora*" *gigantea* Maplestone).

We have not been able to find an Upper Cretaceous fixed-walled species belonging to the Cinctiporidae that would be appropriate as the sister-group of the New Zealand cinctiporids. That is not suprising and does not indicate that one will not be found eventually because so little collecting and publishing of stenolaemate bryozoans have been done in the southern hemisphere.

Phylogeny 2 groups together the two species of fixed-walled cinctiporids (*Attinopora campbelli* and *A. zealandica*, Figures 125–137) as the primitive subgroup of cinctiporids. The free-walled genera *Cinctipora* and *Cylindropora* (Figures 91–111) with their four species and the mixed free-/fixed-walled genus *Semicinctipora* (Figures 112–124) with its two species are inferred to be the two advanced subgroups, each subgroup evolving directly from an hypothetical fixed-walled species appropriate to be the sister-group of the cinctiporids. The two advanced subgroups of this phylogeny are inferred to have evolved separately for the same reasons given in the discussion of Phylogeny 1 above.

Simple application of colonial developmental criteria for determining character polarity suggests that fixed-walled organization is primitive for the family. This is because in the free-walled type species *Cinctipora elegans*, the ancestrula is fixed-walled and the first whorl of zooids in the zone of astogenetic change are mixed fixed-/free-walled. It should be noted that developmental criteria for determining character state polarity have usually been applied to the ontogeny of noncolonial organisms, and their application to colonial animals is rather uncertain. Nevertheless, a good analogue of cinctiporids may exist among cheilostome bryozoans where the occurrence of tatiform ancestrulae in many ascophorans matches expectations that an uncalcified, anascan-like frontal wall is primitive relative to the calcified frontal shield that appears in zooids from zones of astogenetic repetition.

More equivocal support for the inference that fixed-walled organization is primitive in cinctiporids is the occasional presence of regions of fixed-walled growth within zones of astogenetic repetition in the free-walled species *C. elegans*. Regions of free-walled growth have not been observed in the fixed-walled genus *Attinopora*. If fixed-walled growth is indeed primitive, this observation can be explained as atavism—recurrence in descendants of characters possessed by their ancestors.

SUMMARY.—Although the polarity of the family is reversed in the two hypothetical phylogenies, certain relationships remain unchanged. The same three subgroups are inferred to have evolved independently from either a free-walled or a fixed-walled Upper Cretaceous ancestral species. Also, three morphologic trends are evident in the subgroups. The older species from the Upper Cretaceous into the Miocene have zooidal arrangements that are largely annular. The younger species have zooidal arrangements that are largely spiral. The second trend is the increase in zooidal size from generally normal for stenolaemates to uniquely gigantic in all three subgroups. The third trend is an increase in branch diameters within each subgroup that is no doubt related in part to zooidal size. The forces driving the amazing increase in zooidal size are unclear and are likely to remain so until more is known about the functional significance of zooid size in bryozoans. This is not an example of increased variance causing an increase in maximum and mean size through time (Gould, 1988). Instead, it is an absolute increase in minimum, mean, and maximum size through time in three concurrent lineages.

## Genus *Cinctipora* Hutton, 1873

*Cinctipora* Hutton, 1873:102; 1880:198.—Waters, 1887:341.—Gordon in Willan, 1981:242.

*Filicea* d'Orbigny.—Levinsen, 1902:31 [in part].

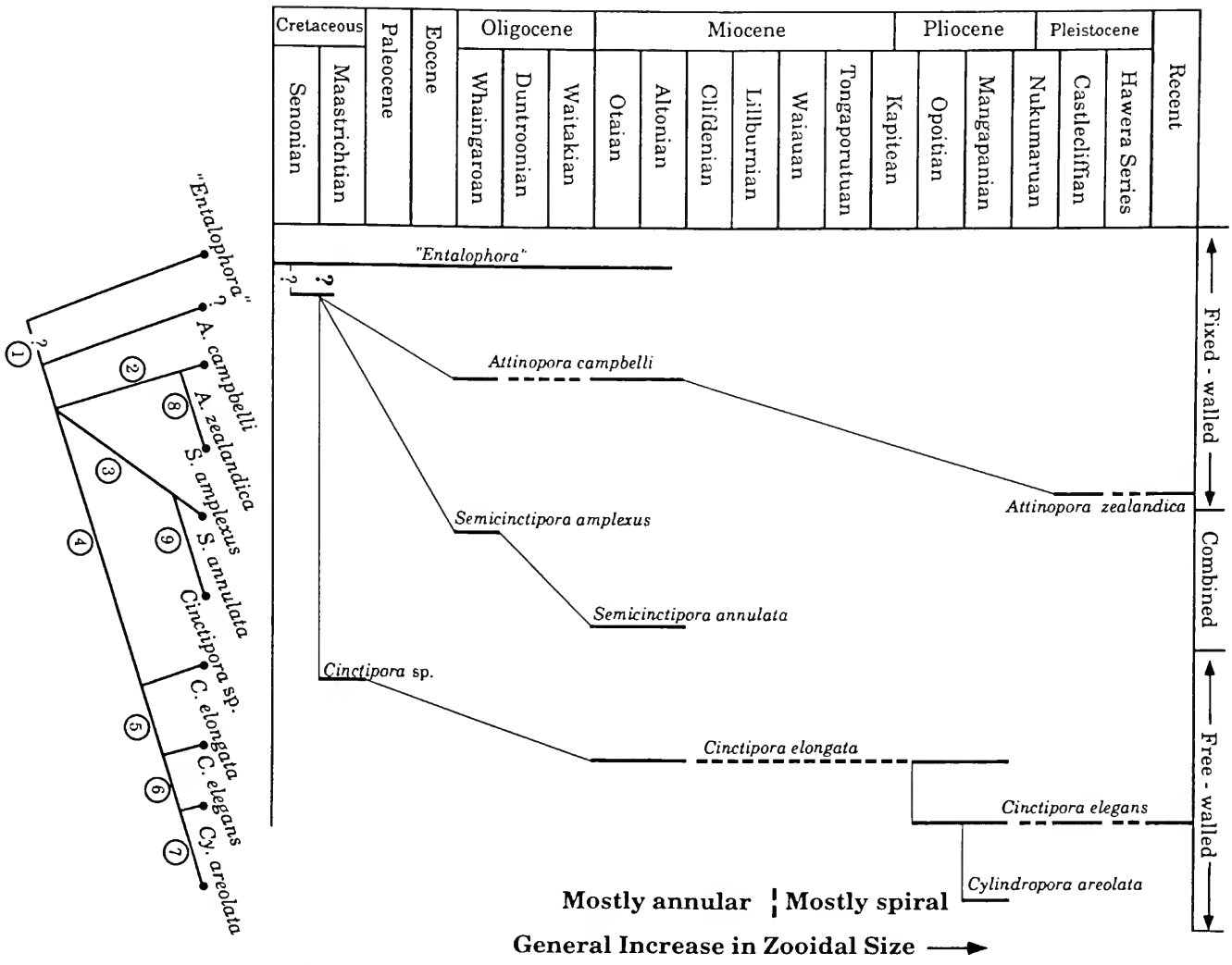



FIGURE 90.—Phylogenetic relationships of the Cinctiporidae starting with fixed-walled "*Entalophora*" as the outgroup; the phylogenetic tree above correlates with cladogram below. Numbered character-state transformations at nodes of the cladogram as follows: node 1, change to annular zooidal arrangement about imaginary axis, loss of gonozooids; node 2, increase in zooidal dimensions; node 3, change to combined free-/fixed-walled species; node 4, change to free-walled species; node 5, increase in zooidal and colonial dimensions; node 6, decrease in skeletal shield length:width ratios, increase in spiral whorls; node 7, change to larger branch diameters because of more zooids and some ontogenetic gradient in exozones, more closely spaced whorls; node 8, increase in zooidal and colonial dimensions; node 9, increase in zooidal and colonial dimensions.

TYPE SPECIES.—*Cinctipora elegans* Hutton, 1873:103, by monotypy.

EMENDED DEFINITION.—Primarily free-walled Cinctiporidae with zooidal apertures in widely spaced spiral whorls or annular rings in slender, bifurcating branches. Zooids small to gigantic in evolutionary clade of species, intersect colony surfaces at small angles, boundaries 5-sided at branch surfaces. Skeletal shields develop from distally extended vertical walls, functional apertures subterminal at bases of shields. Shields longitudinally elongate and subrectangular, generally concave outward with few scattered communication pores, most minutely pustulose. Some older functioning zooids in some species secondarily fixed-walled because of late forming, short, exterior-walled peristomes.

Single transverse rings of depressed attachment scars in skeletal surfaces at points of contact with ligaments of attachment organs in some living chambers. In some zooids pustules of skeletal shields on axial and lateral sides of skeletal

walls inward to region of attachment scar rings, proximally walls smooth or with longitudinal grooves. In other zooids pustules throughout living chambers. Communication pores closely spaced in axial walls of zooids between bases of shields and region of attachment scar rings, scattered proximally.

In primary zone of astogenetic change ancestrula entirely fixed-walled, encrusting with low basal disc (protoecium), lateral to ancestrula one or more branches from small, encrusting colony bases surrounded by space-filling polymorphic zooids of variable sizes. Zooids of first whorl with frontal walls and fixed apertures proximally, free apertures at bases of first skeletal shields distally. Zooids of second whorl free-walled to end of zone of change.

REMARKS.—Waters (1887:341) suggested "doubt as to whether *Cinctipora elegans* is really a Bryozoan." Levinsen (1902:31) placed the species among the Bryozoa by making the generic name of *Cinctipora* a junior subjective synonym of the bryozoan genus *Filicea* d'Orbigny 1854, from the Upper Cretaceous of France. Gordon in Willan (1981:242) re-established *Cinctipora* as a valid genus, noting the difference in budding pattern between it and *Filicea regularis* d'Orbigny, 1854, as described by McKinney (1975:73).

RANGE.—Maastrichtian of South Africa; Miocene-Recent, New Zealand.

### *Cinctipora elegans* Hutton, 1873

FIGURES 2-42, 48, 49, 51-58, 62-84, 91-96

*Cinctipora elegans* Hutton, 1873:103; 1880:198.—Waters, 1887:341.—Gordon in Willan, 1981:242.

*Filicea elegans* (Hutton).—Levinsen, 1902:31.—Livingstone, 1928:80, pl. 4, fig. 6.

*Spiroporina immersa* Tenison-Woods, 1880:23, fig. 24 [new synonomy].

EMENDED DESCRIPTION.—Bush-shape colonies as much as 15 cm in height and 0.5 m square in lateral extent. Arrangement of zooids commonly spiral, varying from continuous with high pitch to interrupted with lower pitch in same colony, rarely annular for few whorls. Feeding zooids pale pink for as much as 10 mm from branch tips. Proximally, branches white, of dormant feeding zooids with skeletal terminal diaphragms. Growing tips of branches flattened. Branch diameters 1.1-2.1 mm, commonly 9-13 zooids around branch circumference. Emergent peristomes sporadic to common in colonies. Average nearest neighbor longitudinally 1.47 mm, calculated nearest neighbor transversely 0.31-0.34 mm.

On branch surface, average zooecial length 1.64 mm, average proximal width of zooecia 0.72 mm, and average minimum width 0.49 mm. Ratio of zooecial length:proximal width about 2.3:1 and length:minimum width about 3.3:1.

Rapid increase of maximum zooidal wall thicknesses from youngest zooids at growing tips for distance of 0.9 mm proximally to outer ends of newest skeletal shields. Thereafter, slower increases in maximum wall thickness of skeletal shields for distance of just over 0.2 mm.

Attachment organ ligaments number 24, some zooids with corresponding attachment scars on skeletal walls, proximally living chamber lining smooth, with longitudinal grooves, or pustulose. Rapid increase in depth of ligament attachments from apertures for distance of 1.1 mm from youngest zooids at centers of growing tips to youngest zooids with permanent attachment positions. Proximally along branches, depths of permanent ligament attachment positions irregularly variable 700-1290 µm. Rapid increase in zooidal chamber diameters at levels of ligament attachments for distance of 0.8 mm proximally from youngest zooids at centers of branch tips to youngest zooids with permanent attachment positions. Proximally from there, zooidal diameters at ligament attachment positions irregularly variable 270-400 µm.

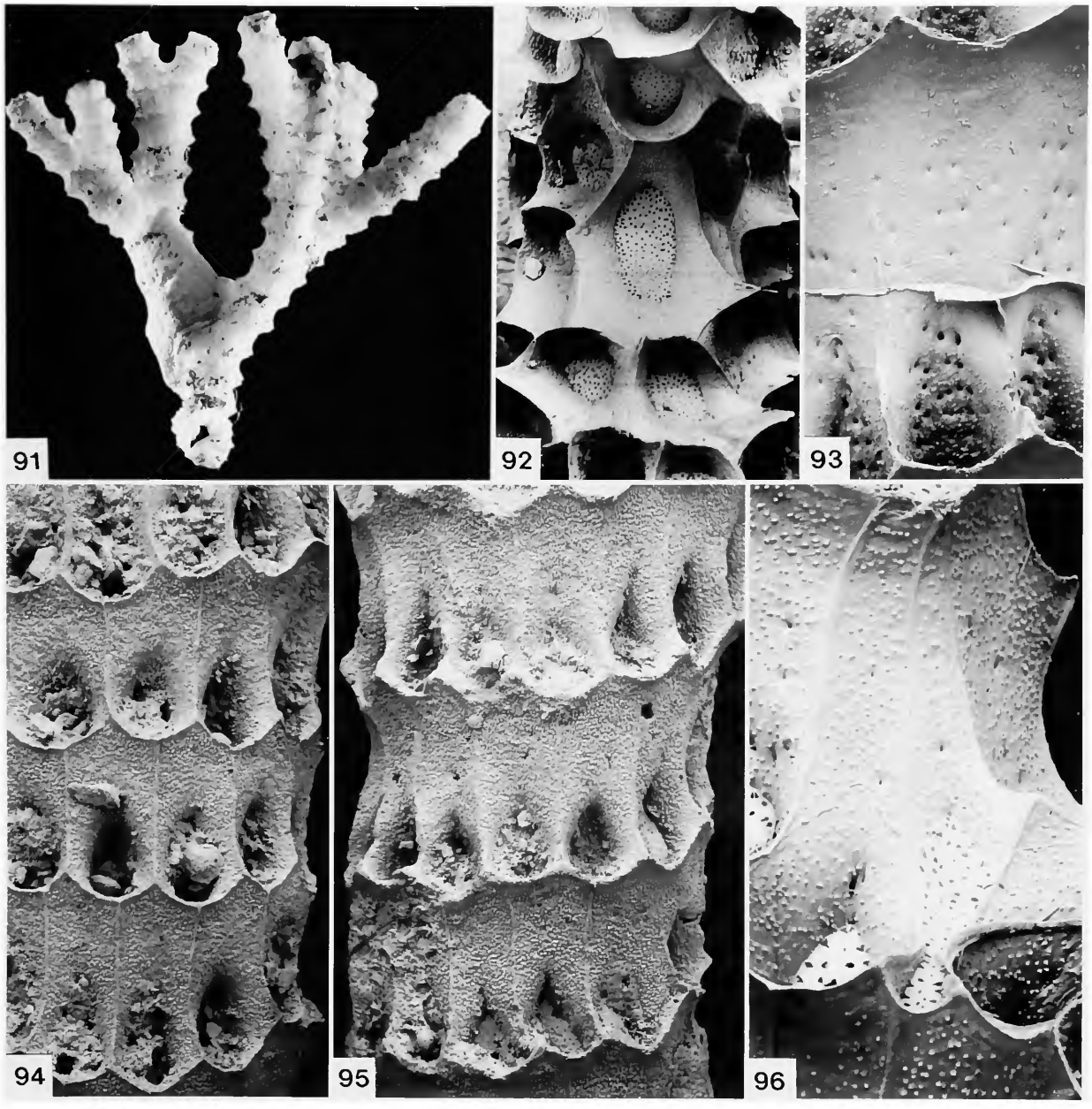
Full-size feeding organs nearly fill living chamber cross-sectional areas from mouth level to near the inner end of the caecum when retracted. Lophophores with 16 tentacles of roughly equal length. In fully regenerated colonies, rapid ontogenetic size increase of tentacles and total lengths of feeding organs for distance of approximately 1.0 mm from youngest zooids at branch tips to youngest zooids with full-size feeding organs. Full-size feeding organs 1000-1800 µm in length and corresponding tentacles 600-900 µm. Proximally from about 3 mm to nearly 8 mm from centers of branch tips feeding organs and tentacles slightly shorter, beyond which zooids generally dormant. Tentacles constitute 31.5%-82.5% of length of retracted feeding organs, proportionally longest in youngest zooids for as much as 1 mm proximally from branch tips.

Single brown bodies in some zooids in endozones at growing tips and exozones in degenerated and regenerating zooids. Brown bodies generally absent in fully regenerated zooids.

In primary zone of astogenetic change, ancestrula with concentrated pseudopores close to basal disc, distally pseudopores more scattered, pustulose lining throughout, some with terminal diaphragms. Some zones of change with second encrusting, fixed-walled, ancestrular zooid attached to ancestrula and leading to first whorl of colony. Some encrusting polymorphs around colony base with pustules and terminal diaphragms.

REMARKS.—All studied populations of free-walled cinctiporids from the Recent are referred to *C. elegans*. The species has a wide distribution around the South Island of New Zealand (Figure 1) and there is considerable variation in external skeletal morphology between populations. Variable characters include branch thickness, length:width ratios of skeletal shields, and degree of shield pustulosity. Nevertheless, this varability does not encompass the range of morphometric separation of *C. elegans* from *C. elongata*, a Miocene and Pliocene species that has skeletal apertures with consistently higher length:width ratios (see below). A genetic study would provide a useful means of testing the hypothesis that only one species of *Cinctipora* is extant in New Zealand.

ECOLOGICAL NOTES.—*Cinctipora elegans* is common on




FIGURES 91–96.—*Cinctipora elegans*. 91, Bleached colony, lectotype BMNH 1875.1.5.37a, locality unknown (×3.5). 92, Giant zooid typical of crotch of bifurcating branches from Otago Shelf, BMNH 1989.10.40.1 (×21). 93, Skeletal shields nearly smooth with few pustules, NZOI sta C624 (×47). 94, Variation in zooidal length, OUM QW 92, Lower Pleistocene from Petane (×24). 95, OUM QW 90, Upper Pleistocene from Wanganui (×22). 96, Morphologic variation due to anastomozing branches, from Otago Shelf, BMNH 1989.10.40.2 (×68).

coarse shell gravel in areas of moderate to strong currents in the Patterson Inlet, Stewart Island. Bushy colonies can be as large as 15 cm high and 0.5 $m^2$ in lateral extent and may form microhabitats colonized by a great variety of encrusting and nestling species (Willan, 1981). *C. elegans* is the dominant bryozoan on the Otago Shelf close to the Otago Peninsula, especially at depths of about 50–70 m ("mid-shelf" in Probert, Batham, and Wilson, 1979; Probert and Wilson, 1984). Current speeds are thought to be high because the north-easterly flowing Southland Current is accelerated as it is squeezed between the Otago Peninsula and colder waters further offshore. According to Nelson, Keane, and Head (1988), *C.*

*elegans* is one of the most important bryozoan species contributing to shelf carbonate deposits around New Zealand and is restricted to localities south of about 40 degrees latitude.

Regeneration of living colonies following damage and breakage is described above and suggests that colony fragmentation may be a means of clonal reproduction in *C. elegans*. Some of the damage and breakage of colonies may be caused by the activities of two echinoid species, *Goniocidaris umbraculum* and *Pseudoechinus huttoni*, reported to graze on *C. elegans* on the Otago Shelf (Barker, 1985:213).

RANGE.—Pliocene to Recent, New Zealand.

TYPES.—*Lectotype, Recent:* designated here, BMNH 1875.1.5.37a, locality in New Zealand unknown.

*Paralectotypes, Recent:* BMNH 1875.1.5.37b–f (f peeled). In 1874, the British Museum (Natural History) received a shipment of specimens as an exchange from F.W. Hutton that included four specimens identified as *Cinctipora elegans*. The covering letter, dated 26 Jul 1874, from Hutton to J.E. Gray, then keeper of Zoology, is letter number 90 preserved in catalog DF200/4 in the Natural History Museum Archives. The letter includes the statement, "A great many of these are types of my new species. ..." Neither the Canterbury Museum at Christchurch nor the Otago Museum at Dunedin, which contains types of some of Hutton's other bryozoan species, have ever had the primary types of *C. elegans*. Therefore, the specimens Hutton sent to the BMNH are considered to be syntypes from which a lectotype and 5 paralectotypes are here chosen.

SECTIONED RECENT MATERIAL.—USNM locality 2681, seven colonies, collected by Dennis P. Gordon for Leigh Marine Research Laboratory, University of Auckland, New Zealand, off Otago Heads, South Island, New Zealand, sta Mu 76-138, 110 m, 2 ft Agassiz trawl, 4 Oct 1976. USNM locality 2689, five colonies, collected by P.K. Probert, Portobello Marine Laboratory, University of Otago, on shelf off Otago Heads, 110 m, Mar 1977. One colony collected by P.J. Schembri from the Otago Shelf, British Museum (Natural History). USNM 2697, one colony, collected by D.P. Gordon, edge of continental shelf off Portobello Laboratory. USNM, University of Southern California sta 1430, 21 colonies, cruise 16, 40 ft Otter trawl, at 165–192 m depth, 22 Jan 1965.

UNSECTIONED RECENT MATERIAL.—New Zealand Oceanographic Institute localities: sta A714, 47°43.5′S 179°04′E, 168 m, 5 Nov 1962; sta A721, 49°39.5′S 178°53′E, 132 m, 6 Nov 1962; sta B230, 46°40′S 168°02.5′E, 26 m, 22 May 1960; sta B482, 46°08.8′S 166°06′E, 88 m, 6 Jun 1961; sta B582, 48°00′S 167°38′E, 143 m, 11 Oct 1962; sta B587, 48°00.2′S 166°39′E 155 m, 12 Oct 1962; sta B592, 48°46′S 167°19′E, 152 m, 13 Nov 1962; sta C60, 41°23′S 174°25.5′E, 143 m, 7 Jun 1956; sta C624, 43°57.5′S 175°52′E, 124 m, 7 May 1961; sta C703; 42°42′S 173°37.8′E, 184 m, 19 Jun 1961; sta C844, 41°38.3′S 175°11.2′E, 88 m, 1 Mar 1962; sta D1, 44°18′S 176°10′E, 141 m, 12 Apr 1963; sta D31, 52°34.5′S 169°17′E, 62 m, 3 May 1963; sta D35, 52°56.4′S, 169°33′E, 188 m, 5 May 1963; sta D53, 50°41.6′S 166°24′E, 81 m, 9 May 1963; sta D75, 50°55.9′S 166°01.5′E, 95 m, 12 May 1963; sta D100, 48°02′S 166°36′E, 161 m, 26 Sep 1963; sta D873, 43°34.5′S 176°38′W, 66 m, 25 Mar 1969; sta E107, 43°45′S 177°0.0′W, 113 m, 11 Oct 1964; sta E817, 46°13.5′S 166°29′E, 218–235 m, 23 Oct 1967; sta E820, 46°35′S 165°58′E, 220 m, 23 Oct 1967; sta E832, 47°21′S 167°05.7′E, 225–251 m, 25 Oct 1967; sta F142, 52°52′S 168°49′E, 168 m, 31 Jan 1965. Portobello Marine Laboratory Stations: sta Mu88-28, 45°50.2′S 170°52.5′E, 82 m, 11 May 1988; sta Mu88-29, 45°51.8′S 170°54.4′E, 87–89 m, 11 May 1988; sta Mu76-138, 45°50.2′S, 170°52.5′E, 110 m, 4 Oct 1976.

FOSSIL MATERIAL.—*Pliocene:* BMNH D58647 (scanned), D59281 (sample), Opiotian-Mangapanian, Whenuataru Tuff, base of cliffs, SW side of Moutapu Point, Pitt Island, Chatham Islands (NZ Fossil Record #CH/f13B, grid reference 721248; see Campbell et al., 1988:305), colld. by A.G. Beu, J.I. Beu, P.A. Maxwell, and H.J. Campbell, 1975 and presd. to P.D. Taylor, Jun 1988.

*Pleistocene:* OUM QW92 (scanned), [?Petane Limestone], Petane, Hawkes Bay. OUM QW90 (scanned) [?Castlecliffian], Shakespeare Cliff, Wanganui. NZGS BZ 113, holotype of *Spiroporina immersa* Tenison-Woods, 1880 (fig. 24A,B), [probably Castlecliffian, ?Tainui Shellbed], Shakespeare Cliff (lower part), Wanganui.

### *Cinctipora elongata*, new species

FIGURES 97–102

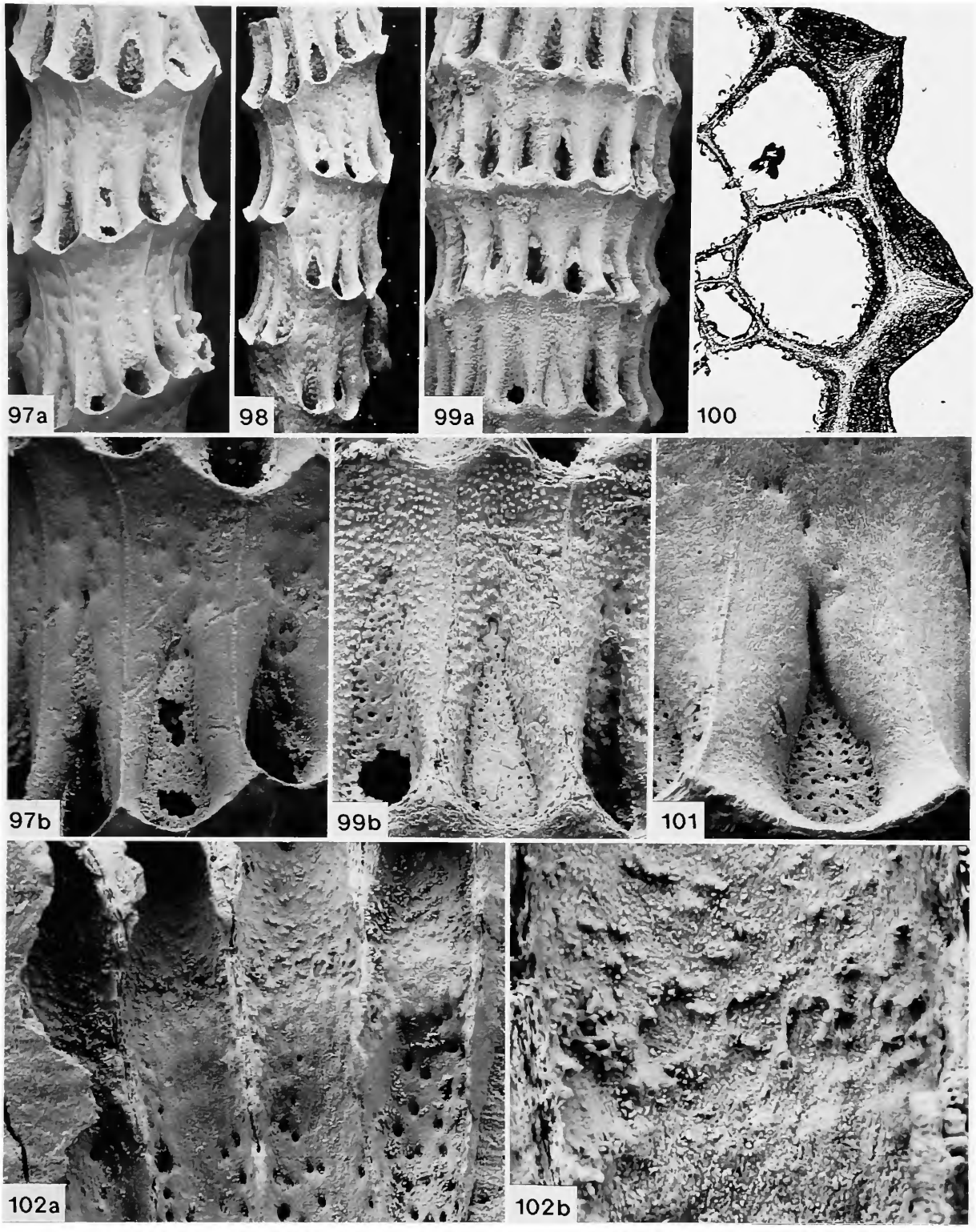
ETYMOLOGY.—Latin for prolonged, in reference to the high length: width ratio of the skeletal shield.

DESCRIPTION.—Colonies erect, branches cylindrical, bifurcating, 1.4–2.4 mm in diameter, averaging 1.8 mm. Zooids in annular rings or spiral whorls with dislocations. Ten to 16 zooids around branch. Emergent peristomes rare, perhaps due to delicateness and lack of preservation. Average nearest neighbor longitudinally 1.21 mm, average nearest neighbor transversely 0.43 mm.

On branch surface, average zooecial length 1.36 mm, average proximal width of zooecia 470 μm, average minimum width of zooecia 350 μm. Therefore, zooecia relatively elongate and narrow, with length:proximal width about 3:1 and length:minimum width about 4:1. Terminal diaphragms elongate, some pointed distally. Shields vary from pustulose to smooth.

Average maximum wall thickness 214 μm. Average chamber diameter 234 μm. Angle between branch axis and zooecial axis in inner exozone 15 degrees on average, and shield at 47 degrees to branch axis on average. Average aperture width 271 μm.

Scars of estimated 16 attachment ligaments in skeletal surfaces at boundaries between pustulose surfaces outward and




FIGURES 97–102.—*Cinctipora elongata*, all Miocene, Otaian-Altonian, Forest Hill Limestone, Lady Barkly Quarry, except Figure 99. 97, Holotype, NZGS BZ 153: *a*, long narrow zooids (×21); *b*, smooth skeletal shields (×54). 98, Offset of spiral whorls, paratype, BMNH D59285 (×15). 99, Paratype, BMNH D59289, from Miocene, Altonian, Clifden Limestone, Clifden Suspension Bridge: *a*, annular rings (×16); *b*, coarse pustules (×56). 100, Peel of transverse section, paratype, BMNH D59332 (×100). 101, Smooth skeletal shields, paratype, BMNH D59282 (×90). 102, Paratype, BMNH D59283, interior of living chambers with pustules above, attachment scar ring, and smooth skeletal lining below: 102*a* (×100); 102*b* (×317).

smooth or grooved surfaces inward. Approximately 20–25 shallow longitudinal grooves in laminar surfaces of some zooids.

REMARKS.—In addition to conspicuous differences of zooids in ratio of length:width in surface expression between *C. elongata* and *C. elegans*, discriminant analysis indicates that the two species differ most in zooecial length, aperture diameter, nearest neighbors transversely, nearest neighbors longitudinally, branch diameter, maximum wall thickness, and chamber diameter. Terminal diaphragms more elongated and pointed than those of *C. elegans* reflect the narrow cross-sectional shape of the zooidal chamber.

RANGE.— Miocene–Pliocene, New Zealand.

TYPES.—*Holotype* NZGS BZ 153, *Miocene:* Otaian-Altonian, Forest Hill Limestone, Lady Barkly Quarry, Winton, Southland (NZ Fossil Record #E45/f168, grid reference 517468, 1984), colld. by P.D. Taylor, Jun 1988.

*Paratypes, Miocene:* BMNH D59282–D59285 (scanned), D59286 (sample), D59287 (sample), D59331–D59342 (peeled), same occurrence data as holotype. OU 39792 (sample), same occurrence data as holotype. BMNH D59288, D59289 (scanned), Altonian, Clifden Limestone, Clifden Suspension Bridge, Southland (NZ Fossil Record #D45/f327, grid reference 009510, 1985; see Hayward, 1988), colld. by P.D. Taylor, Jun 1988.

*Paratypes, Pliocene:* D59290–D59292, D59343–D59347 (paratypes peeled), Opoitian-Mangapanian, Whenuataru Tuff, base of cliffs, SW side of Moutapu Point, Pitt Island, Chatham Islands (NZ Fossil Record #CH/f13B, grid reference 721248; see Campbell et al., 1988:305), recollection by A.G. Beu, J.I. Beu, P.A. Maxwell, and H.J. Campbell, 1977 (DSIR Geology and Geophysics macrofossil collection No. GS 12163), and presd. to P.D. Taylor, Jun 1988.

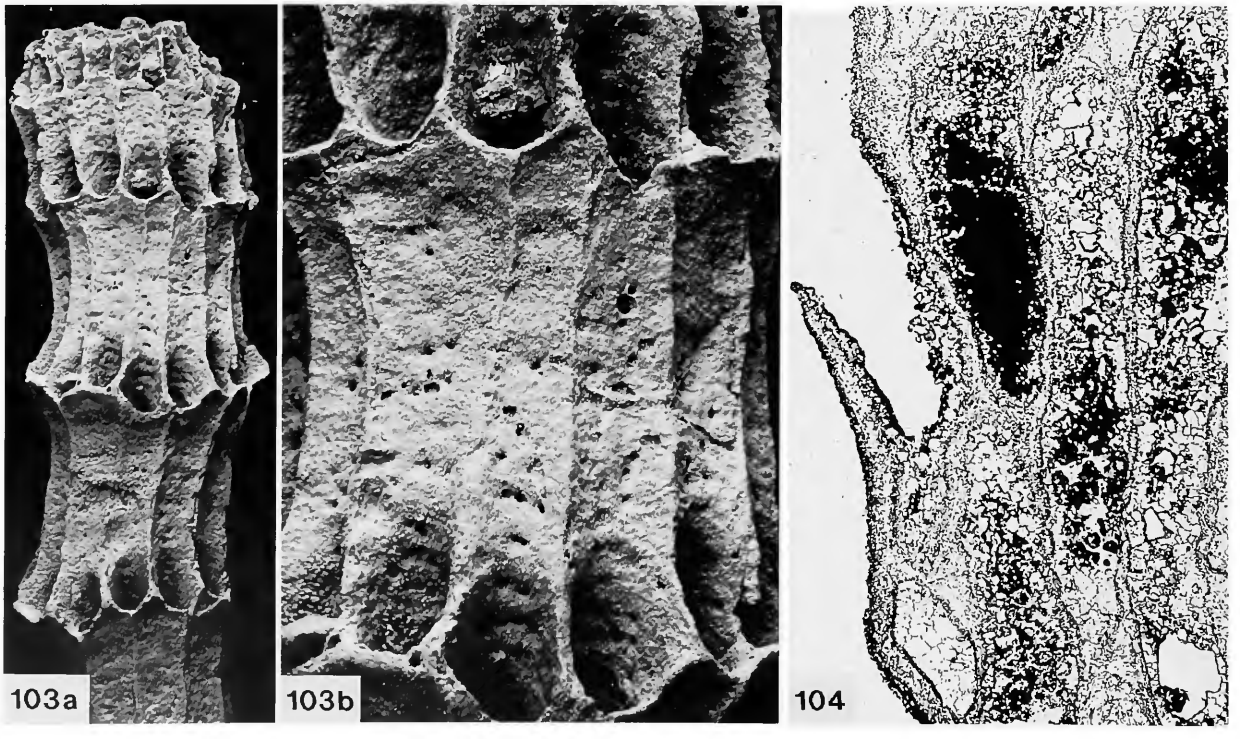
### *Cinctipora* sp.

FIGURES 103, 104

*Spiropora irregularis* Brood, 1977:78 [part], fig. 19A only.

DESCRIPTION.—Colonies erect with cylindrical branches about 0.8 mm in diameter. Eleven to 13 annularly disposed zooids around branch circumference. Average nearest neighbor longitudinally 790 µm. Average maximum wall thickness 58 µm. Ratio of endozone:branch diameter 0.71:1.

Zooids small, skeletal aperture length averages 798 µm, proximal width 254 µm, and minimum width 201 µm. Therefore, zooids relatively narrow, with skeletal aperture length:proximal width about 3:1, and length:minimum width about 4:1.




FIGURES 103, 104.—*Cinctipora* sp., Maastrichtian, Need's Camp, South Africa. 103, BMNH D59325: *a*, relatively long skeletal shields (×34); *b*, shows skeletal shield spanning two distal zooids, cluster of communication pores at functional apertures (×96). 104, Peel of longitudinal section, BMNH D59361 (×100).

Average chamber diameter 141 μm. Angle between branch axis and zooecial angle in endozone 14 degrees on average, in exozone 44 degrees on average. Average functional aperture width 190 μm.

Primary zone of astogenetic change unknown.

REMARKS.—The specimens from the Upper Cretaceous of Need's Camp, South Africa, are not described as a formal species because only three fragmentary specimens are presently available. They resemble New Zealand *Cinctipora* in all essential generic characters. Their branch diameters and zooidal dimensions are considerably smaller than the gigantic zooids of the cinctiporids from New Zealand. However, all three genera of the New Zealand cinctiporids display a trend toward smaller zooids back in time and that trend projected back to the Upper Cretaceous suggests the smaller zooid for earlier ancestors.

One of Brood's (1977) paratype specimens of the fixed-walled species of *Spiropora irregularis* belongs to this *Cinctipora* sp. Brood depicted this specimen in figure 19A and described it as corroded. However, corroded specimens of *S. irregularis* in the BMNH collections have a different appearance, i.e., the distal ends of the zooids are convex and rounded rather than pointed. (The true generic attribution of *Spiropora irregularis* is unclear in the absence of brood chambers, which are essential for the taxonomy of bryozoans of this type; see Voigt and Flor, 1970).

RANGE.—Maastrichtian (?Upper Campanian), Need's Camp, Cape Province, South Africa.

MATERIAL.—*Upper Cretaceous:* BMNH D59325 (scanned), D59361, D59362 (peeled), Upper Campanian or Maastrichtian, Need's Camp, Cape Province, South Africa, Rennie Colln.

## Genus *Cylindropora* Tenison-Woods, 1880

*Cylindropora* Tenison-Woods, 1880:21. [Not *Cylindropora* Eichwald, 1827, sensu Lang et al., 1940.]

TYPE SPECIES.—*Cylindropora areolata* Tenison-Woods, 1880:21, selected herein.

EMENDED DEFINITION.—Free-walled Cinctiporidae with zooidal apertures in closely spaced, irregular spiral whorls in dendroid, bushy colonies with cylindrical branches bifurcating, few anastomosing. Branch diameters typically large for family, mostly because of relatively large number of zooids at any one level so that diameters of endozones large.

Zooids large to gigantic, intersect branch surfaces at moderate angles so that skeletal shields few, shortened, only in younger zooids or those with smaller zooidal angles. Minor ontogenetic increases in exozonal widths in older colonies. Zooidal boundaries at colony surfaces typically hexagonal, marked by sharp keels centered on thick zooidal walls. Zooids of adjacent whorls either in longitudinal rows along branches or offset. Emergent peristomes unknown. Calcified terminal diaphragms in proximal parts of branches.

In thin section, pustules small in laminar layers, communication pores closely spaced in axial walls of zooids behind apertures. Thickened exozonal walls primarily caused by greatly thickened transparent zones.

Primary zone of astogenetic change unknown, can give rise to multiple erect stems.

REMARKS.—Tenison-Woods (1880:21) established a new genus *Cylindropora* in the cnidarian suborder Hydrocorallinae. He referred two new species to *Cylindropora, C. areolata* and *C. spongiosa,* without selecting a type species. No subsequent type species designation apparently has been made (the genus was not mentioned by Bassler, 1953) and, in view of the lack of either an illustration or syntype material of the second named species, *C. areolata* is designated herein as the type species.

*Cylindropora* Tenison-Woods, 1880, is not the same as *Cylindropora* Eichwald, 1829 sensu Lang et al. (1940), an incertae sedis from Estonian drift of ?Silurian age. The original spelling of Eichwald's genus was *Cylindripora* (1829:190, 314) and Lang et al.'s subsequent spelling is an unjustified emendation (see Article 33(b) of the *International Code of Zoological Nomenclature,* ITZN, 1985). Therefore, *Cylindropora* Tenison-Woods is an available name for the cinctiporid genus described here.

*Cylindropora* is a monospecific, free-walled cinctiporid genus characterized by robust branches, apertures closely spaced in spiral whorls, skeletal shields few and shortened, and zooidal boundaries hexagonal at branch surfaces.

The moderate zooidal angles at colony surfaces result in shortened or no skeletal shields and therefore more closely spaced spiral whorls. The moderate angles also make possible continued outward growth of exozonal walls so that some ontogenetic gradient occurs proximally along branches.

### *Cylindropora areolata* Tenison-Woods, 1880

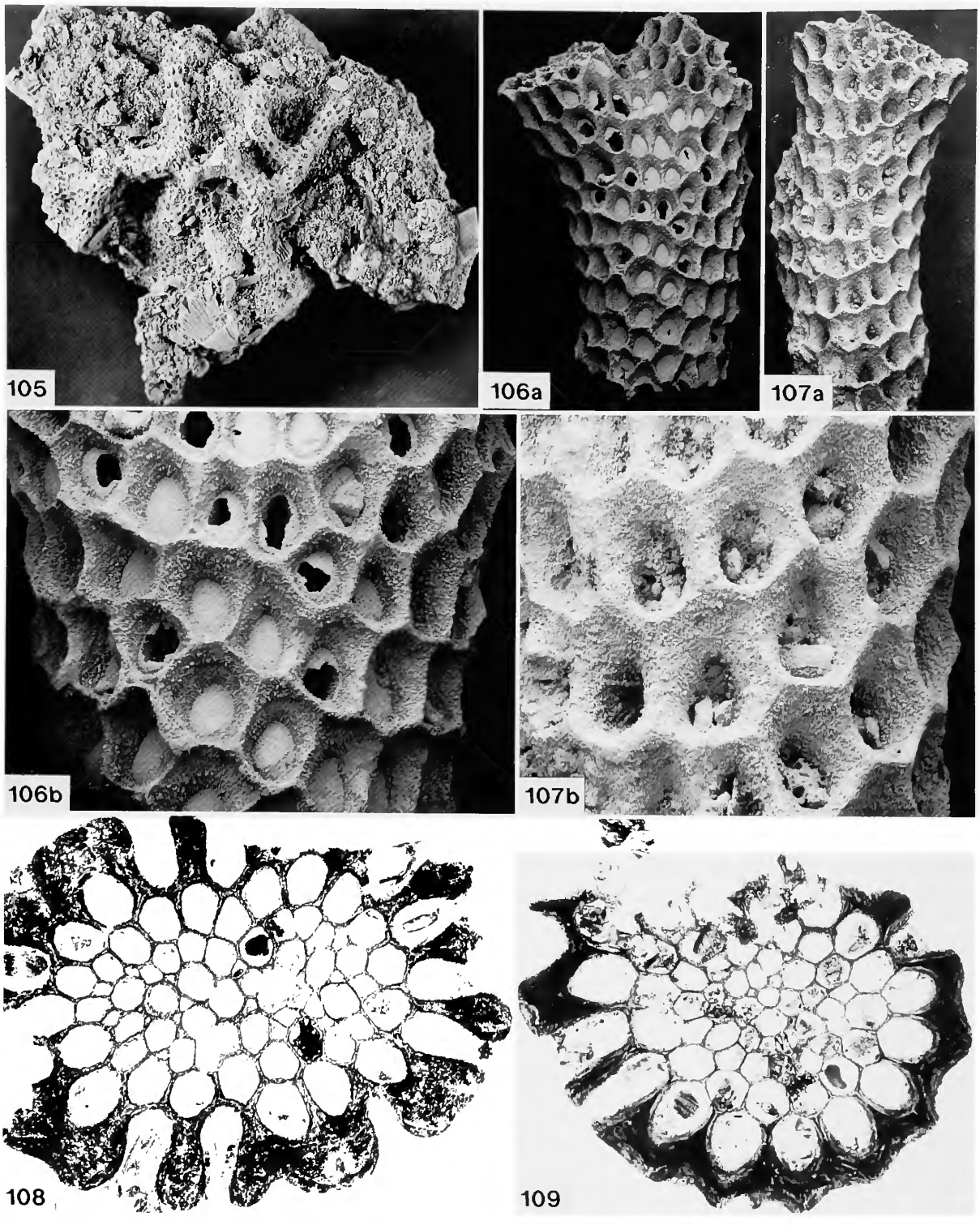
FIGURES 105–111

*Cylindropora areolata* Tenison-Woods 1880:21.

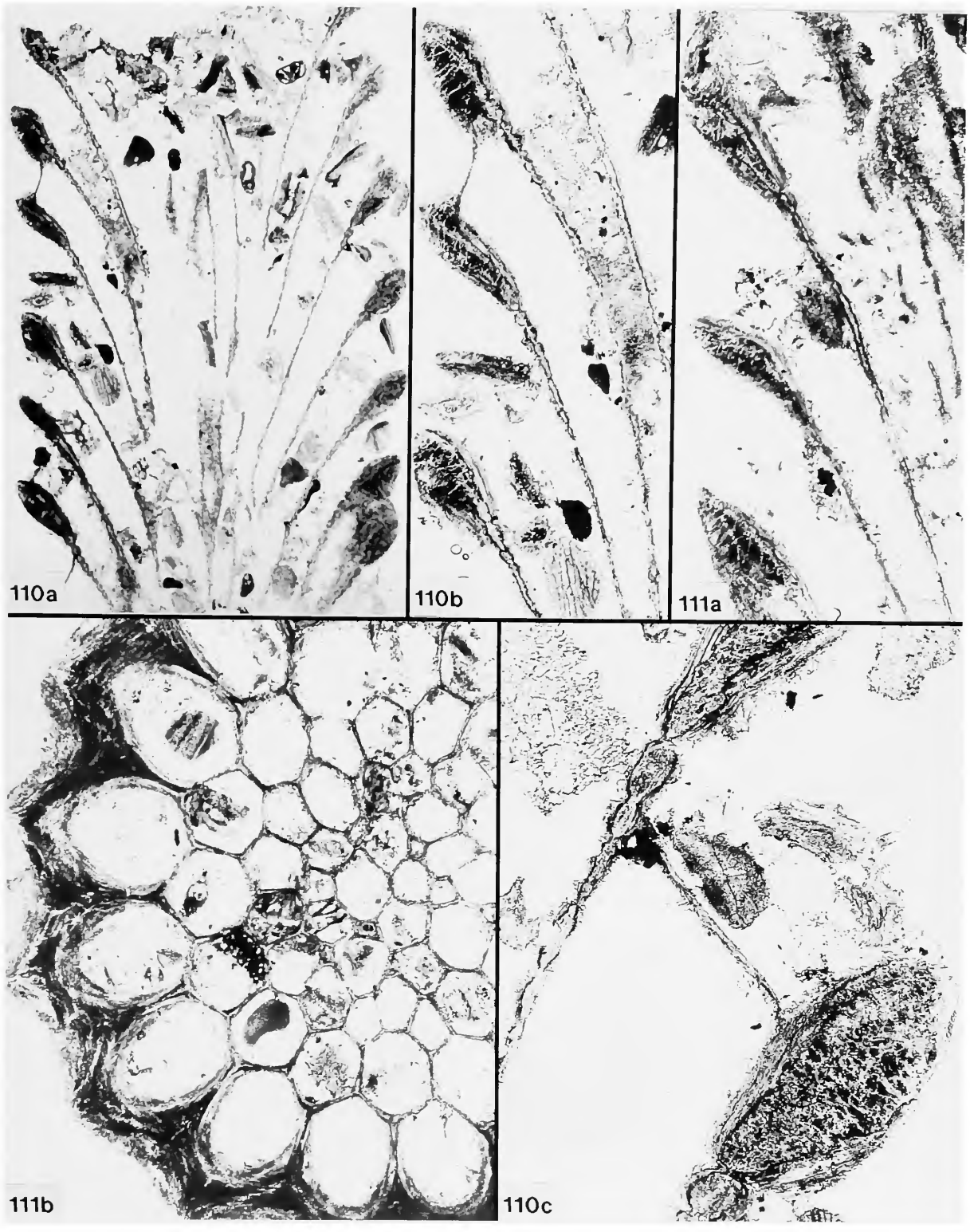
EMENDED DESCRIPTION.—Colonies erect with bifurcating and anastomosing cylindrical branches. Branch diameters 2.3–5.4 mm. Fourteen to 24 zooids around branch. Average nearest neighbor longitudinally 1.03 mm, average nearest neighbor transversely 590 μm. Average wall thickness 240 μm. Ratio of endozone diameter to branch diameter 0.57:1, with moderate variability. Exozonal widths below growing tips ranges from 0.5–0.9 mm indicating some ontogenetic variation.

Thick exozonal walls of both thickened transparent and laminar layers. Pustules small and closely spaced in laminar layers. Zooidal boundaries typically 6-sided, most appear equidimensional, average zooidal length 1.17 mm, average proximal width 460 μm (proximal side of boundary), average minimum width 440 μm (length of proximal or distal boundary, whichever is shorter).

Chamber diameter averaging 396 μm at level of maximum




FIGURES 105-109.—*Cylindropora areolata*, all Pliocene, Mangapanian, Te Aute Limestone. 105, Lectotype, NZGS BZ 110, probably from Dorset's Forty-mile Bush, Wellington (×1.6). 106, 107, From Waipukurau, Napier: 106, BMNH D59293: *a*, closely spaced spiral whorls (×7.6); *b*, skeletal shields short to lacking (×21). 107, BMNH D59295: *a* (×7.6); *b* (×29). 108, 109, Transverse thin sections showing large numbers of zooids at one level in branch, Hatuma Quarry, Hawkes Bay (×20): 108, BMNH D59390. 109, BMNH D59392.




FIGURES 110, 111.—*Cylindropora areolata*, Pliocene, Mangapanian, Te Aute Limestone, Haturna Quarry, Hawkes Bay. 110 BMNH D59391, longitudinal sections, wide transparent layers: *a* (×20), *b* (×40), *c* (×100). 111, BMNH D59392: *a*, longitudinal section (×40); *b*, transverse section (×40).

wall thickness. Angle between outer exozone and branch axis 64 degrees on average. Average aperture width 320 μm.

REMARKS.—*Cylindropora areolata* is free-walled, differing from other cinctiporid species in its generally thicker branches with broad endozones caused by relatively large numbers of zooids, thicker exozonal walls showing some ontogenetic variation, 6-sided zooidal boundaries at surfaces, and closely spaced whorl patterns.

The zone of primary astogenetic change is preserved in specimen OUGD 5050 with encrusting base giving rise to more than five erect stems; the morphology of the zooids is not visible.

The robust branch morphology of *C. areolata* correlates well with its facies distribution. Specimens are common in the "Te Aute Limestone facies" (Beu et al., 1980) of Hawke's Bay. This barnacle-rich limestone with giant cross-beds is interpreted by Kamp et al., (1988) as having been deposited in a current-swept basin. Deposition at inner shelf depths was strongly influenced by strong tidal currents capable of entraining sand and gravel-size skeletons. Indeed, most specimens of *C. areolata* have abraded surfaces suggesting significant predepositional transportation. Specimen preservation is further adversely affected by ubiquitous growth of diagenetic calcite crystals over the surface of the skeleton.

RANGE.—Pliocene, New Zealand.

TYPE.—*Lectotype:* designated here, NZGS BZ 110, (probably Pliocene, Mangapanian, Te Aute Limestone; I.W. Keyes, pers. comm. to P.D.T., Mar 1989), Dorset's, Forty-Mile Bush, Wellington. This specimen was mentioned by Tenison-Woods (1880:21) as "No. 73" and apparently is not the specimen depicted in his fig. 21A-D. The latter might have been his "No. 79," from the Mangapanian Te Aute Limestone of Mount Vernon, Waipukurau, Napier, a specimen that could not be found in the NZGS collections (I.W. Keyes, pers. comm. to P.D.T., Mar 1989).

OTHER MATERIAL.—*Pliocene:* NZGS BZ 145-150, Mangapanian, Te Aute Limestone, Mount Vernon, Waipukurau, Napier, Tenison-Woods colln. BMNH D59293-D59295 (scanned), D59296 (sample), D59297 (sample), D59348-D59351 (peeled), D59390-D59392 (sectioned), Mangapanian, Te Aute Limestone, Hatuma Lime Company quarry, 8.3 km E of Takapau Township at end of Marakeke Station Road, Southern Hawkes Bay (NZ Fossil Record #U23/f6526B, grid reference 045253; see Harmsen, 1984), colld. by P.D.T., Jun 1988. BMNH D59298 (sample) (probably Mangapanian, Te Aute Limestone), Waipukurau, Blake Colln. BMNH D59299 (sample) (probably Mangapanian, Te Aute Limestone), Napier, Blake Colln. OUGD 5050, Te Mata, Napier.

### *Semicinctipora*, new genus

TYPE SPECIES.—*Semicinctipora annulata*, new species.

ETYMOLOGY.—*Semis*, Latin for half, in reference to the similarity with *Cinctipora*, but with skeletal shields of lesser extent. Gender: feminine.

DEFINITION.—Cinctiporidae with widely spaced, annular rings of zooids with combined fixed/free apertures on slender, bifurcating branches. Zooidal arrangement rarely spiral. Branch diameters regularly decrease opposite apertures and shields, increase opposite frontal walls distally to maximum diameters at proximal sides of apertures.

Zooids large to gigantic, at low angles at colony surfaces, endozonal walls extremely variable in thickness among species. Lateral and distal sides of apertures freed by interior vertical walls, proximal sides of apertures fixed by shortened exterior frontal walls; change from vertical to frontal walls at varying positions in proximal half of longitudinal distance between rings of apertures. Shortened skeletal shields from vertical walls so apertures subterminal. Frontal walls with pseudopores form straight proximal edges of functional apertures transverse to branch axes. Externally, change from shields to frontal walls just distal to thickened convex ridges of shields, ridges arched distally on colony surfaces into inverted V- or U-shape. Closely spaced communication pores in axial walls at apertures and pustules throughout skeletons lacking. Emergent peristomes probable, rare.

In sections, zooidal boundaries of vertical walls intersect outer skeletal surfaces at transitions from shields to frontal walls. Convexly thickened ridges of shields largely of thickened transparent layers of vertical walls.

Primary zone of astogenetic change unknown.

REMARKS.—The new genus *Semicinctipora* is created for two new species of cinctiporids, the type species *S. annulata* and *S. amplexus*. They have combined free-/fixed-walled morphologies, in certain respects intermediate between *Cinctipora* and *Attinopora*. Zooids of *Semicinctipora* possess shortened shields (cf. *Cinctipora*) that are transformed distally to shortened exterior frontal walls (cf. *Attinopora*) between adjacent rings or whorls of zooids. Within the family, the genus can be recognized externally by the variation in branch diameters between rings and whorls, the straight proximal edges of apertures, the inverted V- or U-shapes of the thickened ridges at distal ends of shields, the lack of closely spaced communication pores in axial walls behind apertures, and in well-preserved specimens, the position of pseudopores that indicate the extent of shortened frontal walls.

Typical cinctiporid characteristics include the combined fixed-free apertures, skeletal microstructure and ultrastructure, extremely large to gigantic zooids, and annular zooidal arrangement.

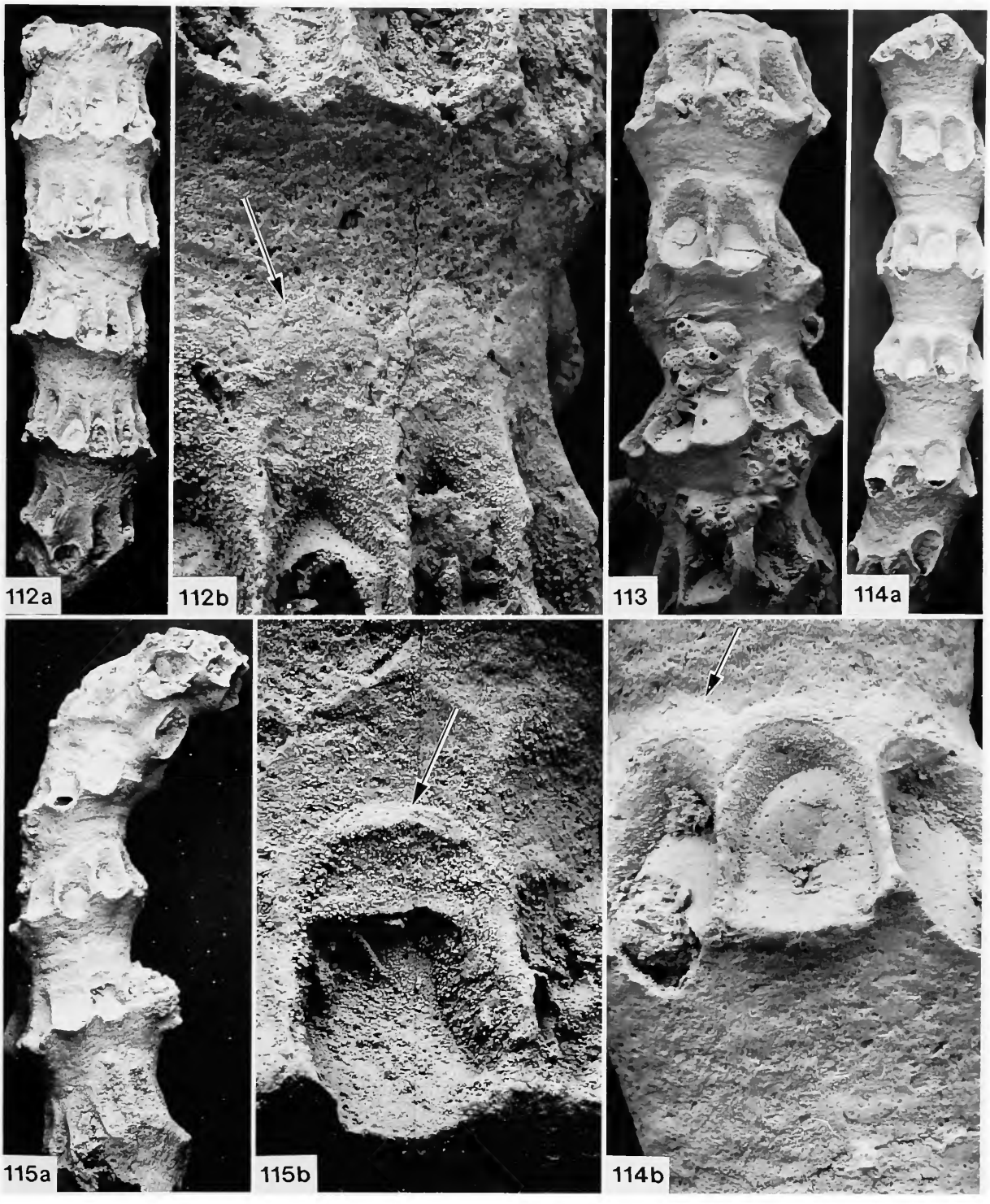
RANGE.—Oligocene-Miocene, New Zealand.

### *Semicinctipora annulata*, new species

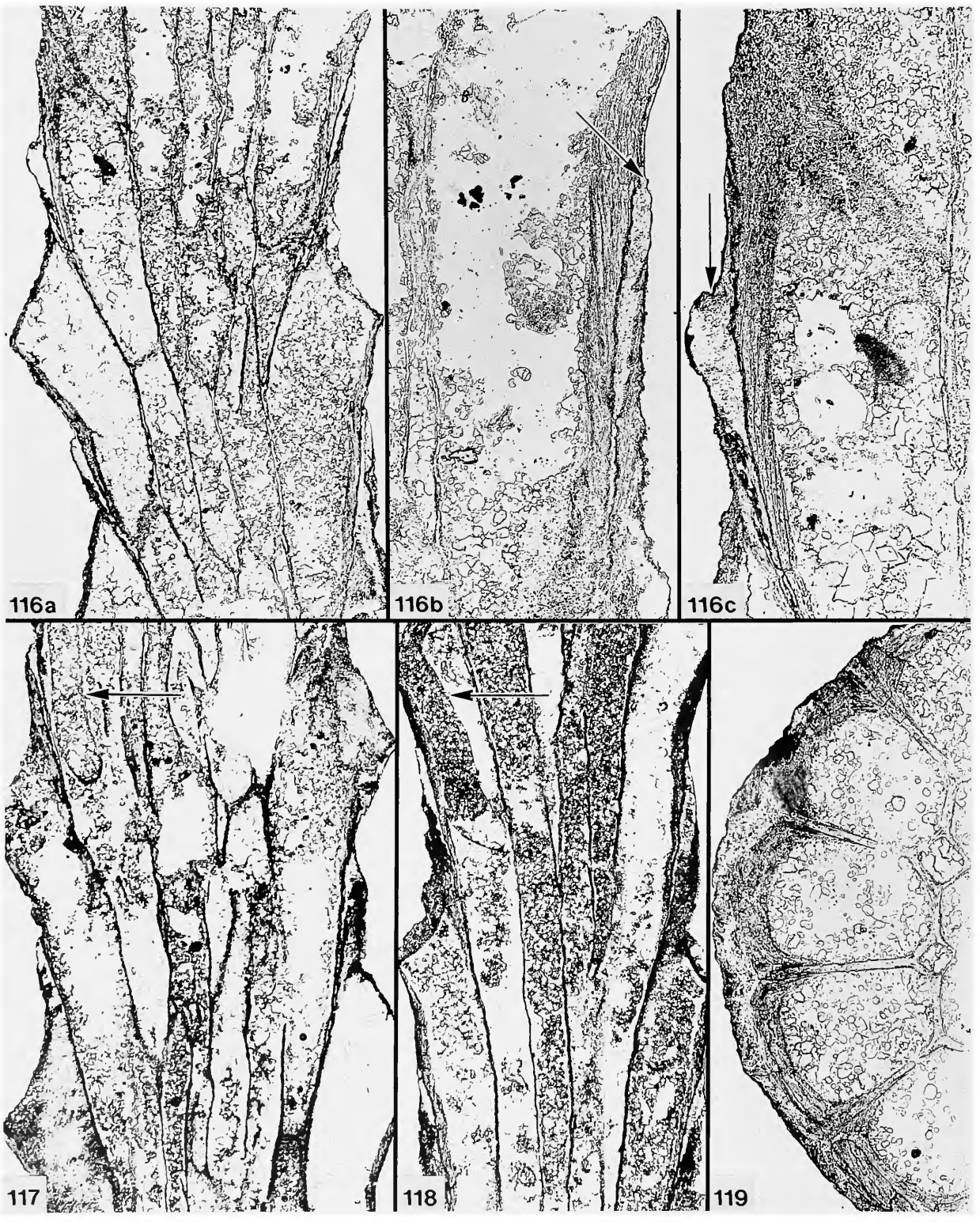
FIGURES 60, 61, 112-119

ETYMOLOGY.—*Annulatus*, Latin for furnished with a ring, in reference to the rings of zooids around the branches.

DESCRIPTION.—Zooids in well-defined to disrupted annular rings, few in spirals. Branch diameter 1.3-1.8 mm, averaging




FIGURES 112–115.—*Semicinctipora annulata*, Miocene, Otaian-Altonian, Forest Hill Limestone, Forest Hill Quarry, Winton. 112, Holotype, NZGS BZ 154: *a*, annular rings of zooids form typical branch shape from cycle to cycle (×12); *b*, massive skeletal shields distal to lower apertures followed distally (arrow at boundary) by frontal wall with pseudopores that form proximal side of upper apertures of next cycle (×75). 113, Paratype, BMNH D58649 (×20). 114, Paratype, BMNH D58648: *a* (×12); *b*, shortened skeletal shields (arrow at shield-frontal wall boundary) (×60). 115, Paratype, BMNH D59300: *a* (×14); *b*, remnant of emerging peristome (arrow) (×98).




FIGURES 116–119.—*Semicinctipora annulata*, Miocene, Otaian-Altonian, Forest Hill Limestone, Forest Hill Quarry, Winton. 116, Paratype, BMNH D59305, longitudinal thin sections: *a* (×40); *b,c*, arrows at junctions between skeletal shields and frontal walls (×100). 117, Longitudinal thin section, thin endozonal walls, probably preserved membranous sac (arrow), paratype, BMNH D59303 (×40). 118, Longitudinal thin section, probably preserved membranous sac (arrow), paratype, BMNH D59302 (×40). 119, Transverse section with thin endozonal walls, annular pattern of endozone, paratype, BMNH D59306 (×100).

1.5, with 10–12 zooids around branch circumference. Strongly convex, inverted, V- or U-shape ridges formed by lateral sides of apertures connected to thickened ridges just proximal to change from shields to frontal walls. Average nearest neighbor longitudinally 1.4 mm, average nearest neighbor transversely 420 μm. Ratio of endozone diameter to branch diameter 0.55:1, with low variability. Endozonal walls extremely thin for cinctiporids.

On branch surface, average zooidal length 1.6 mm, average proximal width 480 μm, and average minimum width 370 μm. Ratio of length:proximal width about 3.3:1, and length:minimum width about 4.3:1. Average chamber diameter 280 μm. Angle between branch axis and zooidal axis averages 26 degrees in outer exozone. Average functional aperture width 300 μm. Emergent peristomes probable, rare.

REMARKS.—Branches of *S. annulata* with short skeletal shields appear superficially to be fixed-walled with extremely thick peristomes. Sections, however, reveal that the convex margins of the lateral and distal sides of the apertures are interior skeleton and the skeletal walls for varying distances up to approximately half way to the next ring of apertures also are interior skeleton. The exterior frontal walls that continue distally from the distal margin of the interior walls to the proximal sides of the next ring of apertures can be identified externally in well-preserved specimens by pseudopores.

In thin sections, thinly calcified sac-shape structures in living chambers suggest membranous sacs.

RANGE.—Miocene, New Zealand.

TYPES.—*Holotype, Miocene:* NZGS BZ 154, Otaian-Altonian, Forest Hill Limestone, Forest Hill Quarry, Winton (NZ Fossil Record #E46/f061, grid reference 575366, 1983), colld. by P.D. Taylor, Jun 1988.

*Paratypes, Miocene:* BMNH D58648, D58649, D59300 (scanned), D59301 (sample), D59302–D59306 (peeled), same occurrence as holotype. OU 39793 (sample), same occurrence as holotype. BMNH D59307 (sample), D59327 (peeled), Forest Hill Limestone, Lady Barkly Quarry, Winton, Southland, (NZ Fossil Record #E45/168, grid reference 517468), colld. by P.D. Taylor, Jun 1988.

### *Semicinctipora amplexus*, new species

FIGURES 50, 120–124

ETYMOLOGY.—*Amplexus*, Latin for encircling, in reference to the skeletal apertures encircling the branches.

DESCRIPTION.—Zooids arranged in semi-regular annular rings. Branch diameter 1.2–1.4 mm, averaging 1.3 mm, contracted between rings or whorls of skeletal apertures, with approximately 9–10 zooids around branch circumference. Skeletal shields short to nearly lacking, ridge just proximal to change to frontal wall convex and rounded. Average nearest neighbor 1.4 mm in longitudinal/sublongitudinal directions, 460 μm in transverse/subtransverse directions. Average vertical wall thickness of zooids in exozones 90 μm just proximal to boundary with exterior frontal wall. Ratio of endozone diameter to branch diameter 0.58:1 with low variability. Endozonal walls extremely thick for cinctiporids.

On branch surface average zooidal length 1.5 mm, average proximal and minimum width both 300 μm. Ratio of length:width of apertures about 5:1. Exterior frontal wall extends for most of length between adjacent rings and whorls. Emergent peristomes not seen.

Average chamber diameter 240 μm. Average angle between branch axis in outer exozone 34 degrees, average functional aperture width 310 μm.

REMARKS.—*Semicinctipora amplexus* differs from the type species *S. annulata* most significantly in the smaller proximal zooidal width and chamber diameter, and greater wall thicknesses in endozones. In addition, zooids are not as well organized into transverse rings in some colonies. Also, frontal walls occupy most of the longitudinal distance between rings and whorls. *S. amplexus* has smaller branch diameters and zooidal lengths than *S. annulata*, but these do not discriminate the two species as well as the features listed above.

*Semicinctipora amplexus* is recorded only in the McDonald Limestone, an Oligocene bryozoan sand that apparently accumulated as banks on volcanic highs in the Oamaru area of North Otago. Although much of the McDonald Limestone is poorly cemented, surface preservation of the bryozoans is not particularly good as a result of predepositional abrasion and diagenetic calcite overgrowth.

RANGE.—Oligocene, New Zealand.

TYPES.—*Holotype, Oligocene:* NZGS BZ 156, Whaingaroan, McDonald Limestone, McDonald's Quarry, Oamaru, North Otago (NZ Fossil Record #J42/f213, grid reference 451579; see Fordyce et al., 1985), colld. by P.D. Taylor, Jul 1988.

*Paratypes, Oligocene:* BMNH D59322, D59323 (scanned), D59324 (sample), D59354–D59360 (peeled), same occurrence as holotype.

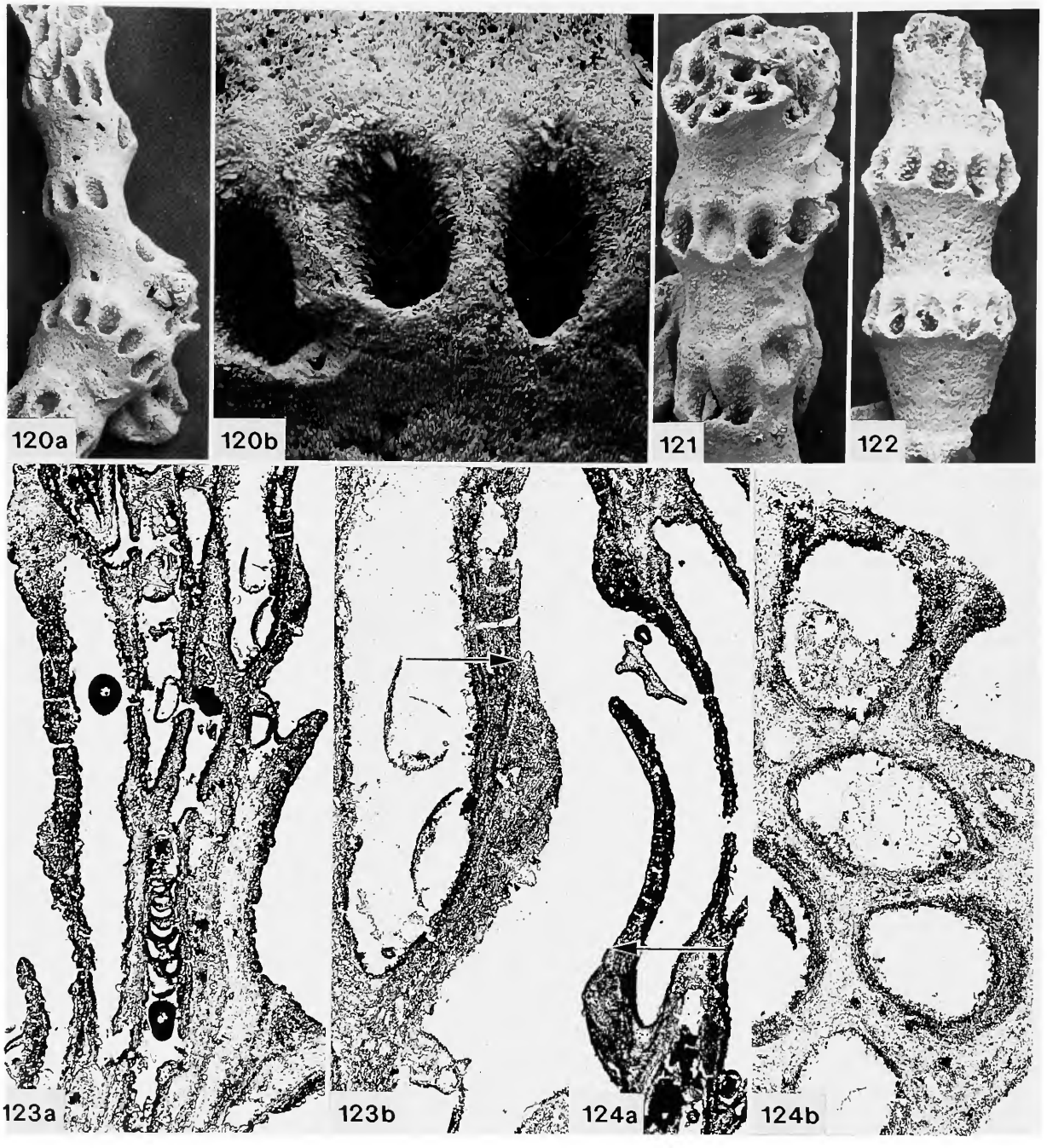
### *Attinopora*, new genus

TYPE SPECIES.—*Pustulopora zealandica* Mantell, 1850.

ETYMOLOGY.—*Attina*, Latin for free-standing wall, in reference to the exterior frontal walls. Gender: feminine.

DEFINITION.—Cinctiporidae with fixed-walled zooids with short peristomes in widely spaced spiral to annular arrangements on cylindrical, bifurcating branches.

Zooids large to gigantic. Fixed apertures subcircular to elliptical, terminal. Proximal and lateral sides of peristomes extensions of frontal walls. Outer surfaces of distal sides of peristomes concave, formed by ends of transparent layers of vertical walls, inner surfaces greatly thickened extensions from laminar and transparent layers of vertical walls with few to no pustules. Emergent peristomes arise from vertical walls within peristomes of frontal walls in some zooids. Externally, frontal walls gently convex between lateral zooidal boundaries, transverse undulations common, small pseudopores sparse.




FIGURES 120–124.—*Semicinctipora amplexus*, Oligocene, Whaingaroan, McDonald Limestone, McDonald's Quarry, Oamaru, North Otago. 120, Holotype, NZGS BZ 156: *a*, widely spaced annular rings (×13); *b*, convex ridge of interior skeleton on distal side of apertures followed above by frontal walls with pseudopores (×73). 121, Thick endozonal walls at broken top of specimen, paratype, BMNH D59323 (×19). 122, Paratype, BMNH D59322 (×16). 123, Paratype, BMNH D59355: *a*, longitudinal peel with thickened endozonal walls (×40); *b*, longitudinal peel with junction (arrow) between convex ridge of skeletal shield and frontal wall above (×100). 124, Paratype, BMNH D59359: *a*, longitudinal peel of structure of convex ridges and frontal wall, arrow at boundary (×40); *b*, transverse peel with wall structure and thick endozonal walls (×100).

Zooidal boundaries either inconspicuous or indicated by shallow grooves externally. Terminal diaphragms in proximal parts of branches, attached to thickened vertical walls inward from apertures.

Internally, laminar layers of vertical walls line living chambers throughout. Pustules spine-like, abundant on axial and lateral sides of living chambers throughout length, less common on linings of frontal walls. Communication pores closely spaced in axial walls of zooids. In thin sections, transparent layers of fibrous crystals transverse to zooidal growth direction as in other cinctiporids, but vague laminations visible in some longitudinal as well as transverse orientations. Zooidal boundaries of ends of vertical walls intersect cuticles of frontal walls on lateral and distal sides of bases of peristomes, junctions visible externally.

Attachment organ strongly thickened, truncated cone-shape in retracted position, attachment ligaments large, probably evenly spaced and fewer than 24. Tentacles as many as 17 per zooid.

Primary zone of astogenetic change unknown, presumed to be completely fixed-walled based on secondary zone of change.

REMARKS.—*Attinopora* is established for fixed-walled cinctiporids with fully developed exterior frontal walls and no skeletal shields in zones of astogenetic repetition. At present, only two species, *A. zealandica* (Mantell) and *A. campbelli*, new species are included in *Attinopora*. However, it is possible that restudy of tubuloporines with narrow cylindrical branches, which are numerous and poorly described, will result in the placement of more species in *Attinopora* and will extend the stratigraphic and geographic distribution of the genus. For example, *Entalophora longipora* MacGillivray, 1895 and *Spiropora gigantea* Maplestone, 1908, both from the Tertiary of Victoria, warrant investigation as possible members of *Attinopora*.

RANGE.—Oligocene-Recent, New Zealand.

### *Attinopora zealandica* (Mantell, 1850)

FIGURES 43-47, 125-132

*Pustulopora zealandica* Mantell, 1850:331, pl. 28, figs. 20, 21.—Tenison-Woods, 1880:22.

*Entalophora wanganuiensis* Waters, 1887:340, pl. 18, fig. 1 [new synonomy].

EMENDED DESCRIPTION.—Colonies bush-shape, of unknown size. Zooid arrangement generally spiral, some annular. Feeding zooids active for approximately 10 mm below branch tips, more proximal zooids dormant and closed by terminal diaphragms. Branches 1.8-2.2 mm in diameter, average 1.9 mm, commonly with 8-10 zooids around branch circumference. Growth tips flattened. Skeletal apertures subcircular or elliptical. Length of peristomes up to one fourth branch diameters. Distal inner surfaces of peristomes sparsely pustulose in some specimens, distal outer surfaces show boundaries between ends of transparent layers of vertical walls and distal frontal walls, and distal and lateral outer surfaces show zooidal boundaries. Some thin emergent peristomes. Average nearest neighbor longitudinally 1.5 mm, average nearest neighbor transversely 760 μm. Ratio of endozone to branch diameter 0.42:1, with high variability.

Vertical interior walls with pustules apparently more dense at level of frontal exterior walls, becoming more sparse proximally in living chambers and distally into peristomes.

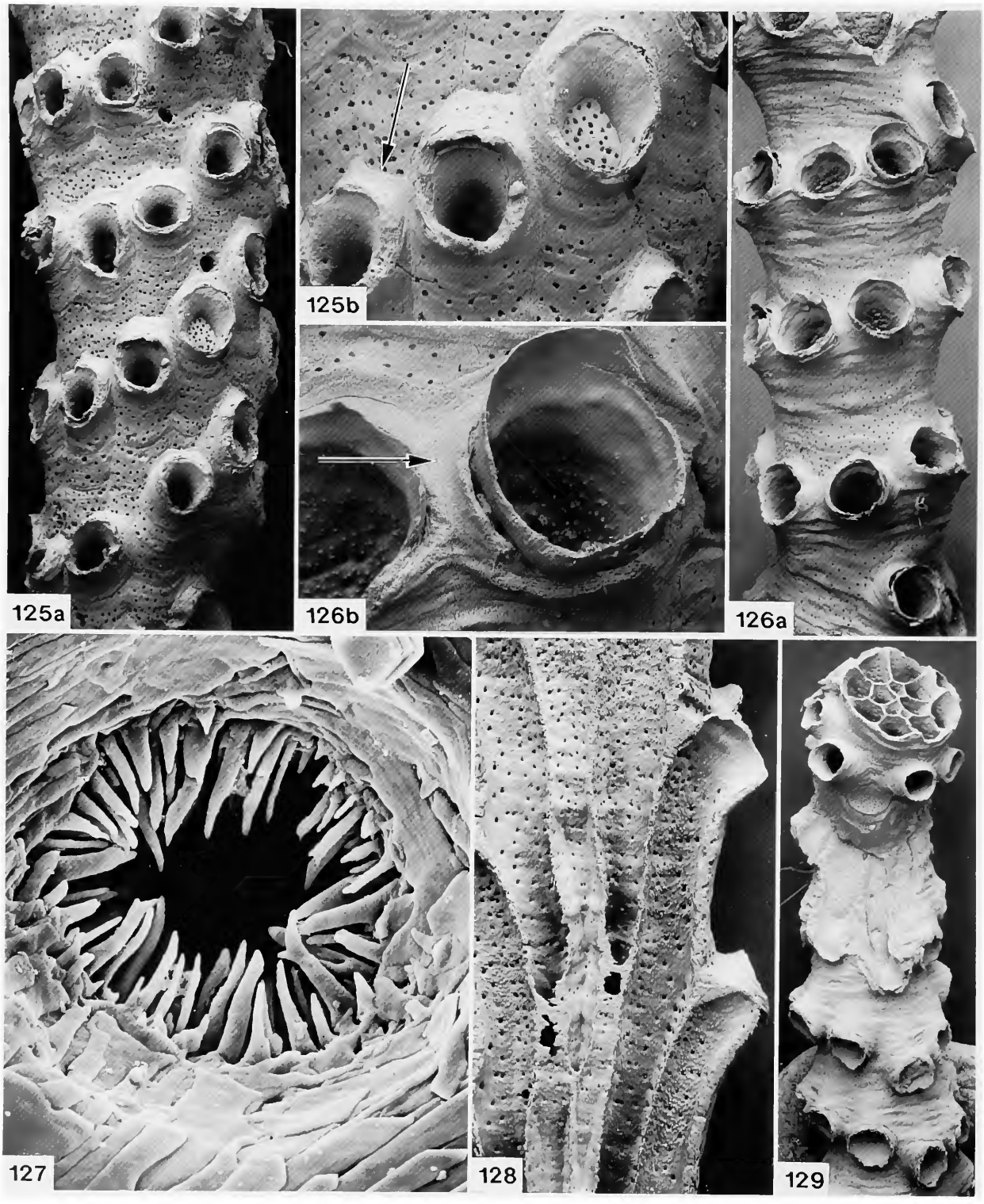
Frontal exterior wall thickness averages 110 μm, increases rapidly in early growth stages, more slowly proximally. On branch surface average zooid length 1.8 mm, average proximal width 510 μm, average minimum width 500 μm. Ratio of length:width about 3.5:1. Angle between branch axis and zooidal axis in inner exozone about 8 degrees, angle between branch axis and zooidal axis in peristome about 62 degrees on average. Average aperture width 480 μm.

Attachment organ ligaments number fewer than 20, estimated at 16. Rapid increase in depth of ligament attachments from youngest zooids at centers of growing tips to youngest zooids in permanent positions in exozones. Average depth of permanent ligament attachment positions 1140 μm in exozones. Correspondingly rapid increase of zooidal chamber diameters at ligament attachment levels from youngest zooids at centers of branch tips to youngest zooids in exozones. Diameter of proximal zooids averages 330 μm at ligament attachment positions.

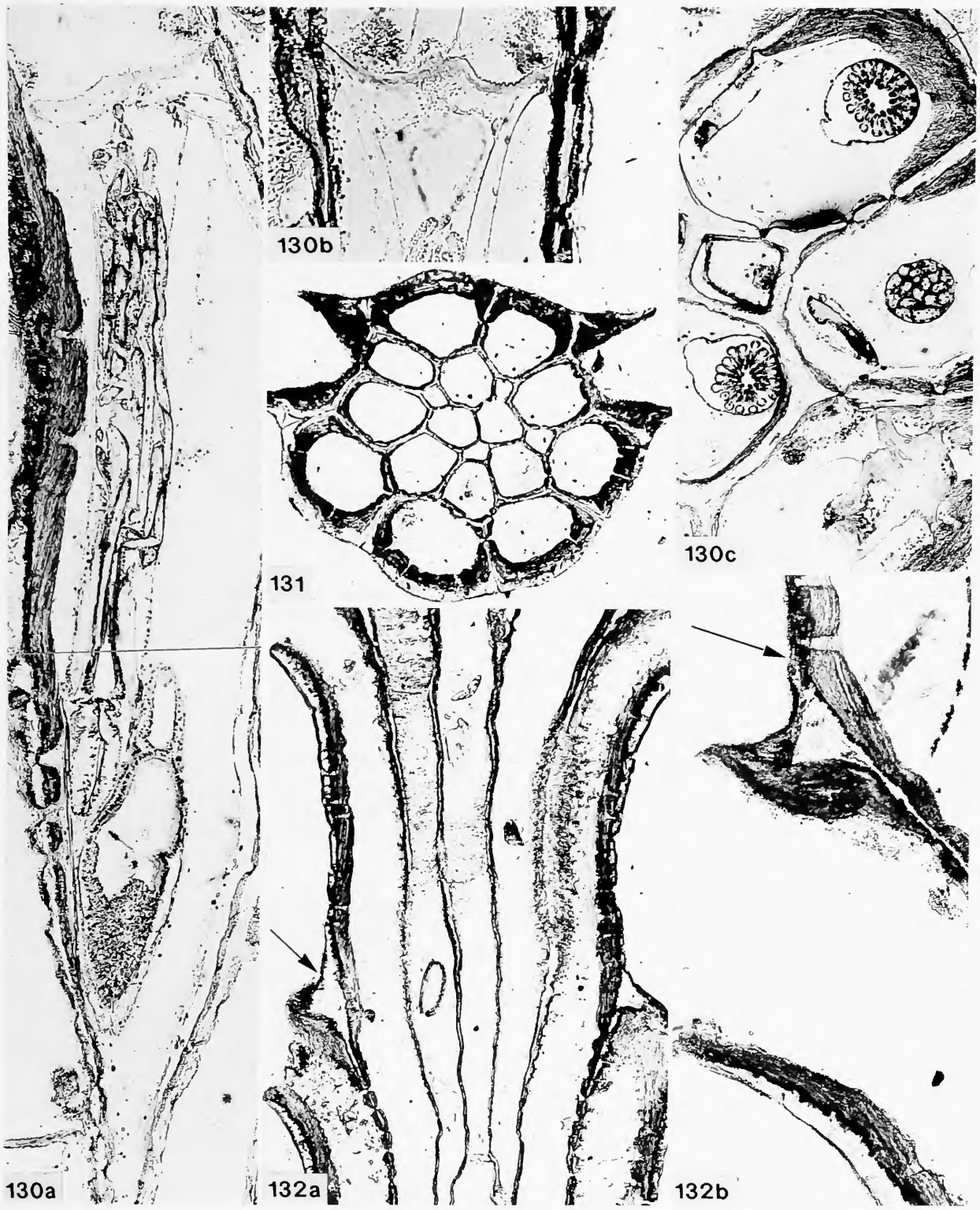
Full-size feeding organs fill over half living chamber cross-sectional area from mouth level to near inner end of caecum when polypide retracted, tentacles occupy half or less of chamber widths. Lophophores with 17 tentacles of about equal lengths, rapid ontogenetic increase of tentacles and total lengths of feeding organs from youngest zooids at centers of branch tips to youngest zooids in exozones. Average full-size feeding organs 1420 μm in length, average tentacle length 870 μm. Brown bodies not accumulated.

REMARKS.—*Attinopora zealandica* was first described as *Pustulopora zealandica* by Gideon Mantell (1850:331) whose description merely states "it is a beautiful species, allied to *Cereopora* [sic] *madreporacea* of Goldfuss." Mantell's figures (pl. 28, figs. 20, 21) are barely adequate for recognition of the species. The provenance of *P. zealandica* was stated as the "blue clay of Onekakara," a locality to the south of Oamaru in Otago. Brown (1952:1) gives the age of this deposit as Eocene (Arnold, Bortonian).

The whereabouts of Mantell's type material is unknown. Specimens of a coral (*Turbinolia*) described by Mantell immediately after *A. zealandica* are registered in the BMNH collections as BM18 and R39637, thus raising the possiblity that the bryozoan may also be in the BMNH collections. Indeed, a specimen identified as *A. zealandica* (BMNH




FIGURES 125–129.—*Attinopora zealandica*. 125, BMNH D1440a, Pleistocene, probably Castlecliffian, Wanganui: *a*, circular to oval apertures, steep spiral whorls (×20); *b*, thickened interior skeleton on inner sides of peristomes, boundary (arrow) between termination of interior vertical wall and distal exterior frontal wall above (×40). 126, NZOI sta E746: *a*, clustered communication pores behind subcircular apertures (×16); *b*, emergent peristome inside normal peristome of frontal wall, zooidal boundary (arrow) in region where interior vertical walls above blend into exterior frontal walls below (×78). 127, Configuration of crystals of laminar layer entering communication pore with radial spines, NZOI sta C760 (×4000). 128, Distribution of pustules in living chambers, NZOI sta E746 (×27). 129, Proximal rejuvenation, secondary zone of astogenetic change fixed-walled, NZOI sta C760 (×13).




FIGURES 130–132.—*Attinopora zealandica*. 130, NZOI E746 (×100): *a*, longitudinal section of complete zooid; *b*, thickened attachment organ; *c*, transverse section, 17 tentacles, part of attachment organ with ligaments in lower zooid. 131, Transverse section, spiral zooidal arrangement in endozone and microstructure of frontal walls, NZOI sta E281 (×40). 132, NZOI sta E281, longitudinal sections: *a*, approximate position (arrow) that zooidal boundary intersects colony surface (×40); *b*, microstructural relationship of vertical wall, frontal wall, and peristome, approximate boundary (arrow) between interior vertical wall and exterior frontal wall above (×100).

D59311) is close in size to Mantell's figured specimen and is stated to be from Onekakara on the label. This specimen, however, is from the J.F. Blake collection, with no documentation to link it with Mantell, and the detailed configuration of the zooids differs from that in Mantell's fig. 21.

The specimens described in Gideon Mantell's paper were collected by his son Walter Mantell and sent to England for description. It may be significant that Walter Mantell's collection also contained Pleistocene material from Wanganui that Gideon Mantell notes (1850:332) "are in the same condition as the shells of Onekakara, and the stratum whence they were obtained is evidently of the same age." This raises the possibility that specimens from the Pleistocene of Wanganui were erroneously attributed to the Eocence of Onekakara; indeed, the preservation and matrix of the BMNH specimens said to come from Onekakara strongly resemble that of the Waganui material. Supporting the theory of a mistaken provinence for *A. zealandica* is the fact that Fleming (1965, fig. 6) when reproducing Mantell's pl. 28, figs. 15–17, gives Wanganui as the locality of two gastropod species said by Mantell to be from Onekakara.

*Entalophora wanganuiensis* Waters, 1887, from the Pleistocene of Wanganui is evidently a junior synonym of *A. zealandica.* Although no type or other material of this species was found in the Waters collection at the Manchester Museum during a visit by PDT in April, 1989, Waters' description and figure are sufficient to establish the identity of the species. Tenison-Wood's (1880) material of *Entalophora zealandica,* also from Wanganui, has been examined by PDT in the NZGS collections and is regarded as *A. zealandica.*

ECOLOGICAL NOTES.—Little is known about the ecology of *A. zealandica.* Living specimens were collected from stations around the North Island of New Zealand at depths of 71 to 267 m. There is no apparent geographical overlap with the South Island species of *Cinctipora elegans.* The strong resemblance in colony morphology between the two species may point to a similar ecology for *A. zealandica* but in lower latitudes. One specimen of *A. zealandica* shows regeneration from the broken proximal end of a branch suggesting the role of fragmentation in clonal reproduction.

Exterior frontal walls of Recent specimens can be fouled by sponges and other encrusters, and bored by small endoliths as far distally as the growing tips of the branches. Endolith borings of a similar type also are present in some fossil specimens (e.g., BMNH D1440a).

RANGE.—Pleistocene–Recent, New Zealand.

TYPES.—No type material of this species is known to exist (see "Remarks").

RECENT MATERIAL.—New Zealand Oceanographic Institute localities: sta C760, 34°10.8′S, 172°8.4′E, 84 m, 18 Feb 1962; sta E281, 34°26.4′S, 172°30′E, 71 m, 8 Apr 1965; sta E746, 40°41.3′S, 176°41.6′E, 267 m, 29 Mar 1967.

FOSSIL MATERIAL.—*Pleistocene:* BMNH D1440a, b (scanned), probably Castlecliffian, Wanganui, G.R. Vine Colln.; NZGS un-numbered, 3 branch fragments labelled *Entalohora zelandica* [sic], Tenison-Woods Colln. 29, Castlecliffian, Wanganui. BMNH D59308–D59311, age unknown, Onekakara.

### *Attinopora campbelli,* new species

FIGURES 133–137

ETYMOLOGY.—Named for Professor J.D. Campbell, University of Otago, in gratitude for his expert guidance of P.D.T. around New Zealand field localities.

DESCRIPTION.—Colonies erect with slender bifurcating branches. Zooid arrangement annular or spiral, some with steep pitch angles. Branch diameters 0.9–1.6 mm with 6–9 zooids around branch circumference. Apertures elliptical, peristomes short, no emergent peristomes seen. Externally, complete zooidal boundaries visible on well-preserved specimens. Terminal diaphragms in proximal zooids, rarely with large central pore reflecting orificial-vestibular membranes. Average nearest neighbor longitudinally 1.0 mm, average nearest neighbor transversely (measured strongly diagonally) 650 μm.

On branch surface, average zooidal length 1.4 mm, average proximal width 320 μm, and average minimum width 220 μm. Ratio of length to proximal width about 4.3:1, and length to minimum width about 6.4:1.

Internally, average maximum frontal wall thickness 80 μm. Ratio of endozone diameter to branch width 0.54:1, with relatively high variability. Average chamber diameter 230 μm. Angle between branch axis and zooidal axis in inner exozone 9 degrees on average, angle between branch axis and zooecial axis in outer exozone 31 degrees on average. Average aperture width 410 μm.

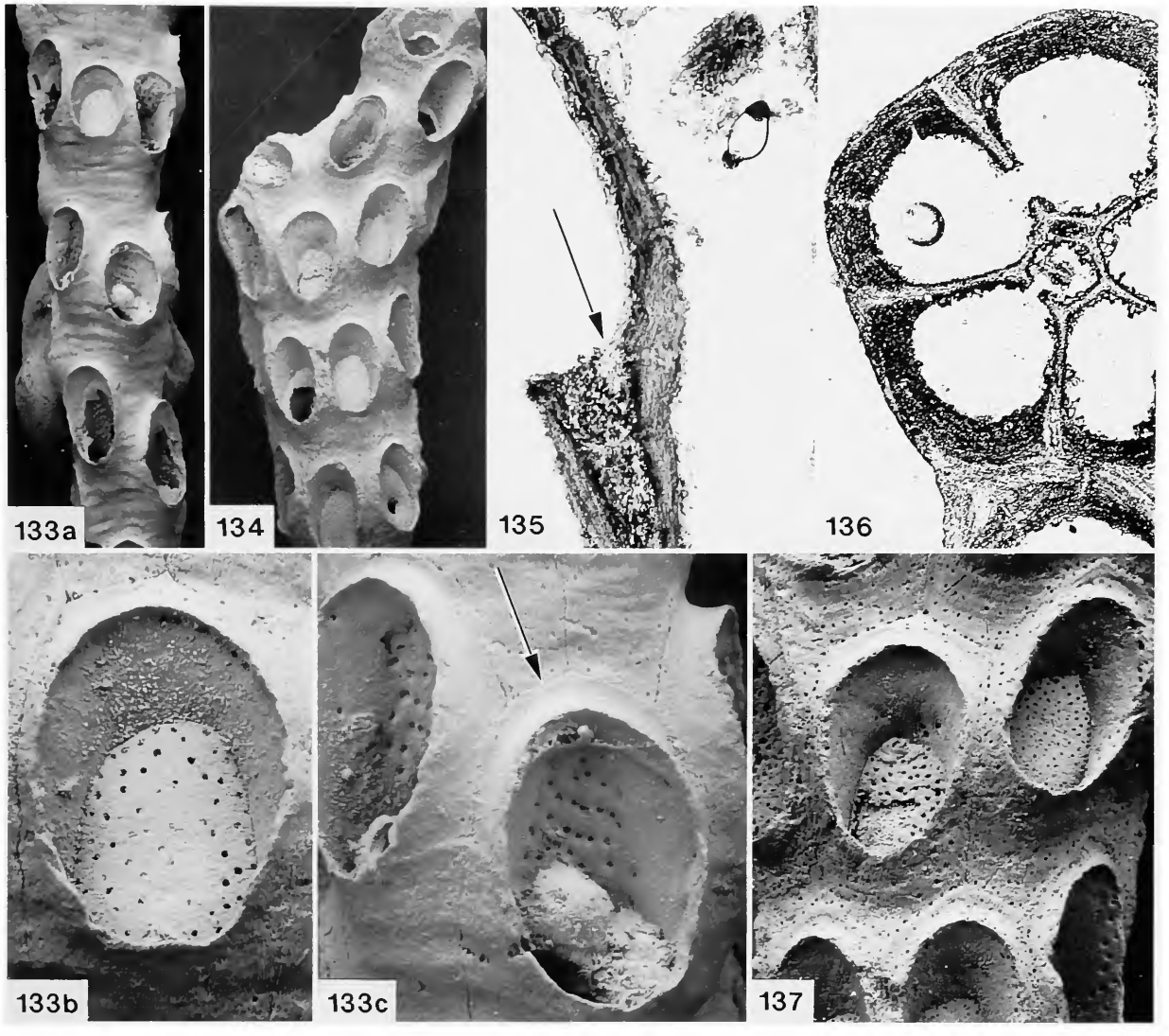
REMARKS.—*Attinopora campbelli* differs from *A. zealandica* most significantly in smaller zooidal and branch dimensions and a smaller angle between branch axes and zooidal axes in outer exozones. In addition, *A. campbelli* has a thinner frontal wall and lesser longitudinal spacing, but these characteristics do not discriminate the two species as well as the features given above.

*A. campbelli* commonly occurs in the same samples as *Cinctipora elongata* in the Miocene Forest Limestone of Southland. In both species, branches from clay-rich horizons are narrower than branches from more calcareous horizons.

RANGE.—Oligocene–Miocene, New Zealand.

TYPES.—*Holotype, Miocene:* NZGS BZ 155, Otaian-Altonian, Forest Hill Limestone, Lady Barkly Quarry, Winton, Southland (NZ Fossil Record #E45/f168, grid reference 517468, 1984), colld. by P.D. Taylor, Jun 1988.

*Paratypes, Miocene:* BMNH D59312, D59313 (scanned), D59314–D59316 (samples), D59328–D59330 (peeled), D59344–D59348, (peeled), same occurrence data as holotype. BMNH D59317 (scanned), D59318 (sample), Forest Hill Limestone, Forest Hill Quarry, Winton, Southland (NZ Fossil Record #E46/f061, grid reference 575366, 1983), colld. by




FIGURES 133–137.—*Attinopora campbelli,* all from Miocene, Otaian-Altonian, Forest Hill Limestone, Lady Barkly Quarry, Winton, Southland. 133, Holotype, NZGS BZ 155: *a,* oval apertures on narrow branch (×14); *b,* peristome and terminal diaphragm (×74); *c,* clustered communication pores, zooidal boundaries between frontal walls and peristomes (arrow) (×56). 134, Two branch sizes, possible reflection of orificial wall and orifice in terminal diaphragm in lower right, paratype BMNH D59313 (×15). 135, Longitudinal section, microstructure of frontal wall and end of vertical wall, approximate position (arrow) of zooidal boundary at skeletal surface, paratype BMNH D59347 (×100). 136, Transverse peel, paratype BMNH D59340 (×100). 137, Scattered pseudopores on lateral and proximal parts of peristome, paratype BMNH D59312 (×39).

P.D. Taylor, Jun 1988. UOGD 39791 (sample), same occurrence data. BMNH D59319 (sample), Altonian, Clifden Limestone, Clifden Suspension Bridge, Southland (NZ Fossil Record #D45/f327, grid reference 009510, 1985; see Hayward, 1988), colld. by P.D. Taylor, Jun 1988. BMNH D59320 (sample), D59340–D59343 (peeled), Otaian, Claremont Limestone (= Mt. Brown A Limestone), Onepunga, Waipara, North Canterbury (NZ Fossil Record #M33/f24, grid reference 757897), colld. by P.D. Taylor, Jun 1988.

*Paratypes, Oligocene:* Whaingaroan, McDonald Limestone, Everett's Quarry, Oamaru, North Otago (NZ Fossil Record #J42/f212, grid reference 450570, 1984), colld. by P.D. Taylor, Jul 1988. BMNH D59349–D59353 (peeled), McDonald Limestone, McDonald's Quarry, Oamaru, North Otago (NZ Fossil Record #J42/f213, grid reference 451579, 1984; see Fordyce et al., 1985), colld. by P.D. Taylor, Jul 1988.

## Conclusions and Implications

1. The primary zone of astogenetic change of *Cinctipora elegans* is unique among those few specimens of primary zones studied that belong to free-walled stenolaemates. The ancestrula is fixed-walled and remains outside the main body of the colony, followed by zooidal apertures of the first whorl that are proximally fixed by frontal walls and distally free at the bases of skeletal shields. In addition, rejuvenations on supporting colonies of *C. elegans* begin as upright secondary zones of astogenetic change similar to the primary zones of change minus the ancestrulae. The partially fixed-walled organization of the zones of change of the free-walled species is part of the evidence for placing both free- and fixed-walled species in the same family.

2. Within species of the cinctiporids zooidal patterns of branches range from annular to interrupted spirals to complete spirals, controlled by increasing pitch angles starting from zero degrees in the annular arrangement. Species from the Upper Cretaceous through the Middle Miocene are mainly annular. Younger species are mainly spiral.

3. Endozones necessarily grow faster parallel to branch axes than exozones grow laterally in order for vertical branching growth habits to form in stenolaemates. With each new polypide cycle in endozones at growing tips of *C. elegans*, attachment organs and polypides apparently degenerate and regenerate in progressively more outward positions until fixed positions near the beginning of exozones are reached. Both skeletons and soft parts grow at high rates in the endozones, and tentacles are longest in proportion to polypide length indicating high ingestion rates. As a result, fully regenerated polypides and skeletal growth are approximately proportional in size in endozones, a relationship that occurs in many if not all Recent stenolaemates.

4. When exozones are reached by outwardly shifting polypides along sides of branches in *C. elegans*, attachment organs attain their permanent positions, additional cycles are few, and lengths of polypides stabilize with relatively shorter tentacles. As a result, outward skeletal growth of exozones virtually ceases so that no skeletal ontogenetic gradients are produced below growing tips and branches have subequal diameters throughout their lengths. The fixed positions of attachment organs in exozones from cycle to cycle occur in other cinctiporids, and possibly in other stenolaemates in which branch diameters are essentially constant throughout their colonies. Fixed-walled stenolaemates that continue polypide cycling after frontal walls and peristomes are formed probably have fixed positions for attachment organs because polypides rarely if ever progress outward to attach to insides of peristomes.

5. In *C. elegans*, polypides in fully regenerated colonies display the maximum range of ontogenetic sizes; fully degenerated zooids lack polypides but have not yet become dormant as indicated by lack of calcified terminal diaphragms; partly regenerated zooids have polypides either uniformly or unevenly undersized in exozones. All parts of a colony are not necessarily in the same stage of a cycle. Apparently, polypide cycling occurs in all stenolaemates in which vertical walls grow much longer than their enclosed polypides. Cycling also is known in many Recent species in which living chambers remain only slightly longer than full-size polypides throughout life.

6. During the regenerating phase of a single cycle in *C. elegans*, polypides in exozones grow inward from attachment organs to their full size. During this presumed continuous growth, retractor muscles are attached to skeletons and polypides ingest and pass faecal pellets. In order to keep their functional positions relative to the lengthening polypides, the ends of the retractor muscles attached to skeletal walls apparently slide inward along the walls while continuing to function. This functional inward growth during polypide regeneration probably is typical for stenolaemates with attachment organs.

7. Assuming that tentacle sheaths are not stretched, undersized polypides of *C. elegans*, during early stages of regeneration, ingest nutrients and eliminate faecal pellets apparently from within living chambers. This is caused by the depths of attachment ligaments within the chambers being greater than the combined lengths of the inverted tentacle sheath and the attachment membranes. Apparently, elimination of faecal pellets through the atrium and vestibule makes that function possible from within living chambers. This elimination path has been observed in other living bryozoans, including gymnolaemates, and may prove eventually to be widespread in the phylum.

8. In stenolaemates, the membranous sac surrounding the coelom is the main hydrostatic organ that protrudes the polypide to its feeding position. The body cavity of a free-walled zooid outside the membranous sac, the pseudocoel, is open to the remainder of the colony under its orificial wall. Zooids of both free- and fixed-walled colonies are open to other zooids through any open communication pores. Theoretically therefore, pseudocoels of most stenolaemates cannot develop hydrostatic pressure within living chambers, so they remain passive as the pressure for protrusion develops within membranous sacs.

9. No communication between neighboring zooids through a funiculus is possible in *C. elegans* because generally it is attached blindly to the skeletal wall of its zooid rather than to a communication pore. Presently, the only known function of the funiculus in stenolaemates is as a retractor muscle.

10. Some functioning polypides of *C. elegans* when retracted indicate the nonfunctioning of funicular muscles by being doubled just below the cardia. Apparently, retractor muscles attached to lophophores can retract polypides by themselves.

11. The skeletal linings of zooids of the cinctiporids and many other stenolaemates consist of a continuous laminar layer

that provides a uniform skeletal surface for soft parts and their attachments to skeletons. The transparent layer next to zooidal boundaries in cinctiporids consists of fibrous crystals oriented with lengths at right angles to the zooidal growth direction. Zooidal boundaries are narrow layers of small irregularly shaped and oriented crystals.

12. A skeletal wall calcified from one side forms against pre-existing membranes. Exterior skeletal walls in stenolaemates are calcified against inner surfaces of exterior cuticles. Cuticles provide a locus for crystal deposition and shape the skeleton. The flexibility and shape of the pre-existing cuticle as it is calcified is reflected in the faithfulness with which basal colony walls adhere to irregular surfaces, and in the linear undulations typical of freely growing exterior walls, including frontal zooidal walls and reverse-side colony walls. The undulations are typically at right angles to growth directions and form approximate growth time lines. Flexibility of cuticle before calcification is also demonstrated in the terminal diaphragms that are modified by adhering foreign particles. In the cinctiporids, the shape of pseudopores in exterior walls commonly points in the direction of local skeletal growth.

13. Emergent peristomes grow from inner surfaces of vertical walls and occur in Recent colonies of *Cinctipora elegans* and *Attinopora zealandica* and in the fossil species *Semicinctipora annulata*. Their function is not apparent because most zooids in the two Recent species function without them. In fixed-walled stenolaemates frontal walls typically form peristomes in feeding zooids. In *A. zealandica*, emergent peristomes form in some zooids just inside the peristomes of the frontal walls and so appear functionally to be a needless duplication. The potential for emergent peristomes to form is apparently genetically controlled and one of the shared characters that results in the inclusion of both a fixed- and free-walled species in the same family. The actual appearance of emergent peristomes is apparently microenvironmentally controlled.

14. Interior vertical walls change to exterior frontal walls at intersections of zooidal boundaries of vertical walls and exterior cuticles. These intersections occur in most fixed-walled stenolaemates at the outer ends of vertical walls near skeletal apertures, producing the frontal walls and peristomes that form the outer skeletal walls of those colonies. The new fossil genus *Semicinctipora* is the only genus known in which the normal change from vertical to frontal walls occurs between whorls, causing apertures to be fixed proximally and free distally, and outer skeletal walls to be combinations of interior skeletal shields and exterior frontal walls. An outer wall can change from interior to exterior distally, but not the reverse.

15. One Pliocene colony of *C. elegans* has zooids with skeletal shields and free apertures followed by zooids with frontal walls and fixed apertures in the same branch. A Recent colony of *C. elegans* has zooids with fixed apertures, free apertures, and apertures that are partly free and partly fixed, all with corresponding frontal walls or shields. These are combinations unknown in other stenolaemates and are the major evidence for placing both free- and fixed-walled species in the same family. Outside the cinctiporids another kind of free-/fixed-walled combination occurs in fasciculate stenolaemates that have clusters of zooids surrounded by rings consisting of exterior zooidal walls (Balson and Taylor, 1982; Boardman, 1983:74).

16. The combination of study techniques employed here, peels, thin sections and SEM micrographs of skeletons, and hard-soft thin sections of skeletons and soft parts together, were all essential in revealing the morphology and anatomy of the cinctiporids as reported.

17. Biometrics based on the detailed measurements of the many exterior and interior taxonomic characters of the cinctiporids were necessary to separate some of the morphospecies described here.

18. Newly inferred phylogenetic trends and classifications that include new taxonomic characters will not always fit into established concepts. For example, the exozonal skeletons of the cinctiporids are much more variable and plastic than the polypides and endozonal skeletons. The results of an equally detailed study of some Paleozoic clades indicated just the opposite, more rapid evolutionary changes in the endozones than in the exozones (Boardman and McKinney, 1976). Further, the cinctiporids are presented here with character states from the two different groups of established suborders. As a result, we suggest two possible phylogenies, each beginning with a different outgroup, one free-walled and one fixed-walled.

# Appendix

## Anatomy of Feeding Zooids

OUTER MEMBRANOUS WALLS.—Outer membranous walls of free-walled stenolaemates are uncalcified exterior body walls that include orificial and vestibular walls of zooids and any walls between orificial walls that connect adjacent zooids. They are generally colony-wide above encrusting bases and provide a barrier between the collective body cavity of the colony and the surrounding environment. In fixed-walled stenolaemates the orificial and vestibular walls of each zooid are isolated from those of neighboring zooids by exterior frontal walls that are calcified.

*Orificial walls* are the parts of outer membranous walls that extend across skeletal apertures and in most stenolaemates are the terminal walls of zooids (Figure 5). They contain simple openings called *orifices* through which tentacles protrude during feeding. Orificial walls merge with *vestibular walls* inwardly within zooidal living chambers. Vestibular walls (Figure 10) terminate inwardly at atrial sphincter muscles or tentacle sheaths and separate vestibules containing sea water from body cavities.

Outer membranous walls are mainly held in place on free-walled colonies by attachment to edges of basal walls of colonies, and by connections through vestibular walls to attachment ligaments and inner ends of retractor muscles, both inserted into skeletal walls of zooids within living chambers (Figure 10).

In an histological study of a species of the genus *Crisia*, a fixed-walled stenolaemate, Nielsen and Pedersen (1979:72) recognized two layers in membranous orificial and vestibular walls: an outermost noncellular periostracum, here called a cuticle; and a thin layer of ectodermal cells, here called an epidermis. Further, they made the assumption, followed here, that orificial and vestibular walls of all stenolaemates have the same two-layered construction (Nielsen and Pedersen, 1979:86).

OUTER ATTACHMENT STRUCTURES.—The outer attachment structures of feeding zooids of stenolaemate Bryozoa are part of the anatomy that attaches outer membranous walls, lophophores, and alimentary canals to zooidal skeletal walls. These structures include an atrial sphincter muscle, an attachment organ inserted directly into skeletal walls by its ligaments, a tentacle sheath, and short tentacle sheath attachment filaments that fasten the tentacle sheath directly to the attachment organ (Figure 10).

Configurations and relative thicknesses of outer attachment structures vary greatly among studied taxa and are among the most readily observed differences, suggesting that they are important sources of taxonomic characters. The attachment structures of some of these species are so different and so complex that detailed histological work will be necessary to understand their anatomy in detail (Boardman and McKinney, 1985:36–43).

The *atrial sphincter muscle* (Figure 10) is located between the *vestibule* and the *atrium*, the space that contains the retracted tentacles. This muscle is interpreted to be of ectodermal origin by Nielsen and Pedersen (1979:83). Functionally, it seems likely that all stenolaemates have an atrial sphincter muscle or some other means of closing off the atrium from the vestibule.

*Attachment organs* are roughly conical or collar-shape membranes that have their outer edges attached to atrial sphincter muscles and their inner edges attached to zooidal skeletons by their *ligaments* (Borg, 1923:2–4; Boardman, 1973:235). In most species studied, these ligaments are separated from each other, thereby providing spaces between them for passage of body fluids from distal to proximal exosaccal cavities during tentacle protrusion (Nielsen and Pedersen, 1979:81). However, perimetrical attachment organs (Boardman, 1973:235) in *Neofungella claviformis* (Waters) appear to be attached to skeletal walls continuously around their perimeters, seemingly prohibiting the transfer of body fluids.

Attachment organs generally are thicker than other membranes but are extremely variable in shape and thickness among taxa. They are absent in some species (Boardman, 1983:92). Attachment organs are considered to be a part of the membranous sac and mesodermal in origin by Nielsen and Pedersen (1979:76).

The *tentacle sheath* surrounds the atrium (Figure 10) and extends from the atrial sphincter muscle to the base of the tentacles. It provides the barrier between the sea water of the atrium and the apposing body cavity and everts to protrude tentacle crowns to the feeding position. Therefore, it is an organ necessarily occurring throughout the phylum Bryozoa.

Nielsen and Pedersen (1979:74) reported that in the genus *Crisia* the tentacle sheath consists of a basement membrane supporting a layer of ectodermal cells on the atrial side and a layer of mesodermal cells and longitudinal muscle cells on the body cavity side. We assume here that this organization is true for stenolaemates in general.

In most taxa studied, *attachment filaments* of the tentacle sheath (Figure 10) connect the tentacle sheath to the attachment organ near its ligaments. Although evidence is inadequate,

these filaments appear to be closely spaced strands of tissue in some species. The combination of attachment organ, attachment filaments, and tentacle sheath limit the amount of outward extension of tentacles when fully protruded.

MEMBRANOUS SAC.—The membranous sac (Figure 10) is a structure unique to the stenolaemates within the Bryozoa. The membranous sac surrounds the *endosaccal cavity* that in the retracted position contains the tentacles, digestive tract, retractor muscles, gametes, and funiculus. Membranous sacs are fastened to skeletal walls of zooids by attachment organ ligaments at their outer ends, by retractor muscles at mid-lengths, and by funicular muscles at inner ends. A membranous sac, therefore, remains in place when tentacles are protruded.

Membranous sacs are an essential organ for the protrusion of tentacles of stenolaemate feeding zooids with their stiffened skeletal body walls. Membranous sacs have been found in all Recent stenolaemates studied and are assumed for all stenolaemates, both Recent and fossil.

The membranous sac was recognized in bud development by Harmer (1898:113) who stated that it "may probably be regarded as the somatic mesoderm." Borg (1923:4) stated that the membranous sac "is an independent formation and has nothing to do with the body-wall of the zoid." Nielsen and Pedersen (1979:79) interpreted the membranous sac to be the detached mesoderm of the zooidal wall. On the same page they reported that in *Crisia*, the inner surface of the membranous sac consists of "a thin inner layer of mesodermal cells covered externally by a slightly thickened, clearly filamentous, basement membrane with a series of ring-shaped muscle cells interposed between them." The muscle cells form a series of annular muscles in the walls of membranous sacs. These annular muscles may be homologues of the transverse parietal muscles in the ctenostome body wall (Larwood and Taylor, 1979; Taylor, 1981) and provide an essential contracting force for the protrusion of tentacles in stenolaemates. Scattered ectodermal cells are reported on the outer surface of the membranous sac (Nielsen and Pedersen, 1979:80).

FEEDING ORGANS.—The feeding organs of stenolaemate Bryozoa include the lophophore and digestive tract (Figure 10). The digestive tract is further divided into the pharynx, cardium, caecum (stomach), pylorus, rectum, and anus. A few seemingly distantly related stenolaemate taxa have a gizzard between the pharynx and cardia (Boardman and McKinney 1985:36; Schäfer, 1986; Markham and Ryland, 1987).

The *lophophore* includes tentacles and a fleshy ring structure that supports the tentacles and forms the mouth of the polypide. Tentacles of just a few species of cheilostome Bryozoa have been described histologically (e.g., Smith, 1973:336; Gordon, 1974:149; Lutaud, 1983:226). They consist of an outermost mucopolysaccharide cuticle, a single layer of epidermal cells in 9 or 10 longitudinal rows on a basal lamina of collagen that surrounds longitudinal muscles, peritoneal cells, nerves, and a central body cavity considered to be a mesocoel. Three longitudinal bands of motor cilia have been reported in some stenolaemates, two lateral bands and one less well-developed frontal band (Borg, 1926:217). Other stenolaemates have just two lateral bands (Nielsen, 1987:232). Apparently some variation may exist among taxa, although Borg's observations need to be reconfirmed with electron microscopy.

The circular base of the lophophore, the fleshy ring structure, supports the tentacles and surrounds the mouth of the polypide. A basal lamina separates the epidermis from the cuticle, as in the tentacles (Gordon, 1974). Within the basal lamina itself are subepidermal circular muscles that are part of the circular muscle system of the digestive tract. Inward from the basal lamina are peritoneal cells, a nerve ganglion, mouth dilator muscles, and a circular body cavity (mesocoel) that is confluent with the body cavities of the attached tentacles. Outward from the basal lamina are ciliated epidermal cells lining the mouth and pharynx. The outer ends of the lophophore retractor muscles are inserted into the basal lamina at the level of the circular body cavity (Gordon, 1974).

The *pharynx* is surrounded by a layer of circular muscles (Nielsen, 1970:229). The lumen of the pharynx is triangular in transverse sections, and the epidermal cells that line part or all of the lumen are ciliated. The cardia has different proportional lengths in different species and the epidermal cells are generally thought to lack cilia.

The *caecum* is a large sac with a blind inner end that produces the U-shape digestive tract characteristic of the phylum. The caecum is lined with high epidermal cells having many vacuoles (Nielsen, 1970:230). The *cardium* enters and the *pylorus* empties at the outer ends of the caecum. The epidermal cells of the pylorus are ciliated. The pylorus opens outward into the *rectum*. The *anus*, in turn, opens through the tentacle sheath into the atrium near the base of the tentacles in the retracted position.

INNER ATTACHMENT STRUCTURES.—The inner attachment structures include retractor muscles and a funicular muscle (Figure 10). *Retractor muscles* have been reported in *Crisia* extending from insertions in skeletal zooidal walls to (1) the base of the lophophore, (2) the cardia, and (3) to the blind end of the caecum (Nielsen and Pedersen, 1979:67). Few of the species we have studied have retractor muscles attached to the cardia. Retractor muscles attached to the base of the lophophore insert through the membranous sac and epidermal cells to the organic matrix of the skeleton (Nielsen and Pedersen, 1979:80) on the side opposite to the rectum and anus.

In all classes of the Bryozoa the *funiculus* is reportedly the site of the formation of testes. In the Phylactolaemata, statoblasts form there also. In the cheilostomes a complex funiculus serves as an organ of interzooidal communication and also apparently serves a placenta-like function (Carle and Ruppert, 1983:182). In stenolaemates the funiculus contains one or two robust retractor muscles surrounded by the membranous sac. The funiculus inserts through the membranous sac and epidermis to the skeletal wall, reportedly either

without connection to communication pores (Bobin, 1977:329, 330), or possibly coinciding with them (Carle and Ruppert, 1983:186). If funiculus insertions occur at communication pores the funiculus in stenolaemates might serve as an organ of interzooidal communications, as in gymnolaemates. If not, the apparent functions of the funiculus in stenolaemates is as a retractor muscle for the polypide and the site for the formation of testes.

BODY CAVITIES.—The fixed-walled stenolaemate genera, *Crisia* and *Tubulipora*, reportedly have two separate body cavities that together fill living chambers within zooids, as well as an additional body cavity within the lophophore (Figure 10; Nielsen, 1970:255; Nielsen and Pedersen, 1979:85). The *exossacal cavity* (Borg, 1926:228) occurs between vertical skeletal walls and the membranous sac, and continues outward from the attachment organ. Unlike Borg (1923:3), Nielsen and Pedersen found no peritoneum lining the skeletal walls, only epidermis. Sides of the cavities opposite to the skeletal walls are lined either by peritoneal basement membranes of membranous sacs and attachment organs, or outwardly, by the epidermis of the vestibular and orificial walls. The exosaccal cavity, therefore, is lined by a single layer of cells on all sides, and Nielsen and Pedersen characterize the cavity as a pseudocoel.

The exosaccal pseudocoel is continuous around the outer ends of zooidal vertical walls through the confluent outer body cavities in all free-walled stenolaemates, apparently providing colony-wide physiological communication among zooids (Figure 5). The pseudocoel also provides apparent interzooidal connections through communication pores in vertical zooidal walls.

A second large body cavity occurs within the membranous sac, between the sac and attachment organ on one side and the digestive tract and tentacle sheath on the other. This is the *endosaccal cavity* of Borg (1926:228). Nielsen and Pedersen (1979:86) interpret the membranous sac and attachment organ to be the detached mesodermal layer of the zooidal walls and the body cavity sides of the tentacle sheath and digestive tract also to be mesodermal. The endosaccal cavity, therefore, apparently is lined by two layers of cells, the inner layer thought to be peritoneal. Nielsen and Pedersen consider this body cavity to be a coelom. In stenolaemates, coeloms are thus restricted to individual zooids and are without direct interzooidal connections.

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**Synonymy** in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

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