

Reflections on the Morphology,
Anatomy, Evolution, and Classification
of the Class Stenolaemata (Bryozoa)

Richard S. Boardman



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ABSTRACT

Boardman, Richard S. Reflections on the Morphology, Anatomy, Evolution, and Classification of the Class Stenolaemata (Bryozoa). *Smithsonian Contributions to Paleobiology*, number 86, 59 pages, 129 figures, 1998.—Thin sections of 37 stenolaemate species with soft parts within the skeletons unexpectedly reveal 10 variations in polypide anatomy and related methods of tentacle protrusion. Six of the variations modify attachment organs, and four occur in species that lack such organs. Attachment organs are required for the majority of “progressive” degeneration–regeneration polypide cycles that advance new polypides as the skeletons grow, so that functionally constant protrusion distances are maintained. In most species lacking attachment organs, polypides retract and regenerate in the bottoms of their living chambers so polypide cycles are “stationary” and protrusion distances increase as the skeletons grow in length.

Internal studies indicate that skeletal microstructure and polypide anatomy in Recent stenolaemates are generally qualitatively uniform within colonies and within species. Unexpectedly, skeletal microstructure and polypide anatomy often do not correlate with each other or with the skeletal structures of the five informal taxa (horneroids, tubuliporines, fasciculates, disporelloids, and heteroporoids) used to group Recent species. These groupings have been established historically using only the relatively few external characters available. Internally, four of the five groupings have more than one kind of attachment organ, and three of the five have polypides both with and without attachment organs. Furthermore, organs that apparently occur in relatively few taxa occur in more than one grouping. Skeletally, more than one microstructure occurs in four of the five groupings. Noncorrelations of internal character states are so numerous that it seems almost any polypide can occur in almost any skeleton.

Genetically controlled taxonomic characters of fossil stenolaemates that seem promising in elucidating relationships are skeletal microstructure, skeletal structures that reflect polypide anatomy and function, such as nutrient exchange systems, and mode of growth. Species in which laminae in the vertical zooidal walls grew inward from zooidal boundaries under outer body cavities dominated throughout the Paleozoic and Triassic and that inward-growing microstructure has continued to the present. Communication pores and frontal walls developed and disappeared in a meager number of species that became extinct in the Paleozoic. Species that grew laminae outwardly from zooidal boundaries, or grew crystallites at right angles to zooidal growth, apparently appeared first in the Jurassic. Three Paleozoic orders are inferred to have survived into the Jurassic, and, with the new Mesozoic clades, to have independently evolved communication pores and frontal walls. The three surviving Paleozoic orders are inferred to have interchanged primitive characteristics with the advanced features of newly evolved Mesozoic clades to produce the detailed noncorrelations described here in Recent species. Post-Triassic stenolaemates, therefore, are inferred to be polyphyletic at the order level.

With just 37 Recent species available, it is not clear whether polythetically described taxa ultimately can be distinguished in a manner that adequately reflects phylogenetic patterns in younger stenolaemates. Differing, but functionally similar, parts might have been so pervasive across clades that the resulting noncorrelations have produced a mosaic distribution of combined primitive and advanced character states that makes any sort of natural classification unlikely.

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Reflections on the Morphology, Anatomy, Evolution, and Classification of the Class Stenolaemata (Bryozoa)

Richard S. Boardman

Introduction

The study of post-Triassic Stenolaemata of the phylum Bryozoa has been hindered historically by too few students and by the almost total reliance on the relatively few taxonomic characters evident on the exteriors of colonies. Unfortunately, stenolaemates generally have opaque calcareous skeletons, and the tubular zooids and other skeletal features of most are oriented at high enough angles to colony surfaces, that little more than apertures and surface arrangements are available for external study. There are only a few different kinds of colony growth habits, and they generally are thought to be subject to environmental modifications; apparently most have evolved more than once in different major taxa. As a result, most of the morphology, anatomy, and basic biology of post-Triassic stenolaemates, so critical to present-day systematics, occurs internally in colonies and has yet to be revealed. Phylogenies and classifications based on adequate numbers of characters have yet to be attempted.

This lack of knowledge of the post-Triassic stenolaemates provides a rare research opportunity among the major classes of invertebrates today. The paucity of species that have been prepared for an internal study of their skeletal morphology and anatomy (probably fewer than 100) adds to the excitement of working with this class. Preparation and detailed study of the interiors of additional species undoubtedly will reveal new internal characteristics and functions, which will lead to major improvements in our understanding of this major class of colonial animals.

The specialized terminology of bryozoans is avoided where possible herein, and the terms used are as self explanatory as

possible. References to the literature are to the Bryozoa volume of the *Treatise on Invertebrate Paleontology* and other easily obtainable sources. Therefore, the earliest references to some items and taxonomy are not indicated but can be traced backward in time from sources cited herein. It is hoped that these simplifications will aid in attracting students and professionals to a major class of complex marine animals that promises a lifetime of exciting basic research.

The purpose of this paper is to demonstrate just how essential the detailed study of both organ anatomy and exterior and interior skeletal morphology is to having a basic understanding of post-Triassic stenolaemate Bryozoa. This paper extends the approach, detailed evidence, and interpretations published for the family Cinctiporidae (Boardman et al., 1992) to 37 species of other stenolaemate taxa. The relatively small number of Recent species that have been sectioned anywhere restricts broad phylogenetic and classificatory understanding of the class at present. These 37 species, however, do demonstrate the scale of the diversity of internal morphology, anatomy, and function, and indicate that these details cannot be ignored in future systematic studies.

The study methods of post-Triassic stenolaemate Bryozoa have evolved into two divergent approaches. The older approach, deeply entrenched and still practiced, is restricted largely to the study of the external skeletal morphology of colonies and their zooids; therefore, it employs relatively simple study techniques that reveal few characters. This approach to the study of post-Triassic stenolaemates is best explained in a monograph on Recent British cyclostome bryozoans (Hayward and Ryland, 1985).

The more recent approach began with the preparation of thin sections, a process that is inexpensive but time consuming, that provides details of the interiors of post-Triassic stenolaemate colonies. Peels of sliced specimens (Boardman and Utgaard, 1964; Merida and Boardman, 1967) require less time and

Richard S. Boardman, curator emeritus, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; present address 3612 East Forest Lake Drive, Sarasota, Florida 34232.

equipment than thin sections, and they adequately reveal the skeletal morphology and microstructure. The technique of thin sectioning skeletal and soft parts together in living relationships featured in this paper is outlined in Nye et al., 1972. Refinements revealing even finer details of colonies can be obtained by the use of scanning electron microscopy of the exteriors, interior surfaces, and broken edges of skeletons (Taylor, 1986; Boardman et al., 1992, SEM work by Taylor; Taylor and Jones, 1993; Taylor et al., 1995; Weedon and Taylor, 1995). Microtome sections illustrated by electron microscopy are necessary to study the histological details of organs (Nielsen, 1970; Nielsen and Pedersen, 1979). Observations of living specimens are essential, and, finally, future genetic studies will judge the many interpretations based on morphology and anatomy.

Little is said herein about brood chambers because their detailed study requires special section orientations that are not available. A recently published and beautifully illustrated monograph (Schäfer, 1991) dealing largely with the brood chambers of stenolaemates, however, demonstrates that they also must be studied both externally and internally in detail, and that considered with other characters, they certainly will continue to be important in classifications.

Specimens used in this study are housed in the following institutions: collections of the former United States National Museum (USNM) now in the National Museum of Natural History (NMNH), Smithsonian Institution, Washington D.C.; The Natural History Museum, London (formerly the British Museum of Natural History) (BMNH); New Zealand Oceanographic Institute, Wellington (NZOI); New Zealand Geological Survey, Lower Hutt (NZGS); and Mediterranean specimens at Centre d'Océanologie de Marseille, Université d'Aix-Marseille, France.

ACKNOWLEDGMENTS.—Interest in Recent stenolaemate species was initiated by Dennis P. Gordon (NZOI), who over 20 years ago sent collections of beautifully preserved specimens to the NMNH. Other New Zealand collectors include P.K. Probert and A. Watson. Specimens also were loaned by Jean-Georges Harmelin (Université d'Aix-Marseille) and Ehrhard Voigt (Universität Hamburg). At approximately the same time as the arrival of the first New Zealand specimens, Donald A. Dean (Department of Paleobiology, NMNH) perfected the preparation of thin sections with both skeletons and soft parts in place. This paper is a celebration of his unique mastery of both sectioning and photography. Mary E. Parrish (Department of Paleobiology, NMNH) compiled the detailed drawing of the zooid of Figure 1 from several sections and drafted the other figures. This paper was reviewed and improved by Alan Cheetham (Department of Paleobiology, NMNH), Dennis Gordon, Frank McKinney (Appalachian State University), Claus Nielsen (Zoological Museum, Copenhagen), and Paul Taylor (The Natural History Museum, London). My thanks to all for their invaluable assistance.

Generalizations about Growth, Anatomy, and Function in the Stenolaemata

NUTRIENT EXCHANGE AND GROWTH

Nutrient exchange within colonies has been a basic requirement for the growth and evolutionary success of the overwhelming majority of stenolaemate species throughout the history of the class. These exchanges can be assumed because of the many structures that have grown outside the boundaries of actively feeding zooids, for example, (1) the growing margins of the newest zooids and the basal and median colony walls in budding zones, (2) the nonfeeding polymorphs from Paleozoic mesozooids to Recent gonozooids and nanozooids, and (3) the extrazoidal skeleton between zooids and on the back sides of branches where feeding zooids are lacking.

It appears that nutrient exchange has been accomplished in two ways in stenolaemates: (1) by confluent outer body cavities outside of skeletal structures, which are enclosed by the outermost membranous exterior walls with cuticles, and (2) by communication pores through vertical skeletal walls. More highly integrated stenolaemates employ both methods.

Budding zones of colonies are covered by expanding membranous exterior walls in all stenolaemates. The membranous walls cover the outer body cavities that provide flexible expanding space and nutrients for the growth of new zooids and adjacent structures. The nutrients come from actively feeding zooids in older parts of colonies.

In colonies with confluent outer body cavities throughout, skeletal apertures are formed by vertical skeletal walls, which are all interior in origin (Figures 2–4; Boardman, 1983, fig. 25). Membranous orificial walls are unattached (free) at skeletal apertures, and these zooids and colonies are termed “free-walled.” Orificial walls are connected to the orificial walls of adjacent zooids and to any other outermost membranous colony walls to provide, in total, the outermost membranous coverings that enclose confluent outer body cavities outside of colony skeletons. The membranous coverings are mainly held in place above the basal colony walls by connections to the skeletons within zooids. The outer body cavities provide colony-wide nutrient exchanges.

In colonies with outer body cavities closed below budding zones, skeletal apertures are formed within the exterior skeletal frontal walls of zooids or in the exterior skeletal peristomes supported by frontal walls (Figures 1, 5–7; Boardman, 1983, fig. 26). Frontal walls begin growth immediately below budding zones from the ends of interior vertical walls of zooids and combine to form a continuous outer skeletal covering of colonies below budding zones and between zooidal apertures. The frontal walls are calcified by the zooids themselves. As the colonies grow, the outermost cuticle layers of outer membranous walls of budding zones continue proximally as the outermost cuticle layers of skeletal frontal walls. Thus, the orificial walls of zooids are attached (fixed) individually to

skeletal apertures and outer body cavities are closed below budding zones. Colony-wide nutrient exchanges are therefore limited to only communication pores in the interior vertical walls of zooids. These colonies are termed "fixed-walled."

The two nutrient exchange systems control the locations of growth of many features. In free-walled colonies with outer body cavities and no communication pores, growth necessarily occurs only on the outer edges and surfaces of existing membranes and skeletons where nutrients are available in the living chambers of feeding zooids or in the outer body cavities. For example, extrazoidal skeleton and both basal and terminal diaphragms in these colonies are necessarily calcified on the outer surfaces of membranes and skeleton. The interiors of colonies that are walled off from the living chambers by diaphragms lack nutrients and living tissue, so they serve only as supports for outer growing surfaces.

In fixed-walled colonies having communication pores, growth generally can occur throughout the colony because all regions apparently are connected to feeding zooids by the pores. The exterior frontal walls of zooids calcify on the inside of membranes, so theoretically they can directly obtain all or most nutrients necessary for growth from their individual zooids. Terminal diaphragms also are calcified only on the inner surfaces of membranes after the final polypide cycles, because nutrients necessary for growth presumably can only be obtained from the living chambers of adjacent, actively feeding zooids via the communication pores. Species with frontal walls became abundant only after communication pores became ubiquitous, probably because each zooid otherwise would have had the theoretical disadvantage of being physiologically isolated after the frontal walls were completed just below budding zones.

Highly integrated colonies having both systems available, therefore, can grow skeletal structures both from within and on the outer surfaces of colony skeletons because nutrients are available throughout the colony. Terminal diaphragms in some of these species are calcified on both sides, presumably using nutrients from both exchange systems.

Not only are these two exchange systems basic to colony growth, but they have been used as the monothetic characteristic for dividing the class Stenolaemata into two taxonomic subgroups, the Cyclostomata (fixed-walled) and the Trepostomata (free-walled) (Borg, 1944). The validity of this split will be investigated in this paper.

POLYPIDE CYCLES AND GROWTH

The growth of feeding zooids of the class Stenolaemata is characterized by cycles of degeneration and regeneration of polypides, and these cycles are indicated primarily by the presence of brown bodies in Recent species. During a single cycle, at least the polypide, including the lophophore, gut, tentacle sheath, membranous sac, and muscles (Figure 1),

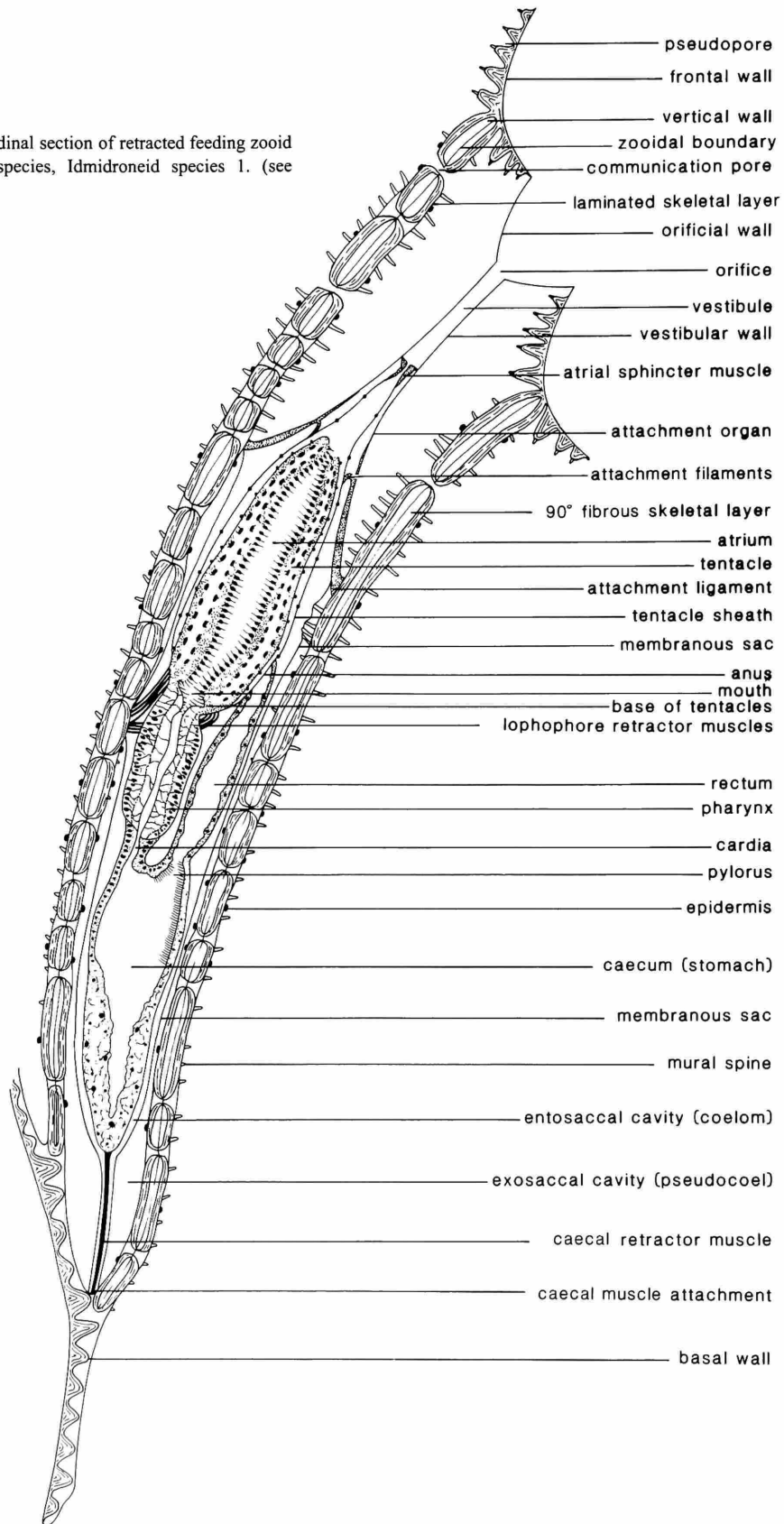
degenerates into a brown body. Each brown body is a concentration of degenerated cells encapsulated within a membrane (Figures 2, 3). Formation of the brown body, in some species at least, starts with a degeneration of the caecum, followed by the entire polypide slumping toward the bottom of the living chamber. The bases of the lophophores slump down below the skeletal attachment points of the lophophore retractor muscles, the polypide membranes compress and wrinkle, and finally the skeletal attachments of the retractor muscles come loose and the spherical to irregularly shaped brown body is formed. Brown bodies are ejected with each new regeneration phase in some species but are retained in the zooidal chambers in other species, which allows at least a minimum number of degenerations to be recorded (Figures 2, 3). The regeneration phase of the cycle begins with the budding of new polypides that continue growth and basic life functions until they in turn degenerate.

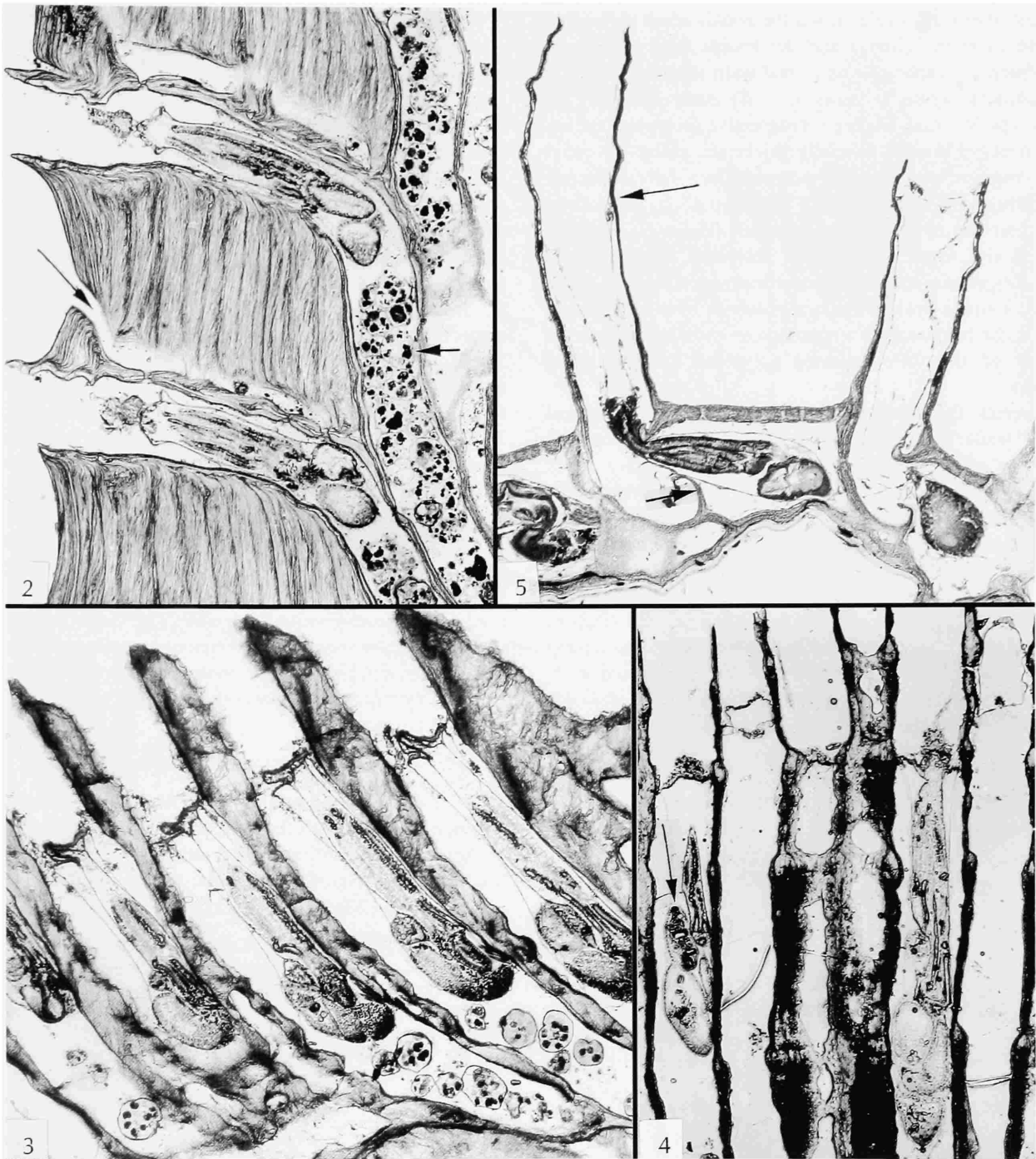
Polypide cycles can determine polypide lengths at any one time in a colony. In some species, cycles occur simultaneously and polypides of older cycles are at comparable lengths during regeneration (Figure 2; Boardman et al., 1992, fig. 64). In other species, cycles occur at different times from zooid to zooid (Figures 4, 5). In Figure 4, zooids with nearly empty living chambers are degenerated and the polypides in two of the zooids are at different stages of regeneration as indicated by their differing lengths. Polypide cycles in some stenolaemates, therefore, produce temporary intracolony polypide size variations that are not reflected in their skeletal dimensions.

Undersized polypides also occur within colonies as the result of ontogenetic sequences expressed as gradients of increased polypide size away from colony edges. A fully regenerated colony shows the progressively increasing lengths of zooidal skeletons and enclosed polypides caused by growth stages (Figure 3; Boardman et al., 1992, fig. 63). Ontogenetic sequences, therefore, are revealed by both polypides and their skeletons.

Polypide cycles also are critical to the positioning of regenerated polypides in their living chambers. Stenolaemates have at least two kinds of cycles. In "progressive" polypide cycles, the living chambers of newly regenerated polypides are positioned outward from the polypides of the preceding cycle. Progressive cycles maintain functionally constant distances from the fully retracted polypide to its skeletal aperture as the zooidal skeleton increases in length so that the tentacles can be fully protruded (Figures 2-4). In "stationary" polypide cycles, newly regenerated polypides maintain the same position within the living chambers as did the polypides of the preceding cycle. The distance between a fully retracted polypide and its skeletal aperture increases if the zooidal skeleton increases in length. Some species have stationary cycles throughout life, and the fully retracted polypides remain at or near the bottoms of their living chambers (Figures 5, 7). In other species, progressive cycles occur in the lengthening zooids of budding zones and

FIGURE 1.—Longitudinal section of retracted feeding zooid of a fixed-walled species, Idmidroneid species 1. (see "Tubuliporines.")





FIGURES 2-5.—Polypide cycles and ontogeny (all $\times 100$): 2, *Hornera* sp., free-walled, advanced growth stage indicated by wide exozone and many brown bodies (small arrow), extrazoidial skeleton with inwardly growing laminae and vacuole (large arrow) between the apertures of feeding zooids, BMNH specimen, Arctic. 3, Disporelloid of seven species complex, free-walled, right to left ontogenetic sequence with shorter polypides and fewer brown bodies in younger zooids, functionally constant distance to skeletal apertures, USNM 488143, Unalaska to Cook Inlet, Alaska. 4, *Neofungella* sp., free-walled, two polypides at different stages of regeneration indicated by different sizes, faecal pellet in regenerating polypide (arrow), at least two zooids degenerated, USNM 488144, off Victor Hugo Island, west coast of Palmer Peninsula, Antarctica. 5, *Harmelinopora indistincta* (Canu and Bassler), fixed-walled species, ontogenetic sequence right to left, regenerating polypide in older zooid to right, edges of hemisepta curved outward (small arrow), attachments of membranous sac and tentacle sheath high in exterior peristome (large arrow), Mediterranean Sea, Port Cros, Gabiniere, France.

change to stationary cycles when the zooids reach permanent positions in erect colonies and the zooids stop growing in length, such as in species with frontal walls (Figure 6).

Attachment organs (Figures 1, 6, 8) occur in nearly all studied species that undergo progressive polypide cycles. Attachment organs are generally thickened, collar- or cone-shaped membranes when the polypides are fully retracted. These attachment organs connect the polypides to the skeletal living chambers by attachment ligaments (Figure 9), and they also give rise to the regenerating polypides. The ligaments presumably remain attached in fixed positions during the active phase of a single cycle. Thus, the positions of the attachment organs at the beginning of a regeneration cycle determines the positions of the fully retracted polypides in their living chambers.

In species that undergo progressive cycles, the vertical skeletal walls of zooids apparently continue to lengthen throughout all phases of a cycle. With each cycle, newly regenerated polypides shift outward to new positions. The distance that they shift is the same distance that the vertical walls advanced since the previous regeneration cycle. This correlation of skeletal growth and new polypide position maintains a functionally constant distance to the skeletal aperture so that the tentacles can be fully protruded (Figures 2–4; Boardman, 1983, fig. 37). In stenolaemates having attachment organs, cycles can be either progressive or stationary, depending on whether the vertical walls of zooids increase or remain the same length.

Retractor muscles connect the lophophore bases and guts to inward positions on the skeletons and, along with attachment organ ligaments, tie polypides to their skeletons (Figure 1). These retractor muscles relax and stretch as the polypides protrude, and they contract instantly when the polypides are retracted. Retractor muscles include those that attach the bases of lophophores to skeletons, which are present in all bryozoans, and also those that attach cardia to skeletons, which are present in just a few stenolaemates (Figure 10).

Additional muscles, the “caecal retractor muscles,” are enclosed by the inner ends of membranous sacs and attach the midpoints of the stomachs of polypides to inward positions on their skeletons (Figures 1, 11; Nielsen and Pedersen, 1979). These caecal attachments have been thought to be a part of the nutrient exchange system among stenolaemate zooids and have been called funicular cords or muscles (Carle and Ruppert, 1983). No nutrient exchange is possible with these coecal attachments, however, because the shifting connections to the skeletal surfaces in Recent species do not typically attach to communication pores (for cinctiporids, see Boardman et al., 1992:35), unlike the funicular cords in cheilostomes. In Paleozoic and Triassic species, the lack of communication pores in the skeletal walls of zooids makes the exchange concept impossible, whether there were caecal muscles or not. It appears that a funiculus as a means of nutrient exchange does not occur in stenolaemates.

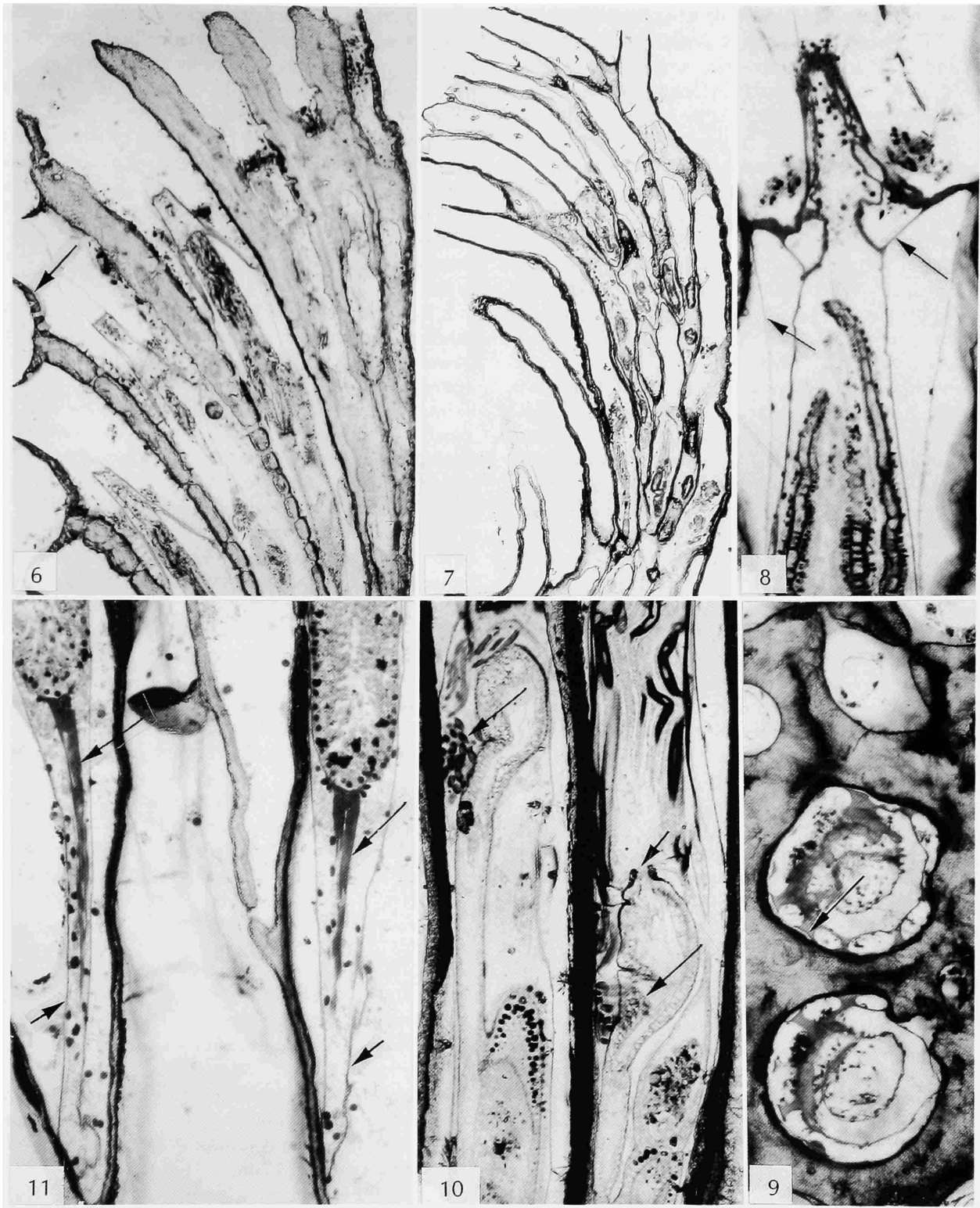
Regenerating polypides of either progressive or stationary cycles feed as they increase in size (Figure 4; for cinctiporids, see Boardman et al., 1992:35). In order for stenolaemates to feed during regenerating phases, functioning retractor muscles must be attached to the skeletal linings in their functioning positions (Figure 1). As regenerating polypides feed and increase in length inward from the attachment organs, which are fixed in position on the polypide, the position of the skeletal attachments of the retractor muscles also must shift inward so that the muscles will always be in position to fully retract the feeding polypides (Figure 4; for cinctiporids, see Boardman et al., 1992:35). The mechanism for shifting the muscle attachments in stenolaemates has not been investigated.

Attachment organs are absent in the species studied in which the polypides retract and are regenerated in the bottoms of living chambers by stationary cycles throughout life (Figures 5, 7). In these species, the connections of the lophophore retractor muscles to the skeletons are in the bottoms of the living chambers and are always in a position to function without having to shift throughout regeneration. In some of these species, the bottoms of the living chambers of older zooids can be filled with brown bodies or large sperm sacs, such that the skeletal bottoms of the living chambers are not always available to regenerating polypides. In these zooids, the retractor muscles attach to the skeletons laterally just below the lophophores and high enough on the skeletal walls to provide room for the pharynx and caecum to grow.

TENTACLE PROTRUSION

The membranous sac (Borg, 1926:207) seems to be a necessary organ in tentacle protrusion for all stenolaemates of all ages. The sac surrounds the retracted internal organs of feeding zooids (Figure 1) and some polymorphs, and it is the

FIGURES 6–11.—Progressive and stationary cycles, anatomy: 6, *Idmadroneid* species 1, budding zone on top, frontal walls along left side (arrow) growing from vertical walls outward to form exterior apertures, fully regenerated polypides with cone-shaped attachment organs and constant, short distances to their skeletal apertures; polypides in budding zone undergoing progressive cycles as vertical walls increase in length, whereas polypides behind frontal walls undergo stationary cycles, which halts the lengthening of vertical walls, USNM 488145, from Cape Rodney to Okakari Point, New Zealand ($\times 100$). 7, *Mecynoea delicatula* Harmelin, budding zone top left, frontal walls and long peristomes below, fully regenerated polypides retracted to the bottoms of their living chambers leaving long protrusion distances to the skeletal apertures; Grand Salaman, Marseille, France ($\times 50$). 8, *Neofungella* sp., outer end of polypide showing attachment organ, attachment filaments (large arrow), tentacle sheath, and membranous sac (small arrow), USNM 488146, near Palmer Peninsula, Antarctica ($\times 200$). 9, *Disporelloid*, species 10, tangential section, showing attachment organ with ligaments (arrow), USNM 488147, Unalaska to Cook Inlet, Alaska ($\times 200$). 10, *Infundibulipora lucernaria* (Sars), cardia retractor muscles (large arrows) and mouth of polypide (small arrow), USNM 250078, Kara Sea, Russia ($\times 200$). 11, *Fasciculipora ramosa* d'Orbigny, inner ends of caecum showing caecal retractor muscles (large arrows) and membranous sacs (small arrows), USNM 488148, McMurdo Sound, Antarctica ($\times 150$).



primary organ that protrudes polypide tentacles (Nielsen and Pedersen, 1979). The body walls of stenolaemate zooids are skeletal and rigid, so the hydrostatic pressure necessary to protrude tentacles must be provided primarily by the annular muscles in the flexible sacs. Starting at the inner end of the sac, the annular muscles contract progressively outward, thus forcing the polypide, with its tentacles extended, to the skeletal aperture. As the polypide protrudes, the inner end of the membranous sac is held in place by the retractor muscles, which pass through the sac membrane to fasten to the adjacent skeletal walls. The effective outer end of the sac with its annular muscles must be within the length of the polypide gut of the skeletal aperture so that the mouth and tentacles can be pushed out to open water. Membranous sacs are considered to be peritoneum (Nielsen and Pedersen, 1979).

The tentacle sheath is a membranous cylinder that surrounds the lophophore when it is retracted (Figure 1). The tentacle sheath is connected to the base of the lophophore at one end and to the membranous vestibular wall at the atrial sphincter muscle at the other end. The orificial wall, vestibular wall, and tentacle sheath (Figure 1) together provide epidermal protection for the body cavity within the living chambers of feeding zooids, a necessary safeguard throughout the phylum. In species studied that have attachment organs, the tentacle sheaths have a second, intermediate connection to the attachment organ. In species lacking attachment organs, intermediate tentacle sheath connections were not found and the tentacle sheaths are connected directly to the atrial sphincter muscles. As the tentacles are protruded, the tentacle sheaths turn inside out about their intermediate or direct connections to the atrial sphincter muscles, thus extending the tentacles into open water. Beyond these apparent constraints, the organs and mechanics of stenolaemate polypide protrusion are widely variable.

PROTRUSION WITH ATTACHMENT ORGANS.—In addition to originating regenerating polypides and positioning polypides in their living chambers, attachment organs limit the distance tentacles can be protruded. The ligaments, which fasten the attachment organs to the skeletons, plus the intermediate connections of the tentacle sheaths to the attachment organs, assist in anchoring the sheaths and attached lophophores to the skeletons. The intermediate connections of the tentacle sheaths are either affixed directly to the attachment organs (Figure 12) or indirectly to the attachment organs by attachment filaments (Figures 1, 8). Attachment filaments encircle the tentacle sheaths and connect them to the attachment organs at varying distances from the ligaments. As the polypide protrudes, the atrial sphincter muscles relax and the attachment organs beyond the attachment filaments fold back out of the way (Figure 13). If the polypide membranes do not stretch, polypide protrusion cannot be extended farther than the cumulative length of the attachment ligament, the segment of attachment organ between the ligament and filaments, the filaments, and the everted tentacle sheath from its intermediate connection with the filaments to the base of the protruded lophophore. This means that species with filaments (protrusion mechanism 1 of

Figure 129) have retracted polypide positions that place the polypide mouth roughly two tentacle-sheath lengths or less from the skeletal aperture. As the living chambers grow longer these functional distances to the skeletal apertures are maintained by progressive polypide cycles.

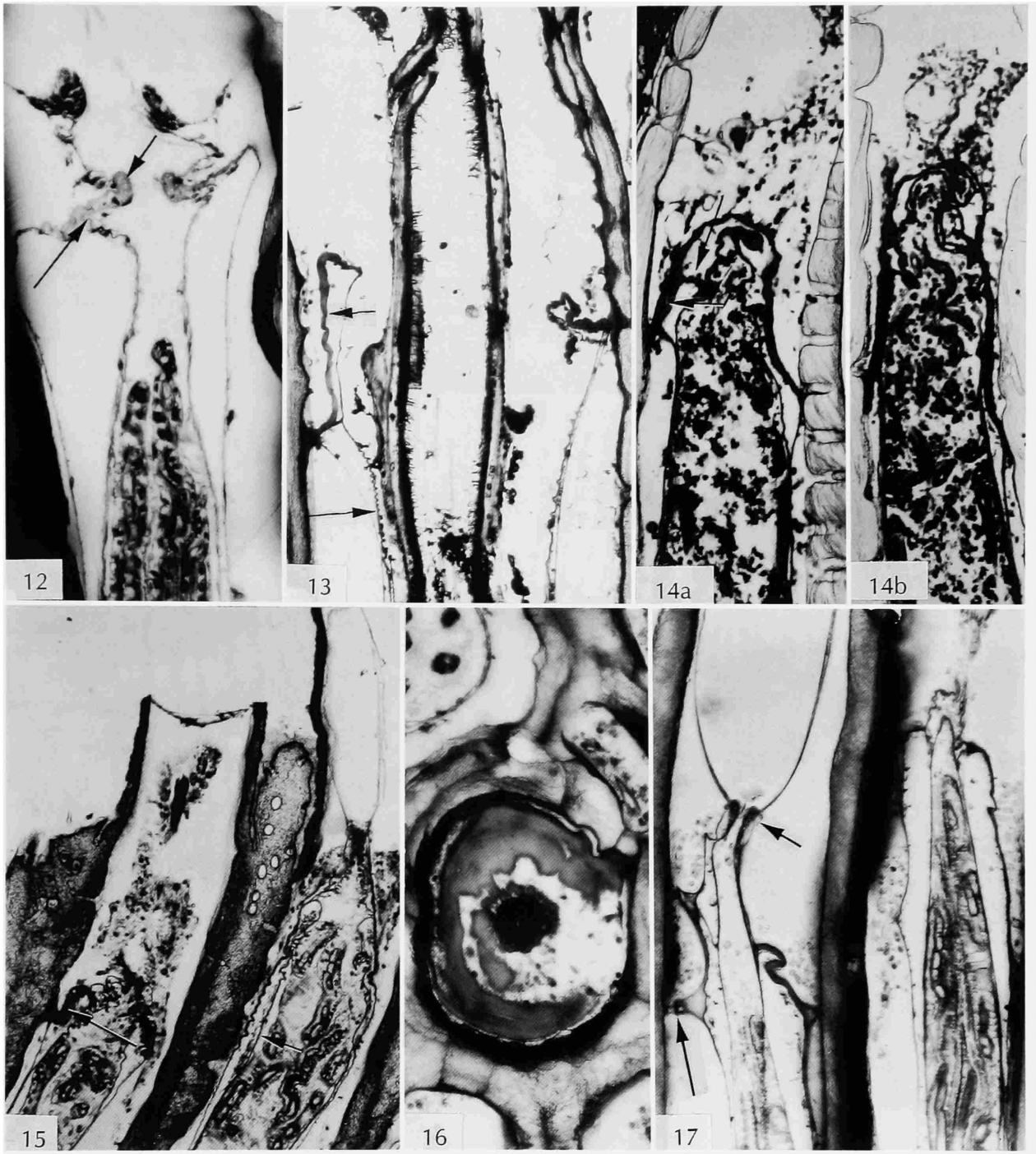
A second variation (2 of Figure 129) of attachment organ mechanisms has attachment organs that are pleated between the ligaments and filaments, thus providing an additional protrusion distance as the pleats unfold (Figure 14). As the living chambers grow longer, these greater functional distances to the skeletal apertures are maintained by progressive polypide cycles.

A third variation (3 of Figure 129) appears in species with attachment organs and no filaments (Figure 12). Protrusion extends through the cumulative length of the attachment ligament, the attachment organ to a direct intermediate connection with the tentacle sheath, and the everted tentacle sheath from its intermediate attachment organ connection to the base of the protruded lophophore. In some of these species, fully retracted attachment organs, which appear to be greatly thickened, are actually compressed into pleats (Figure 15). This provides another attachment organ mechanism variation (4 of Figure 129), one that lacks filaments. As the lophophores protrude, the pleats unfold, further increasing the protrusion distance.

Attachment organs of another modification (5 of Figure 129) are connected perimetrically to the skeletal wall (Figure 16) rather than by ligaments (Figure 9). All detailed accounts of the process of tentacle protrusion require body fluids to pass by attachment organs between ligaments, inward as the tentacles are protruded and outward as they are retracted (Nielsen and Pedersen, 1979; Taylor, 1981). This transfer of body fluids seems prohibited by the perimetrical attachment, so polypide protrusion for this attachment method is not fully understood. Again, the functional distances to the skeletal apertures are maintained by progressive polypide cycles as the zooids grow.

The last variation of attachment organ anatomy (6 of Figure 129) is radically different from those in all other stenolaemates studied. These attachment organs have a bilateral plane of symmetry in the proximal-distal direction and are attached at two or three levels on the distal side and at a single inward level on the proximal side (Figure 17). The membrane on the proximal side is thicker and has a transverse fold when the polypide is fully retracted. Despite this difference in symmetry, the tentacle sheaths have intermediate connections to the attachment organs by filaments, and the tentacles apparently can be protruded similarly to those in species with conventional attachment organs and filaments (Figure 13).

PROTRUSION WITHOUT ATTACHMENT ORGANS.—More flexible arrangements capable of long protrusion distances have evolved in species that lack attachment organs. All but one of these species studied retract the polypides to or near to the bottoms of the living chambers and employ stationary polypide cycles throughout life. The least complicated example occurs in a tubuliporid from Cape Cod, Massachusetts (Figures 18, 19),



FIGURES 12-17.—Attachment organs: 12, Disparelloid of seven species complex, intermediate connection of tentacle sheath connected directly to attachment organ (large arrow), atrial sphincter muscle (small arrow), USNM 488149, Northumberland Island, northwestern Greenland ($\times 300$). 13, *Cinctipora elegans* Hutton, tentacles with cilia partly protruded past collapsed attachment organ (small arrow), vestibular wall connected to inner end of relaxed atrial sphincter muscle and outer end of crenulated tentacle sheath (large arrow), USNM 454184, from edge of Otago Shelf off Otago Peninsula, New Zealand ($\times 150$). 14, Entelophorid species, USNM 186551, Kerguelan Ridge, southern Indian Ocean ($\times 150$). 14a, retracted polypide with pleated attachment organ (small arrow) and attachment filaments (large arrow) just

starting to protrude tentacles and unpleat; 14b, unpleated attachment organ. 15, Disparelloid species #11, polypide fully retracted on left (large arrow), pleated attachment organ without filaments has begun to unpleat in zooid on right as polypide starts to protrude tentacle sheath (small arrow), USNM 488150, Leigh Cove, New Zealand ($\times 200$). 16, Disparelloid species 8, tangential section, showing attachment organ perimetally connected to skeleton rather than by ligaments (as in Figure 9), USNM 488151, Unalaska to Cook Inlet, Alaska ($\times 300$). 17, Disparelloid species 9, unique attachment organ attached to mural spine (large arrow), a bilateral plane of symmetry is seen in the zooid to right, profile to left, atrial sphincter muscle (small arrow), USNM 488152, Leigh Cove, New Zealand ($\times 300$).



FIGURES 18–21.—Protrusion of polypide. 18, 19, *Tubulipora* sp.: Manomet, Cape Cod, Massachusetts ($\times 150$). 18, polypides retracted near the bottoms of living chambers, USNM 488153. 19, membranous sac (small arrow) and tentacle sheath (large arrow) in two feeding zooids of a narcotized colony, tentacle sheaths attached to membranous sacs at points (1) and to base of tentacles at points (2); in zooid to right, tentacles are protruded far enough that point (2) has moved outward past point (1), causing tentacle sheath to turn inside out; point (1) and membranous sac remain in place, USNM 216485. 20, 21, *Telopora* sp., Poor Knights Island, New Zealand: 20a, most of length of colony showing polypides retracted to the bottoms of extremely long living chambers ($\times 30$); 20b, polypides at the bottoms of living chambers with tentacle sheath (large arrow) and strongly pleated membranous sacs (small arrows), USNM 488154 ($\times 200$); 21, cluster of zooids in profile showing frontal walls with fixed apertures on side nearest the center of colony (small arrow) and polypide at aperture (large arrow), USNM 488155 ($\times 50$).

and it is the seventh variation (7 of Figure 129) in the mechanics of tentacle protrusion. The membranous sac is held in place by retractor muscles where they connect to the skeletal wall at or near the bottom of the living chamber. The sac terminates where it connects to the tentacle sheath and vestibular wall at the atrial sphincter muscle without making any connection to the skeleton. The tentacle sheath connects with the vestibular wall at the atrial sphincter muscles to close the epidermal membranes that enclose the body cavity within the zooid. The other end of the tentacle sheath is attached to the base of the lophophore without any intermediate connections. As the polypide is pushed outward by the annular muscles of the membranous sac, the lophophore end of the tentacle sheath passes the connecting atrial sphincter muscle and turns inside out (Figure 19). The possible protrusion distance from a fully retracted position in this species is roughly twice the length of the tentacle sheath of the polypide, so no outward movement of the membranous sac is required.

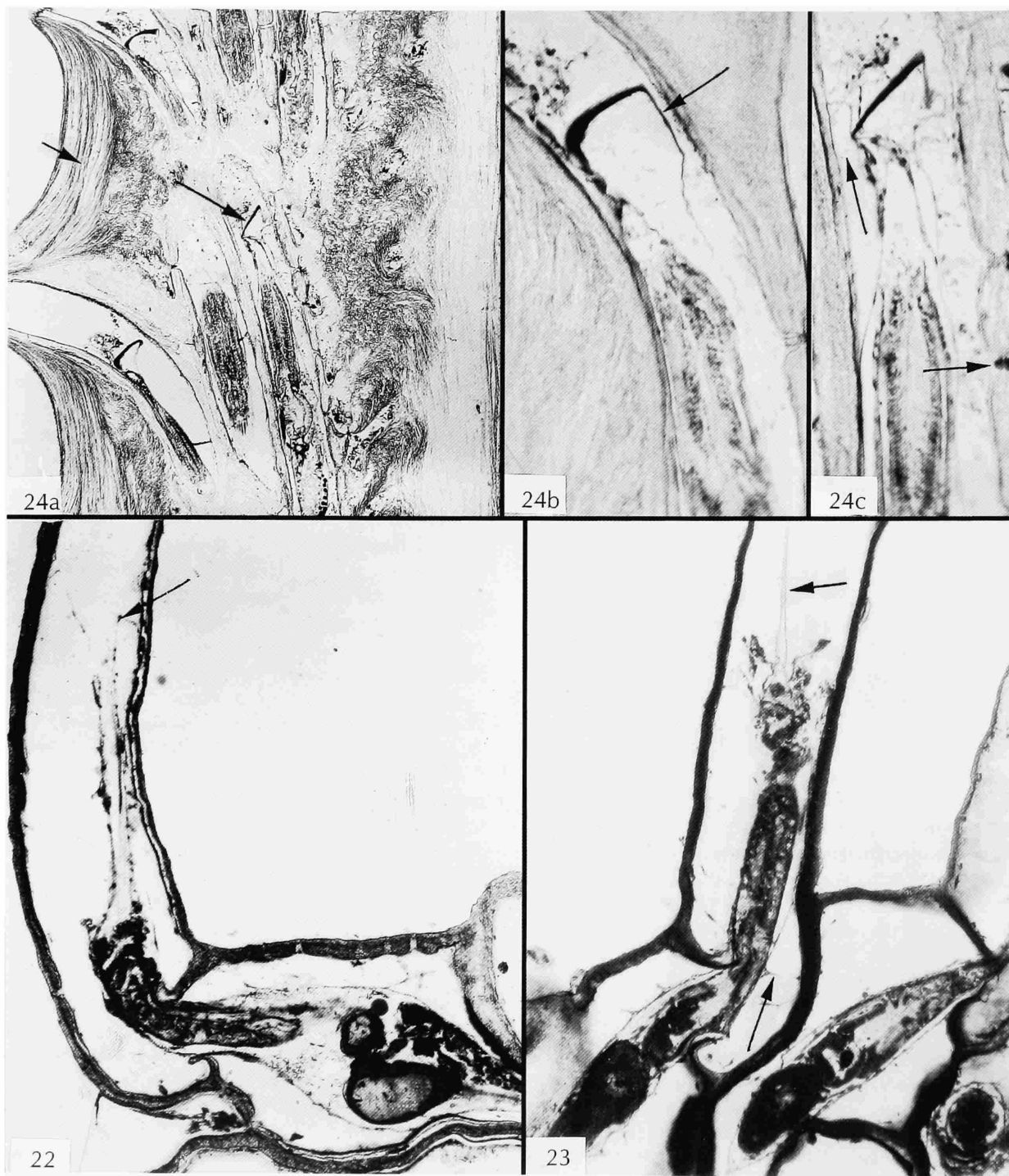
A remarkable variation (8 of Figure 129) of the tubuliporid mechanics described above (Figures 18, 19) is best seen in a New Zealand and Antarctic species of *Telopora* (Figures 20, 21). This variation employs an extremely long membranous sac with movable outer ends. Colonies of *Telopora* develop fin-like radiating clusters of long, parallel zooids from a central trunk (Figure 20a). The polypides undergo stationary cycles and retract into or near the bottoms of the living chambers deep in the center of the colonies. Polypides of the longer zooids retract as much as nine or 10 polypide lengths (McKinney and Boardman, 1985:199). The membranous sac is attached at or near the bottom of the living chamber by retraction muscles, and it must be able to extend to within a gut length of the distant skeletal aperture for the tentacle crown to be pushed out (Figure 21). Thus, the membranous sac is nearly as long as the long living chamber. The outer end of the sac is attached directly to the tentacle sheath and vestibular walls at the atrial sphincter muscles, just as in the tubuliporid described above. In the fully retracted position, the sac-sheath attachment at the sphincter muscle is near the ends of the tentacles near the bottom of the living chamber. The long membranous sac is therefore compressed, causing it to be deeply pleated (Figure 20b). The pleating is perhaps controlled by the annular muscles of the sac. In addition to the pleats, longer zooids develop a major inward fold of the pleated sac, thus accommodating an even longer sac in the inner end of the living chamber (Figure 20b). Membranous vestibular walls proportional to the zooidal length must extend down from the skeletal aperture to the atrial sphincter muscles in order to maintain the body cavity within the long skeletal walls, although this was not seen. The tentacle sheaths are slightly longer than the tentacles, as in most other species, and are also attached to the atrial sphincter muscles to complete the epidermal protection within the living chamber. By necessity, the retractor muscles are able to stretch from their skeletal attachments near the bottom of the living chamber to

nearly to the distant skeletal aperture, so they are extremely long, even when relaxed, and collect in a large mass below the retracted polypide in the longer zooids.

To begin protrusion, a polypide is forced outward by the progressive contraction of the annular muscles starting at the inner end of the membranous sac. As the polypide moves outward, the pleats at the inner end of the sac start to unfold, increasing the sac length. The outer end of the sac at the atrial sphincter muscle follows the outward motion of the polypide. In the longest zooids the major inward fold of the sac straightens out as the sac is pushed outward. Also, as the polypide moves outward, the body cavity behind the polypide lengthens (Figure 21) and the vestibule with its sea water correspondingly shortens. The vestibular wall must necessarily buckle and be pushed out of the way by the advancing polypide, although this was not seen in the available slides. As the polypide approaches the aperture, the membranous sac becomes fully unpleated and extended, halting the advance of the atrial sphincter muscle and the attached tentacle sheath. The annular muscles of the membranous sac continue pushing the polypide outward, turning the tentacle sheath inside out to free the tentacles. It is not clear whether the membranous sac of *Telopora* needs an additional longitudinal force for it to extend outward far enough to protrude the polypide fully (Figure 21). Presuming near neutral buoyancy of the polypide, gravity should not be a factor regardless of the zooidal orientation.

Another solution to the problem of long protrusion distances (9 of Figure 129) occurs in the encrusting fixed-walled species *Harmelinopora indistincta* (Canu and Bassler, 1929) (Figures 5, 22, 23; Harmelin, 1976:90; genus by Brood, 1976). The polypide undergoes a stationary cycle and retracts behind a pair of skeletal hemisepta to the bottom of the living chamber. The frontal wall of the zooid supports a long exterior peristome outward from the hemisepta. The protrusion distances of polypides from the hemisepta to the skeletal apertures are as much as three tentacle lengths.

The problem of enabling tentacle crowns to protrude past distant skeletal apertures is solved in *H. indistincta* by having stationary membranous sacs and tentacle sheaths that are both uncommonly long. The membranous sac is fixed in place by retractor muscles at the bottom of the living chamber and is fastened to the atrial sphincter muscles by the tentacle sheath and vestibular walls up near the skeletal aperture within the peristome (arrows of Figures 5, 22). It is not clear how the sac fastens to the peristome. The sac extends approximately one polypide length outward from where the retracted tips of the tentacles are attached, instead of ending roughly at the tips of the retracted tentacles as in species with attachment organs. In Figure 23, one-third of the polypide is protruded, and the length from the mouth to the sac attachment in the peristome is about equal to the length from the sac attachment to the skeletal aperture. Thus, with an outward extension beyond the retracted polypide, the sac can push the mouth of the polypide to the



FIGURES 22-24.—Protrusion anatomy: 22, 23, *Harmelinopora indistincta* (Canu and Bassler), Mediterranean Sea, Port Cros, Gabiniere, France ($\times 150$): 22, membranous sac and tentacle sheath attached high in exterior peristome, atrial sphincter muscle (arrow) also at attachment level; 23, tentacles partly protruded past hemisepta with ends of tentacles nearly reaching attachment level, vestibular membrane still in place (small arrow), minute strands connecting membranous sac (large arrow) to skeleton at approximately 90 degrees, indicating sac remains stationary during protrusion. 24, *Crisina* sp.,

USNM 216489, Nausen Island, western Palmer Peninsula, Antarctica: 24a, horny valves (large arrow) instead of attachment organs, somehow the polypides undergo progressive polypide cycles as they maintain a constant distance to their skeletal apertures, extrazooidal skeleton with laminae growing inward from the apertures between zooids (small arrow) ($\times 100$); 24b, closeup showing valve attached to membranous sac (arrow) ($\times 300$); 24c, valve tilted slightly, apparently indicating the path (large arrow) of exit for protruding tentacles, cells in communication pore (small arrow) ($\times 300$).

skeletal aperture and still remain stationary, as is indicated by the right angle positions of the strands that connect the membranous sac to the peristome wall during protrusion (Figure 23).

Axial to the membranous sac, the tentacle sheath and vestibular wall must connect to provide the epidermal protection for the body cavity at an atrial sphincter muscle. In Figure 23, the vestibular wall has not started to be pushed aside by the tentacles; therefore, the ends of the tentacles have not passed the sac-sheath connection at the atrial sphincter muscle. Thus, the tentacle sheath also extends well beyond the retracted polypide and ends at the attachment of the sac to the peristome.

The vague connection of the sac and sheath to the inner walls of the peristomes in *Harmelinopora* is not considered to be an attachment organ because it apparently does not have the same regenerative function for the polypide. When polypides regenerate in *H. indistincta*, they start from the bottom of the living chamber (Figure 5). At some point when degenerated, the zooid develops membranous diaphragms across both the peristome and hemisepta (Harmelin, 1976, pl. 16; Boardman, 1983, fig. 40-4), which probably indicates the final cycle. Theoretically, polypides can begin feeding in their early regeneration phases because their retractor muscles are in position to function in the bottoms of the living chambers.

Another mechanism of tentacle protrusion (10 of Figure 129) occurs in an unnamed branching free-walled species of *Crisina* d'Orbigny, from the Antarctic (Figure 24). Unfortunately, only one colony is available, and all the zooids were fully regenerated with their polypides retracted and so revealed little of either protrusion or regeneration. The polypides lack attachment organs, and the exozones widen proximally. The polypides, however, maintain a functionally constant distance from the skeletal apertures through many progressive polypide cycles, which is indicated by the large number of brown bodies stored in the living chambers. Somehow, these polypides undergo progressive cycles without the benefit of attachment organs, a combination that is not understood and might well be considered a third basic method of protrusion.

In the general position of an attachment organ, *Crisina* polypides have a cap or valve-like structure, which is stiffened and horny, and is oriented transversely in the living chamber when the polypide is retracted (Figure 24). It would be an operculum if it was hinged at the skeletal aperture; however, the circumference of the valve is attached to the outer end of the membranous sac except on the proximal side of the living chamber. The sac attachment means that the valve is within the body cavity and is not part of the epidermis. Evidently, an atrial sphincter muscle reduces the diameter of the tentacle sheath as the sheath connects to and passes under the valve to make an epidermal connection with the vestibular wall. On the proximal side of the living chamber, the membranous sac apparently connects to the atrial sphincter muscle to complete the attachment of its outer edge. An unseen skeletal connection

apparently holds the valve and the outer end of the retracted polypide in place.

The valve has a diameter only slightly less than the diameter of the living chamber, so it must act as a flutter valve when opened, that is, it must rotate about its diameter. As the polypide starts to protrude, the atrial sphincter muscle apparently relaxes and the bottom of the valve swings inward out of the way (Figure 24c). The mouths of fully retracted polypides are roughly two tentacle sheath lengths from their skeletal apertures, so the tentacle crowns should open just outside of the skeletal apertures.

In summary, the sectioning of just 37 different stenolaemates species revealed 10 variations of protraction organs. Six variations are based on attachment organs and four occur in species that lack attachment organs. How many more variations are there in Recent species of the class? These differences in anatomy are directly involved with the basic function of tentacle protrusion and should be incorporated into phylogeny and classification wherever possible.

Detailed Morphology and Anatomy of Various Stenolaemata Taxa

Borg (1926, 1944) first demonstrated the importance of detailed descriptions of both the exteriors and interiors of colonies in the systematics of post-Triassic stenolaemates; however, descriptions of interiors have not been included in the great majority of taxonomic papers published since then. This section provides a measure of the diversity of morphology and anatomy that occurs in Recent colony interiors and the importance of that diversity to the systematics of the class. This section also provides the basic evidence for the interpretations that follow in this paper. The described characters are largely internal, and their occurrences and descriptions are organized under the current classification that is based largely on external features.

The class Stenolaemata has been divided into two main subgroups (Borg, 1944) based on the presence of either simple body walls (herein described as exterior frontal walls of feeding zooids with fixed orificial walls) or double body walls (herein described as outermost membranous walls of colonies covering outer body cavities and vertical walls of feeding zooids that have free orificial walls). The experience of placing genera with either fixed, fixed/free, or free walls in the same family, the Cinctiporidae (Boardman et al., 1992), led to a search for other possible exceptions to Borg's two major divisions among stenolaemates.

HORNEROIDS

DESCRIPTION.—Borg (1926:307) gave the following description of the horneroids: "One of the most characteristic features of the genus *Hornera* is the thickening of the

calcareous layer, during the growth of the zoarium, around its entire circumference: the secondary calcification. ... This process is of course made possible owing to the presence of soft tissues outside the calcareous layer; during the entire life of the zoarium the ectodermal epithelium which is the most immediate covering of the calcareous layer seems to continue to secrete new calcareous matter."

As Borg indicated, Recent species commonly placed in the Cenozoic genus *Hornera* Lamouroux have an outermost membranous wall covering a confluent outer body cavity, and they remain free-walled throughout colony life (Figure 25a). Typical *Hornera* colonies are fenestrate (Figure 26a) or are branching with the branches commonly in broad planes (Figure 27). A set of feeding zooids open on the frontal side of branches and are evenly and widely spaced in a rhombic arrangement. Behind the frontal feeding zooids is a layer of lateral feeding zooids, which have longer living chambers and polypides that fan out to open on the sides of branches (Figures 25a, 26–29). The back sides of branches lack zooidal apertures and are covered by massive extrazoooidal skeleton.

Horneroid endozones have zooidal walls with the mirror image microstructure of compound walls centered on zooidal boundary zones, indicating calcification by adjacent zooids. Horneroid boundary zones extend throughout the lengths of the feeding zooids and, in all three orientations, are sharply defined dark to clear layers in transmitted light (Figures 2, 25a,b, 26b). An SEM study reveals that in two species of *Hornera*, the boundary zones consist of small crystallites that are flat rhombs, with many of the rhombs six-sided (Taylor and Jones, 1993, fig. 1c). (Compare the sharpness of definition of boundary zones with those in cinctiporids, Boardman et al., 1992, fig. 40c.) On either side of a boundary zone in the endozonal walls is a thin laminar layer of flattened crystallites that forms skeletal linings throughout the living chambers of horneroid feeding zooids.

As exozones are reached during growth, the frontal feeding zooids turn outward at high angles to the colony surfaces, no new feeding zooids are added, and adjacent zooids separate equally so that the apertures are evenly spaced and rhombic in arrangement (Figures 2, 25a). The space between the diverging zooids is filled with extrazoooidal skeleton. Where zooidal separation is accomplished with a bifurcation of boundary zones, each zooid has its own boundary zone completely surrounding its living chamber and extends its zone outward to form interior peristomes on colony surfaces (Figure 2). If the separation into the exozone is accomplished without the bifurcation of boundary zones, the distal sides of living chambers lack boundary zones and are occupied by extrazoooidal skeleton. On the proximal sides of zooids the boundary zones form lunaria that are U-shaped in cross section and form troughs along which the polypides slide in and out (Figure 25a,b).

Feeding zooids are separated by deposits of massive, laminar extrazoooidal skeleton in exozones, which form skeletal colony

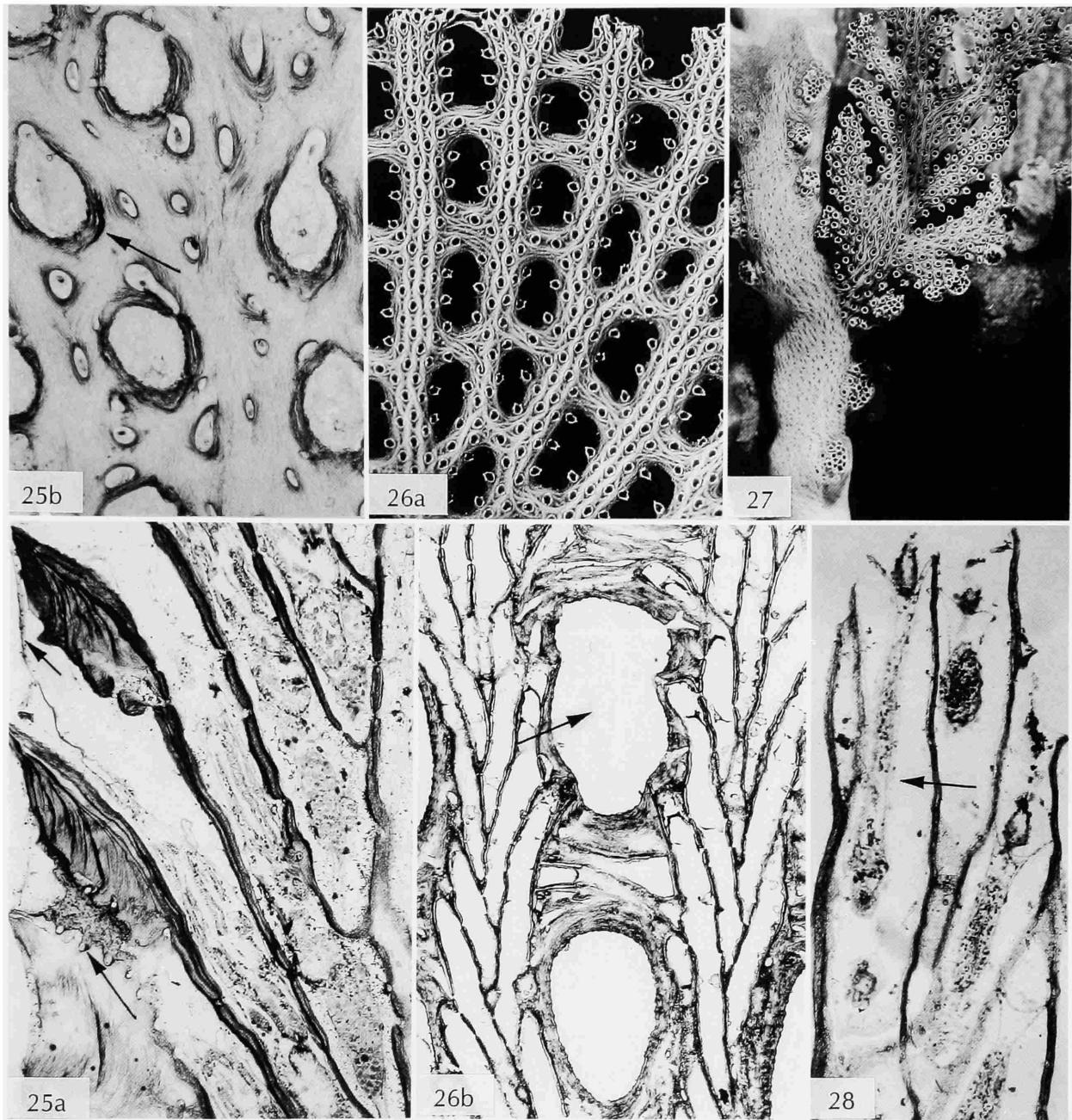
surfaces between the zooids (Figures 2, 25), that continues around to cover the back sides of branches. Incorporated into all the extrazoooidal skeleton are elongated body chamber vacuoles called cancelli that lack organs and their own skeletal walls in the same way that communication pores lack their own walls (Figures 2, 25b). As the term indicates, extrazoooidal skeleton is formed outside of zooidal boundaries and therefore is not assignable to individual feeding zooids.

A detailed SEM study (Taylor and Jones, 1993) indicates that zooidal boundary zones originate both the laminar living chamber linings and the extrazoooidal skeleton. Furthermore, the skeletal laminae of both consist of flattened crystallites, which grow inward, opposite to the direction of zooidal growth. This inward growth direction from the tips of the boundary zones necessarily produces the concave surfaces formed by the parallel laminae of the extrazoooidal skeleton between zooids (Figure 2). This inward growth direction also requires that extrazoooidal laminae from adjacent zooids merge with each other from opposite directions.

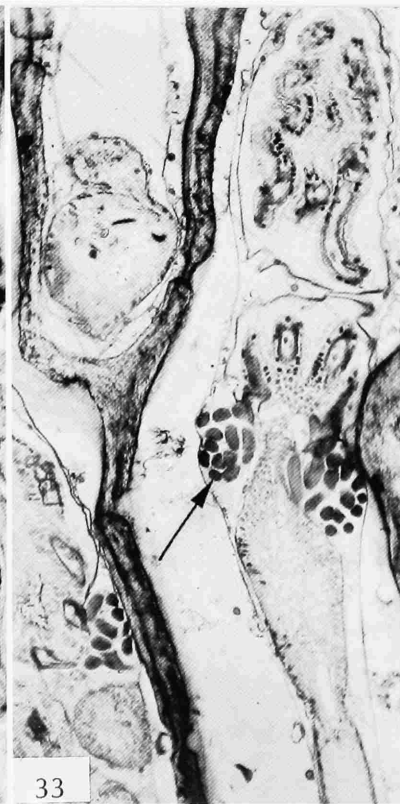
Some sections of *Hornera* display thin layers of darker laminae in the extrazoooidal skeleton that generally parallels the skeletal surface (Figure 2). The areas covered by the darker layers range from small patches to layers that are continuous on the front and back sides of branches. In one slide, a darker layer encircles the extrazoooidal skeleton and is covered by just one or two layers of transparent crystallites, indicating that at least some of these darker layers represent coeval surfaces within the skeleton. The uneven spacing and the differing degrees of darkness permit the identification of the the same layers on both the fronts and backs of branches, just as in tree rings or glacial varves. An SEM photo of a polished section of hornerid skeleton suggests that the darker laminae are denser layers of crystallites, which are smaller than the crystallites between the layers (Schäfer, 1991, pl. 11: fig. 1).

The presence of an outermost membranous wall protecting a confluent outer body cavity makes it possible for skeletal features to be deposited on outer skeletal surfaces throughout a colony at any time. For example, all branches of the colony have frontal sides facing the camera in Figure 27. Extrazoooidal skeleton covers the zooidal apertures of the main supporting branch starting from the base of the colony and progressing distally. Extrazoooidal skeleton that overwhelms feeding zooids to form support structures of several configurations is common in both the Cenozoic hornerids and the Paleozoic fenestrates (see McKinney et al., 1993). The confluent outer body cavities of both groups must be the means of nutrient exchange from the feeding zooids to the regions of extrazoooidal skeleton. The hornerids have communication pores that might also carry some nutrients to extrazoooidal growth. Paleozoic fenestrates, however, do not have communication pores, so their outer body cavities must have been the single means of nutrient exchange.

A second feature of hornerids is the unusual mode of growth of calcified terminal diaphragms. The great majority of terminal diaphragms of feeding zooids of post-Triassic steno-



FIGURES 25–28.—Horneroids: 25, *Hornera* species 1, USNM 488156, off Otago Head, South Island, New Zealand ($\times 100$): 25a, extrazoooidal skeleton oriented inward, orificial membrane continuing distally past extrazoooidal wall to next younger zooid (small arrow), communication pores aligned parallel to growth direction (large arrow), both zooids have lunaria; 25b, tangential section, lunaria on proximal sides of some feeding zooids (arrow) and small diameter vacuoles in extrazoooidal skeleton that separates feeding zooids. 26, *Hornera* sp., USNM 250057, Flinders Island, Australia: 26a, fenestrate growth habit ($\times 15$); 26b, deep tangential section revealing set of larger polymorphic feeding zooids whose apertures project out into large spaces (fenestrules, arrow) between branches in Figure 26a ($\times 50$). 27, *Hornera* species 1, branching colony, the frontal side of main branch to left has zooidal apertures covered by extrazoooidal skeleton with vacuoles, the smaller branches to right show uncovered frontal side with zooidal apertures, a set of larger polymorphic feeding zooids project along sides of branches, USNM 488158, off Otago Head, South Island, New Zealand ($\times 6$). 28, *Hornera* sp., growing tip with a new frontal set of zooids opening to the right, the larger polymorphic zooids (arrow) behind (as in Figure 26b), Mediterranean Sea, Rion, Marseille, France ($\times 100$).



FIGURES 29–34.—Horneroids: 29, Horneroid species, frontal feeding zooids opening to left, larger polymorphic feeding zooids are longitudinal along branch (arrow), the large brood chamber with interior skeletal cover is on well-developed reverse side of branch, indicating brood chamber originated below growing tip, BMNH specimen, Halley Bay, Coats Island, Antarctica ($\times 30$). 30, *Hornera* sp., polypide with thin attachment organ (small arrows) and tentacle sheath (large arrow), BMNH specimen, Blacken Collection, Arctic ($\times 300$). 31, *Hornera* sp., polypide with thin attachment organ and pear-shaped atrial sphincter muscle above (arrow), BMNH specimen, Blacken Collection, Arctic ($\times 300$). 32, *Hornera* species 1, fragile attachment organs that are apparently pulled loose (arrow), USNM 488159, off Otago Head, South Island, New Zealand ($\times 300$). 33, *Hornera* species 2, few and extremely coarse lophophore retractor muscles in each cluster (arrow), USNM 488160, Three Kings Island, New Zealand ($\times 300$). 34, *Hornera* species 3, polypide just starting protrusion, thicker pleated attachment organs and deeper retraction distance, attachment ligaments (arrow), USNM 250097, Poor Knights Island, New Zealand ($\times 100$).

laemates are exterior structures that form as the inner surfaces of membranous diaphragms become calcified. The calcified terminal diaphragms include exterior cuticles and pseudopores (Boardman, 1983, fig. 34-1d; Boardman et al., 1992:27). Presumably, the nutrients for calcification come through communication pores from adjacent actively feeding zooids. An unexpected feature of hornerid skeletons is the calcification from both sides of the terminal diaphragms of feeding zooids. This observation is based on the terminal diaphragms seen in only two slides from one colony. Apparently an infold of the depositing epidermis on one side of a living chamber wall produces two layers of crystallites back to back that grow together to close the aperture. These terminal diaphragms develop entirely within body cavities, so they are interior structures. Also, they do not have the customary pseudopores of exterior terminal diaphragms (Schäfer, 1991, pl. 47: fig. 3). The compound calcification of the interior diaphragms apparently takes advantage of both communication pores in vertical walls and confluent outer body cavities to provide the nutrients for calcification to zooids that have ceased to feed. In the two available slides that show terminal diaphragms, the exterior membranous walls with cuticles are visible and cover regions of the colonies that have zooids with terminal diaphragms, thus keeping the confluent outer body cavities intact.

A third structure that relies on outer membranous walls and confluent body cavities is the hornerid brood chamber. The skeletal walls of brood chambers of many stenolaemate taxa must begin development in budding zones of colonies as the zooidal skeletons form adjacent to them. In contrast, the brood chambers of *Hornera* begin development proximal to budding zones on the back sides of branches. Skeletons at the growing tips of hornerid branches are uniformly thin-walled (Figure 28; Boardman, 1983, fig. 30-2). The proximal development of brood chambers is indicated by the chambers sitting on thicker, ontogenetically more advanced skeletal walls (Figure 29; Boardman, 1983, fig. 30-2). This proximal growth is made possible by the ability of outer body cavities and any

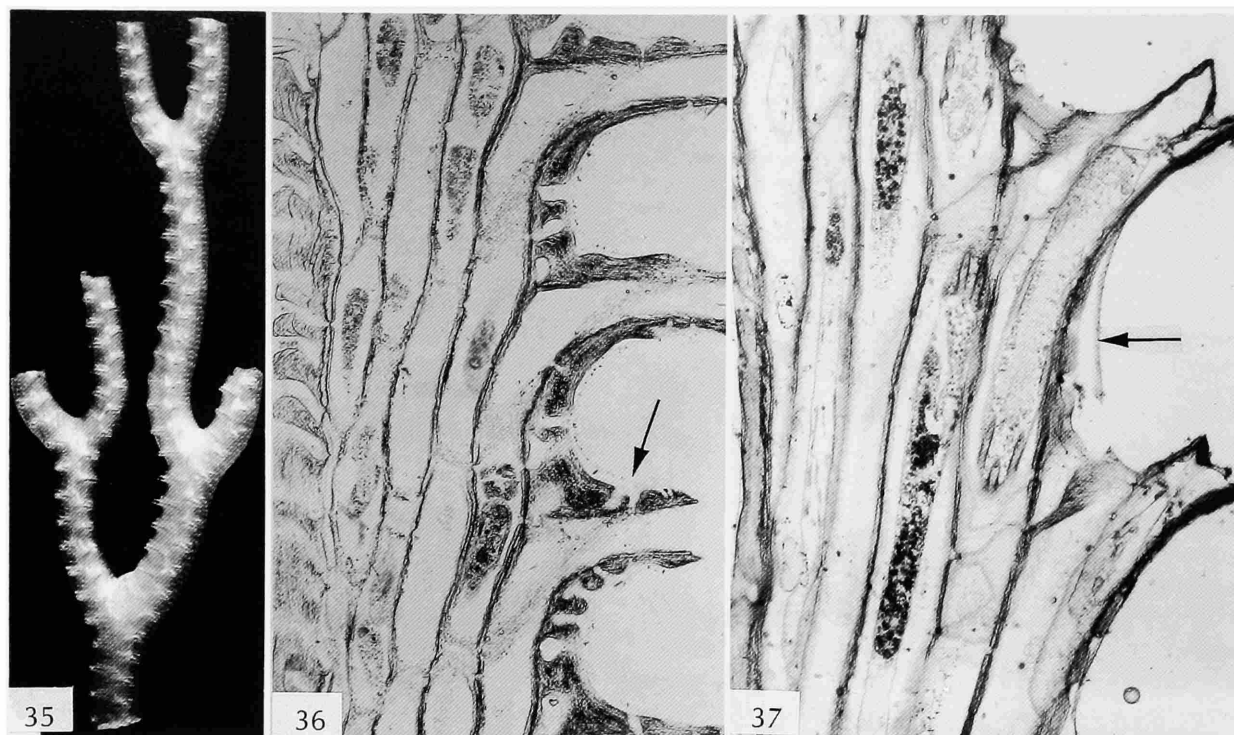
intervening communication pores to supply nutrients to the region.

Hornerids in this collection, which occur in the Arctic, Antarctic, and Mediterranean, have polypides that maintain short functional distances to their skeletal apertures by progressive cycles as the exozones widen (Figures 2, 28). They have thin membranous attachment organs, whose inner ends attach to the skeleton, and whose outer ends attach to the membranous sac (Figures 30, 31; Boardman, 1983, fig. 44-5). The membranous attachment organs extend up to a large, pear-shaped, atrial sphincter muscle, thus keeping the exosaccal and endosaccal body cavities separate. The tentacle sheath connects directly with the membrane of the attachment organ without any attachment filaments and continues on to the atrial sphincter muscle and vestibular wall, thus sealing the atrium from the body cavity.

Hornerids from New Zealand, with skeletons as generally described above, have anatomical differences that readily differentiate species. All three species available in the collection retract their tentacles at least one-third further into their living chambers than do the species of Figures 2, 28, 30, and 31 described above. Unfortunately, two of the New Zealand species have their fragile attachment organs pulled loose, thus giving a first impression of lacking them completely. One of the two species is from South Island (Figure 32) and appears to have its polypide anatomy comparable to that of the species studied from other regions. The second species is from North Island and is distinguished by relatively few, thick lophophore retractor muscles (Figure 33). A third species, which also occurs off North Island, has thick attachment organs that are pleated when the polypides are fully retracted (Figure 34).

It is safe to predict that other genera with hornerid skeletal microstructures also grow crystallites inwardly. For example, *Crisina* is a genus that is externally distinct from *Hornera*, but it has a hornerid microstructure. In an undescribed *Crisina* species from the Antarctic, two vertical rows of paired feeding zooids open on the frontal sides of branches (Figures 24, 35). The zooid pairs are not parallel, thereby making it difficult to bisect the zooids in longitudinal sections. The polypides have horny valves and lack attachment organs as part of their protrusion mechanism, which is described in detail in "Tentacle Protrusion," above. Rather than having valves, a species identified as *Crisina watersi* Borg, 1941, from Tulear, Madagascar, has a hornerid wall structure, but its attachment organs are poorly understood, and it is likely that the two species are not congeneric (Figure 36). *Mesonea radians* (Lamarck), the type species of the genus, from the Great Barrier Reef, also has a hornerid wall structure; however, it has a different looking attachment organ that is also poorly understood (Figure 37).

SUMMARY.—Horneroid colonies are highly integrated and feature both outer body cavities with free orificial walls and



FIGURES 35–37.—Horneroids: 35, *Crisina* sp., exterior of branching colony, USNM 216489, Nausen Island, western Palmer Peninsula, Antarctica ($\times 7$). 36, *Crisina watersi* Borg, interior peristomes and entire skeleton covered by membranous outermost wall (arrow), extrazoooidal skeleton with vacuoles on both front and reverse sides, Tuléar, Madagascar ($\times 100$). 37, *Mesonea radians* (Lamarck), zooids with interior peristomes and what are apparently attachment organs, thin extrazoooidal skeleton is on front and reverse sides, all covered by membranous outermost wall (arrow), BMNH specimen 1932.4.20.10, Low Island, Great Barrier Reef, Australia ($\times 150$).

communication pores in vertical walls. Nutrient exchange through the outer body cavities dominates skeletal growth, this is indicated by the formation of enclosed massive extrazoooidal skeleton on outer surfaces between feeding zooids and on the reverse sides of branches. (This extrazoooidal growth is similar to extrazoooidal structures developed in a host of Paleozoic species that lack communication pores.) That both nutrient exchange pathways function, however, is indicated by the terminal diaphragms that are calcified on both sides. The other requirement for the development of fossil and horneroid extrazoooidal skeleton is the inward growth of skeletal crystallites and wall laminae, which is opposite to the zooidal growth direction. Crystallites in the other Recent species in this paper grow outward or at right angles to the direction of zooidal growth. These other Recent species also apparently cannot grow extrazoooidal skeleton.

Horneroid zooids undergo progressive polypide cycles as the exozones widen. In three species of *Hornera* from New Zealand (Figure 129), two have membranous attachment organs but their polypides are otherwise different, and one has thicker and pleated attachment organs. *Crisina*, another genus with horneroid microstructure, has membranous attachment

organs in one species and the poorly understood horny valves without attachment organs in another species. These three variations in polypide anatomy in just five species indicate that the internal characteristics of horneroid colonies cannot be assumed and must be investigated.

TUBULIPORINES

DESCRIPTION.—The Tubuliporina Milne Edwards, are presently considered a suborder and include taxa having membranous orificial walls fixed to skeletal apertures that are formed by either exterior frontal walls or by exterior peristomes supported by frontal walls. Stenolaemates with frontal walls first appeared in the Ordovician with small encrusting runner, sheet-like, or slender erect colonies. A few species have a restricted number of communication pores (Boardman, 1973; Buttlér, 1989), whereas other species appear to entirely lack pores. These species are mostly from the lower Paleozoic (Brood, 1975). In those species lacking communication pores, physiological connections among the zooids would have been closed by the formation of frontal walls just proximal to confluent budding zones. Jurassic and younger tubuliporines

appeared with communication pores in their vertical walls so that physiological connections could be maintained among zooids throughout colony life. With this theoretical advantage, and no doubt others, tubuliporines diversified and are the most numerous species among living stenolaemates.

The tubuliporines are a much larger taxonomic group than the horneroids described above, and a greater morphologic and anatomical diversity occurs in the species studied. Some shared characteristics, other than frontal walls causing fixed orificial walls, would suggest some confidence in the phylogenetic validity of the suborder. Morphology and anatomy, which are presumed here to be among the major characters of future tubuliporine classifications, include (1) microstructure (ultrastructure) of skeletons, (2) polypide anatomy, (3) zooidal arrangement, and, in this suborder, possibly, (4) colony growth habit.

The most commonly occurring skeletal microstructure in this collection of Recent tubuliporines is similar to that of the cinctiporids (Boardman et al., 1992, figs. 37–42, SEM ultrastructure done by Taylor) and is found in Recent species from New Zealand, the Mediterranean, and the western Atlantic. Using light microscopy, the zooidal boundary zones appear as pink or dark layers, which are actually sharply defined microcrystalline zones. Adjacent to a boundary zone is a thicker layer of fibrous crystallites that have their lengths oriented closely parallel to the boundary zones and at right angles to the zooidal lengths as seen by the SEM. Using light microscopy, this layer appears transparent in longitudinal sections, which is caused by the crystallites being perpendicular to section planes. In transverse and tangential sections the fiber lengths are barely visible, either slightly approaching or diverging from the zooidal boundary zones. Adjacent to the fibrous layer is the laminar living chamber lining in which the crystallites grow outward in the direction of zooidal growth, this is in contrast to the inward growth direction in the horneroids described above.

An idmidroneid species from New Zealand, with a cinctiporid wall structure, has erect colonies with bifurcating branches in broad planes (Figure 38). Idmidroneid branches are triangular in cross section with zooidal apertures on the two front sides only. Zooidal apertures are arranged in single transverse rows that are separated by spaces filled with frontal walls (Figures 1, 40) or brood chambers (Figure 39). The brood chambers extend across the frontal sides of branches and have exterior skeletal covers. The outer margins of branches have single longitudinal rows of smaller zooids; these are offset from the horizontal rows of feeding zooids (Figure 38). The back sides of branches are formed from the coalesced exterior basal walls of the feeding zooids (Figure 39).

Polypides of this New Zealand idmidroneid have prominent attachment organs that are thickened, elongate, and cone-shaped when fully retracted (Figure 40). The intermediate attachment of the tentacle sheaths is by attachment filaments. In

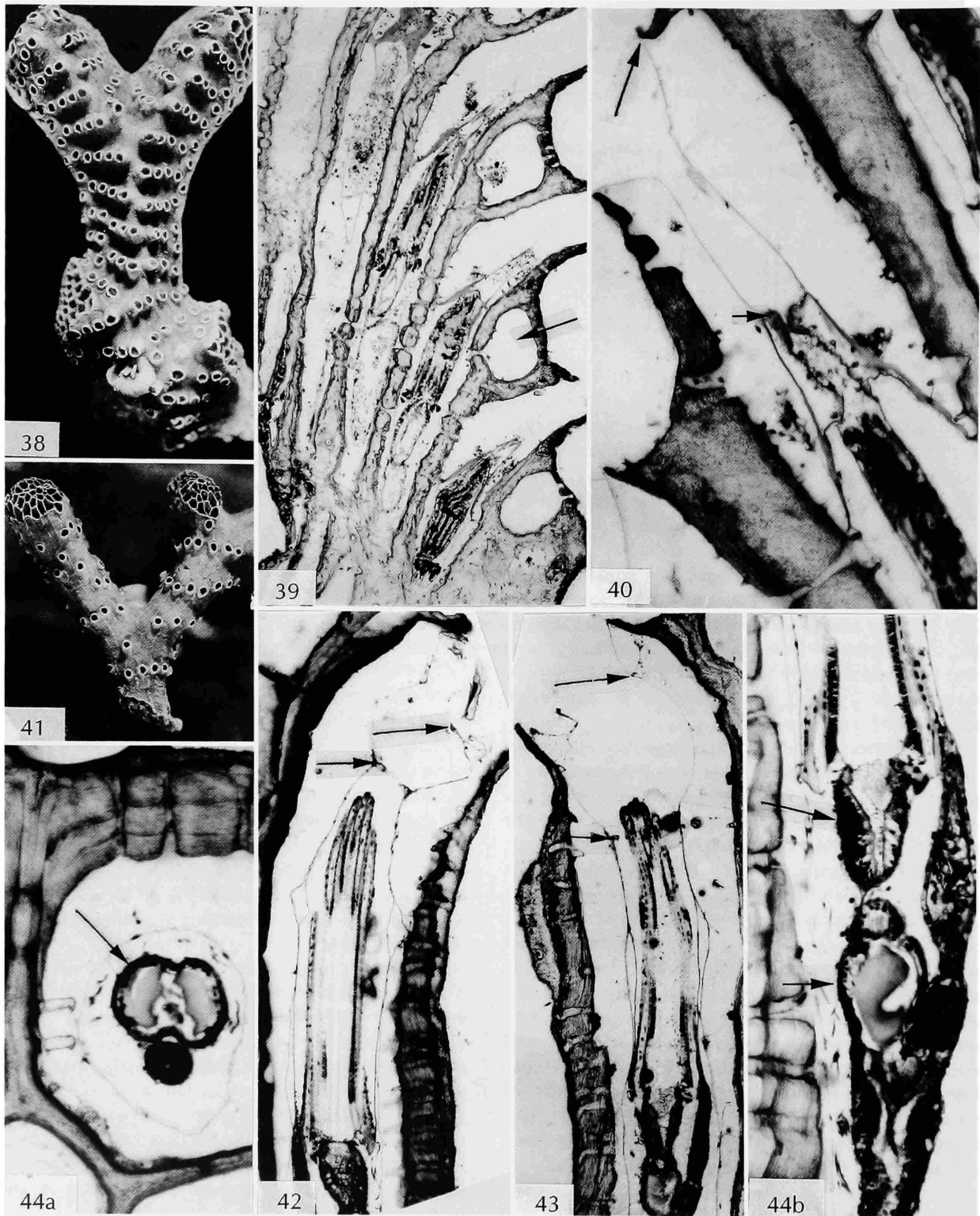
the free-walled budding zones (Figure 6), young polypides maintain a short distance to their skeletal apertures by progressive cycles as their living chambers lengthen. With the development of frontal walls just proximal to budding zones the outward growth of vertical walls is terminated, polypides maintain a fixed position in their living chambers, and subsequent cycles are stationary, as in most, if not all, tubuliporines with attachment organs.

During the ontogenetic development of the polypides in this species, the lophophore retractor muscles of the youngest zooids are attached to the proximal (frontal) sides of living chambers. In subsequent cycles they are attached laterally, and finally, in the last cycles, the retractor muscles are attached on the distal sides of living chambers (Figure 1).

Idmidronea atlantica (Forbes), is a species with a cinctiporid wall structure that has been identified in the Mediterranean (Harmelin, 1976:182). The Mediterranean specimens have a more delicate colony than the New Zealand idmidroneid but the skeleton is qualitatively comparable. The Mediterranean polypides, however, are distinctly different, as they lack attachment organs, which are replaced by valves (Harmelin, 1976, pl. 32: figs. 4–7; Boardman, 1983, fig. 44-3) comparable to those of the Antarctic free-walled horneroid species of *Crisina* described above (Figures 24, 35). Protrusion distances are short as in *Crisina*, indicating that the polypides underwent early progressive cycles without an attachment organ. This Mediterranean fixed-walled species and the free-walled horneroid are the only two species known to have the valves. Their distance both geographically and in current classifications poses a taxonomic puzzle.

Sections of a second Mediterranean species with a cinctiporid wall, *Idmidronea coerulea* Harmelin (1976, pl. 33: figs. 1–10), do not reveal details of the protracting organs. The polypides have neither attachment organs nor valves, however, and fully retracted polypides are deep within the living chambers so the protrusion organs are different from the other two idmidroneids.

Pustulopora purpurascens Hutton, is a New Zealand species with a cinctiporid wall structure that has an erect, branching growth habit with zooids that lack peristomes and are arranged in a spiral around the branches (Figure 41). The polypides have membranous attachment organs that are attached to their living chambers by four ligaments, and they maintain retracted positions near their skeletal apertures (Figures 42, 43). Tentacle sheaths connect directly to the attachment organs without filaments. This is an exceptional species because of two seemingly rare organs, a gizzard that occurs between the pharynx and caecum (Figure 44), and an orificial sphincter muscle (Figures 42, 43) in addition to the normal atrial sphincter muscle. Gizzards have been found in stenolaemates only in a fixed/free species, also from New Zealand (see Fasciculate species below), and in two fixed-wall species of



FIGURES 38–44.—Tubuliporines. 38–40, Idmidroneid species 1: 38, oral side, USNM 488162, Cape Rodney to Okakari Point, Marine Reserve, Leigh, New Zealand ($\times 15$); 39, conical attachment organs, brood chambers covered by frontal walls (arrow) between horizontal rows of zooids, USNM 488163, Poor Knights Island, New Zealand ($\times 100$); 40, orificial membranous wall (large arrow) attached to frontal wall, atrial sphincter muscle (small arrow), same species as Figure 1, USNM 488164, locality same as Figure 38 ($\times 300$). 41–44,

Pustulopora purpurascens Hutton, Poor Knights Island, New Zealand: 41, zooids in spiral arrangement around branch, USNM 488165 ($\times 7$); 42, atrial sphincter muscle (small arrow), orificial sphincter muscle (large arrow), USNM 488166 ($\times 150$); 43, atrial sphincter muscle (small arrow), orificial sphincter muscle (large arrow), USNM 488167 ($\times 150$); 44, USNM 488168: 44a, deep tangential section through gizzard (arrow) ($\times 300$); 44b, pharynx (large arrow), gizzard (small arrow) ($\times 150$).

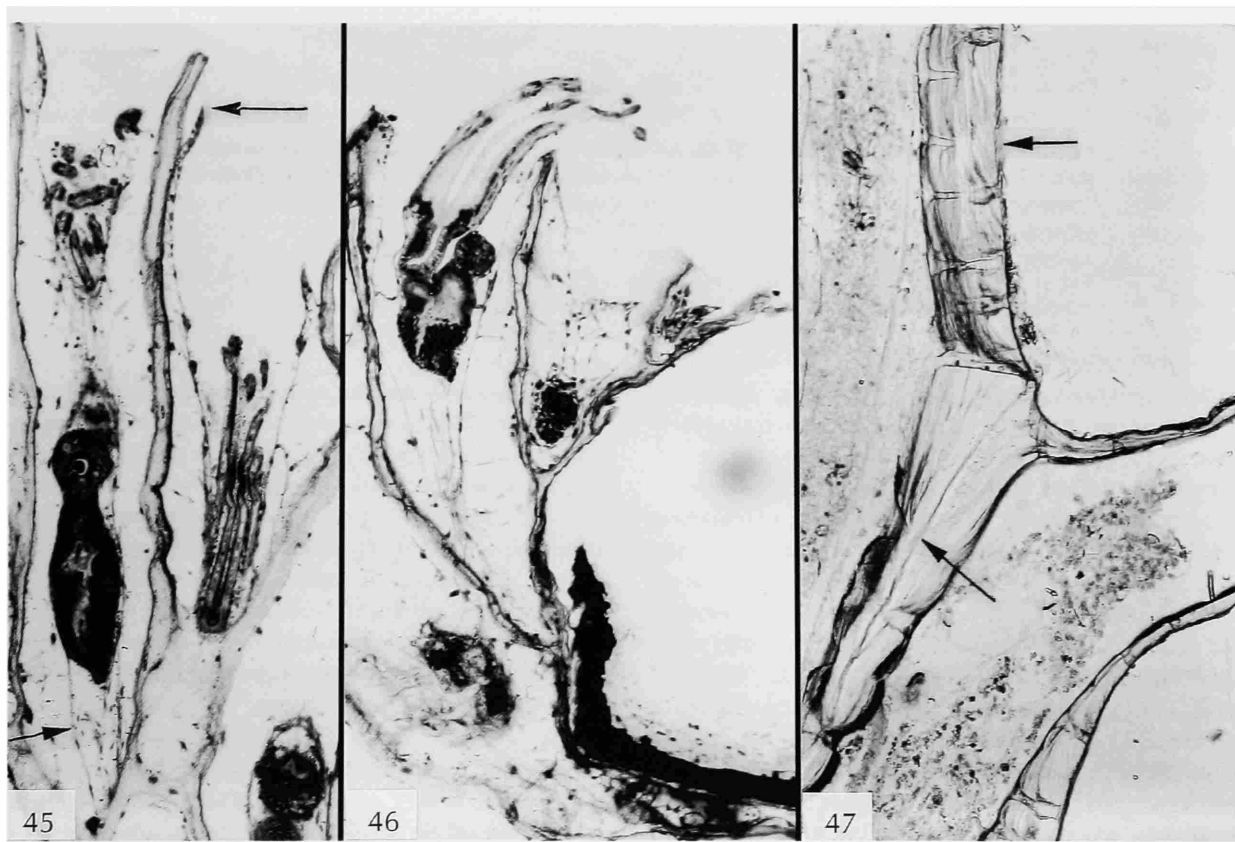
Diaperoecia from the Mediterranean. Gizzards also occur in a few gymnolaemates (for a detailed review see Schäfer, 1986).

The knowledge of orificial sphincter muscles is even more restricted. They occur in species of *Crisia* and *Crisiella* (Nielsen, 1970), which belong to another suborder, the Articulata. Orificial sphincter muscles also occur in a species of *Tubulipora* from Cape Cod, Massachusetts (Figure 45), that has a cinctiporid wall structure. In contrast, however, the Cape Cod species is an encrusting tubuliporid that lacks an attachment organ and possesses the mechanism described in detail in "Tentacle Protrusion," above (Figures 18, 19). Polypide development occurs in the bottoms of living chambers in both the first appearances of polypides in budding zones (Figure 46) and in older regenerating polypides. The membranous sac of the Cape Cod species is attached directly to the tentacle sheath, and the polypide retracts to the bottom of the shallow living chamber.

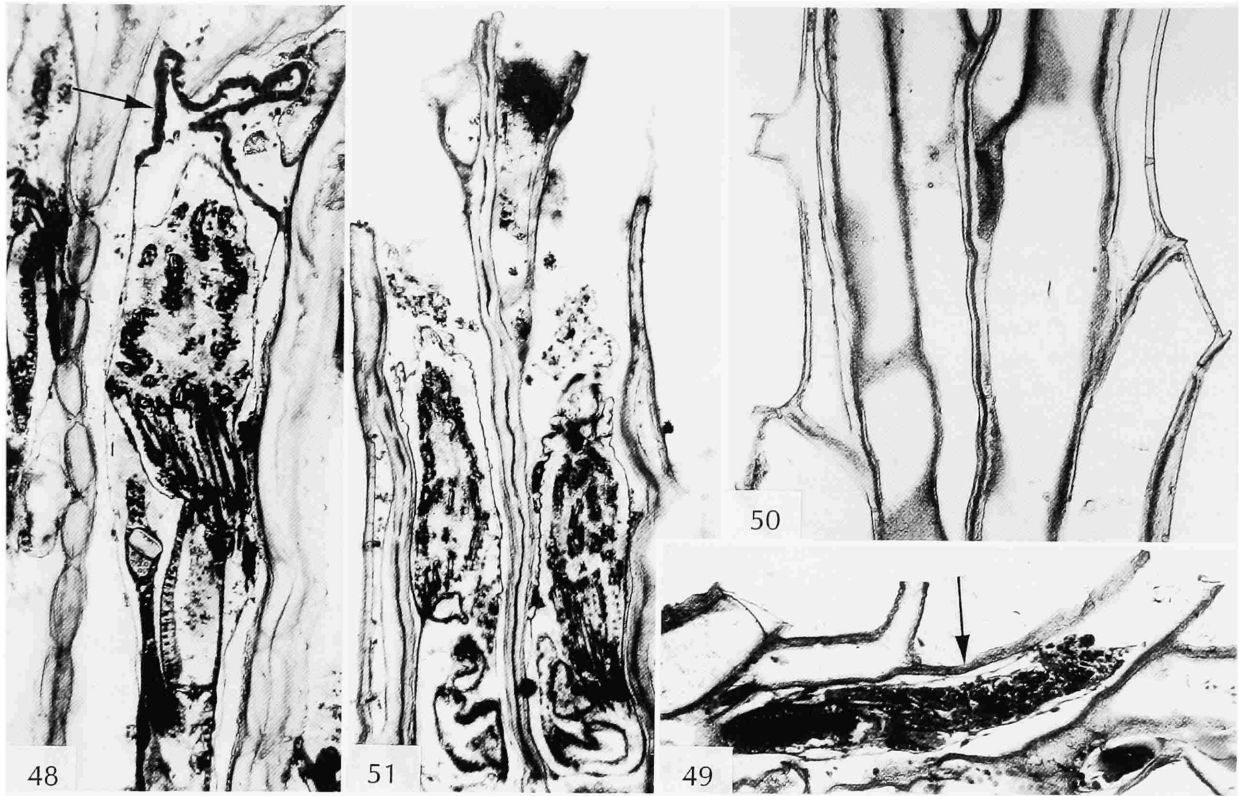
Two Mediterranean species, *Mecynoecia delicatula* (Figure 7) and *Tervia irregularis* (see Harmelin, 1976, for both), also have cinctiporid wall structures and erect branching growth habits, but they are otherwise different from *Pustulopora purpurascens* described above. Both species have long exterior

peristomes, they both lack gizzards and orificial sphincter muscles, and they both lack attachment organs so that the polypides retract at or near to the bottoms of their living chambers, thus placing the retracted mouths of the polypides as much as seven tentacle lengths from their skeletal apertures (Figure 7). Unfortunately, the available slides do not reveal the details of the organs of tentacle protrusion. The two species differ by *M. delicatula* having zooids arranged radially around colony branches and *T. irregularis* having zooids opening on the front sides of branches only in transverse rows.

A second skeletal microstructure occurs in tubuliporine species from the southern Indian Ocean (Figures 14a,b, 47) and in the Antarctic (Figure 48). In transmitted light, the zooidal boundary zones appear as pink layers that are thicker than the boundary zones in cinctiporids, in longitudinal sections they are unbroken lines, and in transverse or tangential sections they are either unbroken or dashed lines. Adjacent to the boundary zones in the vertical walls are layers of coarse laminae that are apparently initiated by and diverge outward from the boundary zones. The laminae consist of flattened crystallites, which are large enough to be seen with a light microscope, and grow outward parallel to the zooidal growth directions (the edgewise



FIGURES 45–47.—Tubuliporines (all $\times 150$). 45, 46, *Tubulipora* sp., Manomet, Cape Cod, Massachusetts: 45, no attachment organ (see Figures 18, 19), polypides are just starting to protrude, bottom of membranous sac (small arrow), orificial sphincter muscles (large arrow), USNM 488169; 46, growing edge, two young, developing zooids on right, partially protruded older zooid on left, USNM 488170. 47, Entelophorid species, zooidal boundary zone (large arrow) and outwardly diverging laminae of vertical wall, frontal walls (small arrow) attached to edge of vertical wall, USNM 186551, Kerguelan Ridge, southern Indian Ocean.



FIGURES 48–51.—Tubuliporines (all $\times 100$). 48, Idmidroneid species 2, polypide just starting to protrude with pleated attachment organ that lacks attachment filament (arrow), BMNH specimen, Halley Bay, Coats Land, Antarctica. 49, *Diplosolen* sp., small nanozooid with terminal aperture, frontal wall of larger feeding zooid (arrow), USNM 250088, Popoff Strait, Alaska. 50, 51, *Diplosolen intricaria* (Smith): 50, nanozooids with apertures at midlengths in their frontal walls that extend from aperture to aperture of the adjacent feeding zooids, USNM 186548, Kara Sea, Russia; 51, budding zone at top, polypides retracted to the bottoms of short living chambers, attachment organs not identified, BMNH 1958.1.26.2, Barents Sea, 60 miles north of North Cape.

multiple laminar growth of Boardman, 1983, fig. 29-2). The living chambers are lined by finer laminae, comparable in appearance to the skeletal linings of other wall structures.

The southern Indian Ocean species is apparently an entalophorid (Figures 14, 47). Colonies have an erect branching growth habit, and the feeding zooids are arranged radially around the branches and have short exterior peristomes. Zooids have thick attachment organs, thick closely-spaced ligaments, and thick filaments that connect to the tentacle sheaths some distance from the ligaments (Figure 14a). The “filament” structure is a flattened ring formed by a thickened membrane instead of a ring of separate strands. The interval of the attachment organ between the ligaments and the “filament” membrane is loosely pleated (pleats not shown in Figure 14a but are visible in other slides of species) and unpleats outwardly as the tentacles start to protrude (Figure 14b). This entalophorid is characterized by having polypides that retract to just inside their skeletal apertures, lophophore retractor muscles that attach to proximal (frontal) or lateral skeletal walls, and polypides with 16 tentacles.

The Antarctic species with the same wall structure is an idmidroneid with erect branches that are triangular in cross section with the zooids opening on the two frontal sides only. Internally, however, this species differs from the idmidroneids described above because it does not have the cinctiporid wall structure and its polypides have thick pleated attachment organs, but they lack filaments or valves (Figure 48). The lack of filaments theoretically allows the polypides to protrude further than the entalophorid described above (Figure 14b), and it compares with the protrusion mechanism of the dispoeloid described in “Tentacle Protrusion,” above (Figure 15).

The generic concept of *Diplosolen* Canu, includes encrusting or bifoliate fixed-walled species that have small primary polymorphs termed nanozooids, which originate in budding zones adjacent to developing feeding zooids (Figures 49–51; Boardman and Cheetham, 1973:152, fig. 30; Harmelin, 1976, fig. 35). Nanozooids contain reduced polypides with only a single tentacle (Borg, 1926:188, 232–239), which is interpreted to have a cleaning function on colony surfaces (Silen and Harmelin, 1974). *Diplosolen obelium* (Johnston), the type

species of the genus, has small, encrusting, generally circular colonies and occurs in the Mediterranean (Harmelin, 1976:144). A species from Alaska has the same growth habit (Figure 49). The feeding zooids bud from the basal walls of the colonies in a rhombic pattern. The nanozooids bud from the vertical walls of adjacent feeding zooids, which have skeletal apertures at the outer ends. Exterior frontal walls of both feeding zooids and nanozooids combine to form the outer skeletal covering of colonies between the skeletal apertures. The skeletal walls inside the colonies are interior vertical walls of feeding zooids or vertical walls shared by the feeding zooids and nanozooids. The wall structure of the two encrusting species appears to be largely microcrystalline.

As a feature of their ontogeny, the feeding zooids of *D. obelium* develop exterior-walled peristomes as much as four times their tentacle length (Silen and Harmelin, 1974). Unfortunately, no interpretable polypides were found in the few sections of the type species available, but the Alaska species has a membranous attachment organ (Figure 49).

A species identified as *Diplosolen intricaria* (Smitt) from the Barents and neighboring Kara seas in this collection has an erect, bifoliate growth habit (Figures 50, 51; Boardman, 1983, figs. 30-4, 42-2, 49-9). The skeletal wall structure is also different from that of the encrusting species. The zooidal boundary zones are dark microcrystalline layers. Adjacent to the boundary zones are laminae that parallel or diverge outward in the vertical walls, so it is assumed that crystallites grow outward in the direction of zooidal growth. Thin patchy layers of laminae line the living chambers. Both communication pores and pseudopores are widely scattered in zooidal walls. No communication pores were found in the thick compound median walls that divide the bifoliate branches, thus separating the two sides of a branch physiologically except at the budding zones.

In the encrusting species, nanozooids have skeletal apertures at their outer ends and provide the exterior frontal walls for the proximal halves of feeding zooids that they front (Figure 49). The feeding zooids themselves provide the exterior frontal walls for their distal halves. In the erect, bifoliate species, nanozooids have apertures at their midlengths, and their frontal walls extend from aperture to aperture of adjacent feeding zooids, thus providing all of the exterior frontal walls for the colony (Figure 50). Also, the interior vertical walls of feeding zooids extend to their skeletal apertures. The frontal walls of the nanozooids attach to the vertical walls of the feeding zooids at their skeletal apertures, thus fixing the orificial walls of the feeding zooids. Extremely short exterior peristomes form beyond some vertical walls. Feeding zooids of this bifoliate species, therefore, do not have frontal walls of their own, unlike the feeding zooids in the encrusting type species and other tubuliporines.

Attachment organs are not positively identified in *D. intricaria*. If present, they are membranous and are torn loose in the several sections available (Figure 51). The polypides are

retracted to the bottoms of their living chambers in at least the youngest zooids.

Harmelinopora indistincta (Canu and Bassler, 1929) is a small encrusting species from the Mediterranean with polypides that retract behind hemisepta (Figures 5, 22, 23). The protrusion mechanism is described in "Tentacle Protrusion," above. The fastening of the membranous sacs and tentacle sheaths to the inside surfaces of the peristomes makes the protracting organs different from those of other sectioned species of tubuliporines. Zooids are arranged in a rhombic pattern on the basal wall of a colony. The wall structure is extremely complicated (Harmelin, 1976, pls. 4, 5, 16; Boardman, 1983, figs. 32-1, 40-2) and also different from that of the other sectioned species. An SEM study will be necessary to fully understand the complexities.

SUMMARY.—Tubuliporines lack outer body cavities below budding zones so they must exchange nutrients only through communication pores in the vertical walls. Orificial walls of feeding zooids are fixed to the apertures of exterior frontal walls or to the peristomes supported by frontal walls. In one species, orificial walls are fixed by the frontal walls of intervening polymorphs. Reverse sides of tubuliporine branches without encrusting growths of polymorphs are necessarily exterior skeletal walls because outer body cavities are lacking. Seven species have a cinctiporid wall microstructure, three have laminae that diverge outwardly, and one is microcrystalline.

Beyond these skeletal generalities there seems to be little correlation of the internal features in tubuliporines. Among the eight species in which the anatomy is complete within sections, five species maintain shallow retraction distances using four different attachment organs. The three other species lack attachment organs, and the polypides in two of them retract to the bottoms of their living chambers using different mechanisms. The third has a shallow retraction distance involving the horny valve mechanism that is also found in one of the horneroids. Seven of the 10 protrusion mechanisms recognized in this paper occur in the tubuliporines. There seems to be no correlation or taxonomic pattern using both skeletal and soft parts in the available tubuliporines.

FASCICULATES

DESCRIPTION.—Fasciculates are characterized by colonies in which long, parallel, feeding zooids grow in clusters called fascicles. The clusters either form branches or prominences on colony surfaces. Some genera are entirely free-walled, with the vertical walls of feeding zooids forming their skeletal apertures and the free-walled polymorphs between fascicles. Other genera have surface areas between the distal ends of fascicles smoothly covered by thick exterior walls with abundant pseudopores. These exterior covering walls are coalesced zooidal walls and are termed "fascicle" walls. Most are parallel to the long feeding zooids of fascicles but range to transverse

orientations that cut off zooids in the crotches of branches. The outermost zooids of these fascicles have exterior walls on the exposed sides (the fascicle walls) and interior vertical walls within the fascicles so that their orificial walls are fixed/free. Zooids entirely within fascicles have interior vertical walls at their apertures and are free-walled. Generally, colonies have a few zooidal walls coalesced with the fascicle walls that ordinarily would be called normal frontal walls. Some species have extremely long living chambers that require correspondingly extreme mechanisms for tentacle protrusion. The clustered feeding zooids are obvious externally, and the genera have commonly been placed in a loose grouping of several families (Borg, 1926:375; Schäfer, 1991:91, for detailed review).

An Alaskan species of *Discocyrtis* d'Orbigny has a short peduncle, or stalk, that supports an expanded capitulum that has irregularly positioned fascicles of feeding zooids separated by polymorphs (Figure 52a,b). The oldest feeding zooids of a colony occur axially in the peduncle. The surfaces of the peduncle are covered by small polymorphs (Figure 53). As the oldest feeding zooids lengthen and diverge into clusters to form the capitulum, younger zooids are added progressively to the outer sides of fascicles (Figures 54, 55a). The polymorphs between fascicles are larger than those on the surface of the stalk. The outermost skeletal surface of the clusters consists of the vertical walls of feeding zooids that thicken and develop pustules common to the interior skeletal surfaces of some other taxa. The skeletal roofs of expanded brood chambers are interior and are covered by the smaller polymorphs (Figure 55a,b).

Colonies of this species of *Discocyrtis* are free-walled, and skeletons are interior above the basal colony walls. Both sizes of polymorphs have their apertures closed by relatively thick terminal diaphragms that are calcified from both sides (Figure 55b), and some even have communication pores. Sheets of exterior membranous walls can be seen in some sections to be intact over the regions of polymorphs. Thin calcified interior diaphragms occur sparsely within the living chambers of feeding zooids. Some of the interior diaphragms are positioned as terminal diaphragms, but they apparently lack pores (Figure 55b). The direction of bending of these thin diaphragms at their junctions with the vertical walls indicates that they were calcified on either inner, outer, or both sides. No calcified diaphragms were found in feeding zooids with polypides. Boundary zones range from thin and pink to dark, and the laminae diverge outward from the zones (Figure 56).

Some polypides are undersized relative to fully regenerated polypides; this is due to either ontogeny or the early regeneration stages in the polypide cycle. The polypides of one colony were all equally undersized, indicating a regeneration stage. Polypides retract into the inner end of their living chamber except where the bottom of the chamber is filled with brown bodies, indicating stationary cycles. The mouths of fully retracted polypides are as much as six tentacle lengths from

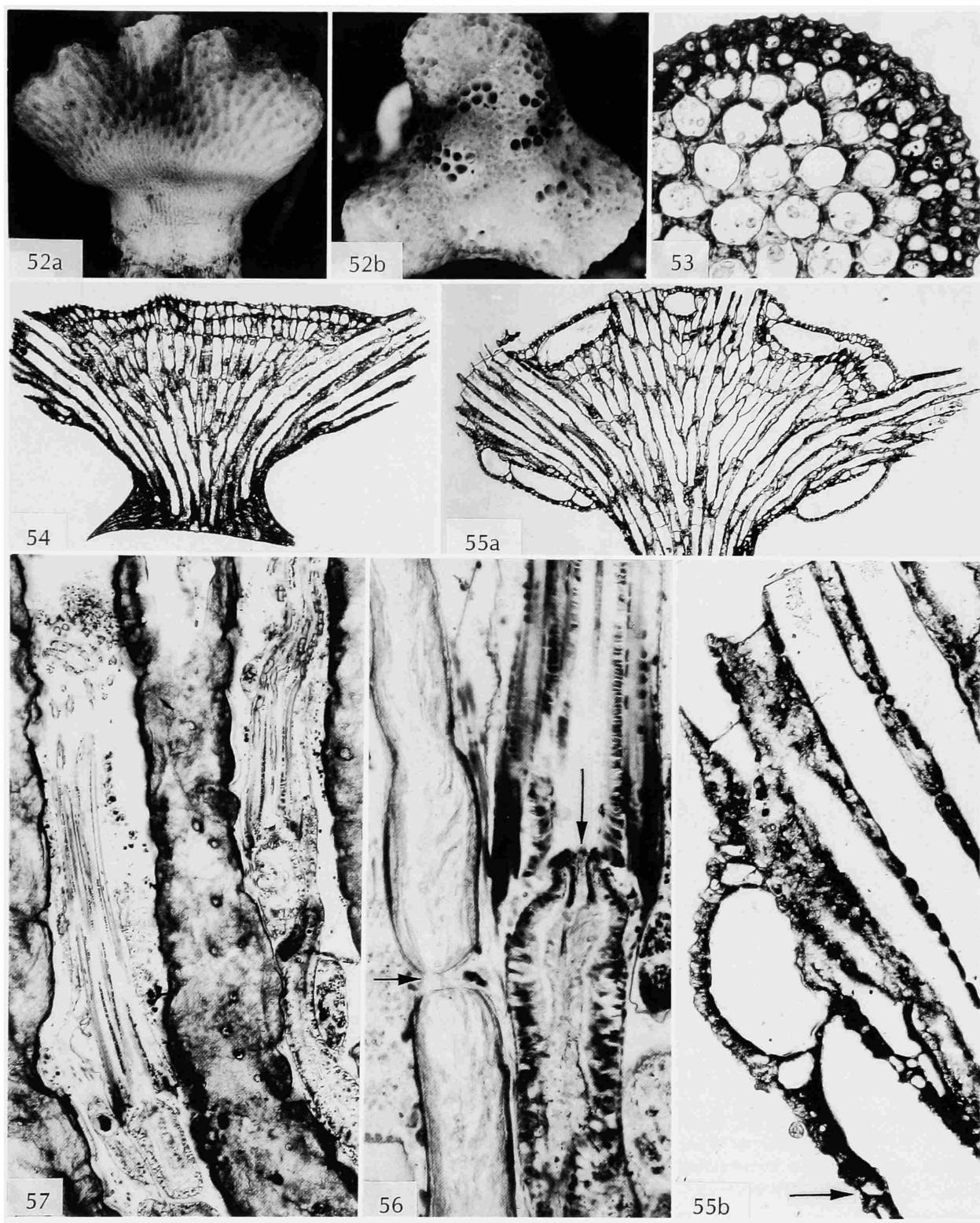
their skeletal apertures. No attachment organs were seen, and, unfortunately, the protrusion mechanism is not directly interpretable in detail in the slides. Polypides have 14 or 15 tentacles. The lophophore retractor muscles of adjacent zooids can be attached on opposite sides of the living chambers (Figure 57).

The type species of the genus *Infundibulipora* Brood, 1972 (see Voigt, 1977, for detailed discussion), is *Defrancia lucernaria* Sars, a Recent species from the Kara Sea. This species compares with the species of *Discocyrtis* described immediately above by having a peduncle and an expanded capitulum of fascicles with feeding zooids (Figure 58a,b). Also, functioning feeding zooids are free-walled throughout, and new feeding zooids are added on the outermost sides of the clusters (Figures 59, 60).

Many skeletal and anatomical differences, however, distinguish the two species. Externally, the fascicles of feeding zooids of *Infundibulipora* are regularly arranged in a circle around the capitulum. Polymorphs are lacking on the outer surfaces of peduncles and large, irregular vesicles occupy the central regions of colonies (Figure 59). The roofs of brood chambers are extremely thick exterior skeletal walls with pseudopores (Figure 58b) instead of interior walls, which are common in free-walled taxa. Skeletal-wall structures appear uniformly microcrystalline rather than laminar.

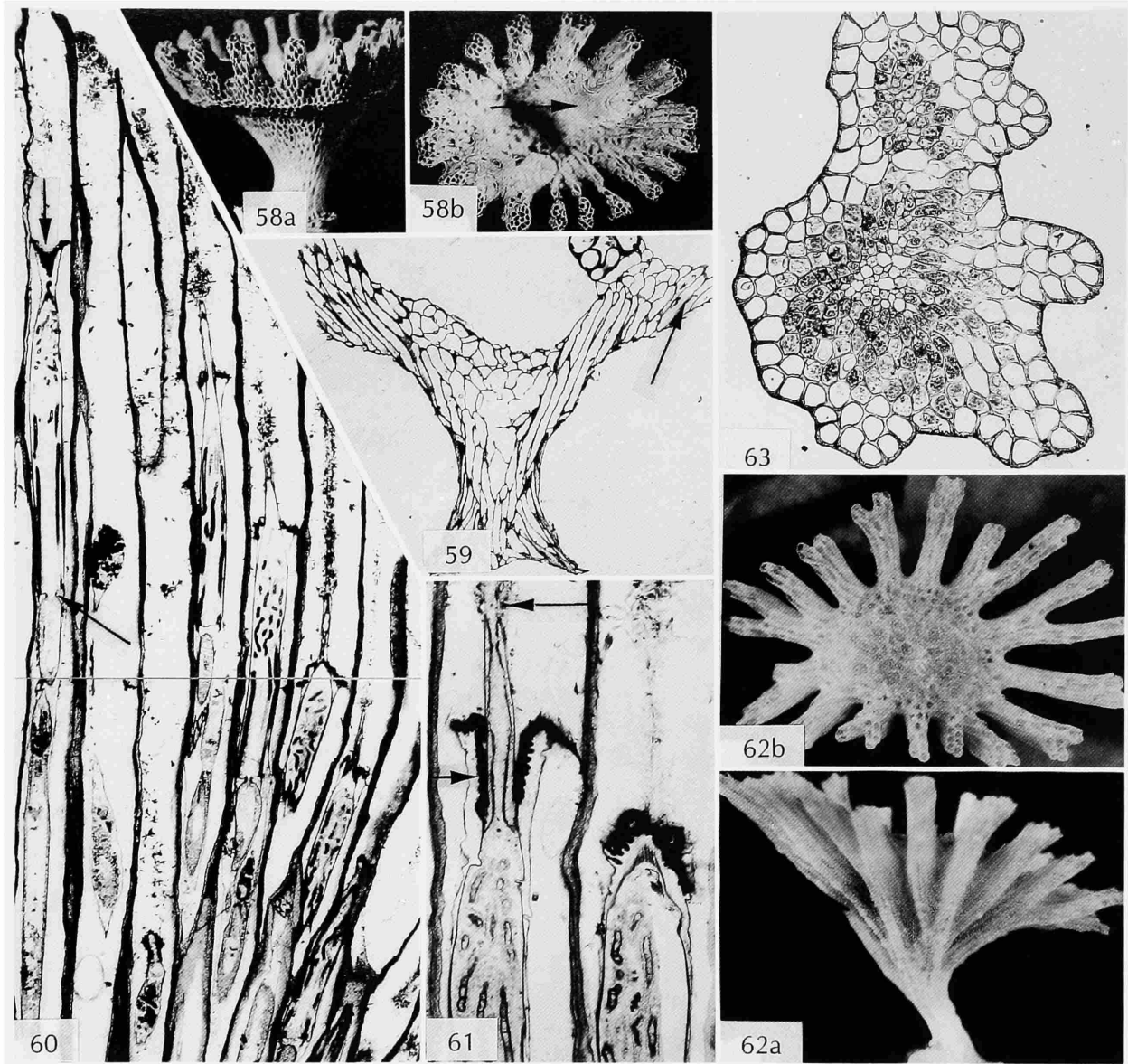
Polypides of *Infundibulipora* adjust to the extremely long living chambers very differently than those of *Discocyrtis*. *Infundibulipora* polypides have shallow retraction distances, and the oldest zooids are incredibly long, nearly filling the living chambers (Figure 60). They have pleated attachment organs that lack filaments (Figure 61). (See description of a similar protrusion mechanism under "Tentacle Protrusion," above; Figure 15.) Polypides also have both cardinal and lophophore retractor muscles (Figure 10) that apparently attach only to the distal sides of feeding zooids, and they have 12 rather than 14 or 15 tentacles. The positions of the mouth of most retracted polypides is within two tentacle lengths of their skeletal aperture; this is consistent with polypides having attachment organs that undergo progressive cycles (Figure 60). A few polypides are retracted slightly further, and apparently the unpleating of the attachment organs provides the extra length needed to extend polypide mouths to their skeletal apertures.

Colonies of the genus *Telopora* Canu and Bassler, 1920, from New Zealand and the Antarctic (Figure 62a,b) look superficially like the free-walled *Infundibulipora* described immediately above, but their skeletal construction is more complicated and the interiors of colonies are very different. The outermost skeletal walls of the peduncles are thick exterior walls with abundant pseudopores (Figure 63) that continue up the outer sides of the radially arranged fascicles of the feeding zooids to their skeletal apertures, the fascicle walls (Figures 20a, 21). The orificial walls at the skeletal apertures are fixed



FIGURES 52-57.—Fasciculates. *Discocythis* species, Unalaska to Cook Inlet, Alaska: 52a,b, colony showing short peduncle and expanded capitulum, fascicles of large feeding zooids surrounded by smaller polymorphs, USNM 488171 ($\times 10$). 53, cross section of the peduncle of colony with axial feeding zooids and peripheral small polymorphs, USNM 488172 ($\times 50$). 54, longitudinal section through the center of colony with feeding zooids diverging in clusters, USNM 488173 ($\times 10$). 55a,b, longitudinal section showing brood chambers

with interior covers of small polymorphs, thick terminal diaphragms of polymorphs calcified from both sides (arrow), USNM 488174: 55a ($\times 10$), 55b ($\times 50$). 56, vertical wall with laminae diverging outward (upward in figure), communication pore (small arrow), mouth of polypide (large arrow), USNM 488175 ($\times 300$). 57, polypides apparently lacking attachment organs retracted to the bottoms of their living chambers, lophophore retractor muscles on opposite sides of adjacent zooids, USNM 488176 ($\times 100$).



FIGURES 58–63.—Fasciculates. 58–61, *Infundibulipora lucernaria* (Sars): 58a,b,c, colony with fascicles of feeding zooids arranged radially around center of capitulum, brood chamber in 58b (arrow), USNM 488177, Kara Sea, Russia ($\times 6$); 59, longitudinal section through the colony, young feeding zooids (arrow), USNM 488178, SW of Star Island, Sta. 44b collected by Verril, 1874 ($\times 10$); 60, longitudinal section through the radial fascicle showing the extremely long living chambers and polypides, progressively younger zooids are to the right, attachment organ (small arrow in oldest zooid on left), mouth of polypide (large arrow), USNM 250078, Kara Sea, Russia ($\times 50$); 61, pleated attachment organ (small arrow), atrial sphincter muscle (large arrow), USNM 250078, Kara Sea, Russia ($\times 150$). 62, 63, *Telopora* sp.: 62a,b, fascicles of feeding zooids arranged radially, USNM 488180, 49°40'S, 178°53'E, Antarctica ($\times 10$); 63, cross section at the base of radial fascicles, polypides retracted to the bottoms of living chambers located in the center of colony (see Figures 20, 21), exterior zooidal skeletal walls surround outside of colony, USNM 488154, Poor Knights Island, New Zealand ($\times 30$).

by the exterior walls and are free over the interior walls, so the outermost ring of zooids of a fascicle are fixed/free and the remainder are free (Figure 20a). Along the inner sides of fully developed fascicles, that is, toward the vertical axes of

colonies, extremely thin frontal walls with short peristomes develop on older zooids, thus fixing orificial walls and terminating outward growth (Figure 21). Feeding zooids projecting through the exterior-walled brood chambers are also

fixed. The ontogenetic sequence within a fascicle proceeds from its outermost side towards the vertical axis of the colony, opposite to the sequence seen in *Discocyttis* and *Infundibulipora* described above.

The skeletal-wall structure of *Telopora* seems to compare with the cinctiporid wall structure of the tubuliporines described above. A large brood chamber(s) occupies the floor of the capitulum in some colonies and is roofed over by exterior skeletal walls with closely spaced pseudopores.

The living chambers of *Telopora* are extremely long, even for fasciculates. Instead of developing long polypides that nearly fill the living chamber, as in *Infundibulipora*, the short polypides of *Telopora* retract to the bottoms of living chambers, which are as much as 12 or 13 times the tentacle length from the skeletal apertures (Figure 20a). Polypides manage protrusion without attachment organs by employing pleated membranous sacs that are nearly as long as the living chambers when they are unpleated. The outer ends of the sacs are attached to the tentacle sheaths. Using their annular muscles, the sacs push the polypides outward, the tentacle sheaths then move outward taking the outer ends of the attached sacs with them. The sacs unpleat and extend far enough outward to free the tentacle crowns (Figures 20b, 21; see detailed discussion under "Tentacle Protrusion," above).

The type species of the genus *Fasciculipora* d'Orbigny, is *F. ramosa* from Patagonia. Colonies of this species have bifurcating branches, which are circular in cross section. Each branch is a separate fascicle completely surrounded by thick exterior fascicle walls that enclose the interior vertical walls (Figures 64, 65), producing both fixed/free and free orificial walls. The polypides of feeding zooids are restricted to the outer ends of branches where the only skeletal apertures of the colonies are located. As the cylindrical branches grow in length some older feeding zooids develop extremely long living chambers. Others zooids lose their polypides and are walled off by new feeding zooids budded in close enough alignment that the cylindrical branches maintain reasonably constant diameters.

The microstructure of the vertical walls includes a narrow, pink boundary zone and laminae that diverge outward with thin patchy laminar living chamber linings. Cylindrical brood chambers (Schäfer, 1991, fig. 53b) have exterior skeletal walls.

At the ends of branches, polypides maintain shallow positions in long living chambers with attachment organs that produce progressive polypide cycles (Figure 66). Fully regenerated polypides can become extremely long and may grow to the bottoms of the newer shorter living chambers (Figure 67). The main characters for *Fasciculipora* polypides include the lack of attachment filaments, lophophore retractor muscles that can be attached on opposite sides of neighboring zooids, thick caecal retractor muscles (Figures 11, 67), and 15 to 16 tentacles, a high number for stenolaemates. When the polypides are fully retracted, the rectum extends outward

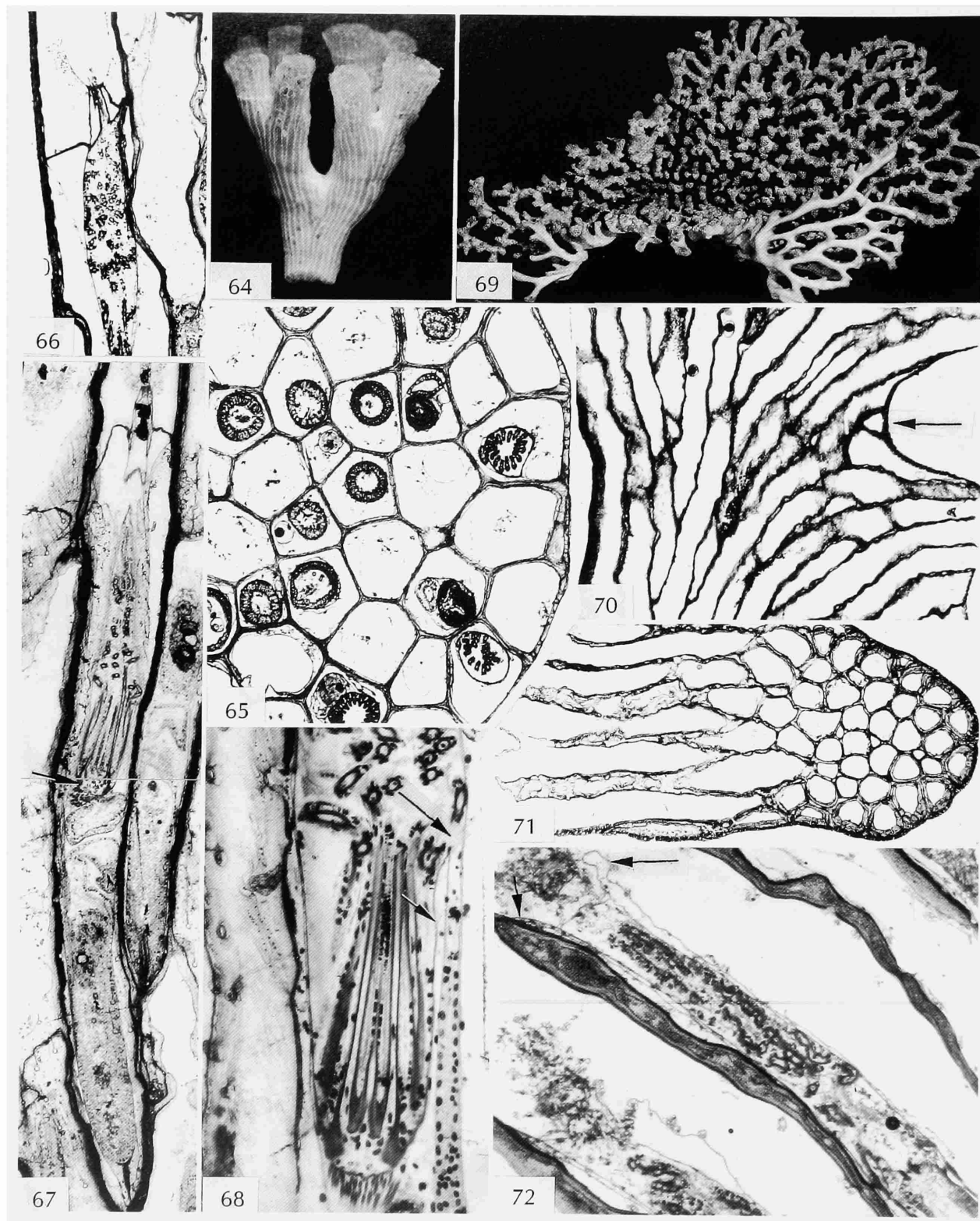
one-half to two-thirds of the way up the tentacle sheath, which is a condition not seen in other species (Figure 68).

The fasciculate genus *Fron dipora* Link has its type species from the Mediterranean, *F. reticulata*. Another Mediterranean species, *F. verrucosa* (Lamouroux), has irregularly shaped fascicles of feeding zooids opening only on the front sides of irregularly anastomosing branches (Figure 69; Harmelin, 1976:192). Coalesced exterior fascicles and a few frontal zooidal walls cover colonies thereby forming smoothly curved outer surfaces (Figures 70, 71). The orientation of these exterior fascicle walls relative to the polypides ranges from parallel to transverse. Most feeding zooids bud from the vertical walls of other feeding zooids within the branches, but a few bud on the outer edges of fascicles from the exterior walls. The vertical walls have a thick microcrystalline layer covered by a thick laminar living chamber lining, thus requiring SEM study to understand.

The frontal openings of the feeding zooids of *F. verrucosa* result in shorter living chambers (Figure 70) than those of *Fasciculipora* (Figure 67). Orificial walls are either free within fascicles or are fixed/free around the edges. Polypides have membranous attachment organs (Figure 72), shallow retracted positions, and undergo progressive polypide cycles, all similar to the hornerids. Polypides have 11 tentacles, no attachment filaments were seen, and the lophophore retractor muscles can be attached on the opposite sides of living chambers in adjacent zooids.

A fasciculate species from the Antarctic (Figures 73, 74a,b) has fascicles opening radially around the branches that develop fixed/free and free orificial walls. Fascicles are enclosed and broadly connected by exterior fascicle walls, including a few frontal walls. Vertical walls are annularly thickened with a microstructure that appears to be either a fibrous or laminar layer, covered by a thick laminar living chamber lining (Figure 74a). The fibers or laminae diverge outward from the boundary zones in the direction of zooidal growth.

The protrusion mechanism is basically comparable to that of the *Telopora* species, with movable and pleated membranous sacs that lack attachment organs. The sacs are thickened in some polypides where they are attached at midlength by lophophore retractor muscles (Figure 74a,b). The sacs apparently have a skeletal attachment of their own, at least on opposite sides of the retraction muscles (Figure 74a). This second sac attachment at the midlength position has not been observed in other species, and therefore may well indicate still another kind of retraction mechanism. Polypides retract to the bottoms of their living chambers; however, two polypides seem to retract to well above their bottoms, near to their skeletal apertures. More sections are needed to understand this attachment style. The tentacles number 9 or 10. As with other fasciculate genera, the lophophore retractor muscles in this species can be attached on opposite sides of the living chamber in neighboring zooids (Figure 74a).



FIGURES 64–72.—Fasciculates. 64–68, *Fasciculipora ramosa* d'Orbigny: 64, 65, Edisto Station ED-8, McMurdo Sound, Antarctica: 64, each branch a separate fascicle surrounded by enjoined exterior zooidal walls termed fascicle walls, apertures of feeding zooids at ends of branches, USNM 488182 ($\times 3$); 65, cross section of branch showing exterior fascicle walls on outside of branch, USNM 488183 ($\times 50$); 66, attachment organ lacking filament, USNM 179007, sta. 1A Atka, 12/20/56, Deep Freeze III McMurdo Sound, Antarctica ($\times 50$); 67, 68, Edisto Station ED-8, McMurdo Sound, Antarctica: 67, extremely long polypide, caecal retractor muscle at bottom, attachment organ at top of figure, base of tentacles in retracted position (arrow), USNM 488184 ($\times 50$); 68, rectum extends two-thirds of the way up retracted tentacle sheath (large arrow), tentacle sheath (small arrow), USNM 488185 ($\times 150$). 69–72, *Fron dipora verrucosa* (Lamouroux): 69, irregular anastomosing branches, USNM 220033, Mediterranean Sea, Oran, Algeria ($\times 1.5$); 70, 71, Mediterranean Sea, Naples, Italy ($\times 30$): 70, exterior fascicle walls connect fascicles on the front side of colony, here transverse to feeding zooids, USNM 488186; 71, cross section of branch through fascicle, USNM 250068; 72, membranous attachment organs, attached (small arrow), pulled loose (large arrow), USNM 488187, Mediterranean Sea, Gulf of Tunis ($\times 150$).

A fasciculate species from New Zealand (Figure 75) closely resembles the Antarctic species (Figure 73) externally, and, reasonably, it should have internal similarities. It too has exterior fascicle and frontal skeletal walls, and the orificial walls are fixed/free and free. The wall structure of the New Zealand species is cinctiporid, however, with fibers oriented at 90 degrees to the zooidal growth direction and thick laminar chamber linings (Figure 76). The outer walls of the brood chambers are exterior with abundant pseudopores.

This New Zealand species apparently has membranous attachment organs that are generally pulled loose in the available sections (small arrows, Figure 76). No attachment filaments are seen, and the polypides retract well above the bottoms of the living chambers. The larger polypides in the collection are apparently fully regenerated and have shallow retraction distances. Many of the polypides, however, are undersized (Figure 77) and are only partly regenerated in the polypide cycle. Some polypides are retracted as far as five of their tentacle lengths from their skeletal apertures. Food is found in only one gut (Figure 76) and the polypides are poorly preserved. The twin polypides in the same living chamber (Figure 77) are curious; the inner one is equally undersized and its gut is degenerated, suggesting that it failed to get through the degeneration stage and was superceded by another polypide.

This New Zealand species is unique among the fasciculate species studied, and from the great majority of stenolaemates, by having a gizzard (Figures 76, 78). The other species in this study with a gizzard is also from New Zealand, *Pustulopora purpurascens*, a tubuliporine described above (Figures 41–44). Taxonomically, the two species are considered to be quite distant based on their external characters. Internally, both have a cinctiporid wall structure and membranous attachment organs. The rare orificial sphincter muscles of *P. purpurascens*, however, do not occur in the fasciculate species.

SUMMARY.—Fasciculates are characterized by long, parallel, feeding zooids that grow in clusters and develop extreme

modifications of the polypides. Two species have colonies with outer body cavities and some diaphragms calcified on both sides, but they have different skeletal microstructures. One has brood chambers with interior roofs that are unique to fasciculates studied herein, and it has polypides of moderate length that retract to the bottoms of their living chambers and apparently lack attachment organs. The other species has brood chambers with exterior roofs and has extremely long polypides with pleated attachment organs that maintain short distances to their skeletal apertures.

The other five fasciculates have clusters of free-walled feeding zooids with communication pores, surrounded by the outermost zooids of the clusters that are fixed/free by exterior fascicle walls. Four of the five also have some frontal walls that contribute to fixed/free zooids. Internally, three of the five have polypides with attachment organs, one is different from the other two, and three skeletal microstructures are included in the five. One of the two with comparable attachment organs has a gizzard, a condition that is apparently rare in stenolaemates. Two species lack attachment organs and have pleated movable membranous sacs. The lack of correlation of the diverse internal features in these seven randomly chosen species adds only confusion to any possible classification of species with clustered feeding zooids.

DISPORELLOIDS

DESCRIPTION.—One of the most simple and most often invented colony growth habits through Paleozoic to Recent stenolaemate history (Utgaard, 1983a, fig. 152; Boardman, 1983:51, 122) is the small, discoidal, encrusting colony with feeding zooids that open onto the upper colony surfaces. Taxonomist of Recent species have considered them to be a monophyletic clade. The zooids grow from the encrusting colony wall that extends out beyond the circle of zooids as an apron (Figure 79a). For convenience, this ubiquitous growth habit is designated here as “disporelloid” after one of the generic names most commonly applied to Recent species, *Disporella* Gray.

In contrast to the internal differences found in individual species described above, seven Recent disporelloid species in this study are inferred to be comparable enough both externally and internally to be congeneric, or at least closely related. The internal characteristics are known for so few disporelloid species that all that can be said now is that the seven species are more comparable to each other than to the other disporelloids described herein. The generic-level description below, based on the seven species, does not include study of the type species of *Disporella*, *D. hispida* Fleming. The original types are not available (Patricia L. Cook, pers. comm., 1984) and their detailed characteristics were largely unreported. A neotype has been designated but was not included in this study (Alvarez, 1992). There is no reason to assume that the description



FIGURES 73–78.—Fasciculates. 73, 74, Fasciculate species 1, USARP-USC, Eltanin Program, Ref. #180, sta. 1425, May 17, 1965, Antarctic ($\times 5$): 73, part of colony, USNM 488188 ($\times 5$); 74, USNM 488189: 74a, membranous sac with midlength skeletal attachment (large arrow), also attached by lophophore retractor muscles (small arrow) ($\times 150$); 74b, membranous sac (small arrow) attached by lophophore retractor muscles where thickened (large arrow) ($\times 200$). 75–78, Fasciculate species 2: 75, part of colony, USNM 488190, Cape Rodney to Okakari Point, Marine Reserve, Leigh, New Zealand ($\times 4$); 76, polypide showing indication of membranous attachment organ (two small arrows) and gizzard (large arrow), USNM 488191, off Otago Heads, South Island, New Zealand at 110 m ($\times 150$); 77, 78, Cape Rodney to Okakari Point, Marine Reserve, Leigh, New Zealand: 77, exterior fascicle wall at transverse position (large arrow), two polypides in one zooid (small arrows), lower arrow points to degenerated caecum, USNM 488192 ($\times 100$); 78, gizzard (arrow) with pharynx immediately above and caecum below, USNM 488193 ($\times 300$).

immediately below includes the characteristics of the neotype. Therefore, the description is informal and is not a description of *Disporella*. The description serves only as a standard to compare or contrast other species that have a similar growth habit but have some different internal skeletal and/or anatomical characteristics.

INFORMAL GENERIC DESCRIPTION.—Colonies free-walled, most species small, encrusting, circular, flattened to hemispherical (Figure 79a), two species with larger compound colonies of circular subcolonies (Figure 80). Feeding zooids in poorly to well-defined rows radiating from central areas, growth stages progressively younger outward along rows (Figures 3, 79b). Brood chambers in central areas of colonies in some species (Figures 79b, 82), others with central chambers plus apparently isolated chambers scattered through colonies. Most roofs of chambers of interior skeletal walls with small shallow polymorphs called alveoli, which have circular to subpolygonal free-walled apertures. Skeletal apertures of brood chambers large, flared (Figures 81, 82).

Shallow free-walled alveoli between rows of feeding zooids, and, in some species, between feeding zooids within rows (Figures 79b, 83); apertures circular to subpolygonal. Alveoli walls with communication pores shared with adjacent vertical walls of feeding zooids.

Feeding zooids with lunarial skeletal structures on proximal sides of vertical walls (towards colony centers) (Figures 3, 79b, 80–84). Lunarial deposits extend throughout zoecial lengths and well beyond adjacent polymorphs. Deposits consist of lunarial spines (Brood, 1972:40, his pseudolunaria), circular to U-shaped in cross section (Figure 83); lunarial spines, in combination with attached extensions of vertical walls, form smoothly curved skeletal troughs for passage of polypides in and out (Figure 84). Cross sections of living chambers oval (Figure 83) to drop-shaped (Boardman, 1971, pl. 2: fig. 2), broader sides of drop-shaped chambers with polypides and lunaria on proximal sides. Vertical walls irregularly to annularly thickened with communication pores (Figures 3, 82).

Skeletal microstructure of one species appears laminar, diverges outward (Figures 3, 83; Taylor et al., 1995); others

uniformly microcrystalline. Zooidal boundary zones in both range from dark to light. Microcrystalline microstructure requires additional SEM study.

Attachment organs flattened to cone-shaped when polypides retracted (Figures 3, 79b, 82); attachment filaments present in all but one species (Figure 12). Progressive polypide cycles maintain shallow retraction distances; some species have shorter polypides than living chambers (Figure 3), others have long polypides that extend to bottoms of living chambers when fully retracted (Figure 79b). Lophophore retractor muscles attached to lunaria on proximal sides of feeding zooids (Figure 79b). Caecal retractor muscles apparently absent in some species (Figure 3), present in others (Figure 82), and both present or absent in one compound colony. Tentacles range from 8 in some species, up to 12 in others. One species with 6 to 8 tentacles.

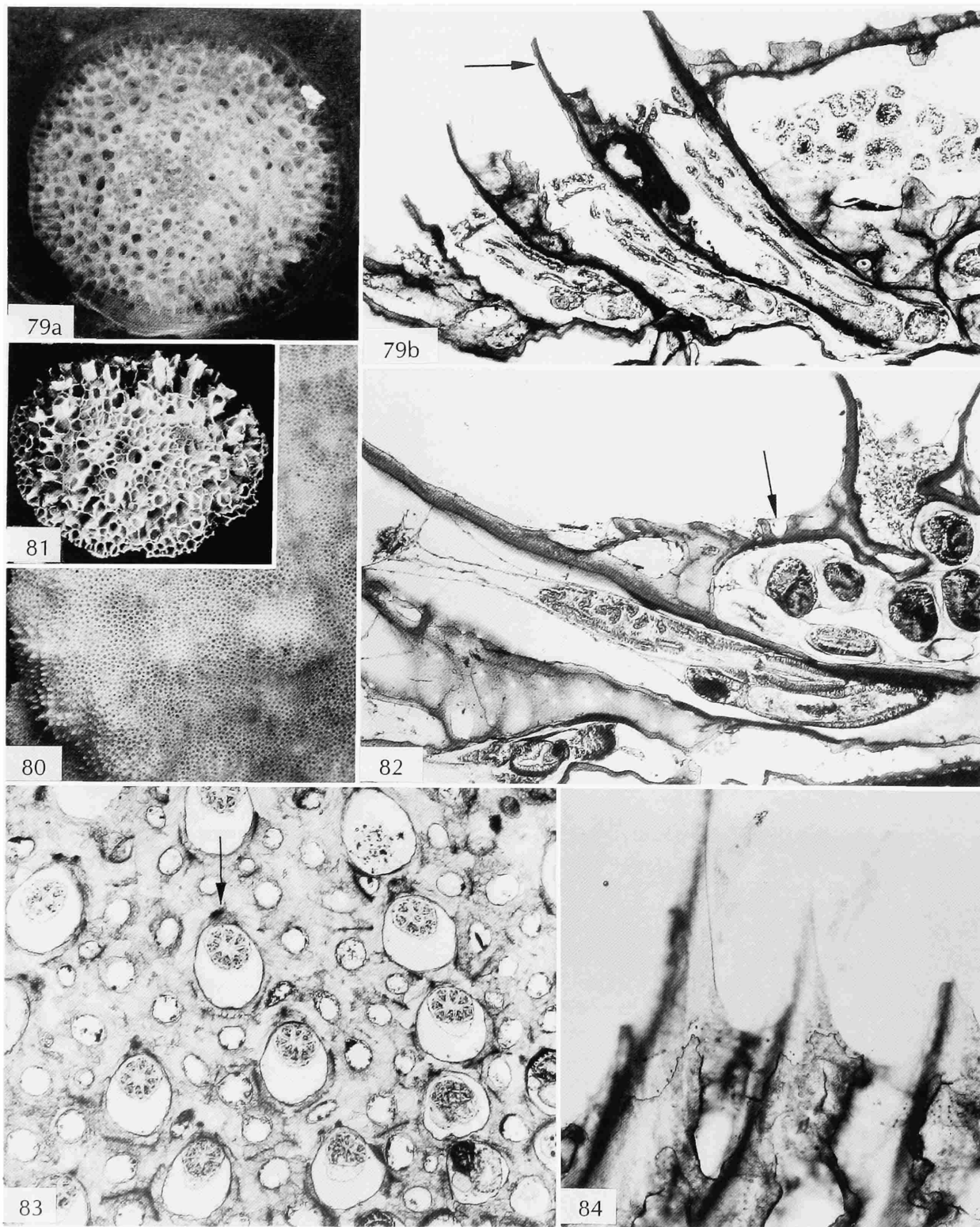
The seven species of disporelloids come from Alaska, Greenland, the Mediterranean, and New Zealand.

REMARKS.—Some variations in these seven species occur from species to species, such as two different skeletal wall structures and the presence or absence of attachment filaments or caecal retractor muscles. With the knowledge of additional related species, these differences could well place some of these species in other genera.

VARIANT DISPORELLOID SPECIES.—The following two species have skeletons that, externally, compare with the seven congeneric species, and they would be considered congeneric with them were it not for the knowledge of their internal characteristics. The polypides of the two species are so different that they appear to belong to other genera and probably to other families.

A free-walled species from Alaska has the standard disporelloid growth habit (Figure 85a). Other similarities with at least some of the seven congeneric species include a laminar skeletal wall, projecting lunaria, and central brood chambers covered by the interior walls of small alveoli (Figure 85b). The polypides have attachment filaments and no caecal muscles (Figures 85b, 86), as seen in species illustrated in Figures 3, 79b, and 82. The polypides, however, do have significant differences. The atrial sphincter muscles are larger than those of the seven disporelloids and they stain deeply (Figures 16, 85b, 86). The attachment organs are connected perimetrically to the living chamber walls (Figures 16, 86) rather than by ligaments (Figure 9). As indicated in the discussion under "Tentacle Protrusion," above, attachment ligaments permit the passing of body fluids out and in past the attachment organs as the polypides protrude and retract, which theoretically seems necessary to function. The perimetrical attachment seems to prohibit that body fluid transfer. These internal differences, especially that of the perimetrical attachment organ, seem to separate this species generically from the seven congeneric disporelloids.

A free-walled species from New Zealand also has a



FIGURES 79-84.—Dispirelloid seven species complex. 79, USNM 488194, Unalaska to Cook Inlet, Alaska: 79a, colony ($\times 7.2$); 79b, ontogenetic sequence right to left, polypides on the proximal sides of living chambers with extended lunaria (arrow), large brood chamber with interior skeletal covering on right ($\times 100$). 80, compound colony with circular subcolonies, USNM 488195, Middleton Island, Gulf of Alaska ($\times 7$). 81, colony, probably conspecific with Figure 82, USNM 488196, Umanak, Greenland ($\times 15$). 82, central brood

chamber with large aperture, interior skeletal cover, outer membranous wall (arrow), USNM 488197, Northumberland Island, northwestern Greenland ($\times 100$). 83, tangential view with polypides and central lunular spines (arrow) on proximal sides of living chambers, center of colony above figure, USNM 488143, Unalaska to Cook Inlet, Alaska ($\times 100$). 84, partly protruded tentacles in extended lunaria, center of colony to left, USNM 488198, Cape Rodney, New Zealand ($\times 100$).

dispoirelloid growth habit with distinctive well-defined radial rows of feeding zooids that have interior-walled peristomes instead of lunaria (Figure 87). Small, apparently isolated brood chambers occur in the centers of some colonies and are covered by alveoli that range from circular to rectangular in cross section (Figure 89). The wall microstructure appears microcrystalline without any visible zooidal boundary zones.

The attachment organs of this New Zealand species (Figures 17, 88*a,b*; see discussion in "Tentacle Protrusion," above) are radically different from those seen in all other stenolaemate species studied. They have a bilateral plane of symmetry in the proximal-distal direction and, in profile, are attached at two or three places on the distal side and at a single inward position on the proximal side. The membrane on the proximal side is thicker and has a fold when fully retracted. The radial rows of feeding zooids develop younger growth stages outwardly as in other dispoirelloids (Figure 88*b*), but in one thin section, a second generation of younger (shorter) polypides has developed in the oldest living chambers of a row (Figure 89).

INTERMEDIATE SPECIES.—In the descriptions above, polypide anatomy taxonomically separates two free-walled species from the seven free-walled dispoirelloids thought to be congeneric. Two other species with dispoirelloid growth habits are described herein that are skeletal intermediates between free-walled dispoirelloids and fixed-walled tubuliporines. Two of the tubuliporine genera are *Plagioecia* and *Desmeplagioecia*, which are Recent species from the Mediterranean that were described by Harmelin (1976, pls. 18–22, 24, 25). These two genera are readily differentiated externally from the free-walled dispoirelloids described above by having frontal walls, exterior peristomes, exterior brood chamber covers, and by the lack of alveolar polymorphs and lunaria. The wall structure and anatomy of the feeding zooids has not been studied.

One of the two skeletally intermediate species occurs in Alaska. Externally, the Alaskan colonies have a dispoirelloid growth habit (Figure 90); however, many feeding zooids in the central regions develop short exterior frontal walls as in the tubuliporines, and other zooids are free-walled comparable to the dispoirelloids. The frontal walls can only be developed on the exposed proximal sides of zooids because the zooids are nearly recumbent (Figure 91). As a result, their orificial walls are fixed on proximal sides by the frontal walls and are free on distal sides formed by the vertical interior walls. The frontal walls apparently develop as they are needed to complete skeletal apertures. Neighboring zooids can be without frontal walls and completely free-walled. This apparent lack of pattern suggests that the positioning of frontal walls is controlled by the microenvironmental demands from zooid to zooid and their positions within colonies are not genetically programmed.

The central areas are surrounded by a thick development of younger, free-walled feeding zooids that are arranged rhombically (Figures 90, 92). Polymorphs are rare and scattered, lunaria are lacking, and brood chambers are covered by exterior

skeletal walls (Figure 93), all characters that differ from dispoirelloids.

Internally, the polypide anatomy, especially the conical attachment organs and filaments, seems comparable with that of the seven dispoirelloids (Figures 93, 94). The microstructure of the skeleton has coarse laminae diverging outward from wide zooidal boundary zones, which contain dark rod-shaped structures that are parallel to growth directions (Figures 91, 92).

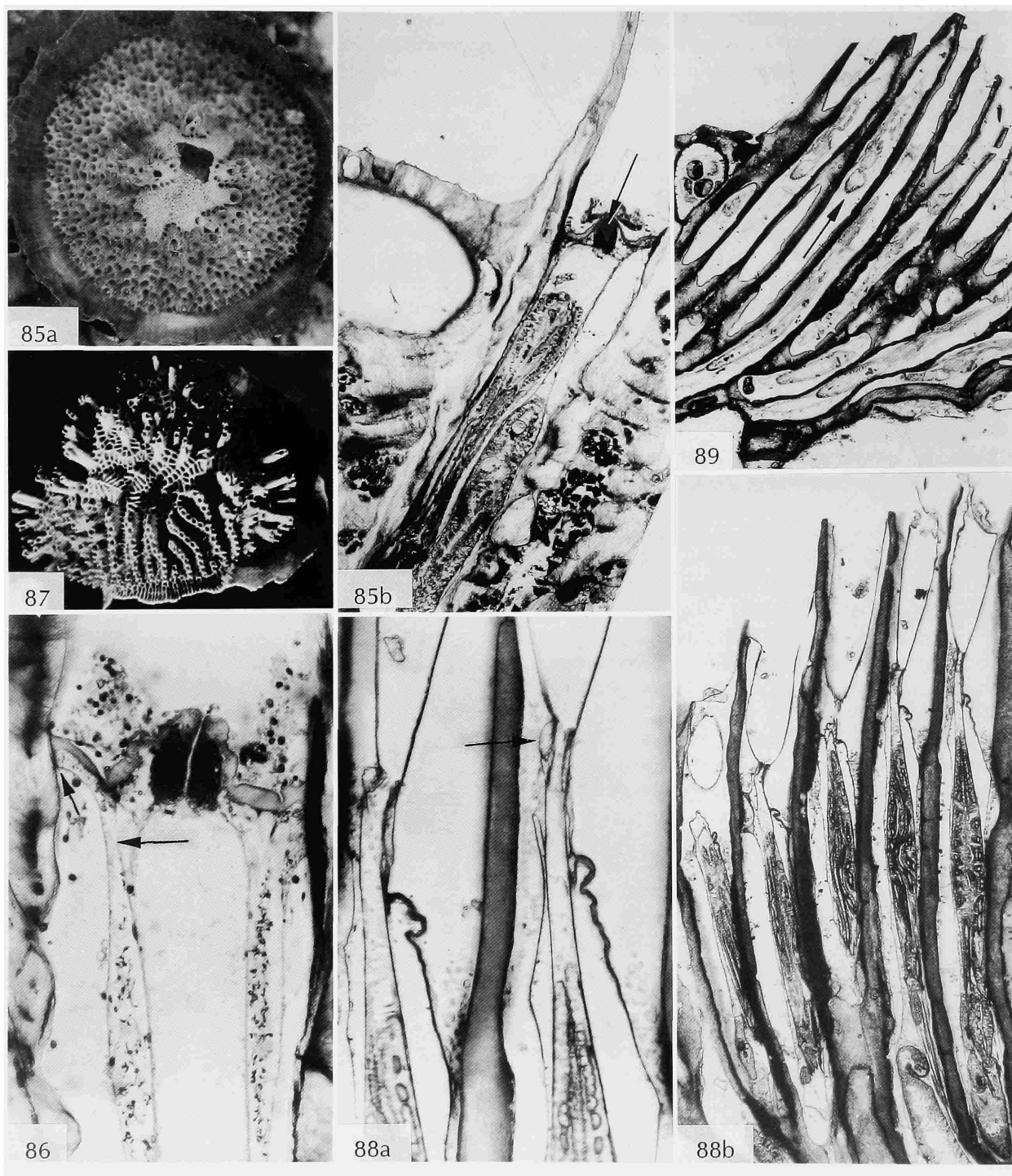
The second intermediate species (Figure 95) occurs in New Zealand and shares with the Alaskan intermediate a central region of zooids with either frontal walls (Figure 96) and fixed/free apertures, or scattered free-walled apertures, again surrounded by a younger region of rhombically arranged free-walled zooids. Brood chambers are covered by exterior walls with pseudopores. This species differs skeletally from the first intermediate species, however, by having a uniformly microcrystalline wall structure. Its polypides differ from the first intermediate species and other dispoirelloids studied herein by having strongly pleated attachment organs (Figures 15, 96), described in detail, above, in "Tentacle Protrusion." Again, internal characteristics divide these two transitional species taxonomically, even though they appear comparable externally.

SUMMARY.—Dispoirelloids feature small discoidal, encrusting colonies. The growth habit has evolved independently several times during the history of the stenolaemates, beginning in the Paleozoic, so that diversity in the internal morphology and anatomy is expected; however, seven species are comparable enough to be considered possibly congeneric. These colonies have outer body cavities with free orificial walls, lunaria, scattered communication pores, interior brood chamber covers, two skeletal microstructures (the microcrystalline microstructure is not understood), and similarly shaped and thickened attachment organs, although one species lacks filaments. All nine free-walled dispoirelloid species studied have attachment organs. Four of the six kinds of attachment organs recognized in this study occur in these dispoirelloids, and two of these are very different and unique to their species, attesting to the taxonomic diversity of the group.

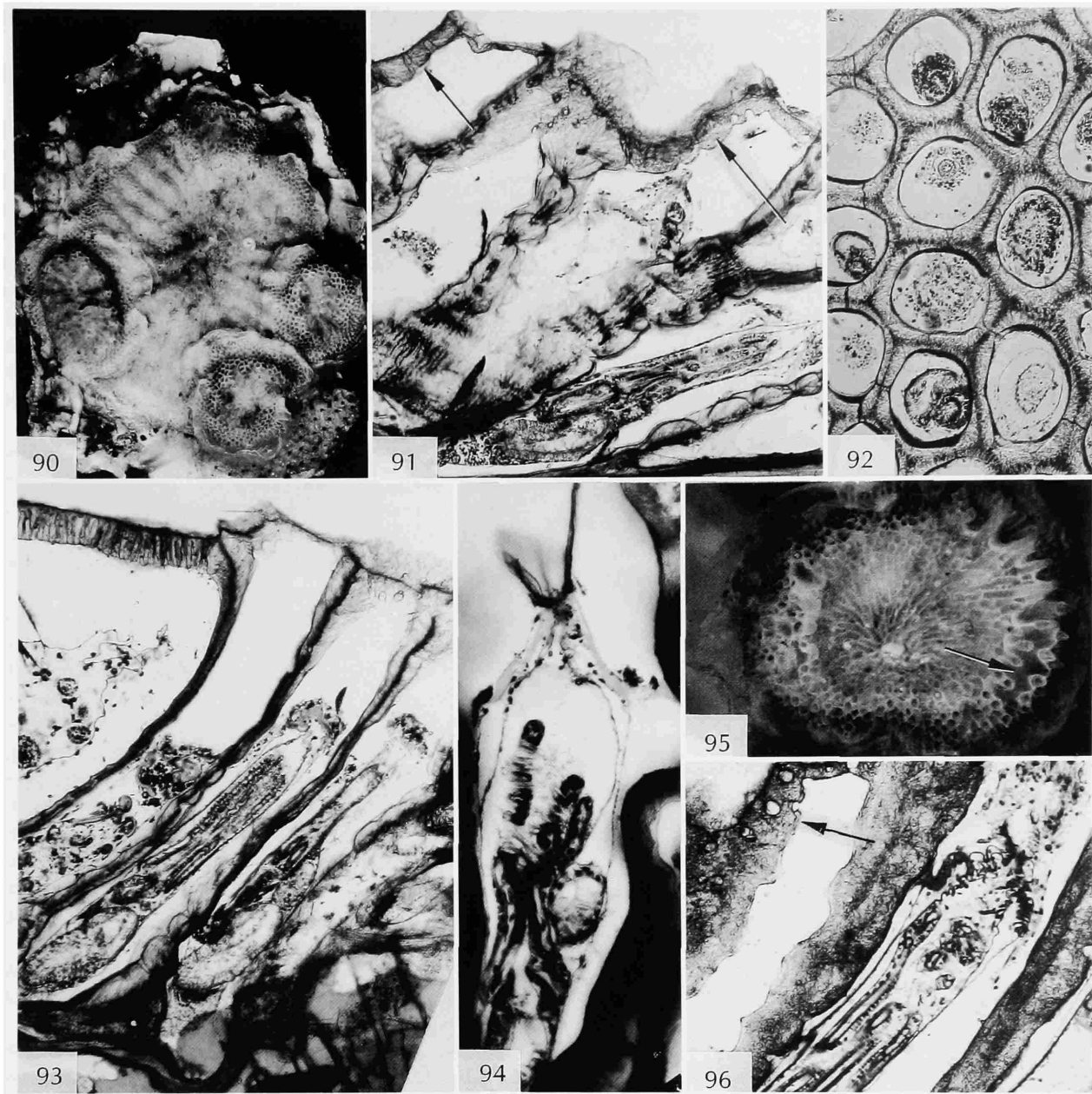
Two species with dispoirelloid growth habits develop exterior brood chamber covers and frontal walls on the proximal sides of some feeding zooids so that the orificial walls are both free and fixed/free within colonies. Each species has a different wall microstructure and attachment organ. Any taxonomy based on the exterior appearances of dispoirelloids will miss the higher categories necessary to reflect a complex phylogeny that is certainly polyphyletic.

HETEROPOROIDS

DESCRIPTION.—The species placed in the genus *Heteropora* de Blainville range from Jurassic to Recent. Most assignments have been based on external appearances without the study of colony interiors. The type species of the genus, *Ceripora cryptopora* Goldfuss, is from the Maastrichtian of the Nether-



FIGURES 85–89.—Disyporelloids. 85, 86, Disyporelloid species 8, Unalaska to Cook Inlet, Alaska: 85, USNM 488199: 85a, colony with central brood chamber ($\times 10$); 85b, brood chamber with interior skeletal cover on left, extended lunarium, polypide with perimetrical attachment organ and large, darkly stained atrial sphincter muscle (arrow) ($\times 100$); 86, polypide with membranous sac apparently attached just below (small arrow) perimetrical attachment organ, attachment filament (large arrow) and darkly stained atrial sphincter muscle, USNM 488200 ($\times 300$). 87–89, Disyporelloid species 9, Leigh Cove, Leigh, New Zealand: 87, colony with interior peristomes in well-defined rows, USNM 488201 ($\times 10$); 88, USNM 488152: 88a, bilaterally symmetrical attachment organs, atrial sphincter muscle (arrow) ($\times 300$); 88b, ontogenetic sequence right to left ($\times 100$); 89, older zooids to the left with two smaller polypides near apertures (arrow), apparently a second generation of polypides, USNM 488202 ($\times 50$).



FIGURES 90-96.—Dispirelloids. 90-94, Dispirelloid species 10, Unalaska to Cook Inlet, Alaska: 90, parent colony with three smaller attached colonies, USNM 488203 ($\times 5$); 91, exterior frontal walls on proximal sides of zooids (arrows), USNM 488204 ($\times 100$); 92, tangential section, USNM 488205 ($\times 100$); 93, brood chamber with exterior skeletal covers, USNM 488206 ($\times 100$); 94, undersized polypide with thickened conical-shaped attachment organ, USNM 488207 ($\times 300$). 95, 96, Dispirelloid species 11, Leigh Cove, New Zealand: 95, colony, brood chamber on right with exterior skeletal cover (arrow), USNM 488208 ($\times 15$); 96, zooid with frontal wall (arrow), polypide with pleated attachment organ, USNM 488150 ($\times 200$).

lands. Syntypes of the species were sectioned and redescribed (Nye, 1976:115). Nye correctly interpreted the Recent species described by Borg under the genus *Heteropora* to belong to a different genus. Until an appropriate genus is named, which is beyond the scope of this paper, it seems less confusing here to continue to use the name *Heteropora* for Borg's Recent species.

Borg published a salient monograph (1933) on the Recent species of the family Heteroporidae, followed by a monograph on the stenolaematous Bryozoa from Antarctica (1944). He characterized the genus *Heteropora* as arborescent colonies having numerous robust smooth branches (Figure 97a) of evenly scattered circular feeding zooids separated by numerous smaller polymorphs termed kenozooids. He described both

kinds of zooids as intercepting colony surfaces at nearly right angles and interpreted the zooids as double-walled (herein termed free-walled).

Borg (1933:369, text-fig. 24) maintained that the calcified terminal diaphragms of both the polymorphs and the feeding zooids of *Heteropora* were interior diaphragms that were calcified from both sides. He interpreted the genus, therefore, to be double-walled after the calcified terminal diaphragms were formed. That is, colony skeletons were completely covered by the outermost membranous walls that protected the confluent outer body cavities, and the orificial walls of feeding zooids were unattached to their skeletal apertures throughout colony life. Later (1944:19), he split the stenolaemates into two groups, a single-walled and a double-walled group, and retained his 1933 concept of *Heteropora*, placing his "Divisio Heteroporina" into his double-walled group (Borg, 1944:208). Borg's double-walled interpretation of heteroporids certainly contributed to his two part division of the stenolaemates into single- and double-walled taxa.

The great majority of Borg's sections were decalcified and prepared with a microtome, so he did not have the benefit of sections showing soft parts in living positions in skeletons. Following Borg's work, sections of skeletons and skeletons plus soft parts of heteroporids and other post-Triassic stenolaemates demonstrate overwhelmingly that the great majority of terminal diaphragms of both polymorphs and feeding zooids are exterior structures calcified from the inner sides only (see homeroids and fasciculates, above, for exceptions). Furthermore, the cuticle of the outermost membranous walls opposite the polymorphs and most feeding zooids is incorporated as the outermost layer of calcified terminal diaphragms (Boardman, 1983, fig. 34-1d) where it can be observed in place in some sections.

Using exterior characters only, Borg (1933) recognized three species of *Heteropora* from the Puget Sound region: *H. pelliculata*, having kenozooids closed by terminal diaphragms and no peristomes; *H. pacifica*, having closed kenozooids and peristomes; and *H. magna*, having stouter colonies, kenozooids either open or closed, and no peristomes. In a study based on detailed collecting at different depths in the region, Ross (1973) found that Borg's key features of the three species can be found in different stages of development in a single colony. "Further, different combinations of characters used to key out species occur in several colonies so that a single colony could be assigned to two or three species" (Ross, 1973:477).

Using Borg's external taxonomic characters, colonies of *Heteropora* from Puget Sound and adjacent Pacific waters have kenozooids that isolate functioning feeding zooids (Figures 97b-100). Kenozooids are commonly closed by thick exterior terminal diaphragms below budding zones (Figures 97-100). In addition, most colonies (Ross, 1973:480) have fixed-walled patches of feeding zooids with exterior-walled peristomes (Figures 97c, 100), and a few zooids can develop isolated

exterior frontal walls where needed to complete skeletal apertures (Boardman, 1983: figs. 34-1b).

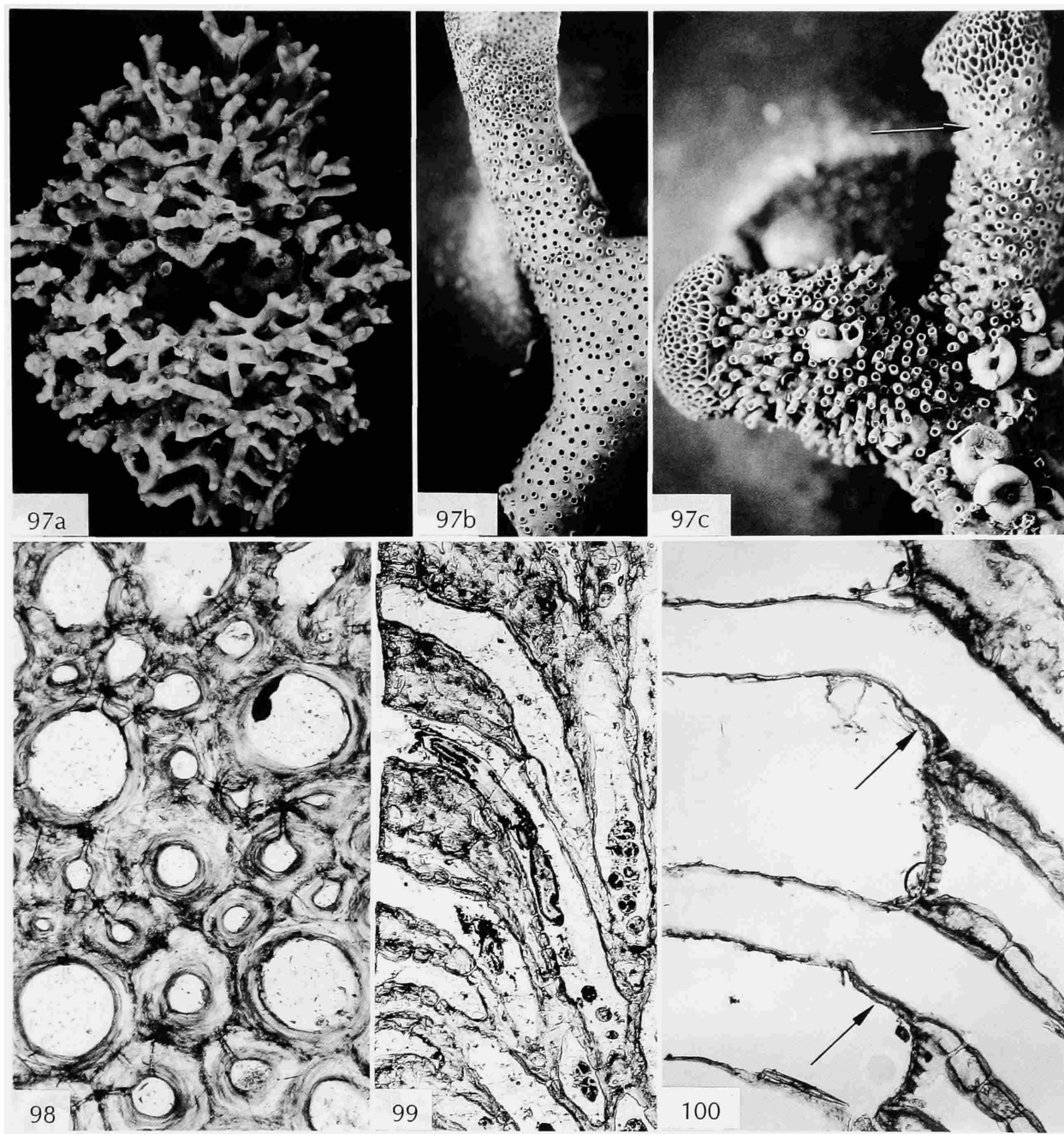
The thin peristomes of the feeding zooids of heteroporoids are exterior structures and therefore have cuticle as their outermost layer. Commonly, the proximal sides of zooids, which begin with short thick outward extensions, are aborted frontal walls followed outwardly by the thin walls of the peristomes, which are extensions of the skeletal linings of the aborted frontal walls (Figure 100). The proximal sides of other zooids lack the aborted frontal walls and are merely exterior extensions of the skeletal linings of the supporting vertical walls (Boardman, 1983, fig. 34-1a). The distal sides of the peristomes are commonly exterior extensions of the skeletal linings of the supporting vertical walls. Generally, peristomes develop after the terminal diaphragms of the intervening kenozooids (Figure 97c).

The formation of exterior terminal diaphragms in kenozooids claims the outermost cuticular layer of the outermost membranous walls and compresses the orificial walls of isolated feeding zooids against their skeletal apertures. The effect is to close outer body cavities as in fixed-walled species. In addition to being free or "compressed," orificial walls within colonies of some heteroporids can be fixed by clusters of feeding zooids having exterior peristomes and, less commonly, by frontal walls (Figure 97b), as described immediately above.

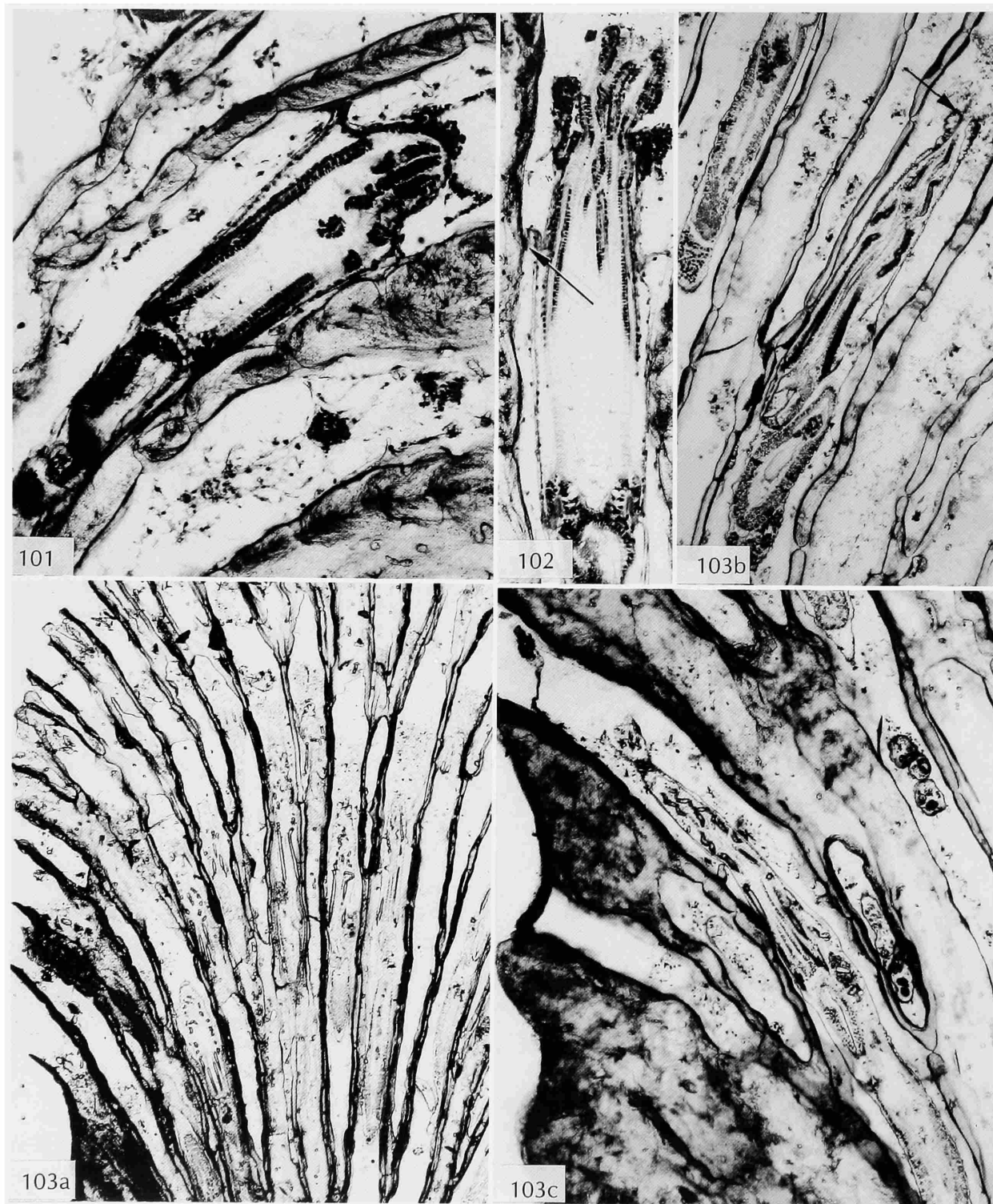
The irregularity of the development of peristomes within colonies suggests that their expression is microenvironmentally controlled. Peristomes conceivably could give a cluster of feeding zooids an advantage in focusing and strengthening feeding currents compared to a neighboring cluster that is lacking them, an interesting research problem for the future.

Borg (1933) redescribed a branching New Zealand species, *Heteropora neozealandica* Busk, 1879, as having no terminal diaphragms in the kenozooids, thus making it free-walled. All combinations seem possible.

Heteroporoids from the Puget Sound region and southern Alaskan waters, as identified by comparable external characteristics, have two entirely different interiors, including both microstructures and enclosed polypides. One interior has coarse laminae that diverge outward from distinct zooidal boundary zones (Figures 98, 99, 101, 102; Boardman, 1975, pl. 2: fig. 4). In transmitted light, the boundaries are meandering and extremely thin and pink in thinner sections and dark in thicker sections. More finely laminated living chamber linings range from thick to discontinuous. An SEM study by Kenneth Towe (NMNH) indicated that the tabular crystallites of both laminar layers are shingled and grow outward by edgewise growth (Boardman and Cheetham, 1969, text-fig. 2b, pl. 28: figs. 2, 3). The polypides that occur in these skeletons have 14 tentacles anchored by attachment organs (Figure 101) that have a shallow retraction distance (Figure 99). Attachment filaments were not found, and attachment organs are not pleated. The polypides undergo progressive cycles until the outward growth of the vertical skeletal walls is halted by the terminal



FIGURES 97–100.—Heteroporoids. 97–99, *Heteropora* species 1: 97, USNM 488209, Middleton Island, Alaska: 97a, colony ($\times 0.5$); 97b, colony surface, kenozooids lacking terminal diaphragms at top of figure, kenozooids with terminal diaphragms isolating feeding zooids below ($\times 5$); 97c, growing tips form a capitulum, feeding zooids isolated by kenozooids covered by exterior diaphragms (arrow), feeding zooids with exterior peristomes proximally ($\times 8$); 98, tangential view, smaller kenozooids isolate larger feeding zooids, USNM 186550, Neah Bay, Washington ($\times 100$); 99, short retracted polypide distance, string of brown bodies in bottom of living chamber, BMNH O'Donaghue Collection 1963.2.6.1, Pacific ($\times 50$). 100, *Heteropora* species 2, laminae of vertical wall diverge inward, distal side of exterior peristomes of feeding zooids extend from skeletal lining of feeding zooids, proximal side of peristomes supported by short frontal walls (arrows), terminal diaphragms of large kenozooids, USNM 186549, Middleton Island, Alaska ($\times 100$).



FIGURES 101–103.—Heteroporoids. 101, 102, *Heteropora* species 1, BMNH O'Donoghue Collection 1963.2.6.1, Pacific ($\times 150$): 101, vertical wall laminae diverging from the zooidal boundary zones outward, polypide with attachment organ; 102, polypide just starting to protrude tentacles past attachment ligaments (arrow). 103, *Heteropora* species 2, USNM 488210, Gulf of Alaska, west side of Middleton Island, Alaska: 103a, fully retracted polypides deep within living chambers ($\times 50$); 103b, deeply retracted, relatively long polypide, movable and pleated membranous sac, atrial sphincter muscle (arrow) ($\times 100$); 103c, long polypide with movable membranous sac in relatively short living chamber ($\times 100$).

diaphragms of the kenozooids, after which, polypide cycles are stationary.

The second heteroporid interior could hardly be more different. Vague skeletal laminae diverge inward in vertical walls from unseen zooidal boundary zones (Figures 100, 103a–c). The polypides in this skeleton retract deeply into their living chambers, lack attachment organs, are longer, and have 10 instead of 14 tentacles. Instead of attachment organs, the polypides are protruded by a membranous sac that has its outer movable end pleated (Figure 103b,c) and fastened to the tentacle sheath.

A capitulate species from Alaskan waters has a growth habit and internal characteristics that suggest it to be transitional between tubuliporines and heteroporids (Figure 104a). The colonies combine peduncles having orificial walls fixed by combinations of frontal walls and peristomes, as in the tubuliporines (Figure 105), and capitulate expansions of free-walled zooids, which are comparable to heteroporids (Figure 106). Peduncles begin development from an external protoecium (Figure 104a); they can be branched, and they lack polymorphs. The frontal walls extend outward to form the proximal sides of peristomes (Figure 105). On the distal sides of apertures, the same peristomes are a thin exterior extension of the vertical walls or the chamber linings of vertical walls (Figure 104b) comparable to those of the Puget Sound heteroporids.

The free-walled capitulate structures (Figure 104a) seem to terminate branch growth and appear to compare with the terminal expansions in the Puget Sound heteroporids (Figure 97c). The free-walled expansions have numerous small zooids among the obvious feeding zooids. Some of the small zooids could be the beginnings of feeding zooids, but most are polymorphs lacking terminal diaphragms. The wall structure of vertical walls (Figures 104b, 105) is comparable to that of the heteroporid with outwardly diverging walls, but it is also comparable to some species now placed in the tubuliporines (Figure 47).

Polypides of the transitional species have membranous attachment organs and shallow retraction distances (Figures 104b, 105). They have 16 to 19 tentacles, the highest number seen so far in stenolaemates. This species has characteristics of both heteroporids and tubuliporines, but more collecting and lab work is needed in both major taxa to determine the phylogenetic and taxonomic relationships of this species.

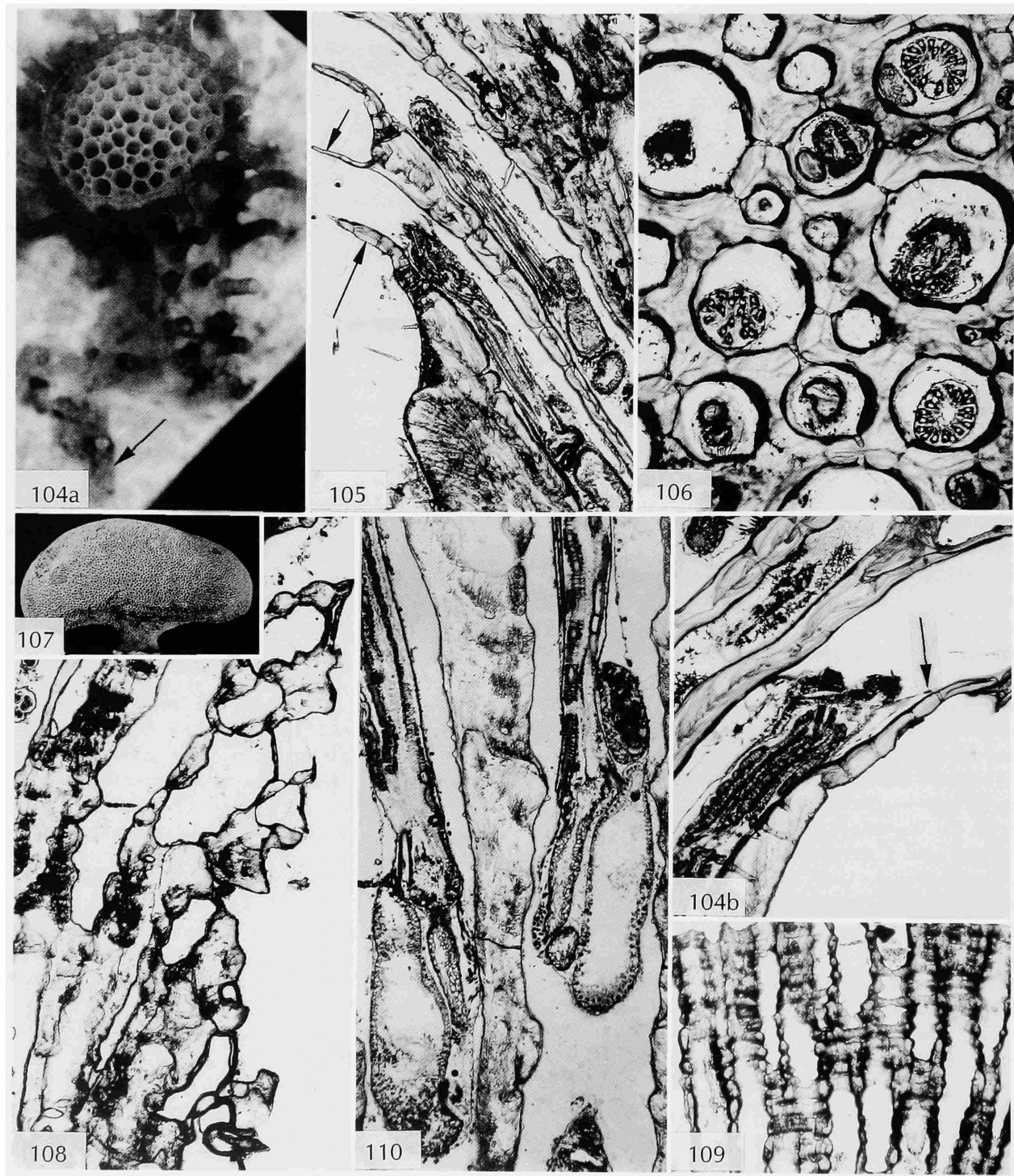
Borg described the genus *Neofungella* and placed it in the family Heteroporidae (1933:259) with three other genera, *Heteropora*, *Densipora* MacGillivray, and *Canuella*, another new genus. Later (1944:209), Borg restricted the family to *Heteropora* and *Neofungella*. He (1933:259) described *Neofungella* as follows: "Zoarium simple, capitulate, with a short peduncle; autozooids and kenozooids about equally numerous, opening both on the peduncle and the capitulum; brood-chamber a spacious cavity covered under the surface of the capitulum."

Colonies of *Neofungella* are free-walled throughout (Figures 4, 107, 108). Zooids in the peduncles are somewhat smaller and some patches of zooids have exterior terminal diaphragms (Figure 108). The capitulate part of a colony expands its diameter like most massive colonies throughout the stenolaemates. Massive colonies expand their diameters from within by having new zooids bud between the distal ends of established exozonal zooids as needed to keep colony surfaces uniformly level. The ontogenetic gradient, therefore, is dispersed throughout the colony so that polypide sizes and the time of cycles can differ among adjacent zooids (Figure 4). Smaller polypides can be either fully regenerated and younger or in the process of regenerating. Neighbors can be fully regenerated or fully degenerated at the same time (Figure 4).

Wall structure in *Neofungella* is markedly different from that of the heteroporids. The vertical walls of zooids are annularly thickened, typical of many species with massive growth habits (Figure 109). Zooidal boundary zones are microcrystalline in appearance and dark and pronounced in thickened segments. Apparently they produce fibers or laminae (an SEM study is necessary to determine which) of the remainder of the skeletal walls (Figure 110). One slanting component of the fibers or laminae of vertical walls can be seen, in longitudinal sections, to diverge outward at low angles from the boundary zones. In sections perpendicular to zooidal growth, the slanting component is at high angles to the boundary zones. No chamber lining was seen.

Polypides of *Neofungella* also differ from those of the heteroporids described above. They have thickened cone-shaped attachment organs with filaments (Figure 8). The filaments are close to the attachment ligaments so that protrusion of the tentacles occurs much like it does in cinctiporids (Figure 13). Polypides have just eight tentacles in contrast to the higher numbers of tentacles in the heteroporids described above. Retractor muscles include a set connected to the cardia, and these muscles are not found in heteroporids (Figure 110). Both cardia and lophophore retractor muscles can be attached on opposite sides of the skeletons in adjacent zooids; this arrangement is typical of many colonies having massive growth habits (Figure 110). These internal differences strongly suggest that *Neofungella* does not belong in the same family as the heteroporids.

SUMMARY.—Heteroporoids (Figures 97–106) studied here are species from the Puget Sound and southern Alaskan waters whose outer body cavities below budding zones are closed by the exterior terminal diaphragms of polymorphs, which isolate the feeding zooids. The terminal diaphragms compress the orificial walls of individual feeding zooids against their skeletal apertures, thus effectively fixing them. In addition, orificial walls are fixed by the exterior peristomes that develop secondarily in patches within colonies and by a few frontal walls, suggesting that their distribution is controlled by microenvironmental demands. Another species, not sectioned, reportedly lacks terminal diaphragms in its polymorphs, so it is free-walled with outer body cavities. Still another species is



FIGURES 104–110.—Heteroporoids. 104–106, transitional genus, Unalaska to Cook Inlet, Alaska: 104, USNM 488211: 104a, protoecium (arrow), peduncle or stem with frontal walls and long exterior peristomes, capitate expansion or capitulum with free walls except around margin where they are fixed/free ($\times 10$); 104b, polypide of stem with membranous attachment organ attached to proximal frontal wall (large arrow) ($\times 100$); 105, section of stem with frontal walls supporting peristomes on proximal sides of zooids (large arrow), distal side of peristomes an extension of vertical-wall lining (small arrow), laminae of

vertical walls diverging outward, USNM 488212 ($\times 50$); 106, feeding zooids isolated by small polymorphs in capitulum, USNM 488213 ($\times 100$). 107–110, *Neofungella* species, USS Edista off Victor Hugo Island, west coast of Palmer Peninsula, sta. 28, Antarctica: 107, colony with broad capitulum and small peduncle, USNM 488214 ($\times 2$); 108, polymorphs of peduncle, USNM 488215 ($\times 50$); 109, annular thickenings of vertical walls, USNM 317028 ($\times 30$); 110, cardia and lophophore retractor muscles attached on opposite sides of adjacent zooids, USNM 488216 ($\times 100$).

seemingly transitional with the tubuliporines by having orificial walls free, fixed/free, and fixed in different regions of colonies. The orificial walls are fixed by frontal walls with exterior peristomes, which is typical of tubuliporines.

Two strikingly different interiors occur in those species having comparable exteriors that include isolating polymorphs with terminal diaphragms, exterior peristomes in patches, and a few frontal walls. One interior has inwardly diverging laminae in the vertical walls, and polypides that lack attachment organs and retract to near the bottoms of their living chambers. The second interior has outwardly diverging laminae in the vertical walls, and polypides with attachment organs and short retraction distances. Certainly these two interiors belong to different higher taxonomic categories. In the transitional genus having zooidal skeletons of both heteroporids and tubuliporines, laminae are outwardly diverging and polypides have attachment organs. Nothing can be assumed from the outside in the heteroporoids.

Family CINCTIPORIDAE

DESCRIPTION.—The family Cinctiporidae Boardman et al., 1992, is significant to this study because it provides extreme skeletal diversity, which is unmatched in other stenolaemate families as presently understood. The family also provides additional evidence against dividing the class Stenolaemata into Borg's single-walled taxa (with frontal walls) and double-walled taxa (with outer body cavities).

The Cinctiporidae are presently known to range from latest Cretaceous to Recent in the Southern Hemisphere. Family-wide features (Boardman et al., 1992:50) include bushy colonies having bifurcating branches, which in rare instances are anastomosing. Branches are uniformly slender because polypide cycles become stationary several generations below the budding zones, followed by the zooids themselves becoming dormant. Zooids are monomorphic and evolve from annular to spiral budding patterns about imaginary branch axes. The zooidal size generally increases through the evolutionary history of the family (Figure 111) such that the younger species have gigantic zooids compared with most other stenolaemates. Zooids intercept colony surfaces at low angles to form skeletal shields (Figure 112, greatly reduced in some genera). These shields are actually exposed internal surfaces of the distal sides of interior vertical walls that extend distally beyond skeletal apertures. This condition is apparently unique to the family and to some species of its presumed Cretaceous outgroup (Figure 114). Clusters of communication pores perforate the bases of skeletal shields where the functional skeletal apertures open (Figure 112). Skeletal apertures are tightly defined in some genera by emergent peristomes, which are calcified by the zooids themselves. The peristomes are exterior skeletal structures that develop in clusters of zooids within colonies (Figure 113a). The skeletal-wall microstructure is constant throughout the family, and polypide anatomy is comparable in

the two Recent species available, one free-walled and the other fixed-walled.

In addition to the shared character states above, the Cinctiporidae contain genera with extreme skeletal diversity. The primary zooidal growth of individual genera in astogenetic zones of repetition is either free-walled, fixed/free-walled, or fixed-walled. The skeletal walls of zooids on colony surfaces are either (1) interior skeletal shields in free-walled species (Figures 112, 113, 115–117); (2) skeletal shields that transform distally to the proximal exterior frontal walls of the zooids in the next younger whorls in fixed/free species (Figures 118–124); or (3) frontal walls that surround apertures and reduced remnants of skeletal shields in fixed-walled species (Figures 125–128).

The skeletal diversity claimed for the family is justified partly by the shared character states listed above that are interpreted to indicate phylogenetic relationships at the family level. Perhaps equally important, evidence for the skeletal diversity included in the family is found in the zones of astogenetic change of *Cinctipora elegans* Hutton, which includes all three skeletal morphologies listed above (Boardman et al., 1992, figs. 5, 30, 31). The earliest one or two zooids in the zone of change, the ancestrula and periancestrula, have exterior skeletons and are fixed-walled throughout life. The second generation of zooids is fixed/free with exterior frontal walls proximal to their apertures and interior skeletal shields distal to their apertures. Distal to the second generation all zooids are free-walled. Unfortunately, similar zones of change are unknown at present in other cinctiporid species, so the overall significance of their diverse morphology is unknown.

Because of growth restrictions, it is apparent that an ancestrula and any periancestrula with exterior skeletons throughout life cannot directly produce interior skeletal walls in the next generation (Boardman et al., 1992, fig. 5). Actually, throughout branching stenolaemate colonies in both zones of change and repetition, zooids with distal frontal walls apparently can grow only proximal frontal walls in the next younger zooids (Boardman et al., 1992, fig. 59).

The extraordinary development of skeletal diversity within a single branch of *Cinctipora elegans* is displayed by groups of free-walled zooids with skeletal shields alternating irregularly along the branch with groups of fixed/free and fixed-walled zooids (Boardman et al., 1992, fig. 57). The exterior walls that fixed the orificial walls were interpreted (Boardman et al., 1992:29–32) to be primary exterior frontal zooidal walls, just as they appear to be (Figure 113b). This interpretation intermixes normal free-walled zooids (Figure 113a) in the same colony with zooids having complete primary frontal walls in the zone of astogenetic repetition. This combination has never before been reported and actually has been thought to be most unlikely, if not impossible.

A second look at the branch indicates an alternative interpretation that seems more likely, given its skeletal

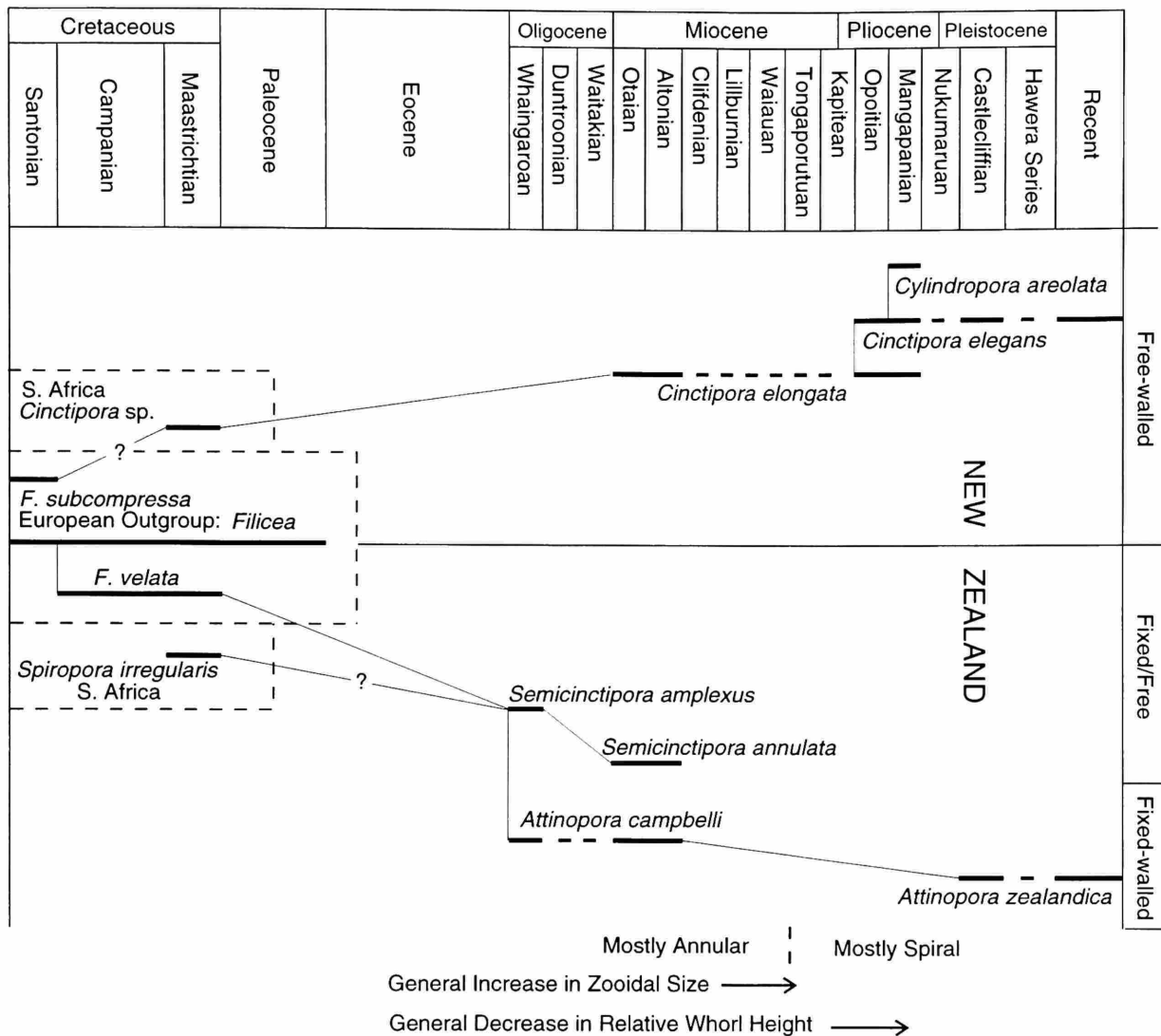


FIGURE 111.—Phylogenetic tree of the Cinctiporidae of the Southern Hemisphere starting from the genus *Filicea* of Europe as the outgroup. The Santonian through the Oligocene are approximately proportional to time in height.

characteristics and the present knowledge of the modes of stenolaemate growth. The most confusing, and at the same time revealing, interval of the branch displays exterior skeletal walls over most of the zooids (Figure 113b). The two zooids on the right side of the branch between the short arrow and dashed line (showing the angle of a whorl) display interior skeletal shields, a species characteristic. Therefore, these two zooids grew, originally at least, as fixed/free zooids, if not as standard free-walled zooids. Laterally to the left in the same whorl, however, are what appear to be fixed-walled zooids with exterior frontal walls. This frontal wall interpretation requires that just under the budding zone the distal-most interior skeletal shields (Boardman et al., 1992, figs. 3, 33b, 63, 65) grew opposite the exterior frontal walls (Boardman et al., 1992, fig.

44) of the fixed/free-walled zooids of the next younger whorl. This seems most unlikely.

So, are the exterior skeletal walls opposite the interior skeletal shield really primary frontal zooidal walls? The only other possibility is that they are thin secondary exterior walls similar to those that form the scattered growths on shields typical of *Cinctipora elegans* (Figure 113a). These thin exterior walls are secondary because they grow on established primary zooidal skeletons. The secondary skeletons are extremely thin (Boardman et al., 1992, figs. 7, 48b) and they commonly have smaller and more widely scattered pseudopores than occur in the terminal diaphragms and primary frontal walls (Figure 126). The smaller and more widely spaced pseudopores of the exterior walls of the *C. elegans* branch (Figure 113b) suggests

that these walls in combination with emergent peristomes are also secondary. Furthermore, on the left margin of the pair of skeletal shields is a broken remnant of the exterior wall, which if unbroken, appears to have arched over the shields. It seems possible that the exterior walls are an extraordinary development of thin secondary skeleton covering normal free-walled zooids that are comparable to the rest of the branch and to the species (Figure 113a).

If true, the exterior skeletal covering is necessarily the calcified outer membranous wall that covered the outer confluent body cavity and calcified itself. The loose membranous outer walls, characteristic of all free-walled colonies, are tied down and kept in place by skeletal connections within the zooids and, in this branch, by the exterior emergent peristomes formed by the individual zooids. Calcification of the outer membrane by itself indicates that its inflated position stretched from peristome to peristome during the life of the colony. The segment of the same branch lacking skeletal covering (Figure 113a) would compare in size if similarly covered.

The external appearance of a branch of a fixed-walled cinctiporid with zooidal frontal walls (Figure 126) is much tighter, and the boundaries of the zooids are more evident because each zooid separately grew its own frontal wall (Boardman et al., 1992, fig. 45). The long distal extensions of the skeletal shields between whorls also contributes to the impression that the secondary exterior skeletal covering was a series of frontal zooidal walls.

The preferred interpretation here of the branch segment (Figure 113b) is that the exterior walls are secondary and cover normal free-walled zooids of the species. If true, the covering skeleton is the calcified membranous exterior wall of the free-walled colony, thus the covering is of colony origin.

CINCTIPORID PHYLOGENY.—Two possible evolutionary histories of the Cinctiporidae were suggested originally, based on different outgroups (Boardman et al., 1992:51). The outgroup preferred in this paper for the family is the genus *Filicea* d'Orbigny, 1854, from the Late Cretaceous to Paleocene of Europe (Boardman et al., 1992:52), even though the cinctiporid family presently is known only from the Southern Hemisphere (Figure 111). The cinctiporids apparently formed two main branches, genera that characteristically evolved with skeletal shields, free orificial walls, and outer body cavities (Figures 111–113, 115–117), and genera that retained skeletal shields and added frontal walls with fixed/free and fixed orificial walls (Figures 122–128). *Filicea subcompressa* d'Orbigny, 1854, from the Santonian of France is interpreted to have given rise to the free-walled branch. This species is free-walled and has clustered communication pores at the bases of its skeletal shields (Figure 114). The rhombic arrangement of zooids differs from the annular-spiral arrangement of cinctiporids, but this arrangement need not be a significant difference based on the detailed studies of flexible zooidal arrangements in some other stenolaemates (Voigt, 1968; Boardman et al., 1992:53).

Zooids are small for the cinctiporid family but are consistent with the evolutionary increase in zooidal size through time.

Through the known history of the Cinctiporidae, the distance between whorls became shorter relative to the zooidal width at apertures, the dimensions of the zooids increased to gigantic, and the whorls changed from annular to spiral (Figure 111; Boardman et al., 1992:52).

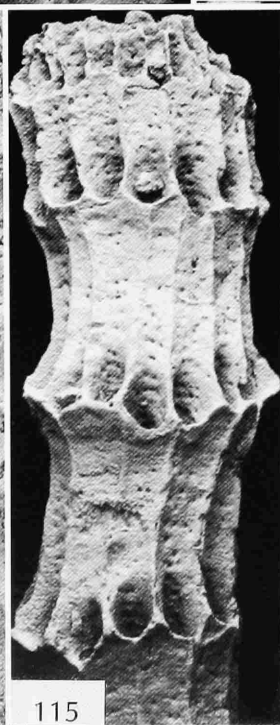
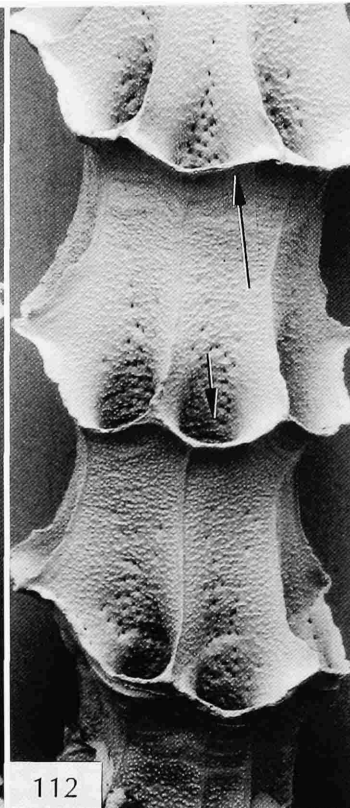
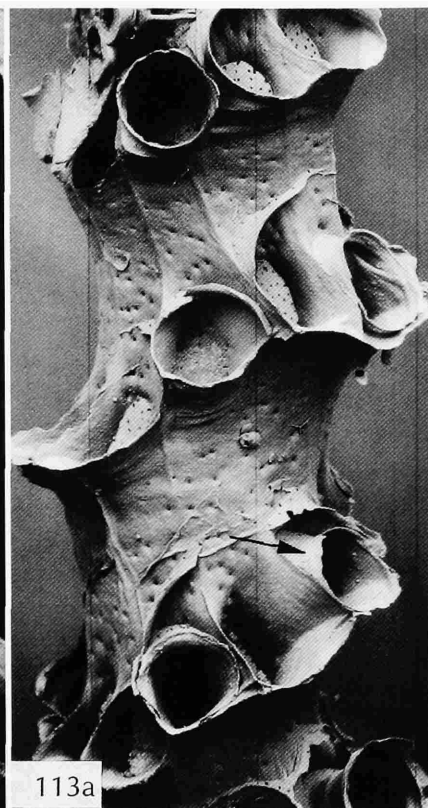
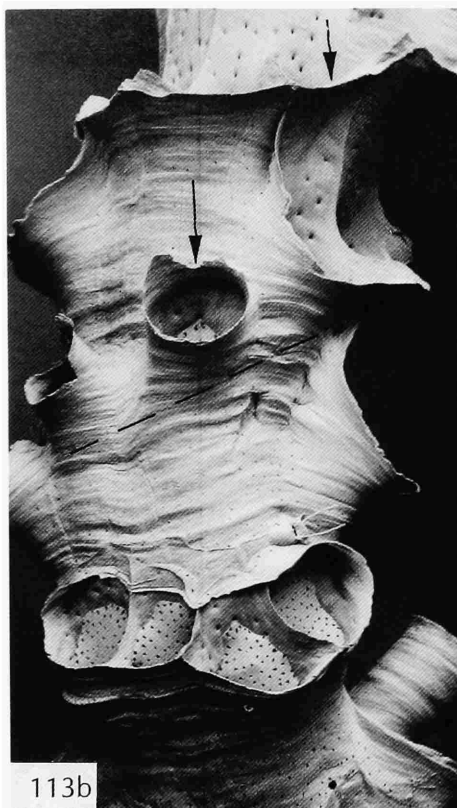
In the branch of the family with skeletal shields and free walls, the oldest available species is from the Maastrichtian of South Africa, *Cinctipora* sp. (Figure 115; Boardman et al., 1992:60). The zooids are arranged in annular whorls similar to those of other older cinctiporids found in the Southern Hemisphere. The zooids are free-walled and small. The heights of the whorls (zooidal lengths at colony surfaces) are proportionally long relative to the proximal widths of the zooids (3:1 to 4:1), and the zooids have clusters of communication pores at their bases.

The next youngest free-walled cinctiporid species available is *Cinctipora elongata* Boardman et al., 1992, from the lower Miocene and Pliocene of New Zealand (Figure 116; Boardman et al., 1992:58). The species is interpreted to have evolved, probably through several intervening species, from the South African Maastrichtian species. The zooids are arranged annularly or spirally, and the heights of the whorls are proportionally shorter relative to the proximal widths of the zooids (2:1 to 3:1) than are those of the South African species.

The youngest species of this branch is *Cinctipora elegans* from the Pliocene, Pleistocene, and Recent of New Zealand (Figures 112, 113; Boardman et al., 1992:56). This is the species in which colonies are free-walled in the zone of repetition (Figure 112), but one colony has a few zooids covered with secondary exterior walls (Figure 113; Boardman et al., 1992, figs. 56, 57). The zooids are mostly arranged in spirals and are immense in size, but the heights of the whorls are proportionally shorter (2.3:1 or less) than the earlier species of the genus.

Another genus, *Cylindropora*, occurs in the Pliocene of New Zealand (Figure 117; Boardman et al., 1992:61) and apparently evolved from *Cinctipora*. Zooids of the genus are large, are arranged in irregular spirals, and are free-walled. The skeletal shields are so short that the zooidal boundaries at the branch surfaces are nearly equidimensional.

The branch of the cinctiporid family that developed frontal walls throughout is more complicated as presently understood. Two Late Cretaceous species with frontal walls are now available that add information to the phylogenetic relationships suggested in 1992. One of the newly available species is *Filicea velata* von Hagenow, from the Campanian and lower Maastrichtian of Germany; the specimens were kindly supplied by Professor Ehrhard Voigt (Figures 118–120). The zooids are in a rhombic arrangement similar to the European outgroup species of *Filicea*. This arrangement is in contrast to the annular-spiral zooids of the Southern Hemisphere cinctiporids. The microstructure of the vertical walls, however, is typically



FIGURES 112–117.—Phylogenetic branch of the Cinctiporidae primarily with skeletal shields. 112, 113, *Cinctipora elegans* Hutton: 112, functional apertures and concentrations of communication pores at the bases of skeletal shields at proximal ends of zooidal skeletons at colony surface (small arrow), distal ends of zooidal skeletons (large arrow) at distal ends of skeletal shields, NZOI sta. E820 ($\times 28$); 113, NZOI sta. C624 ($\times 26$): 113a, part of branch with interior skeletal shields and secondary skeleton of scattered growths and emergent peristomes (arrow) defining functional apertures; 113b, part of the same branch with whorl angle indicated at attachment ligament level (dashed line), distal end of interior skeletal shield is distal end of zooidal skeleton (small arrow) on colony surface, distal end of skeleton at colony surface of adjacent zooid of same whorl if exterior skeleton is primary frontal wall (large arrow). 114, *Filicea subcompressa* d'Orbigny, possible outgroup species, zooids with skeletal shields, concentration of communication pores, and functional apertures in rhombic zooidal arrangement, BMNH D58182, Santonian, Craie de Villedien, France ($\times 60$). 115, *Cinctipora* sp., small zooids with relatively long skeletal shields, concentrations of communication pores, and functional apertures in annular arrangement, BMNH D59325, Maastrichtian, Need's Camp Quarry, South Africa ($\times 34$). 116, *Cinctipora elongata* Boardman et al., offset of spiral whorls of zooids of moderate size and relative length, paratype, BMNH D59285, Miocene, Otaian-Altonian, Forest Hill Limestone, Lady Barkly Quarry, Southland, New Zealand ($\times 35$). 117, *Cylindropora areolata* Tension-Woods, irregular, closely spaced spiral whorls of zooids with short skeletal shields, BMNH D59295, Pliocene, Mangapanian, Te Aute Limestone, Waipukurau, Napier, New Zealand ($\times 11$). (SEM photographs supplied by Paul Taylor.)

cinctiporid, and pronounced skeletal shields with clusters of communication pores at their bases (seen in sections not illustrated) develop on the distal sides of the apertures of *F. velata*. Functional skeletal apertures at the bases of skeletal shields are indicated by the exterior emergent peristomes that occur in patches of zooids, which is typical of cinctiporids. Frontal walls with pseudopores develop on the proximal and lateral sides of apertures in most zooids (Figures 118, 119), thus closing off outer body cavities. As a result, orificial walls lacking peristomes are fixed/free. Distal frontal walls are lacking, so fixed zooids are not developed. Where proximal and lateral frontal walls between the skeletal shields of adjacent zooids are lacking (Figure 120), the zooids presumably can communicate around the ends of the vertical walls, but this apparently occurs only in patches. The zooids are huge, typical of younger cinctiporids and not older species, indicating that much is yet to be learned about the evolution of the family.

The second newly available species is *Spiropora irregularis* Brood, 1977, from the Maastrichtian of South Africa (Figure 121). Externally, the specimen is worn, but it occurs with specimens of *Cinctipora* sp. (Figure 115). The annular arrangement of the zooids and pseudopores, which indicates frontal walls, produces a generalized external appearance comparable to *Semicinctipora amplexus* Boardman et al., 1992, from New Zealand (Figure 122). The zooidal apertures are small in diameter, and the height of whorls (zooidal length at colony surfaces) relative to zooidal width at the apertures is long for the family and is comparable to *Cinctipora* sp., at almost 4:1. Both measurements are consistent with the family trend and are intriguing. Unfortunately, the species must be

sectioned to determine if zooids are fixed/free or fixed and if the species has a cinctiporid skeletal structure.

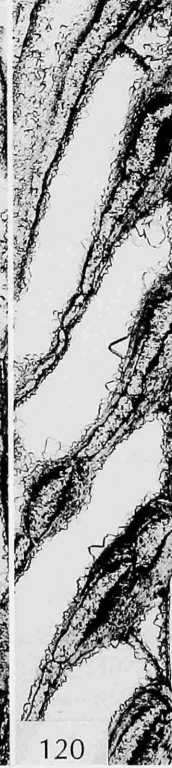
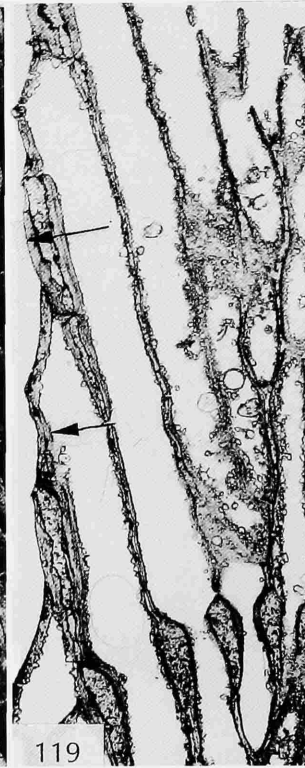
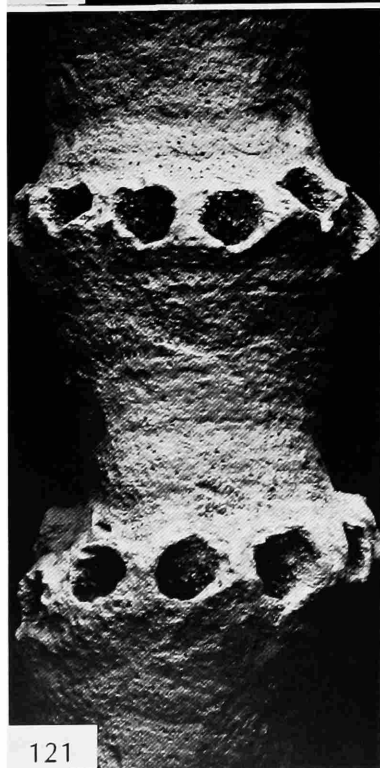
One or perhaps both of these Maastrichtian species could have been involved in the evolution of *Semicinctipora* (Figures 122–124) and *Attinopora* (Figures 125–128) (both Boardman et al., 1992), the branch of the family with frontal walls. The detailed morphology of *Filicea velata* is most convincing and strengthens the relationship between the European outgroup genus and the cinctiporids; however, the significance of the species' occurrence in Europe rather than in the Southern Hemisphere with the cinctiporids needs investigating.

Two species of *Semicinctipora*, *S. amplexus* Boardman et al., 1992, from the lower Oligocene (Figure 122) and *S. annulata* Boardman et al., 1992, from the lower Miocene (Figures 123, 124), have much the same basic skeletal morphology as *Filicea velata*, the Maastrichtian species from Germany, except for the annular arrangement of zooids in the branches. At colony surfaces, the proximal sides of orificial walls are fixed by proximal frontal walls. The distal sides of apertures are formed by interior skeletal shields so that the distal sides of orificial walls are free. The lateral walls lack frontal walls, in contrast to *F. velata*, so the zooids in an annular ring presumably can exchange nutrients laterally around the ends of the vertical walls. The junctions of the distal ends of the vertical walls that form the skeletal shields of *S. annulata* with the proximal frontal walls of the next younger zooids are visible externally (Figure 123).

The new species of *Attinopora*, *A. campbelli* Boardman et al., 1992, from the lower Oligocene and lower Miocene (Figure 125), and *A. zealandica* (Mantell), from the Pleistocene and Recent (Figures 126–128), are fixed-walled species. The ends of the vertical walls support short distal and long proximal frontal walls that surround skeletal apertures as in other fixed-walled species (Figure 127). The ends of the vertical walls are unusual, however, in that they develop thickenings that are considered greatly reduced skeletal shields. The thickenings also form external collars around the distal halves of apertures at junctions with the proximal frontal walls of the next younger zooids. The collars are distinguished externally from the frontal walls by a lack of pseudopores.

SUMMARY.—Certainly, *Cinctipora elegans* and the family Cinctiporidae are critical evidence against the first division of the class into free-walled and fixed-walled taxa. Extreme intracolony skeletal variation in *C. elegans* indicates that polypides and their life functions have advanced enough to be remarkably independent of enclosing skeletal morphology.

The family Cinctiporidae (Figures 13, 112, 113, 115–128) features the greatest and most unpredictable skeletal diversity of the six major groupings considered. The two Recent species available have comparable polypides but widely diverse skeletons. One of the species has fixed-walled zooids (Borg's single-walled skeleton with frontal walls). The other species largely develops free orificial walls (Borg's double-walled



FIGURES 118–124.—Phylogenetic branch of the Cinctiporidae with both skeletal shields and frontal walls. 118–120, *Filicea velata* von Hagenow, possible outgroup species, Campanian and Maastrichtian, Island of Ruegen, Germany, specimens provided by Ehrhard Voigt: 118, skeletal shields, frontal walls on proximal sides of apertures (large arrow), and emergent peristomes (small arrow) in lower portion of branch, Voigt cat. no. 10577, lower Maastrichtian ($\times 30$); 119, Cinctiporid wall structure, thickened walls of abandoned growing tip in endozone, frontal walls proximally (small arrow), skeletal shields distally (large arrow), USNM 488155, Campanian ($\times 50$); 120, Cinctiporid wall structure, abandoned growing tips, skeletal shields, no frontal walls, USNM 73180-6, Campanian ($\times 50$). 121, *Spiropora irregularis* Brood, relatively widely spaced annular whorls of small zooidal apertures and frontal walls with pseudopores, Maastrichtian, Need's Camp Quarry, South Africa ($\times 55$). 122, *Semicinctipora amplexus* Boardman et al., moderately spaced annular whorls of fixed/free zooids with reduced skeletal shields changing (arrow) to frontal walls distally between succeeding whorls, holotype, NZGS BZ 156, Oligocene, Whaingaroan, McDonald Limestone, McDonald's Quarry, Oamaru, North Otago, New Zealand ($\times 37$). 123, 124, *Semicinctipora annulata* Boardman et al., Miocene, Otaian-Altonian, Forest Hill Limestone, Forest Hill Quarry, Winton, Southland, New Zealand: 123, moderately spaced annular whorls of fixed/free zooids, skeletal shields change to frontal walls (arrow at boundary) between apertures of succeeding whorls, holotype, NZGS BZ 154 ($\times 30$); 124, longitudinal section with boundary (arrow) between skeletal shield below and frontal wall above, paratype, BMNH D59305 ($\times 100$). (Specimens and SEM photograph in Figures 118–120 supplied by Ehrhard Voigt; SEM photographs in Figures 121–123 supplied by Paul Taylor.)

skeleton). Another skeletal irregularity includes secondary emergent peristomes that occur in patches, comparable in colony distribution to those in the heteroporoids. Available species from the fossil record add a genus with fixed/free orificial walls and suggest evolutionary paths that could have developed the skeletal extremes of the two Recent species. Shared skeletal characteristics throughout the family include skeletal shields, which are rare elsewhere, and wall microstructure.

Implications

SKELETAL AND POLYPIDE NONCORRELATIONS

The skeletal and anatomical features within five of the six groupings of genera (initially presumed to be clades) used in the organization of this paper are distributed with a disquieting lack of correlation (Figure 129). Certainly, just one kind of polypide and one wall microstructure for each of the groupings would be most reassuring that they were phylogenetically significant. A single skeletal microstructure and polypide anatomy, however, occurs only in the Cinctiporidae (Boardman et al., 1992), a family that was originally defined on both external and internal characters. The defining characteristics of the other five groupings have been largely external. Noncorrelations among skeletons and polypide anatomy in the five groupings are summarized as follows:

Horneroids considered herein (Figures 2, 24–37) feature both outer body cavities and communication pores; free orificial walls; crystallites and laminae that grow inward, opposite to the direction of zooidal growth; and extrazoooidal

skeleton. Two species have comparable membranous attachment organs, but the polypides are otherwise different; another species has thicker, pleated attachment organs; and another genus has horny valves without attachment organs.

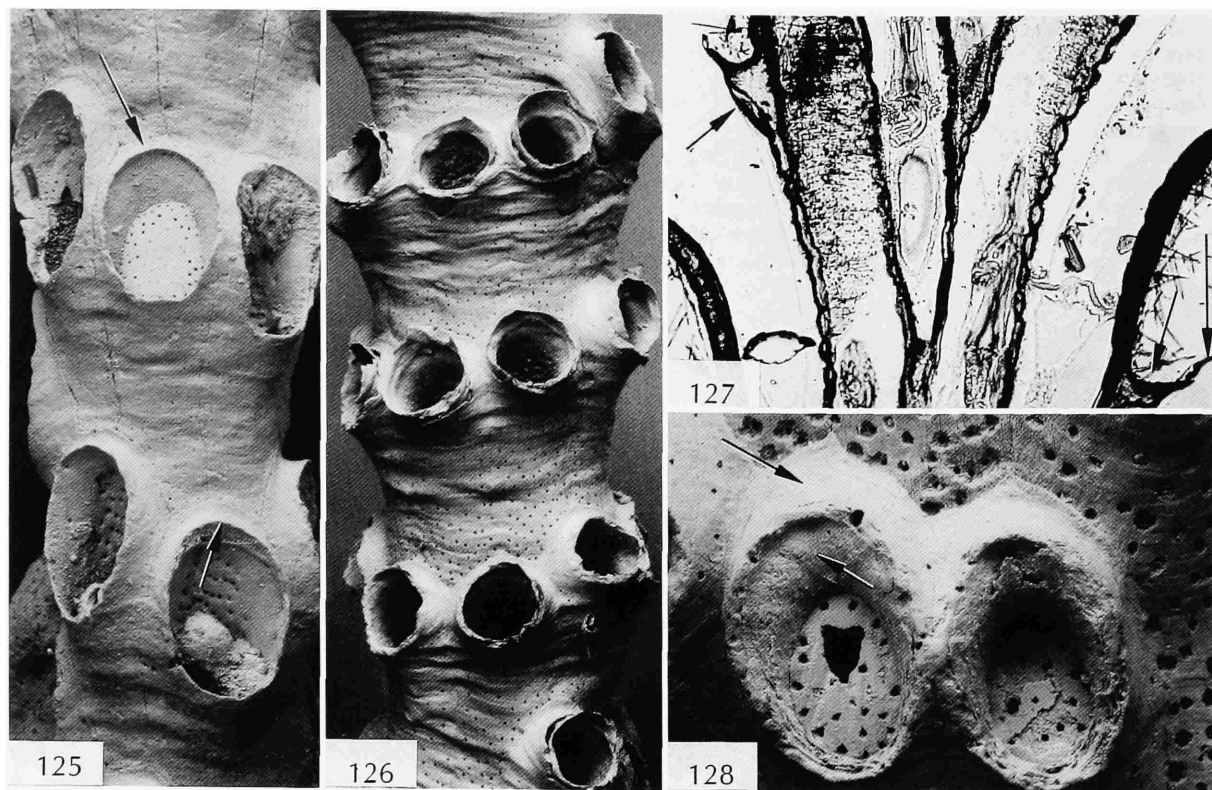
Tubuliporines (Figures 5–7, 14, 18, 19, 22, 23, 38–51) have frontal walls and fixed orificial walls and thus lack outer body cavities below budding zones. The vertical walls have three different microstructures. Five species have four different attachment organs, and one of these has a gizzard. Three other species lack attachment organs, two of these protrude polypides from the bottoms of their living chambers in different ways, and one has horny valves and short protrusion distances similar to those found in a species of the horneroids.

Fasciculates (Figures 10, 11, 20, 21, 52–78) are characterized by clusters of long, parallel, feeding zooids. Two species are free-walled with outer body cavities, but they have different microstructures and polypides, and only one has attachment organs. Five species have clusters of feeding zooids surrounded by exterior fascicle walls, so orificial walls are both fixed/free and free. One of these species also has some fixed walls. Three microstructures are included in the five species. Three have polypides with attachment organs, and one of these has a gizzard. The remaining two species lack attachment organs and have movable pleated membranous sacs.

Disporelloids (Figures 3, 9, 12, 15–17, 79–96) include small discoidal encrusting colonies, a growth habit that has been independently evolved several times throughout stenolaemate history. Seven free-walled species, which have conical attachment organs and brood chambers with interior skeletal covers, are similar enough to be informally considered a genus. Two more species are also free-walled with brood chambers having interior skeletal covers, but they have widely different kinds of attachment organs. Two other species develop scattered frontal walls that are on the proximal walls of zooids only, such that the orificial walls are either free or fixed/free and brood chambers have exterior skeletal covers. Each of the two species, however, has a different skeletal microstructure and polypide.

Heteroporoids considered herein (Figures 97–103) are generally robust, with orificial walls commonly surrounded and compressed by exterior terminal diaphragms of the intervening polymorphs. Also, within individual colonies, the orificial walls can be free or fixed, either by exterior peristomes in clusters or by scattered frontal walls. Two strikingly different interiors occur in these colonies of comparable exterior appearance: one has inwardly diverging laminae and polypides that lack attachment organs, the other has outwardly diverging laminae and polypides with attachment organs.

The phylogenetic significance of the present classification would be enhanced if some of the less common anatomy occurred in just one of the major groupings used herein; however, just the reverse is true (Figure 129). Polypides with pleated and movable membranous sacs occur in two fasciculate species and one heteroporoid. Polypides lacking attachment



FIGURES 125–128.—Genus *Attinopora*, youngest genus in the branch of Cinctiporidae with reduced skeletal shields and frontal walls. 125, *Attinopora campbelli* Boardman et al., spirally aligned oval fixed-walled apertures of frontal walls proximally and extremely short exterior peristomes (small arrow) distally on collars (large arrow) made of ends of vertical walls around distal ends of zooids, clustered communication pores in reduced skeletal shields, holotype, NZGS BZ 155, Miocene, Otaian-Altonian, Forest Lake Limestone, Lady Barkly Quarry, Winton, Southland, New Zealand ($\times 35$). 126–128, *Attinopora zealandica* (Mantell): 126, clustered communication pores in greatly reduced skeletal shields, aligned fixed-wall apertures and zooidal boundaries with collars, emergent peristomes inside apertures, NZOI sta. 746 ($\times 18$); 127, longitudinal section with reduced skeletal shields (small arrow), collar (medium arrow), short exterior peristome (large arrow) with frontal walls, NZOI sta. 746 ($\times 40$); 128, collars of ends of vertical walls (arrow) at distal halves of zooids, BMNH D1440, Pleistocene, probably Castlecliffian, Wanganui, New Zealand ($\times 64$). (SEM photographs supplied by Paul Taylor; thin section and photograph supplied by Frank McKinney.)

organs, but having the mysterious valves, occur once in the horneroids and once in the tubuliporines, the two groupings supposedly least related. Polypides with pleated attachment organs and filaments again occur just once in the horneroids and once in the tubuliporines. Polypides with perimetrical attachment organs, which seem difficult to understand functionally, occur in one species of dispoirelloid and in an Antarctic species of *Neofungella*, a genus presently difficult to classify (Boardman, 1973, pl. II: fig. 1b). Gizzards appear only in a tubuliporine and a fasciculate. This is indeed a taxonomic jumble.

From the apparent chaos in the distributions of morphology and anatomy described above, it seems evident that stenolaemates have evolved a number of functionally comparable parts that occur in different combinations across the boundaries of the presumed groupings. It seems as if almost any protrusion

mechanism can function in almost any skeleton. Comparable, rarely observed organs occur in more than one grouping. Comparable skeletal structures occur in skeletons of different microstructures. Different skeletal microstructures appear in the same grouping. Unfortunately, not enough information is available concerning other post-Triassic species to reveal additional distributions and the evolutionary processes and resulting patterns that have produced the many noncorrelations across informal taxonomic boundaries in the Recent species studied herein. Major features of the evolutionary process must have included a complex of taxonomically broad divergences that produced new recruitable characteristics resulting in increased speciation, plus extinctions, convergences, and parallelisms. With no more evidence than is available now, however, the evolution of the seemingly chaotic noncorrelations remains unknown.

TAXONOMIC CHARACTERS AND STENOLAEMATE PHYLOGENY

INTRODUCTION.—So far, skeletal and anatomical differences have been emphasized for the recognition of diversity and species. The similarities and correlations of comparative morphology and anatomy are required for the recognition of phylogenies and taxonomic categories above the species level. At this point, finding some uniformity of character states and their correlations would be most encouraging.

Within the Recent species studied, some consistency and correlation can be found in the nutrient exchange systems and in the skeletal wall microstructures and their growth directions (Figure 129). Also, certain skeletal structures are necessarily correlated with the presence or absence of communication pores, outer body cavities, and growth directions of laminae, so they can be used as associated characters in higher categories. For example, within the horneroids all species have inward-growing skeletal laminae under their outer body cavities. Therefore, they can grow extrazoooidal skeletons and originate brood chambers below budding zones. In other groupings, communication pores through which nutrients can be exchanged are required for the development of exterior zooidal walls and terminal diaphragms, all calcified only on the inner surfaces of membranes and on skeletal walls.

The growth directions of skeletal crystallites and their laminae, and the methods of nutrient exchange are long-lasting characters in the fossil record of the class. Fortunately, Paleozoic taxa have been described using sections and internal characters since the 1880s (Nicholson, 1881), so they are reasonably well known. Unfortunately, not enough post-Triassic species have been sectioned to indicate any more than spot occurrences in time and space of internal characters, even though their internal characters are more diverse.

Species with crystallites and laminae that grew inward in vertical walls occur throughout stenolaemate history, the overwhelming majority grew under outer body cavities through which nutrient exchange could occur. Most, if not all, post-Triassic species evolved communication pores. Many new post-Triassic species also developed outwardly growing skeletal laminae or crystallites that grew at right angles to zooidal growth directions, either with or without outer body cavities.

CYSTOPORATA.—In the overwhelming majority of Paleozoic and Triassic bryozoans, the laminae of vertical walls grew inward under confluent outer body cavities. In post-Triassic stenolaemates, the inward orientation and free orificial walls continued in some stenolaemate species without break to the present day, where they are seen in horneroids, whatever their phylogenetic relationships might have been. For example, an undescribed species from the Ordovician of Estonia (Boardman and Cheetham, 1973, fig. 38B–D) belonging to the ceramoporid family of the order Cystoporata (Utgaard, 1983b:358) would be considered a horneroid minus the thicker endozonal walls, communication pores, and gonozooids, if it were a post-Cretaceous species. The Ordovician species has free-walled

zooids, inward-growing laminae, extrazoooidal skeleton between feeding zooids and on the reverse sides of branches, and a similar living chamber shape and proportions, all in common with Cenozoic horneroids.

Several other genera of ceramoporinids, from Middle Ordovician to Lower Devonian (Utgaard, 1983b:358), have some skeletal characteristics of horneroids. In the Ordovician, a few genera even developed communication pores in their vertical walls comparable to many of those in post-Triassic species (Boardman and Cheetham, 1973, fig. 36C,D; Utgaard, 1973, figs. 46, 73; 1983b, fig. 160-1h,i). The calcification of terminal diaphragms on their inner surfaces (Utgaard, 1983a, fig. 146) indicates that these Ordovician communication pores distributed nutrients just as they did in post-Triassic stenolaemates. Comparable skeletal morphology, except for the thicker endozonal walls and communication pores of post-Triassic stenolaemates, continued on in some of the genera of the Cystodictyonidae (Utgaard, 1983b:422) and in other upper Paleozoic Cystoporata (Boardman, 1984, fig. 8A–F). *Cystitrypa cassiana* Schäfer and Fois-Erickson (1987) and an unnamed species (Boardman, 1984, fig. 4D,E) are typical cystoporatid species described from the Triassic.

In the Lower Jurassic, two species have been found with cystoporatid characteristics, at least one of them with scattered large communication pores in relatively thick-walled endozones. Both have solid extrazoooidal skeleton between widely spaced feeding zooids and pronounced lunaria (Boardman, 1984, fig. 8E–H). The primary types of *Seminodicrescis nodosa* from the Aptian have a jumbled zooidal arrangement but have definite lunaria and inward-growing laminae. Still younger from the Maastrichtian, the primary types of *Semicrescis tubulosa* d'Orbigny, 1854, have crude vesicular extrazoooidal skeleton, inward-growing laminae, communication pores, and lunaria (Boardman, 1984, fig. 9B,C). These examples document the continuing Mesozoic record of species with characteristics of the order Cystoporata, an order that begins in the Ordovician.

Not enough is known of post-Triassic species to evaluate the possibility of direct relationships between the cystoporates and the horneroids, even at the order level. By the Eocene, however, an undescribed species of *Hornera* from North Carolina has the required generic traits of the genus *Hornera*, including the enlarged feeding zooids behind the frontal feeding zooids (McKinney et al., 1993, fig. 5-1) that are found in Recent species (Figures 28, 29, 34).

CRYPTOSTOMATA.—Comparable skeletal morphology and microstructure occur through major segments of evolutionary time in other stenolaemate orders. Skeletons similar in many characteristics to those of the Paleozoic rhabdomesinids of the order Cryptostomata (Blake, 1983b:569) also occur in Triassic and post-Triassic species. These species are characterized by slender dendroid growth habits and inward-growing skeletal laminae under their outer body cavities. Feeding zooids typically bud from endozonal structures, such as linear axes or axial tubes, resulting in precise zooidal arrangements on colony

FIGURE 129.—Compilation of data on Recent species of this study. Polypide cycles are represented by A = progressive; B = progressive to stationary; and C = stationary. Within "Attachment Organs" and "Number of Attachment Organs," the numbers 1 to 10 indicate the different protrusion mechanisms, which are keyed to the numbers in the text that describes them under the section "Generalizations about Growth, Anatomy, and Function in the Stenolaemata."

FIGURE 129.—Compilation of data on Recent species of this study. Polypide cycles are represented by A = progressive; B = progressive to stationary; and C = stationary. Within “Attachment Organs” and “Number of Attachment Organs,” the numbers 1 to 10 indicate the different protrusion mechanisms, which are keyed to the numbers in the text that describes them under the section “Generalizations about Growth, Anatomy, and Function in the Stenolaemata.”

FIGURE NUMBERS				GROWTH HABIT					ZOOIDAL PATTERN							MICRO STRUCTURE				
				Erect branching	Fenestrate, anastomosing	Encrusting	Bifoliate.	Capitulate	Frontal apertures only	Radial apertures, erect	Fasciculate	Radial apert. encrust.	Rhombic	Vertical rows.	Transverse rows	Annular-spiral	Laminae diverge in	Fibers at 90°	Laminae diverge out	Microcrystalline
HORNEROIDS	<i>Hornera</i> species complex	2, 28, 30, 31	Arctic, Mediterranean	X					X				X				X			
	<i>Hornera</i> sp. 1	25, 27 32	New Zealand	X	X				X				X				X			
	<i>Hornera</i> sp. 2	33	New Zealand	X					X				X				X			
	<i>Hornera</i> sp. 3	34	New Zealand	X					X				X				X			
	<i>Crisina</i> sp.	24, 35	Antarctic	X					X					X			X			
	<i>Crisina wateri</i>	36	Madagascar	X					X					X			X			
	<i>Mesonea radians</i>	37	Australia	X					X				?				X			
TUBULIPORINES	<i>Idmidroneid</i> sp. 1	6, 38 - 40	New Zealand	X					X						X			X		
	<i>Idmidronea atlantica</i>	-	Mediterranean	X					X						X			X		
	<i>Idmidronea coerulea</i>		Mediterranean	X					X						X			X		
	<i>Pustulopora purpurascens</i>	41 - 44	New Zealand	X													X		X	
	<i>Tubulipora</i> sp.	18, 19, 45, 46	Cape Cod			X							X						X	
	<i>Mecynoecla delicatula</i>	7	Mediterranean	X						X				X					X	
	<i>Tervia irregularis</i>		Mediterranean	X					X						X				X	
	<i>Entelophorid</i> sp.	14, 47	S. Indian Ocean	X						X				X						X
	<i>Idmidroneid</i> sp. 2	48	Antarctic	X					X							X				X
	<i>Diplosolen</i> sp.	49	Alaska			X								X						X
	<i>Diplosolen intracaria</i>	50, 51	Arctic				X							X						X
	<i>Harmelinopora indistincta</i>	5, 22, 23	Mediterranean			X								X						?
FASCICULATES	<i>Discocytis</i> sp.	52 - 57	Alaska					X			X									X
	<i>Infundibulipora lucernaria</i>	10, 58-61	Arctic					X			X									X
	<i>Telopora</i> sp.	20, 21, 62, 63	New Zealand, Antarctic					X			X								X	
	<i>Fasciculipora ramosa</i>	11, 64-68	Antarctic	X							X									X
	<i>Froncipora verrucosa</i>	69-72	Mediterranean		X				X		X									X
	<i>Fasciculate</i> sp. 1	73, 74	Antarctic	X							X									X
	<i>Fasciculate</i> sp. 2	75-78	New Zealand	X							X							X		
DISPORELLOIDS	<i>Dispoirelloids</i> , 7 species	3, 12, 79 - 84	Alaska, Med., Greenland, NZ			X						X							X	X
	<i>Dispoirelloid</i> sp. 8	16, 85, 86	Alaska			X						X							X	
	<i>Dispoirelloid</i> sp. 9	17, 87-89	New Zealand			X						X								X
	<i>Dispoirelloid</i> sp. 10	9, 90 - 94	Alaska			X						P	P						X	
	<i>Dispoirelloid</i> sp. 11	15, 95, 96	New Zealand			X						P	P							X
HETEROP.	<i>Heteropora</i> sp. 1	97 - 99,101,102	Pacific	X						X										X
	<i>Heteropora</i> sp. 2	100,103	Pacific	X						X							X			
	Transitional genus	104 -106	Alaska			P		P		X			X							X
?	<i>Neofungella</i> sp.	4, 8, 107 -110	Antarctic					X												X
CINCT.	<i>Cinctipora elegans</i>	13, 112, 113	New Zealand	X													X		X	
	<i>Attinopora zealandica</i>	126 -128	New Zealand	X													X		X	

SKELETAL STRUCTURE							ORIFICIAL WALLS						POLYPIDE CYCLES					ATTACH. ORGANS				NO ATTACH. ORGANS					
Extrazoidal skeleton	Interior peristomes	Inter. brood c. covers	Lunaria	Frontal walls	Exterior peristomes	Exter. brood c. covers	Exter. fascicle walls	Free	Fixed	Fixed/free	Fixed by frontal walls	Fixed by fascicle walls	Fixed by polymorphs.	Progressive cycles	Shallow retraction.	Prog. to stat. cycles	Stationary cycles	Deep retraction	Ligaments	Perimetrical attach.	Filaments	Pleated	Bilateral symmetry	Tent. sheath attached to mem. sac in liv. ch.	Tent. sheath to mem. sac in peristome	Mem. sac pleated	Valves
X	X	X						X						A	A				3								
X	P	X	P					X						A	A				3								
X	X	X						X						A	A				3								
X	X	X						X						A	A				2		2	2					
X	X	X						X						A	A									10			10
X	X	X						X						A	A				X		?						
X	X	?						X						A	A				X		?						
				X	X	X			X		X				B	B			1		1						
				X	X	X			X		X				B	B								10			10
				X	X	X			X		X						C	C						?	?		
				X		X			X		X				B	B			3							Gizzard	
				X	X	X			X		X						C	C						7			
				X	X	X			X		X						C	C						?	?		
				X	X	X			X		X						C	C						?	?		
				X	X	X			X		X				B	B			2		2	2					
				X	X	?			X		X				B	B			4			4					
				X	X	?			X		X				B	B			3								
					X	?			X				X				X	X	?					?			
				X	X	?			X		X						C	C							9		
		X						X									C	C						7			
					X			X						A	A				4			4					
				P	P	X	P	P	P	P	P	P	P				C	C						8			8
					X		P	P			P		P	A	A				3								
				P	X	P	P		P	P	P	P	P	A	A				3								
				P	?	P	P		P	P	P	P	P	P	P		P	P						8			8
				P	X	P	P		P	P	P	P	P	A	A				3							Gizzard	
		X	X					X						A	A				1,3		1						
		X	X					X						A	A					5	5						
		X	X					X						A	A				6		6		6				
				P		X		P		P	X			A	A,B	B			1		1						
				P		X		P		P	X			A	A,B	B			4			4					
		X		P	P			P	P		P		P		B	B			3								
		X		P	P			P	P		P		P				C	C						8			8
		?		P	P	?		P	P	P	P				B	B			3								
		X						X						A	A				1		1						
				P	P			P	P	P	P				B	B			1		1						
				X	P				X		X				B	B			1		1						

surfaces. Feeding zooids are widely spaced by intervening extrazoooidal skeleton, and exozones and endozones are sharply delimited. A Triassic species has extrazoooidal skeleton and abundant metapores typical of rhabdomesinids, although it is classified as a trepostome (Schäfer and Fois-Erickson, 1987, pl. 9). Some Cretaceous species have hemisepta and some have metapores in extrazoooidal skeletons, both characteristic of some Paleozoic rhabdomesinids (Boardman, 1984, figs. 10, 11). The small metapores are cylindrical body cavities in extrazoooidal skeleton that lack their own wall structure, which is comparable to vacuoles in horneroids. The endozonal walls in Mesozoic species are thicker than those of Paleozoic species, and communication pores are either not found or are extremely small and are restricted to endozones in some Cretaceous species (Boardman, 1984:31).

TREPOSTOMATA.—Skeletons having the characteristics of the Paleozoic order Trepostomata also occur in Triassic and post-Triassic species; they all have inward-growing skeletal laminae under outer body cavities. Trepostome characteristics include feeding zooids that typically have long body cavities partitioned by closely spaced basal diaphragms calcified on the outer surfaces that shorten the living chambers of polypides (Boardman, 1984, fig. 5B). Extrazoooidal skeleton is rare, and the zooidal apertures are closely spaced and lack discernable patterns at colony surfaces, unless small polymorphs with their own body walls intervene.

Trepostomes have the largest representation of species in the much reduced bryozoan fauna of the Triassic (Schäfer and Fois-Erickson, 1987). In the late Paleozoic, some genera developed annularly thickened zooidal walls, with the thickenings becoming more closely spaced and pronounced and continuing into the Permian (Gautier, 1970; Boardman, 1984, fig. 6). In the Triassic, endozonal walls became typically thicker than in Paleozoic species, and pronounced annular thickenings have not been found. Three Middle Jurassic species, classified as cerioporinids of the order Cyclostomata, have trepostome characteristics, including inward-growing laminae, closely spaced basal diaphragms, and pronounced annular thickenings of the vertical walls (Nye, 1976, pls. 1–6, 41–44; Boardman, 1984, fig. 7A–C). Communication pores lie in the thin intervals between annular thickenings (Nye, 1976). They are inferred to have had their origin in the Lower Jurassic (Boardman, 1984). The combination of annular thickenings and basal diaphragms occurs as late as the Miocene (Nye, 1976, fig. 13; Boardman, 1984, fig. 7F). Recent heteroporoids have long been compared with Paleozoic trepostomes because of their external appearance (Nicholson, 1880), but the internal differences are numerous, and the detailed transitional morphology leading to Recent heteroporoid species has yet to be discovered.

The few Triassic stenolaemates are generally accepted to be holdovers from Paleozoic clades (Schäfer and Fois-Erickson, 1987). The endozonal walls of feeding zooids throughout the Paleozoic stenolaemates are uniformly thin, structureless, and

dark in thin section. In the Triassic, endozonal walls of stenolaemates are typically thicker and laminated (Boardman, 1984, fig. 4; Schäfer and Fois-Erickson, 1987; Zagorsek, 1992, among many others), so that the boundaries between endozones and exozones are generally poorly defined based on zooidal wall thickness. Thickened endozonal walls apparently appeared first in the Triassic and are typical of post-Triassic stenolaemates.

COMMUNICATION PORES.—Because of the differences in order-level classification, geologic time, and pore morphology, it is inferred herein that communication pores evolved independently first in the Ordovician in (1) the aberrant fixed-walled genera of *Kukersella* and *Diploclema*, presently placed in the Paleozoic Cyclostomata (see below), and in (2) the free-walled ceramoporinids belonging to the order Cystoporata (discussed above and below). With the exception of another aberrant genus, *Corynotrypa* (see below), undoubtedly communication pores have not been found again anywhere in the stenolaemates from the end of the Ordovician until the Jurassic, such that the lower Paleozoic species with communication pores are presently inferred to have become extinct (Boardman, 1984, fig. 12). In the Jurassic, it is inferred that communication pores evolved independently again in (1) a free-walled species with large endozonal communication pores and the essential characteristics again of the order Cystoporata (Boardman, 1984, fig. 8 G,H), (2) the free-walled cerioporinids discussed immediately above with the essential characteristics of the Trepostomata (Boardman, 1984, fig. 7A–C), (3) the free-walled species with the characteristics of the order Cryptostomata (Boardman, 1984, figs. 10, 11), and (4) the many post-Triassic species, either fixed-, fixed/free-, or free-walled, with vertical walls having either skeletal laminae that diverge outward or crystallites that are oriented at right angles to zooidal growth with outwardly growing laminae in chamber linings.

To explain further, the Ordovician fixed-walled genera *Kukersella* and *Diploclema* are considered aberrant herein because they have erect colony branches with unique internal configurations and because the living chambers of zooids are entirely enclosed by thick exozonal skeletal walls with a single communication pore at each end. *Kukersella* has frontal walls with large pseudopores, a single communication pore that connects with the thick-walled exozonal living chambers of adjacent zooids (Buttler, 1989), and axial thin-walled endozonal zooids with evenly spaced diaphragms that connect to the exozonal zooids (Boardman and Cheetham, 1973, fig. 11). *Diploclema* has frontal walls that lack pseudopores and has a single pore that connects the living chamber of zooids to unique unpartitioned extrazoooidal spaces (Boardman and Cheetham, 1973, figs. 12, 35). Stratigraphically between these two aberrant Ordovician genera and the Jurassic cyclostomes are approximately a dozen mostly early Paleozoic genera with delicate encrusting or erect colonies having frontal walls (Bassler, 1953), some of them reportedly lacking pseudopores

and communication pores (Brood, 1975). All of these genera need to be restudied. To demonstrate how poorly they are known, *Osburnostylus* was considered an Ordovician cyclostome genus with exterior frontal walls (Bassler, 1953:G43; Brood, 1975, pl. 8: fig. 2, pl. 11: figs. 1, 2), however, thorough sectioning revealed that the "frontal walls" were actually external homeomorphs consisting of interior extrazoooidal skeleton and that the genus is actually a free-walled articulated arthrostylid cryptostome (Blake, 1983b:563). Presently, excepting the genus *Corynotrypa*, no communication pores have been reported in cyclostomes between the single communication pores of the two Ordovician genera and the ubiquitous communication pores of the post-Triassic stenolaemates.

Corynotrypa has the simplest zoooidal skeleton possible for a bryozoan. Colonies are uniserial, and the single aligned zooids are drop-shaped with the wide ends oriented distally with subterminal skeletal apertures. Skeletons are entirely exterior with no interior vertical walls or outer body cavities, so nutrient exchange was only possible through skeletal pores. Asexual growth requires a skeletal pore connecting parent and daughter zooids (Boardman and Cheetham, 1973, fig. 33A,B). These single connecting pores are at least reproductive pores that exchanged nutrients during the formation of daughter cells. The exchange of nutrients among fully developed zooids apparently continued throughout life, as is indicated by the later inner-surface calcification of exterior terminal diaphragms, one of them apparently a calcified orificial wall (Taylor and Wilson, 1994, figs. 2, 4). These reproductive/communication pores are the only communication pores that are known to penetrate the exterior skeletal walls in stenolaemates. The genus *Corynotrypa* ranges from the Middle Ordovician to the Upper Permian (Taylor, 1985; Taylor and Wilson, 1994).

The lower Paleozoic suborder Ceramoporina of the free-walled order Cystoporata is partly characterized by vertical walls with laminae that grow inward and by communication pores that occur in seven of the nine genera of the suborder (Utgaard, 1983b:358). Five of the seven genera with communication pores are known only in the Ordovician, the other two genera are from the Silurian. The remainder of the Cystoporata, along with the orders Trepostomata and Cryptostomata, are well documented by thin sections through the Paleozoic (Moore, 1983), and no other communication pores have been reported until the Jurassic. This is certainly a time gap long enough to infer an independent origin of communication pores in the Ordovician/Silurian separate from the Jurassic communication pores, unless evidence is found to the contrary.

The mode of growth of communication pores is suggested by a stained cell or concentration of cells that are seen in each side of the pores in a few well preserved specimens (Figure 24c, small arrows; Boardman and Cheetham, 1973, fig. 28D). It is probable that the pores are formed by a cell or cells on each side of a zoooidal boundary that prevents calcification (Claus Nielsen, pers. comm., 1990). Once a communication pore is functioning, the special cells could regulate the transfer of

nutrients but not allow free passage of fluids (D.P. Gordon, pers. comm., 1989). The configuration of the laminae that surround the pores indicates no secondary solution of skeleton to open up the pores, so it is evident that the inhibiting cells from adjacent zooids must be in place at the edges of growing walls as calcification begins. Positioning together before calcification begins would permit cells from adjacent zooids to be perfectly superimposed as they are (Boardman et al., 1992:46, fig. 83a). Partial pore development from one side only does not seem to occur. Several rows of pores parallel to zoooidal growth occur in some taxa indicating that the cell, and therefore pore, locations in these species are precisely coordinated by adjacent zooids (Figure 25a). If all of this is true, these pore cells and their controls are herein inferred to have evolved independently in several different clades in stenolaemate history, and the communication pores are an automatic result each time.

FRONTAL WALLS.—A seemingly rare skeletal combination in post-Triassic stenolaemates includes inward-growing laminae in the vertical walls along with thick pseudopore-bearing frontal walls of Jurassic (Nye, 1976, pls. 23–26) and Lower Cretaceous (Nye, 1976, pls. 16–19; Boardman, 1983, fig. 33–4,5) genera, now placed in the cerioporinids. Another cerioporinid genus mixes inward-growing laminae with frontal walls of a different configuration in the Maastrichtian (Nye, 1976, pl. 50). These are potential Mesozoic examples of skeletal noncorrelations: comparable frontal walls that occur in a few species having inward-growing laminae and in the many species of the tubuliporines that have outward-growing laminae. The addition of communication pores in post-Triassic species of cerioporinids having the characteristics of Paleozoic trepostomes otherwise certainly provided new possibilities for morphologic inventions, such as independently evolved frontal walls.

Again for reasons of differences in order-level classification, geologic time, and morphology, the independent development of frontal walls is inferred herein for the three Mesozoic cerioporinid genera with inward-growing laminae cited in the preceding paragraph, and for the abundant post-Triassic tubuliporines with outward-growing laminae. Much earlier, there is no evidence that the frontal walls of the dozen or so encrusting and erect species of mostly early Paleozoic cyclostomes reportedly lacking pseudopores, and the three genera with huge pseudopores (Boardman and Cheetham, 1973, figs. 33D,F,G, 34, 35) had phylogenetic connections with Mesozoic frontal walls. Furthermore, Recent disporoloids (Figures 90–96) and heteroporoids (Figure 103a) demonstrate how readily frontal walls can be added within colonies, wherever needed, to complete apertures in species where they are not typical.

HISTORY AND SUMMARY.—The brief outline of stenolaemate evolution given above infers that the Paleozoic orders Cystoporata, Cryptostomata, and Trepostomata evolved directly into post-Triassic stenolaemates and independently

added communication pores to the inward-growing laminae of their vertical walls. Therefore, post-Triassic stenolaemates derived from the three Paleozoic orders are inferred herein to be primitive and polyphyletic at the order level. Not enough species have been studied internally to have an understanding of post-Triassic evolutionary patterns of species inferred to have this diverse Paleozoic heritage. One or more of these primitive clades could have become extinct by or within the Tertiary.

If this polyphyletic phylogeny proves to be generally true, the major problem remaining in understanding the order-level origins of post-Triassic stenolaemates is reduced to the origin or origins of the post-Triassic stenolaemates that have vertical walls with crystallites that grow perpendicular to zooidal growth, or vertical walls with laminae that grow outward parallel to zooidal growth. These two wall structures occur in five of the six Recent higher groupings used in the organization of this study.

The commonly accepted version of stenolaemate evolution, however, infers or implies that all post-Triassic stenolaemates are derived from encrusting runner- to sheet-like stomatopods, which are generally one layer of zooids thick, and that these simple species were the single source of the post-Triassic species and their ubiquitous communication pores (Brood, 1975; Taylor and Larwood, 1988, 1990; Anstey, 1990; Schäfer, 1991; McKinney, 1993). Stomatopods, as currently identified, apparently first appeared in the post-Paleozoic record in the Upper Triassic (Taylor and Sequeiros, 1982; Taylor and Michalik, 1991) and have fixed orificial walls with frontal walls and vertical interior walls, thus they are placed in the order Cyclostomata. Therefore, in this version, all post-Triassic stenolaemates are considered to belong monophyletically to the cyclostomes.

This monophyletic phylogeny requires that all Paleozoic orders, except for the Cyclostomata, became extinct by the end of the Triassic. The simple stomatopod cyclostomes are inferred to be the source of the newly evolved Mesozoic stenolaemates, which have the correlated primitive characteristics of the three major Paleozoic orders. At the same time, the stomatopods had to begin evolving the root stocks of the advanced and even more complex taxa of most of the future stenolaemates. This requires an explosion of viable mutations and high evolutionary rates in all directions, and it requires the order Cyclostomata to embrace a greater morphologic diversity than all four of the complex Paleozoic orders combined. Although there have always been many times more species than can be recovered as fossils, this phylogeny also infers that the future of the stenolaemates was hanging by a thread, the stomatopods, the only known cyclostomes around the time of the Triassic/Jurassic boundary (Anstey, 1990, fig. 10.2; Taylor and Larwood, 1988, fig. 5.5B).

It is important to investigate the Mesozoic species with stomatopod growth habits because nothing of significance has been published concerning their interiors (only published

sections of runner-like species in Boardman and Cheetham, 1973, fig. 33C–G, one Ordovician and one Pliocene). We know nothing of their heritable potential because we know nothing of the growth direction of crystallites and laminae in the vertical walls, the occurrence of communication pores, nor how the colonies grew. This basic information is required as a starting point in looking for possible species that can give rise to the necessary transitional morphology that leads to the more complex post-Triassic stenolaemates. For example, stomatopods apparently have ancestrulae with exterior outer skeletons throughout life that fix their orificial walls, as in the complex cinctiporids (Boardman and Cheetham, 1973, fig. 10). Because of growth restrictions, the zooids immediately following must have proximal exterior walls, so their orificial walls must either remain fixed or be fixed/free (Boardman et al., 1992, fig. 5). It would be most reassuring if the early Mesozoic stomatopods with outward-growing laminae and communication pores led through transitional species to the more complex taxa with comparable fixed-walled ancestrulae, laminae, and pores.

The long ranging patterns of comparative, correlated, and transitional skeletal evidence occurring in the fossil record, accompanied by a basic understanding of biologic function and significance, must provide some measure of phylogenetic and taxonomic information without polypides being available, as has always been assumed. The communication systems, skeletal microstructures, and polypides are protected by enclosed body chambers and are uniform within the overwhelming majority of colonies and species. In addition, intrazooidal skeletal features, such as basal diaphragms, hemiphagms, cystiphagms, and hemisepta should have some direct relationships with polypide morphology, and, as these features are also protected by the enclosed body chambers, they should be significant taxonomic characters that are largely genetically controlled.

NONCORRELATED PARTS THROUGH TIME

There is no convincing evidence as yet of the origin or origins of early Paleozoic bryozoans (see Larwood and Taylor, 1979, for review), but the earliest fossilized species certainly had much less skeletal diversity and probably much less anatomical diversity than is found in post-Triassic stenolaemates. The lower diversities should have resulted in a higher percentage of correlations of polypide and skeletal features among major clades. If true, these correlations should make possible nested classifications having phylogenetic significance in early stenolaemates.

Fortunately, thin sections have been made and internal characteristics have been described from Paleozoic stenolaemate since the 1880s, so we can say with some assurance that the classifications of early Paleozoic stenolaemates do seem to be relatively straightforward and without noncorrelations at higher taxonomic levels. As described above, many character states are long ranging, providing reasonably clearcut

differences among taxa above the species level. Some occurrences of comparable skeletal structures across presumed clades require polythetic descriptions of taxa (taxa based on possession of characteristics common to a majority of the members), but these descriptions seem usable at the family and order level. After a long and complex evolutionary history of extinctions and newly evolved morphology, however, transitional and noncorrelated skeletal morphology appears between the upper Paleozoic trepostomes and dendroid cryptostomes, which make some taxonomic assignments controversial, even at the order level (see also Blake, 1980).

Little can be said about polypides in fossil stenolaemates, of course. In the Paleozoic, remnants of polypide outlines are preserved in a few trepostomes (Boardman, 1971; Boardman and McKinney, 1976) and cystoporates (Utgaard, 1973). In both orders, the living chambers of many lower Paleozoic species are shortened by basal diaphragms, and polypide remnants indicate that the relatively short polypides retracted to the bottoms of the chambers and filled the available space. Each regenerated polypide probably sat on its own newly calcified basal diaphragm, thus a progressive polypide cycle is indicated as the zooidal skeletons grew in length. Attachment organs, however, are not surely identifiable. A general type of polypide is perhaps indicated, as the polypide outlines sitting on basal diaphragms are quite uniform. If this is true, the occurrence of basal diaphragms extending into the post-Triassic stenolaemates is most significant. Calcified basal diaphragms have not been found in most post-Triassic stenolaemates or in all Recent species studied to date.

Some higher taxonomic categories in the Paleozoic, such as the fenestrates, have such short zooidal body chambers that there seems no room for progressive polypide cycles. Thus, stationary polypide cycles apparently prevailed.

A less direct indication of restricted polypide anatomy in the Paleozoic might be inferred from the unusual, perfectly square and aligned cross sections of zooids in the endozones of six trepostome genera scattered throughout the Paleozoic (Boardman and McKinney, 1976). If polypides have a measure of control over budding and zooidal arrangements in branches, it would seem reasonable that only one general kind of polypide could produce such a geometrically perfect arrangement in these six genera. The outlines in two of these Ordovician genera indicate relatively short polypides of the same general shape. Five of the six genera were identified with different families, based on exozonal characters, and the family of the sixth was undetermined. Consequently, the genera were not linked phylogenetically at the family level in the study. Ancestral species were found for three of the genera based on comparable exozones and transitional endozones. Thus, the quadrate zooids were interpreted to have developed independently at least five times. This repeated convergence of a rare skeletal characteristic suggests that comparable polypides were capable of producing exozonal skeletal morphology in these six Paleozoic genera (probably families) as varied as the skeletal

morphology produced by the polypide of the Recent cinctiporids described above.

Indications of relatively long polypides occur in a Devonian (Boardman, 1971, fig. 4) and a Mississippian (McKinney, 1969, figs. 1–8) species in the form of actual preserved membranes, which probably indicate at least one other kind of polypide in the Paleozoic.

In the Jurassic, the stenolaemates underwent a rapid radiation of new taxa (Taylor and Larwood, 1990, fig. 10.3). It is inferred herein that the new taxa, evolved from surviving Paleozoic clades with primitive character states, were joined by new clades with advanced character states, as described in "Taxonomic Characters and Stenolaemate Phylogeny," above. All the clades evolved communication pores for nutrient exchange that permitted growth throughout colonies. Communication pores made possible the development of many advanced features, including exterior zooidal skeletal walls, exterior peristomes, exterior terminal diaphragms, and brood chambers with exterior skeletal covers. Brood chambers first appeared in the Paleozoic (for a review see Taylor and Larwood, 1990:221), but, lacking communication pores, they apparently could only develop interior skeletal covers. Also with the development of communication pores, orificial walls could be commonly fixed, compressed, or fixed/free, in addition to being free. Communication pores even made possible the extreme morphological variations within colonies of exterior and interior skeletal structures found in the dispoirelloids, heteroporoids, and cinctiporids.

The nutrient exchanges made possible by communication pores in post-Triassic species apparently contributed to the increasing numbers of noncorrelations of morphology and anatomy across primitive and advanced clades beginning in the Jurassic. The potential for the wider distribution of non-correlated parts was available, apparently to the level seen in the Recent species discussed herein. It seems that the longer the evolutionary history, (1) the greater the diversity of character states available, (2) the more numerous the distribution of noncorrelated parts across clades, and (3) the less inclusive and adequate polythetic descriptions become, thus phylogenies and assignments to higher categories become more controversial.

Conclusions

SKELETAL FEATURES

The free-walled Stenolaemata have outermost colony-wide membranous walls that cover confluent outer body cavities. The vast majority of Paleozoic and Triassic species are free-walled, have inward-growing laminae, and lack communication pores. Necessarily, they calcify all skeletons, including extrazoidal structures, only on their outer membranous and skeletal surfaces open to nutrients from outer body cavities. As a result, these species grow interior skeletal walls but not

exterior skeletal walls above exterior basal colony walls. Diaphragms are calcified on the outer surfaces of membranes and are interior structures. In some Paleozoic species, the directional effects of the laminae growing on outer surfaces can be seen where the laminae overlap edges of the hemisepta, hemiphragms, and ring septa and turn inward (illustrated by Gautier, 1970; Blake, 1983b).

The fixed-walled *Stenolaemata* with primary frontal walls have outermost colony-wide skeletal walls of exterior frontal walls of zooids that close confluent outer body cavities below budding zones. The vast majority of fixed-walled species are post-Triassic. Their interior vertical walls have communication pores and laminae that either grow outward or crystallites that grow at right angles to the zooidal growth directions. Necessarily, they calcify skeleton only on the inner surfaces that receive nutrients through communication pores, and, apparently, they cannot grow extrazoidal skeleton. As a result, these species grow interior vertical walls at budding zones and proximally attach primary exterior frontal walls and exterior terminal diaphragms to them. In some post-Triassic species, the directional effects of laminae growing on the inner surfaces can be seen where the laminae overlap the edges of hemisepta and hemiphragms and turn outward (Figures 5, 22, 23), just the opposite of Paleozoic species.

In a few Ordovician and all post-Triassic species, which are highly integrated with both confluent and outer body cavities and communication pores, terminal diaphragms are calcified on the inner surfaces of membranes and are exterior, indicating that communication pores are a source of nutrients after polypide life activities end. A few post-Triassic species having outer body cavities, communication pores, and inward-growing laminae in vertical walls can calcify terminal diaphragms on both surfaces to form interior structures. Post-Triassic colonies that have some free-walled zooids, plus zooids that combine exterior and interior walls in the same zooids, also have exterior terminal diaphragms.

Exterior skeleton that is calcified on inner surfaces reliably predicts the presence of communication pores in species where they are few and difficult to find in sections.

Because of growth restrictions, zooids with frontal walls can only produce proximal frontal walls in the next generation, whether they are fixed-walled ancestrulae or, in later generations, fixed-walled feeding zooids. Therefore, zooids of a generation immediately following a fixed-walled generation can only be fixed or fixed/free-walled (Boardman et al., 1992, figs. 5, 59).

The spacing of the apertures of feeding zooids on colony surfaces of most *stenolaemates* having inward-growing laminae under their outer body cavities is achieved by either the thickness of vertical walls, the intervening polymorphs, the extrazoidal skeleton, or by a combination of these factors. In most fixed-walled species with communication pores, the wider spacing of apertures of feeding zooids on colony surfaces is achieved by exterior frontal walls.

In heteroporoids and cinctiporids, extremely thin exterior skeletal peristomes are calcified by the zooids themselves, and their distribution apparently is subject to microenvironmental pressures because they are irregularly distributed within colonies.

Based on the observations of the skeletal microstructure of *stenolaemates* of all ages and the more definitive ultrastructural studies recently published by others, it seems that crystallites originate predominantly at the ends of vertical walls at zooidal boundary zones. As crystallites grow away from the boundary zones, they either grow at right angles to the zooidal growth direction or they combine to form laminae that grow either inward or outward relative to the zooidal growth direction.

The microstructure of each of the skeletal structures within a colony or a species of *stenolaemates* is generally constant and, therefore, seems to provide reasonably reliable genetically controlled character states. Skeletal microstructures and intra-zooidal skeletal structures are calcified within the body cavities, so theoretically they are protected to some degree from the external environment.

In contrast, the configurations of primary exterior frontal walls can be extremely adaptable and can vary within colonies as required to complete zooidal walls or to react to external microenvironments. For example, free-walled disporoids can develop scattered partial exterior frontal walls to complete fixed/free skeletal apertures, and free-walled heteroporoids can develop partial frontal walls to support peristomes or to complete apertures.

Apparently, membranous exterior walls can secondarily calcify themselves locally in colonies of the free-walled species *Cinctipora elegans*. The resulting exterior skeletal walls are of colony origin and indicate the position of membranous walls during life, extending from zooidal peristomes over skeletal shields and simulating primary frontal walls.

POLYPIDE FEATURES

The anatomical diversity found in this collection of unique hard/soft sections of Recent *stenolaemates* is greater than anticipated. Interpretations of the anatomy and the accompanying skeletal morphology relative to the most general mode of growth and life functions of the zooids seem understandable and tend to reinforce each other.

Recent *stenolaemate* polypides have evolved at least three basic mechanisms for the protrusion of tentacles, one with attachment organs and two lacking them. The species that have attachment organs maintain polypide positions in the living chambers within short, functionally constant distances from the advancing skeletal apertures by progressive polypide cycles so that the tentacles can always be protruded fully. Progressive polypide cycles are accomplished by the attachment organs taking up new outward positions and originating new regenerating polypides with each cycle. Early in regenerative growth,

undersized polypides begin to feed, thus requiring the retractor muscles to shift their functional attachment positions to the skeletons inward as polypide growth proceeds. Six variations in attachment organ anatomy are readily recognizable in 29 species in this collection.

Species that lack attachment organs demonstrate a wide variety of solutions to solving the problems of tentacle protrusion. All but one of the species, throughout life, retracts the polypide to a constant position at or near the bottom of the living chamber. Polypide cycles in these species are stationary, and no shifting of retractor muscle attachments to the skeleton is required for feeding during regenerative growth. Protrusion distances increase as the feeding zooids grow in length, and they can be extremely long relative to the polypide length. The full protrusion of tentacles in these species is accomplished primarily either by fixed or by movable and pleated membranous sacs, which are long enough to squeeze the polypides outward to the most distant skeletal apertures. Three major variations in the protrusion anatomy of this group are recognized in just six available species.

The third basic mechanism for tentacle protrusion occurs in just two species and features progressive polypide cycles, which lack attachment organs, and instead have horny transverse valves. Unfortunately, little is understood about their growth and function.

It is apparent from colonies that have combinations of free, compressed, fixed, and/or fixed/free orificial walls below budding zones that the same stenolaemate polypides can function adequately in all four circumstances. Those terms describing orificial walls, therefore, are descriptive and have significance in describing mode of growth and nutrient exchange but have little, if any, significance in defining tentacle protrusion. This is further evidence that membranous sacs confine the hydrodynamics of tentacle protrusion to the endosaccal cavities (coeloms) as originally described (Nielsen and Pedersen, 1979), thus making the exosaccal cavities (pseudocoels) and either solid or porous skeletal walls merely passive supporting structures.

In summary, this collection of just 37 species chosen haphazardly contains 10 variations in protrusion anatomy, a rich and unexpected harvest. How many more variations would be revealed by internal studies of a representative number of species in the class is an exciting question.

PHYLOGENY AND CLASSIFICATION

The unexpected diversity of polypide anatomy discovered, together with the confusing noncorrelations between the characteristics of skeletons and soft parts, indicates that species concepts must include both external and internal characters of colonies for use in phylogenetic studies and for future supraspecific classifications.

This diversity and its noncorrelations indicate that phylogen-

etic trends and natural classifications of stenolaemates are more complex and more difficult to recognize than previously supposed. It seems that they can only be realized, if at all, by extensive evidence of comparative morphology and anatomy closely spaced in time and geography. It is also evident that the evolution of the post-Triassic stenolaemates has been too complex and their features are too interwoven to divide the class into Borg's monothetically stated single- and double-walled divisions.

Qualitative polypide anatomy and skeletal microstructure are commonly uniform within Recent colonies and species. This uniformity means that routine taxonomic procedures generally require just one determination of these internal characters per species. Other internal characters require more evidence.

The growth directions of skeletal crystallites and laminae, the methods of nutrient exchange, and the associated characteristics in the fossil record apparently provide some measure of phylogenetic patterns and taxonomic information where polypide anatomy is not available. Contrary to prevailing thought, these skeletal characteristics suggest that some of the Paleozoic and Triassic Cystoporata, Cryptostomata, and Trepostomata evolved directly into post-Triassic species to join with new Mesozoic clades, so that post-Triassic stenolaemates are considered polyphyletic at the order level.

The lack of correlation of the complex polypide anatomy and skeletal morphology in five of the six groupings of genera and species used to organize this paper, plus the fossil record of the stenolaemates suggests that the longer the evolutionary history (1) the greater the diversity of character states available, (2) the more numerous the distribution of noncorrelated parts across groupings, and (3) the less inclusive and adequate polythetic descriptions become, thus phylogenies and assignments to higher categories become more controversial.

Given the great diversity of features and their lack of correlation in Recent species, not enough species are available in this study to hope to recognize detailed skeletal/anatomical phylogenetic patterns. A detailed study of many more Recent species, would, no doubt, further divide the five groupings used herein. If so, some phylogenetic and related classifications might be determined by starting from clusters of Recent species having comparable polypides and skeletal characteristics and, as was done with the cinctiporids, work backwards in time using transitional skeletal characteristics.

The lack of skeletal/anatomical correlation in this study, however, also suggests the possibility that so many noncorrelations have developed across clade boundaries that Recent stenolaemates are an example of a "mosaic distribution of primitive and advanced states. ... Mosaic patterns, in which primitive states of one character frequently persist or occasionally reappear in combination with advanced states of another, typify much of cheilostome morphology" (Cheetham, 1986:165). If this is also generally true for stenolaemates, any sort of natural classification for much of the post-Triassic and Recent species seems unlikely.

Literature Cited

- Alvarez, J.A.
1992. Sobre algunas especies de la familia Lichenoporidae Smitt, 1866 (Bryozoa, Cyclostomida) en la region Atlantico-Mediterranea; Parte I: genero *Disporella* Gray, 1848. *Cahiers de Biologie Marine*, 33(2):201–243, 18 figures.
- Anstey, R.L.
1990. Bryozoans. In K.J. McNamara, editor, *Evolutionary Trends*, pages 232–252, 5 figures, 2 tables. London: Belhaven Press.
- Bassler, R.S.
1953. Bryozoa. In Raymond C. Moore, editor, *Treatise on Invertebrate Paleontology*, Part G, Bryozoa, 253 pages, 175 figures. Lawrence, Kansas: The University of Kansas Press for the Geological Society of America.
- Blake, D.B.
1980. Homeomorphy in Paleozoic Bryozoans: A Search for Explanations. *Paleobiology*, 6(4):451–465, 5 figures.
1983. Systematic Descriptions for the Suborder Rhabdomesina. In Raymond C. Moore, editor, *Treatise on Invertebrate Paleontology*, Part G, Bryozoa, Revised, (1):550–592, figures 271–295. Lawrence, Kansas: The University of Kansas Press for the Geological Society of America.
- Boardman, R.S.
1971. Mode of Growth and Functional Morphology of Autozooids in Some Recent and Paleozoic Tubular Bryozoa. *Smithsonian Contributions to Paleobiology*, 8: 55 pages, 6 figures, 11 plates.
1973. Body Walls and Attachment Organs in Some Recent Cyclostomes and Paleozoic Trepostomes. In G.P. Larwood, editor, *Living and Fossil Bryozoa. Proceedings of the Second Conference International Bryozoology Association*, pages 231–245, 4 figures, 3 plates. London and New York: Academic Press.
1975. Taxonomic Characters for Phylogenetic Classifications of Cyclostome Bryozoa. In S. Pouyet, editor, *Bryozoa 1974. Documents des Laboratoires de Geologie de la Faculte des Sciences de Lyon*, 3(2):595–606, 4 plates.
1983. General Features of the Class Stenolaemata. In Raymond C. Moore, editor, *Treatise on Invertebrate Paleontology*, Part G, Bryozoa, Revised, (1):49–137, figures 25–63. Lawrence, Kansas: The University of Kansas Press for the Geological Society of America.
1984. Origin of the Post-Triassic Stenolaemata (Bryozoa): A Taxonomic Oversight. *Journal of Paleontology*, 58(1):19–39, 12 figures.
- Boardman, R.S., and A.H. Cheetham
1969. Skeletal Growth, Intracolony Variation, and Evolution in Bryozoa; a Review. *Journal of Paleontology*, 43:205–233, 8 figures, plates 27–30.
1973. Degrees of Colony Dominance in Stenolaemate and Gymnolaemate Bryozoa. In R.S. Boardman, A.H. Cheetham, and W.A. Oliver, Jr., editors, *Animal Colonies*, pages 21–220, 40 text-figures. Stroudsburg, Pennsylvania: Dowden, Hutchinson, and Ross.
- Boardman, R.S., and F.K. McKinney
1976. Skeletal Architecture and Preserved Organs of Four-sided Zooids in Convergent Genera of Paleozoic Trepostomata (Bryozoa). *Journal of Paleontology*, 50(1):25–78, 18 figures, 16 plates.
- Boardman, R.S., F.K. McKinney, and P.D. Taylor
1992. Morphology, Anatomy, and Systematics of the Cinctiporidae, New Family (Bryozoa: Stenolaemata). *Smithsonian Contributions to Paleobiology*, 70: 81 pages, 137 figures.
- Boardman, R.S., and John Utgaard
1964. Modifications for Study Methods for Paleozoic Bryozoa. *Journal of Paleontology*, 38:768–770.
- Borg, Folke
1926. Studies on Recent Cyclostomatous Bryozoa. *Zoologiska Bidrag fran Uppsala*, 10:181–507, 109 figures, 14 plates.
1933. A Revision of Recent Heteroporidae (Bryozoa). *Zoologiska Bidrag fran Uppsala*, 14:253–394, 29 text-figures, 14 plates.
1941. On the Structure and Relationships of *Crisina* (Bryozoan, Stenolaemata). *Arkiv för Zoologi*, 33A(11):1–44, 16 text-figures, 4 plates.
1944. The Stenolaematous Bryozoa. In S. Bock, editor, *Further Results of the Swedish Antarctic Expedition 1901–1903*, 3(5):1–276, 26 figures, 16 plates. Stockholm: P.A. Norstedt and Söner.
- Brood, Krister
1972. Cyclostomatous Bryozoa from the Upper Cretaceous and Danian in Scandinavia. *Stockholm Contributions in Geology*, 26:1–464, 148 figures, 78 plates.
1975. Cyclomatous Bryozoa from the Silurian of Gotland. *Stockholm Contributions in Geology*, 28(3):45–119, 19 figures, 16 plates.
1976. Wall Structure and Evolution in Cyclostomatous Bryozoa. *Lethaia*, 9:377–389, 11 figures.
1977. Upper Cretaceous Bryozoa from Need's Camp, South Africa. *Palaeontologia Africana*, 20:65–82.
- Buttler, Caroline J.
1989. New Information on the Morphology and Skeletal Ultrastructure of the Ordovician Cyclostome Bryozoan *Kukersella* Toots, 1952. *Palaeontologische Zeitschrift*, 63:215–227, 6 figures.
- Canu, Ferdinand, and R.S. Bassler
1920. North American Early Tertiary Bryozoa. *United States National Museum Bulletin*, 106: 879 pages, 279 text-figures, 162 plates.
1929. Bryozoa of the Philippine Region. *United States National Museum Bulletin*, 100(9): 685 pages, 94 plates, 224 figures.
- Carle, K.J., and E.E. Ruppert
1983. Comparative Ultrastructure of the Bryozoan Funiculus: A Blood Vessel Homologue. *Sonderdruck aus Zeitschrift für Zoologische Systematik und Evolutionsforschung*, 21:181–193, 19 figures.
- Cheetham, A.H.
1986. Branching, Biomechanics and Bryozoan Evolution. *Proceedings of the Royal Society of London*, 228:151–171, 13 figures.
- Gautier, T.G.
1970. Interpretive Morphology and Taxonomy of Bryozoan Genus *Tabulipora*. *University of Kansas Paleontological Contributions, Paper*, 48: 21 pages, 8 plates, 9 figures.
- Harmelin, J.-G.
1976. Le sous-ordre de Tubuliporina (Bryozoaires Cyclostomes) en Mediterranee ecologie et systematique. *Mémoires de l'Institut Océanographique*, Monaco, 10:1–326, 50 text-figures, 38 plates.
- Hayward, P.J., and J.S. Ryland
1985. Cyclostome Bryozoans: Keys and Notes for the Identification of the Species. *Synopses of the British Fauna, new series*, 34:1–147.
- Larwood, G.P., and P.D. Taylor
1979. Early Structural and Ecological Diversification in the Bryozoa. In M.R. House, editor, *Systematics Association Special Volume*, 12, pages 209–234, 8 figures. London and New York: Academic Press.
- Merida, J.E., and R.S. Boardman
1967. The Use of Paleozoic Bryozoa from Well Cuttings. *Journal of Paleontology*, 41:763–765, plate 100.
- McKinney, F.K.
1969. Organic Structures in a Late Mississippian Trepostomatous Ectoproct (Bryozoan). *Journal of Paleontology*, 43:285–288, 1 figure, 1 plate.

McKinney, F.K., and R.S. Boardman

1985. Zooidal Biometry of Stenolaemata. In Claus Nielsen and G.P. Larwood, editors, Bryozoa, Ordovician to Recent. *Proceedings of the Sixth Conference International Bryozoology Association*, pages 193–203, 8 figures. Fredensborg, Denmark: Olsen and Olsen.

McKinney, F.K., P.D. Taylor, and V.A. Zullo

1993. Lyre-shaped Hornerid Bryozoan Colonies: Homeomorphy in Colony Form between Paleozoic Fenestrata and Cenozoic Cyclostomata. *Journal of Paleontology*, 67(3):343–354, 7 figures.

Moore, Raymond C., editor

1983. *Treatise on Invertebrate Paleontology*. Part G, Bryozoa, Revised, (1): 625 pages, 295 figures. Lawrence, Kansas: The University of Kansas Press for the Geological Society of America.

Nicholson, H.A.

1880. On the Minute Structure of the Recent *Heteropora neozelanica* Busk, and on the Relations of the Genus *Heteropora* to *Monticulipora*. *Annals and Magazine of Natural History*, series 5, 6(35): 329–339, 414–423, 5 figures. [Paper in two parts.]

1881. *On the Structure and Affinities of the Genus Monticulipora and Its Subgenera, with Critical Descriptions of Illustrative Species*. 240 pages, 50 text-figures, 6 plates. Edinburgh, Scotland: William Blackwood and Sons.

Nielsen, Claus

1970. On Metamorphosis and Ancestrula Formation in Cyclostomatous Bryozoans. *Ophelia*, 7:217–256, 41 figures.

Nielsen, Claus, and K.G. Pedersen

1979. Cystid Structure and Protrusion of the Polypide in *Crisia* (Bryozoa, Cyclostomata). *Acta Zoologica*, 60(2):65–88, 24 figures.

Nye, O.B., Jr.

1976. Generic Revision and Skeletal Morphology of Some Cerioporid Cyclostomes (Bryozoa). *Bulletin of American Paleontology*, 69(291): 222 pages, 20 figures, 51 plates.

Nye, O.B., Jr., D.A. Dean, and R.W. Hinds

1972. Improved Thin Section Techniques for Fossil and Recent Organisms. *Journal of Paleontology*, 46:271–275, 1 plate.

Orbigny, A.D., d'

1854. Bryozoaires. In *Paléontologie Française, Terrains Crétacés*, 5: 985–1192, plates 600–800. Paris: Masson.

Ross, J.R.P.

1973. Calcification in the Colonial Stenolaemate, *Heteropora*. In G.P. Larwood, editor, Living and Fossil Bryozoa. *Proceedings of the Second International Bryozoology Association*, pages 475–483, 4 figures. London and New York: Academic Press.

Schäfer, Priska

1986. On the Gizzard in the Bryozoan Genus *Diaperoecia* Canu (Order Tubuliporata). *Senckenbergiana Maritima*, 17:253–277, 3 figures, 3 plates.

1991. Brutkammern der Stenolaemata (Bryozoa): Konstruktionsmorphologie und phylogenetische bedeutung. *Courier Forschungsinstitut Senckenberg*, 136: 147 pages, 76 figures, 56 tables.

Schäfer, Priska, and E. Fois-Erickson

1987. Systematics and Evolution of Triassic Bryozoa. *Geologica et Palaeontologica*, 21:173–225, 2 text-figures, 14 tables, 15 plates.

Silen, Lars, and J.-G. Harmelin

1974. Observations on Living Diastoporidae (Bryozoa, Cyclostomata) with Special Regard to Polymorphism. *Acta Zoologica*, 55:81–96, 22 figures.

Taylor, P.D.

1981. Functional Morphology and Evolutionary Significance of Differing Modes of Tentacle Eversion in Marine Bryozoans. In G.P. Larwood and Claus Nielsen, editors, Recent and Fossil Bryozoa. *Proceedings of the Fifth Conference International Bryozoology Association*, pages 235–247, 4 figures. Fredensborg, Denmark: Olsen and Olsen.

1985. Carboniferous and Permian Species of the Cyclostome Bryozoan *Corynotrypa* Bassler, 1911 and Their Clonal Propagation. *Bulletin of the British Museum (Natural History)*, Geology, 38(5):359–372, 13 figures.

1986. Scanning Electron Microscopy of Uncoated Fossils. *Palaeontology*, 29(4):685–690, plate 52.

Taylor, P.D., and C.G. Jones

1993. Skeletal Ultrastructure in the Cyclostome Bryozoan *Hornera*. *Acta Zoologica*, 74(2):135–143, 5 figures.

Taylor, P.D., and G.P. Larwood

1988. Mass Extinctions and the Pattern of Bryozoan Evolution. In G.P. Larwood, editor, Extinction and Survival in the Fossil Record. *Systematics Association Special Volume*, 34:99–119, 6 figures.

1990. Major Evolutionary Radiations in the Bryozoa. In P.D. Taylor and G.P. Larwood, editors, Major Evolutionary Radiations. *Systematics Association Special Volume*, 42:209–233, figures 10.1–10.6.

Taylor, P.D., and J. Michalik

1991. Cyclostome Bryozoans from the Late Triassic (Rhaetian) of the West Carpathians, Czechoslovakia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 182(3):285–302, 7 figures.

Taylor, P.D., and L. Sequeiros

1982. Toarcian Bryozoans from Belchite in North-east Spain. *Bulletin of the British Museum (Natural History)*, Geology, 36(2):117–129, 10 figures.

Taylor, P.D., M.J. Weedon, and C.G. Jones

1995. Skeletal Ultrastructure in Some Cyclostome Bryozoans of the Family Lichenoporidae. *Acta Zoologica*, 76(3):205–216, 6 figures.

Taylor, P.D., and Mark A. Wilson

1994. *Corynotrypa* from the Ordovician of North America: Colony Growth in a Primitive Stenolaemate Bryozoan. *Journal of Paleontology*, 68(2):241–257, 14 figures.

Utgaard, John

1973. Mode of Colony Growth, Autozooids, and Polymorphism in the Bryozoan Order Cystoporata. In R.S. Boardman, A.H. Cheetham, and W.A. Oliver, Jr., editors, *Animal Colonies*, pages 317–360, 74 figures. Stroudsburg, Pennsylvania: Dowden, Hutchinson, and Ross.

- 1983a. Paleobiology and Taxonomy of the Order Cystoporata. In Raymond C. Moore, editor, *Treatise on Invertebrate Paleontology*, Part G, Bryozoa, Revised, (1):327–357, figures 142–155. Lawrence, Kansas: The University of Kansas Press for the Geological Society of America.

- 1983b. Systematic Descriptions for the Order Cystoporata. In Raymond C. Moore, editor, *Treatise on Invertebrate Paleontology*, Part G, Bryozoa, Revised, (1):358–439, figures 156–215. Lawrence, Kansas: The University of Kansas Press for the Geological Society of America.

Voigt, Ehrhard

1968. Homoeomorphy in Cyclostomatous Bryozoa as Demonstrated in *Spiropora*. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale*, 108:43–53, 3 figures.

1977. *Infundibulipora huckriedei* n. sp. (Bryoz. Cyclostomata) from the Upper Cretaceous of Iran and Western Europe; With Remarks on the Genus *Infundibulipora* Brood, 1972. *Journal of the Palaeontological Society of India*, 20:230–236, 5 plates.

Weedon, M.J., and P.D. Taylor

1995. Calcitic Nacreous Ultrastructures in Bryozoans: Implications for Comparative Biomineralization of Lophophorates and Molluscs. *Biological Bulletin*, 188:281–292, 18 figures.

Zagorsek, Kamil

1992. Comparison between Triassic Trepostomata, Recent Cyclostomata and Paleozoic Trepostomata (Bryozoa); and One Question in Addition. *Acta Universitatis Carolinae—Geologica*, 1–2:145–149, 2 plates.