ULTRASTRUCTURE AND SKELETAL DEVELOPMENT IN CHEILOSTOMATE BRYOZOA

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Calcification of cheilostomate bryozoan skeletons is often rapid, so that intermediate morphologies can be difficult to observe, even in living colonies. Most of the ontogenetic gradient is in the fragile, distal colony margin, which is most susceptible to breakage, abrasion, or corrosion. Banta (1970, p. 52–53) and Cook (1973b, p. 259) noted that it is difficult to determine ontogenetic differences in fossil or dry material lacking cuticle or epidermal layers, or even in dissected mature colonies. Nevertheless, the data available in fossil cheilostomates are the skeletons, without soft tissues, but with diverse, distinctive morphologic features and ultrastructural details. Even many modern species are known only from dry material. Morphologic features, mainly of the frontal wall, have been of major importance in taxonomic and functional studies of cheilostomates.

Bryozoan skeletons, like mollusk and brachiopod shells, grow by continuous additive calcification. Earlier ontogenetic states are preserved in each zooecium, but are mostly covered by later skeletal increments. As noted by Banta (1970), major developmental differences may be obscured by the similar mature morphology of such ontogenetically different groups as **umbonuloids** (ascophorans with the frontal shield formed by calcification on the lower side of an **epifrontal fold**) and **lepralioids** (ascophorans with the frontal shield formed as a cryptocyst). Despite morphological similarities even at the microscopic structural level in the mature state, bryozoan skeletons developed by different ontogenetic modes should show recognizable differences at the ultrastructural level. In this discussion I briefly characterize skeletal ultrastructure among cheilostomates and consider to what degree ultrastructure can provide data for ontogenetic reconstructions and for taxonomic-phylogenetic inferences. First, however, it is advisable to consider whether studies of skeletal ultrastructure have actually accomplished their stated objectives. Following are some major reasons for ultrastructure studies and at least a preliminary evaluation of the usefulness of such studies.

ULTRASTRUCTURE AS A TAXONOMIC KEY

In a paleontologic parallel of the reductionist philosophy championed by some biologists, one might engage in ultrastructure studies in the hope that the very fine skeletal structure will afford a highly refined criterion for determining taxonomic relationships. Certainly, some organisms do produce skeletal crystals that, individually or in aggregate structural units, are distinctive. Most notable among these are the monocrystalline skeletal elements of echinoderms and the crossed-lamellar structure of mollusks. These, and various other distinctive arrangements of skeletal crystals, are indeed usable for taxonomic recognition, even in very fine fragments of skeletal debris (Majewske, 1969; Hay, Wise, & Stieglitz, 1970; Stieglitz, 1972). However, only fairly high-level taxonomic differentiation is possible, and, more importantly, not all organisms produce skeletal ultrastructures that are so distinctive or diagnostic, even at the class or phylum level. Indeed, small fragments of spherulitic aragonite produced by scleractinian corals, cheilostomate bryozoans, the modern cephalopod *Nautilus,* some codiacean algae, or even by inorganic, submarine cementation can be very difficult to distinguish (Sandberg, 1975a). It is usually the size and morphologic features of such ultrastructurally similar fragments that are diagnostic.

As the skeletal ultrastructure of bryozoans and diverse other groups has become better understood, it has become evident that ultrastructures are largely not taxonomically dependent. Rather they reflect the degree and nature of the **biological interference** that the organism exerts upon the calcification process. This vital effect is manifested in such things as the composition of the fluid medium from which skeletal precipitation occurs and the amount and distribution of organic matrix. Depending on the nature of that interference, the properties (for example, mineralogy, crystal morphology, cation makeup, stable carbon and oxygen isotope composition) of the resulting skeletal carbonates may resemble or differ by varying degrees from equivalent properties of actually or potentially coprecipitated inorganic carbonates (Sandberg, 1975a). On the basis of ultrastructural and mineralogical studies, it appears that biological interference with calcification may vary greatly both topographically or ontogenetically within skeletons of a single taxon, but also may show great similarities even among skeletons of diverse phyla. In addition to the common spherulitic structures discussed above, for example, much morphologic similarity exists among lamellar or "nacreous" skeletal units of cheilostomate bryozoans, brachiopods, and bivalves in their development of similar **screw-dislocation** structures (Fig. 102,*4,5*; 103,*3,4*; Williams, 1971b; Wada, 1972). It should be noted that, despite the morphological resemblance, the lamellar crystals are calcite in the bryozoans and brachiopods, but aragonite in the bivalves, presumably reflecting differences in biological interference.

Contrary to earlier hopes, ultrastructure is not a panacea for resolving questions of taxonomic relationships. Used cautiously within well-defined taxonomic units, ultrastructure can be taxonomically useful. However, because of the relationship between ultrastructure and both the general functional-structural properties of skeletons and the variable degree to which different organisms interfere with calcification, ultrastructure is not a broadly applicable, general taxonomic criterion.

ULTRASTRUCTURE AND SKELETAL GROWTH MODES AND SUCCESSIONS

Despite these taxonomic limitations, ultrastructure can be quite useful in understanding modes of skeletal development and ontogenetic or even phylogenetic changes in the nature of the skeletal material deposited. The basic patterns of skeletal growth in cheilostomates and their relationship to skeletal growth in other groups, notably mollusks, will be treated in greater detail later. For the moment, it is sufficient to say that distinctive ultrastructures and ultrastructural successions afford considerable information on growth of cheilostomate skeletons, the location of cuticles, and the structural-functional role of the skeleton in various groups. Successful interpretation of some fairly complex examples of cheilostomate skeletal growth has been possible on the basis of ultrastructure, even in fossil material. Such interpretations would previously have been available only from suitably prepared histologic samples or from observation of growth in living colonies. The implications for bryozoan paleontology are obvious.

The ultrastructural feature most promising for growth mode interpretations was called "parallel fibrous" ultrastructure (Sandberg, 1971) (see later discussion of exterior wall recognition). That term (parallel fibrous) has been used in various earlier papers, but leaves the reader with the question "parallel to what?" The growth to which that term has been applied is a form of two-dimensional **spherulitic ultrastructure** of the type discussed by Bryan (1941) and Bryan and Hill (1941). For the sake of clarity and to minimize proliferation of new terms, their descriptive term **planar spherulitic ultrastructure** will be used in this discussion. In cheilostomate bryozoans, this ultrastructure is the first calcification against the cuticle in exterior walls. It is fundamentally a two-dimensional spherulitic growth. An equivalent ultrastructure occurs on the undersides of dissepiments of scleractinian and tabulate corals. Significantly, in those latter groups it is also useful in selecting among various theories of dissepiment growth (WELLS, 1969). CHEETHAM (1971) related zooid structure to colony form, particularly with reference to calcification of frontal walls and its relationship to structural support of the colony. Knowledge of ultrastructural successions and of distributions of individual ultrastructures, particularly the planar spherulitic ultrastructure, can provide a clearer picture of development of the fundamental skeletal "box" of the zooecium and its later calcareous embellishments, and their relationship to such things as zooidal function, colonial morphology and stress distribution, and physiological changes during zooid ontogeny.

ULTRASTRUCTURE AND THE INTERPRETATION OF ANCIENT SKELETAL REMAINS

The skeletons we observe as fossils are the products of not only the biological interference that the organisms exerted on the calcification process, but also the vagaries of postmortem diagenetic effects. If we are to use ultrastructure for interpretation of fossil skeletons and their genesis, we must have a better understanding of the extent and nature of recrystallization than has been evident in much paleontologic literature. Some excursions into the areas of carbonate petrography and geochemistry are required for proper appreciation of the processes involved (for discussion of problems and reference to much of earlier literature, see BERNER, 1971; LIPPMANN, 1973; MILLIMAN, 1974; BATHURST, 1975; SANDBERG, 1975a,b).

It appears that, in the paleontological literature, "recrystallization" has been sometimes overworked and sometimes underestimated. The reasons for these two extremes are quite distinct. Overuse of inferred recrystallization to explain observed textures in fossil skeletons has resulted from too strict an adherence to analogy with modern inferred relatives and their skeletal products. For example, one argument that had rather wide acceptance earlier was—"The rugose corals, an extinct group, have lamellar or spherulitic calcite skeletons; these must have originally been spherulitic aragonite, the exclusive skeletal material of the modern relatives, the scleractinian corals." In interpretation of the original skeletal makeup of extinct taxa, the sort of analogy described above becomes increasingly less reliable as the taxonomic distance between the two groups increases. Furthermore, as discussed elsewhere (SANDBERG, 1975a) and briefly reviewed below, there are certain predictable patterns of diagenetic behaviors for the various skeletal carbonate phases. Knowledge of these patterns can be used to support or, as in the case of the rugose corals, refute inferences of original state of fossil skeletons.

Since the time of ROSE (1859) and SORBY (1863, 1879) it has been recognized that carbonate skeletons or skeletal parts of differing mineralogies and cation composition have varying susceptibilities to textural disruption by diagenesis. Solid-state processes have

FIG. 102. Growth surfaces of interior walls.——*1,2. Metrarabdotos tenue* (BUSK), rec., Caroline Sta. 68 off NE. Puerto Rico; *1,* frontal exterior, growth surface, etched, note numerous superimposed layers accreting laterally simultaneously in a manner analogous to gastropod nacre, ×8,000 (bar = 1 μm); *2,* detail of lower left region of *1,* ×16,000 (bar = 1 μm); both USNM 209434.——*3,4. Tremogasterina robusta* (HINCKS), rec., Perim Is., Aden, Red Sea; basal interiors, distal toward top of photograph; note rhombic crystal shapes, accretionary banding, and occasional screw dislocations; both ×5,000 (bar = 2 μm), BMNH 1966.2.24.1.——*5. Arachnopusia unicornis* (HUTTON), rec., N.Z.; basal interior; screw dislocations more common than in *3,4* and accretionary banding virtually absent; ×2,000 (bar = 5 μm), BMNH 1886.6.8.4–5.——*6. Labioporella calypsonis* COOK, rec., Konakrey, Senegal; frontal exterior of cryptocyst near distal edge; note overlapping flat crystals and numerous, minute screw dislocations; ×4,900 (bar = 2 μm), BMNH 1964.9.2.31.

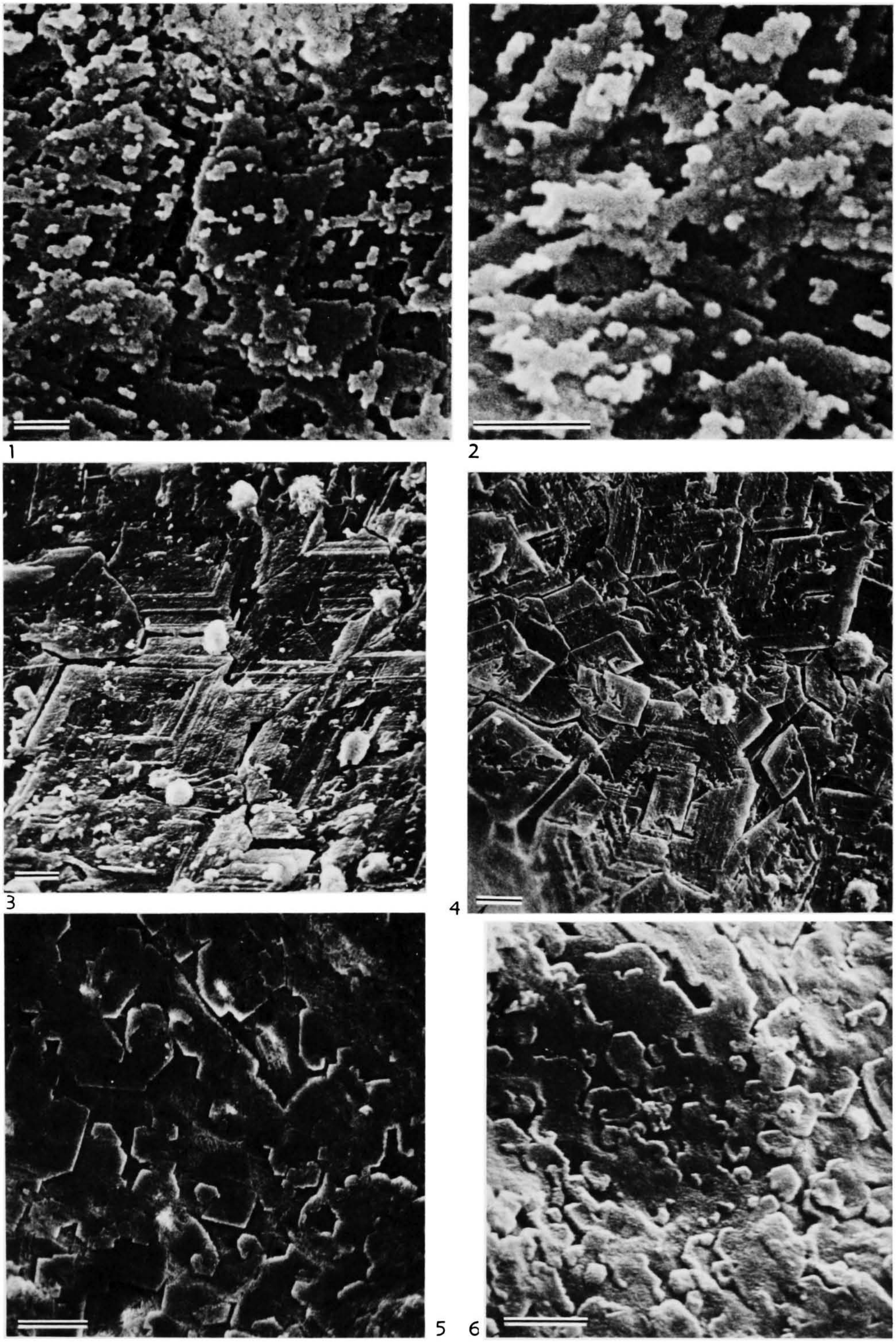

FIG. 102. *(For explanation, see facing page.)*

sometimes been invoked to explain observed textural states of fossils. Although these may well be influential in cation exchange, they are not generally regarded as significant in producing textural changes in shells in comparison to the temperature-pressure region in which diagenesis occurs (Fyfe & Bischoff, 1965; Bathurst, 1975).

Over the past century, numerous workers have studied fossil carbonate skeletons of known or inferred original composition. Compilation of their observations allows a few generalizations about preservation or disruption of skeletal detail that are independent of taxonomy.

Aragonite skeletons.—Fossil skeletons or skeletal parts that were originally aragonite, unless protected by such unusual, generally impermeable deposits as the Buckhorn Asphalt and Kendrick Shale (Pennsylvanian) (Stehli, 1956; Hallam & O'Hara, 1962), will undergo solution removal (leaving a mold) or else transformation to calcite by microscale solution-redeposition, but with profound disruption of original crystal texture (Sorby, 1879; Hudson, 1962; Bathurst, 1975). In microscale replacement, the new calcite crystals are several orders of magnitude larger than the original skeletal aragonite crystals and may be traversed by fine relics of the organic sheets occurring at growth surfaces or ultrastructural unit boundaries. Unfortunately, those organic relics have been misconstrued by some as indications of preservation of fine skeletal detail, despite the transformation to calcite. This is a good example of the underestimation of the effect of recrystallization. Although some few crystallites of original aragonite may occur as inclusions in the replacement calcite (Sandberg, Schneidermann, & Wunder, 1973; Sandberg, 1975a,b), it should be emphasized that these are only scattered relics and that the main mass of such shells has been drastically altered to coarse calcite. Otherwise, preserved aragonite shells, which are not especially common in older rocks, will retain their original ultrastructure, sometimes in a chalky state, because of partial solution removal.

Calcite skeletons.—Fossil skeletons that were calcite in their original state commonly show little if any change in texture, at least at the light-microscopic level. However, varying amounts of $MgCO_3$ may exist in solid solution in the skeletal $CaCO_3$. High-Mg calcite is metastable relative to low-Mg calcite and, in diagenetic environments, alters by microscale solution-redeposition or by surface exchange or solid-state diffusion processes to produce calcite and an Mg^{++} enriched solution. Various workers have observed that this alteration occurs without textural disruption at the light-microscopic level (Sanders & Friedman, 1967; Land, MacKenzie, & Gould, 1967; Purdy, 1968) and in some cases even at the electron microscopic level (Towe & Hemleben, 1976), but

Fig. 103. Frontal walls and organic matrices.——*1. Petraliella crassocirca?* (Canu & Bassler), rec., Albatross Sta. D4880, off Japan; frontal shield element between two tremopores; note that initial calcite frontal (C) has concentric lamellae around a more massive core; lamellae later overlain, on frontal side only, by superficial spherulitic aragonite (A); etched transv. sec., USNM 209443, ×1,680 (bar = 5 μm).——*2. Watersipora subovoides* (d'Orbigny), rec., locality unknown; single bar in cryptocyst; note concentric laminations reflecting secretion on all sides of frontal shield; heavily etched transv. sec., BMNH 1970.6.1.32, ×3,500 (bar = 2 μm).——*3,4. Labioporella calypsonis* Cook, rec., Konakrey, Senegal; *3,* detail of etched cryptocyst, note abundant screw dislocations of thin rhombic crystals, ×2,000 (bar = 5 μm); *4,* detail of another region of cryptocyst surface, ×5,000 (bar = 2 μm); both BMNH 1964.7.2.31.——*5. Adeona* sp., rec., locality unknown; basal-lateral wall junction; aragonite forms short, broad laths between very numerous, close-spaced organic sheets; etched transv. sec., BMNH 1934.2.10.20, ×9,000 (bar = 1 μm).——*6. Melicerita obliqua* (Thornely), rec., Antarctic; zooecial lining layers, very heavily etched, zooecial interior toward top; massive, spherulitic zooecial lining with some accretionary banding, and organic sheets, shown in this photograph, very closely spaced; BMNH 1967.2.8.119, ×9,500 (bar = 1 μm).

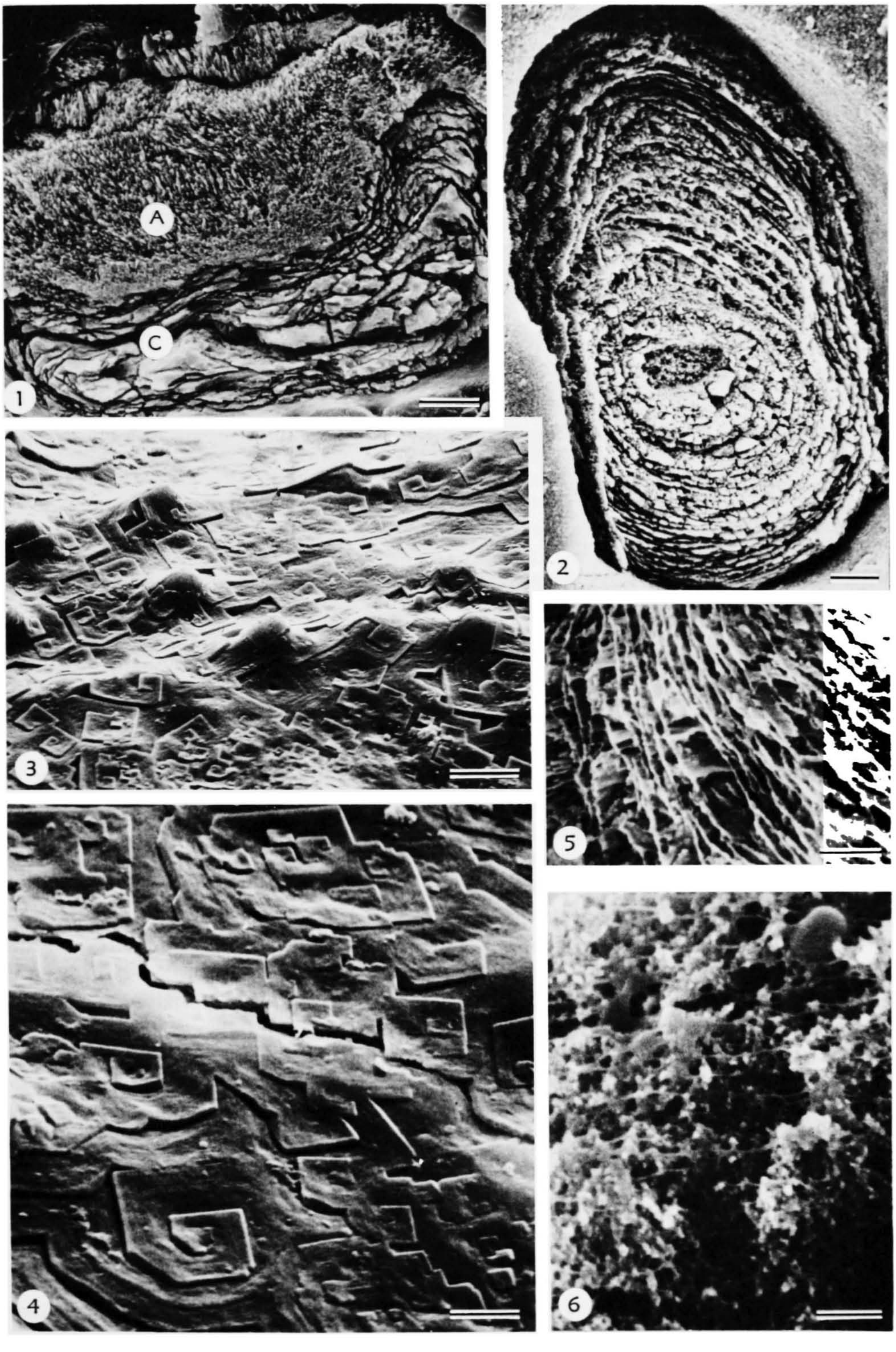

FIG. 103. *(For explanation, see facing page.)*

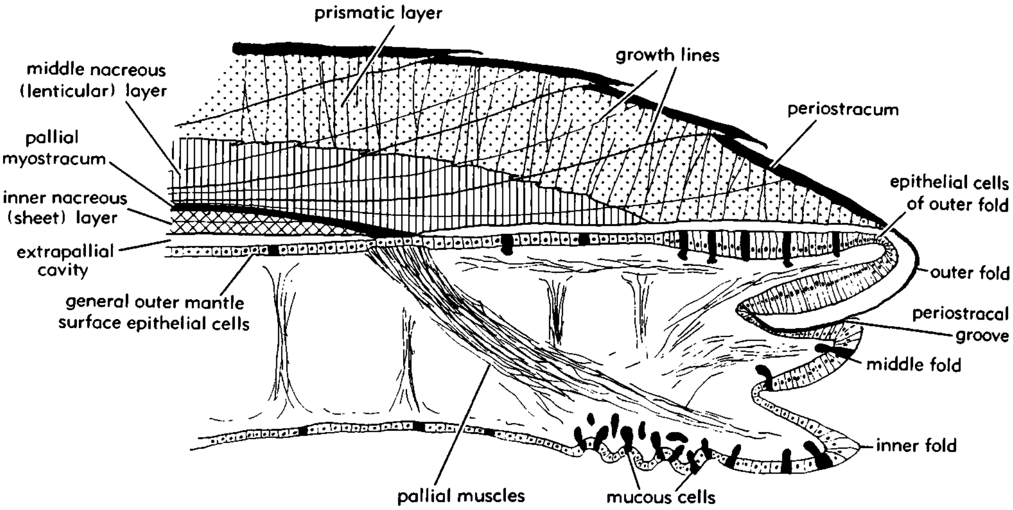

FIG. 104. Skeletal growth. Radial section of the shell and mantle at the valve margin in the bivalve *Anodonta cygnea* Bosc (after Taylor, Kennedy, & Hall, 1969).

others (BANNER & WOOD, 1964; SCHNEIDERMANN, 1970) have found an apparent relationship between original $MgCO_3$ content and diagenetic textural disruption. More recently, SEM work has shown that significant textural reorganization not clearly evident in the light microscope can occur during Mg^{++} loss from even low-Mg calcite (bryozoan skeletons; SANDBERG, 1975a).

From the foregoing we can expect, in the fossil record of bryozoans (and other groups as well), that originally calcitic skeletons will preserve much of the original texture—more so with lesser original $MgCO_3$ content. At least in many ancient stenolaemate bryozoans, textural preservation appears excellent. That textural retention is most likely related to an initially low $MgCO_3$ content, like that found in skeletons of modern stenolaemates (cyclostomates) (SCHOPF & MANHEIM, 1967). The textural disruption commonly observed in skeletons of some stenolaemates, such as *Nicholsonella,* may well be a function of higher original $MgCO_3$ content.

Statements about the degree of resemblance between observed state (texture, mineralogy, cation, and stable isotope composition) of a fossil skeleton and its original state are thus dependent on knowledge of first, stability of the various skeleton-forming carbonates in diagenetic environments, and second, the nature of the skeletal products of modern forms (or rare, unusually well-preserved fossil forms) most closely related to the fossils of interest. This latter application of "biological uniformitarianism" (BEERBOWER, 1960) is much more reliable than a uniformitarian comparison between nonskeletal carbonates in modern sediments and similar nonskeletal carbonates in ancient limestones. This is because the composition of those nonskeletal carbonates will closely reflect the physical-chemical conditions of the general environment and will vary with temporal changes in those conditions. In contrast, biological interference with calcification and the nonequilibrium stability of biological systems (PRIGOGINE, NICOLIS, & BABLOYANTZ, 1972) act as buffers, tending to minimize the influence that any temporal changes in external environmental conditions would have on the resulting skeletal carbonates.

Terminology.—Although qualifying adjectives (calcareous, skeletal) have generally been used in reference to walls in this discussion, it should perhaps be further emphasized that this discussion deals almost

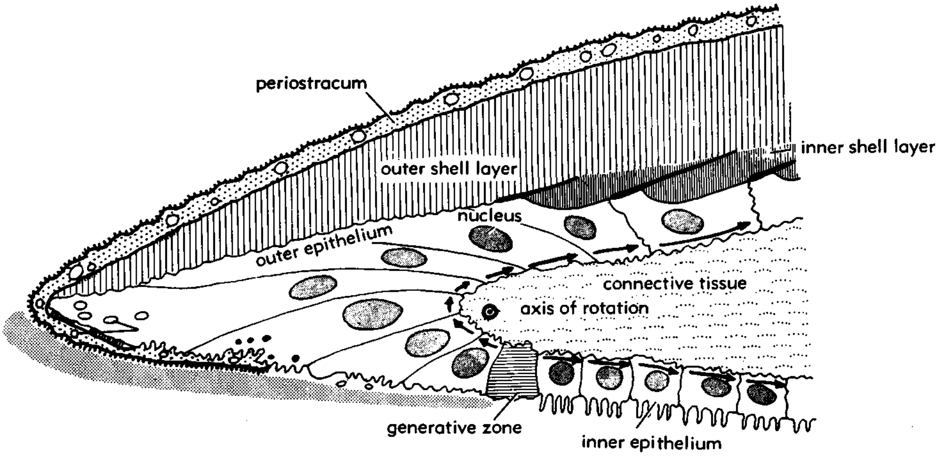

FIG. 105. Skeletal growth. Conveyor-belt model of shell growth, as exemplified by the brachiopod *Notosaria* (after Williams, 1971a).

exclusively with skeletal walls. In order to underscore this skeletal emphasis, HARMER's (1902) term "frontal shield" has been used to differentiate calcified walls in the frontal region from the original membranous frontal wall (see Fig. 65).

BANTA (1968) discussed the interpretation of skeletal walls in cheilostomates as intracuticulate. It should be emphasized that statements on cuticulate or noncuticulate walls in this discussion refer not to that possible intracuticulate condition, but rather to the presence or absence of an outermost boundary cuticle (BANTA, 1968, p. 498).

COMPARISON OF SKELETAL GROWTH IN CHEILOSTOMATES, BRACHIOPODS, AND MOLLUSKS

General models of growth can be most useful in understanding developmental patterns, both ontogenetically and phylogenetically, in skeletons of diverse organisms. Growth models can be derived from observation of such features as skeleton-tissue relationships, the distribution of organic partitions or bounding layers (e.g., cuticle, periostracum) and ultrastructural successions in the skeletons, the orientation of skeletal growth lines and surfaces, or by a more theoretical or function-analysis approach (particularly significant with extinct organisms).

The growth model proposed for cheilostomate bryozoans by SILÉN (1944a,b) is no longer fully satisfactory, largely because of the great diversity of morphologies and observed or inferred skeletal-epithelial relationships subsequently discovered among members of that group. Nevertheless, the nature of cheilostomate skeletal development can be compared and contrasted with skeletal growth in groups for which well-established growth models exist, such as the brachiopods and the mollusks, especially bivalves. TAVENER-SMITH and WILLIAMS (1972) implied some similarities, in details of fine skeletal structure, between bryozoans and brachiopods. However, if one compares the higher level skeletal development of bryozoans (particularly cheilostomates) and brachiopods-mollusks, certain major distinctions and dissimilarities emerge.

Brachiopod-molluscan growth model.—The fundamentally open-ended, one-sided growth of brachiopod and bivalve shells involves dimensional expansion and lateral displacement of the skeletal accretion surface along

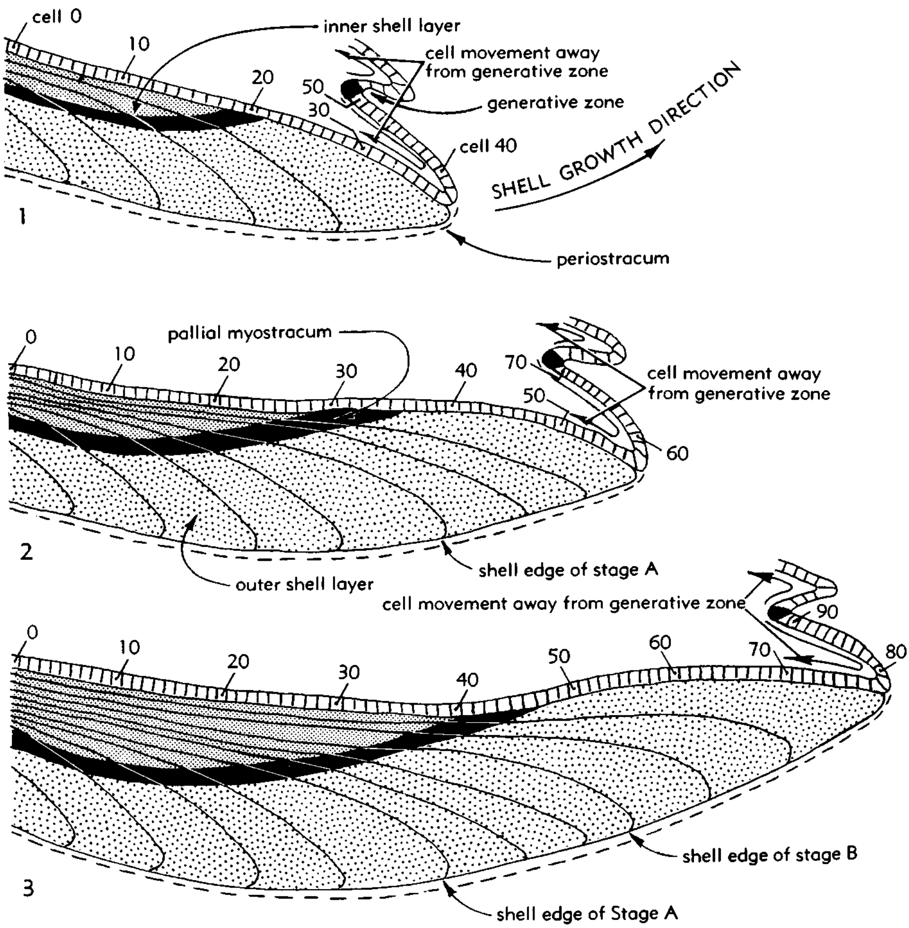

FIG. 106. Skeletal growth. "Road-paver" model of shell growth in mollusks and brachiopods. Note the fixed position of each cell relative to the shell surface and the continual distal generation of new cell "pavement" (by the "paving machine," the generative zone) and the later development of subjacent shell. Note the change in secretory function of the numbered cells as the valve-mantle margin and generative zone move away distally. Growth lines marking the positions of the shell edge at earlier stages are indicated in *2* and *3*.

a growth spiral (YONGE, 1953; RAUP, 1966). That surface is divided into zones whose skeletal products are distinctive and whose positions relative to one another are, with few exceptions, fixed. Dominance and areal extent of any given ultrastructural unit may vary, such as the variations in thickness and distribution of the myostracal layer in the mussel *Mytilus* as described by DODD (1963). However, such variations are merely topological distortions of skeletal units in a fixed succession.

Secretion begins on the outer surface, at a periostracum, and the shell is thickened by successive accretions added medially (toward the mantle cavity and body) across the entire inner surface of the shell in more or less uniform, concentric zones (Fig. 104). The nature of mantle formation and the successive secretory regimes through which a mantle epithelial cell passes have been portrayed by a "conveyor-belt" model (WILLIAMS, 1968). This model is commonly represented by a radial section through the shell and mantle showing the positional and physiological change in cells as shell growth progressively alters their loca-

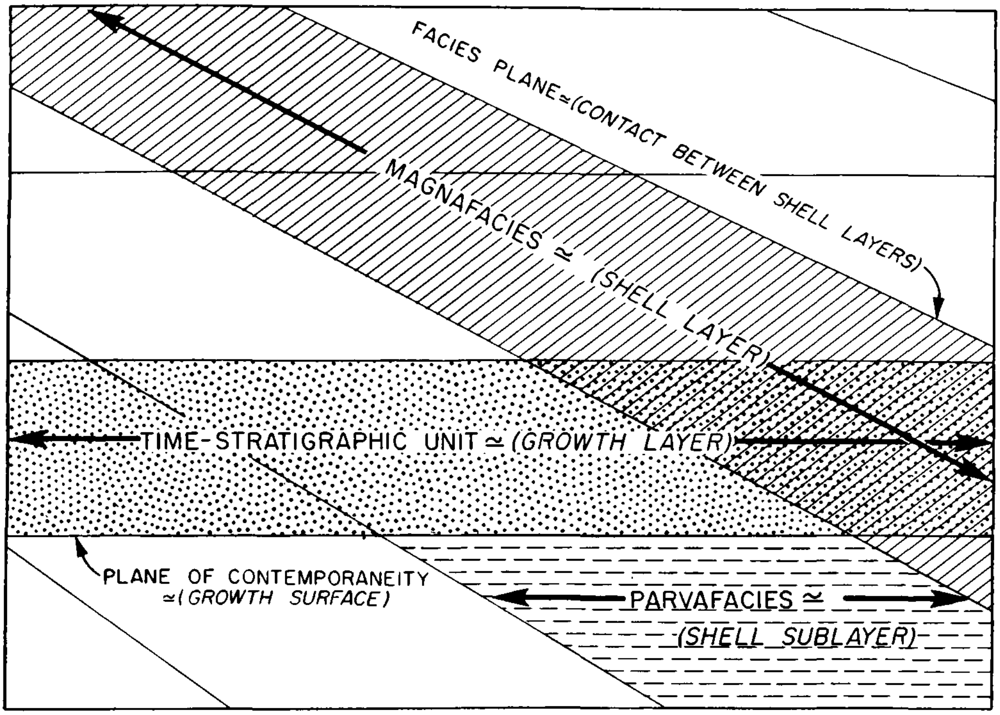

FIG. 107. Skeletal growth. Diagrammatic comparison of shell-unit and growth-increment boundaries with facies concepts of CASTER (1934) (after McClintock, 1967).

tion relative to the shell margin (Fig. 105). Along any radial sector line, cells may be expected to pass through all secretory regimes present proximally (adapically), with the obvious exceptions of spatially limited adductor attachments and, in some groups, discontinuous pallial attachment. If it is a conveyor belt, it is an odd one with one end attached and the other continuously generating new belt and moving forward. The conveyor-belt analogy is perhaps not a good one, because the cells, once in position adjacent to the shell, are each "nailed down," that is they do not move laterally relative to that shell. Rather they undergo a series of physiological changes in secretory function dependent on their positive relative to the mantle-generative zone.

The mantle system would be better portrayed as a road-paving system in which the moving "paving machine" (the mantle-generative zone) produces a fixed "pavement" of cells as it moves distally (Fig. 106). Even that analogy is limited because the cells, unlike the passive macadam pavement formed by a real road paver, are active producers of new subjacent layers (the shell), migrate vertically relative to the shell surface as new shell is secreted, and change in function as the "paving machine" of the generative zone moves away distally.

MACCLINTOCK (1967) pointed out the analogy between molluscan skeletal ultrastructural units with their "outcrop bands" on the inner shell surface and CASTER's (1934) stratigraphic concepts of magnafacies and parvafacies, respectively (Fig. 107; see also WESTBROEK, 1967). The ultrastructural types present on the interior of the shell are thus analogous to laterally adjoining, temporally equivalent depositional environments. Vertical successions of ultrastructures through the shell reflect the lateral (distal) shift of those "environments" in a microscopic corollary of

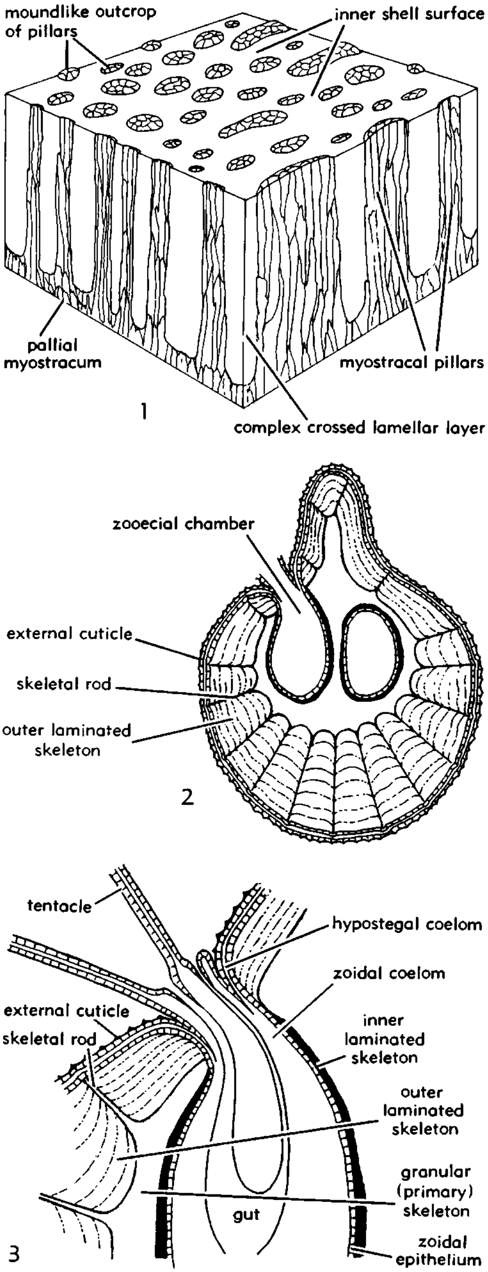

FIG. 108. Skeletal growth. Comparison of myostracal pillars in the bivalve *Chama rubea* REEVE (*1*) (after Taylor, Kennedy, & Hall, 1969) with the rods of "primary" skeleton extending through the lamellar "secondary" skeleton in a fenestellid stenolaemate bryozoan (*2,3*) (after Tavener-Smith, 1969).

a transgressive sequence. Attempts at demonstration of "correlation" or, more correctly, "lithic equivalence" (i.e., not necessarily contemporaneous deposition but simply "same unit") among shells of different bivalves using the myostracal layer (prismatic aragonite formed at the line of mantle attachment) as a datum plane have not been totally successful (TAYLOR, KENNEDY, & HALL, 1969, p. 9). This is because, in some forms, numerous myostracal layers are interleaved with other shell units, and, in some other forms, mantle attachment is absent or secondary.

Any given skeletal unit is obviously not contemporaneous throughout, but the generally clear growth lines allow determination of earlier instantaneous growth surfaces and of time-equivalent skeletal deposits, whether in brachiopods or in mollusks (Fig. 104, 106, 107).

In the molluscan-brachiopod model there is a single open-faced secretory surface whose dimensions are continually expanding (even in successive chambers of cephalopods). The resulting individual skeleton produced at that secretory surface is composed of skeletal layers that are essentially continuous sheets or wedges from their distal exposure at the growth surface back toward the proximal region of the larval shell. There are some discontinuous units, such as the myostracal pillars in *Chama* (TAYLOR, KENNEDY, & HALL, 1969). As indicated in Figure 108, those pillars are analogous at least in appearance to the rods of the primary layer extending through the laminated secondary layer of fenestellid stenolaemate bryozoans (TAVENER-SMITH, 1969).

Parenthetically, it should be noted that the one-sided, external shell model given here for mollusks does certainly have some unusual, if relatively rare exceptions or modifications. Notable ones includes extreme mantle extension and envelopment of the shell by secondary deposits (as in the gastropods *Cypraea* and *Calyptrophorus*) and the development of an internal shell in belemnites. The chambered shells of ectocochlear cephalopods, which are external and one-sided, are the closest molluscan approximation of the compartmentalization of the colonial skeleton in bryozoans.

Cheilostomate bryozoan skeleton.—The bryozoan skeleton (like shells of brachiopods and bivalves) is epidermal in origin (i.e., an exoskeleton), regardless of the often complex, infolded topological distortions of that epidermis into the colonial coelom (BOARDMAN & CHEETHAM, 1973, p. 124). The "standard" growth pattern (see later definition and discussion) among cheilostomates is, like the brachiopod-bivalve model, one-sided. That is, calcification occurs in one direction from an exterior wall with a bounding organic layer (periostracum in bivalves-brachiopods, cuticle in cheilostomates). However, in cheilostomates and other bryozoans, that exterior wall surface may comprise only the basal side of the ancestrula.

One may reasonably expect significant differences between skeletons of solitary and colonial animals, the most obvious being some degree of compartmentalization of the colonial skeleton, delineating the individuals. The distinctiveness of that delineation varies greatly among cheilostomates. In fact, the significance of boundaries between individuals in a bryozoan colony is a subject of some controversy, relating primarily to the degree of integration or of separateness in functioning of individuals. Some work, such as the recent study of response to mechanical stimuli by THORPE (1975), suggests a high degree of integration of individuals. Even when superficial calcification of the frontal shield occurs without breakdown of intercalary cuticles, the amount of such calcification is closely determined by the position of the individual zooid. A striking example of this occurs in adeonids, in which **dendritic thickenings** extend over the zoarium (Fig. 109,*2*). Along those axial dendritic zones, normal zooids are overlain by a thick sequence of heavily calcified kenozooids quite distinct from the outer, laterally adjacent zooids. Despite the extreme thickening, the lateral intercalary cuticles persist throughout (Fig. 109,*1*).

In the cheilostomates, the general colonial growth field, the equivalent of the valve interior in the brachiopod-mollusk model, is subdivided into numerous, repeated skeletal compartments, the zooecia. There is a clear developmental gradient of morphological change from the zooecial buds at the leading edge of the colony through the heavily calcified, sometimes occluded zooecia in the proximal region. However, the zooecial unit dimensions are fixed early, and, except for small variations produced in zones of astogenetic change or as a result of crowding, similar sized units (sometimes polymorphic) are repeated as the colony growth continues.

Once the fundamental calcareous box or structural framework of each zooid is formed, the coelomic volume tends to decrease as skeletal secretion continues for a time on the interior of that box (Fig. 110,*2*). Although brachiopod and mollusk shells also grow by secretion inward, continuing marginal expansion of the open-ended skeletal enclosure more than compensates in living space for the inwardly growing skeleton (Fig. 110,*1*).

Recognition of contemporaneous skeletal deposits.—The ultrastructurally distinctive shell layers that compose the skeletons of mollusks and brachiopods are all present in the postlarval shell, and the secretory regimes in which they are each produced are displaced laterally as the shell grows. This lateral displacement is generally rapid relative to the rate of thickening of the skeletal unit formed in any of those regimes, and the boundaries between resulting shell layers tend to be at relatively low angles to the secretory surface. Nevertheless, distinctive growth lines allow recognition of contemporaneous parts of the different molluscan shell layers (Fig. 104).

For several reasons, such easy demonstration of contemporaneity of deposition is not generally possible for parts of cheilostomate bryozoan skeletons. It should be emphasized here that, because of compartmentalization of the developmental gradient from the colony margin inward, the major problem is determination of contemporaneity of skeletal

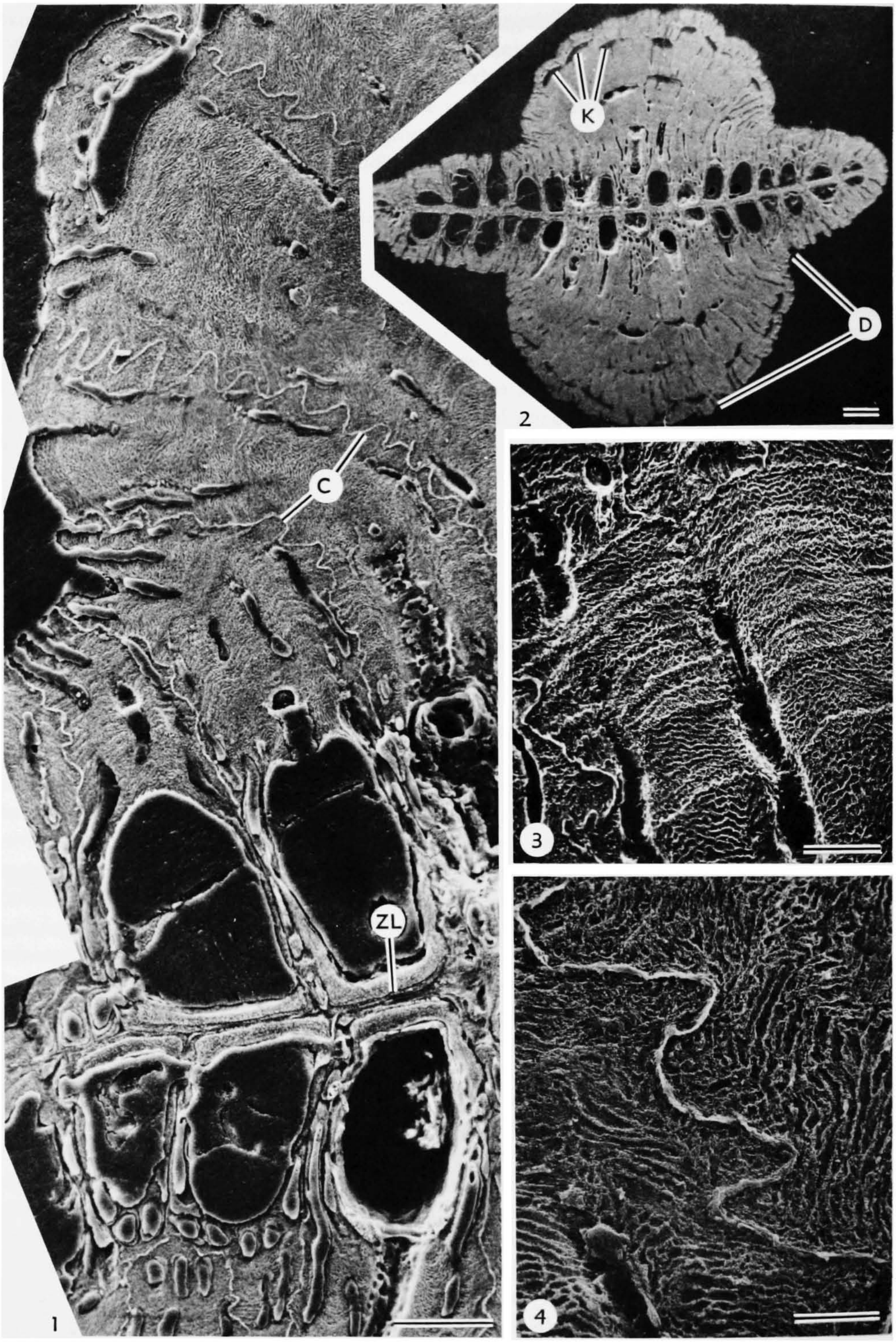

FIG. 109. *(For explanation, see facing page.)*

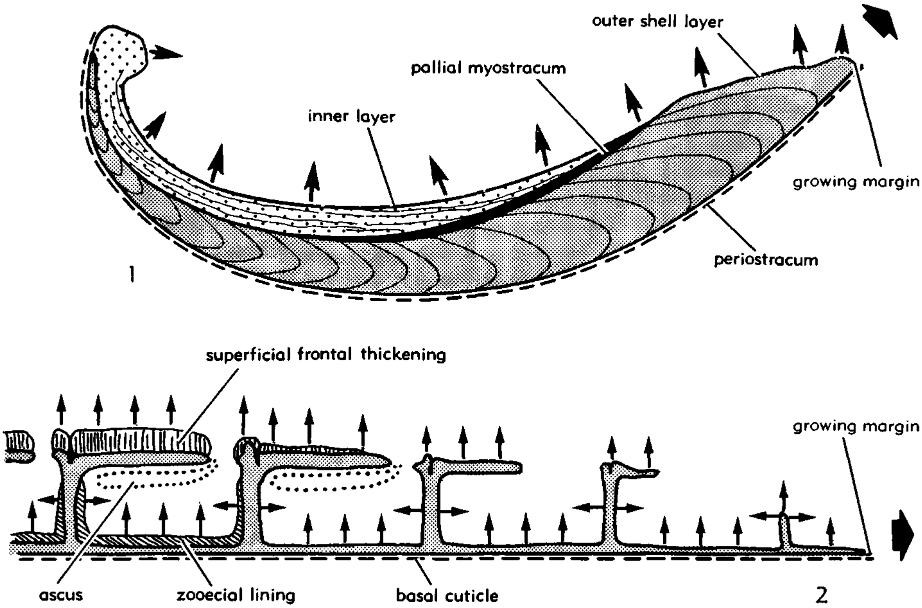

FIG. 110. Skeletal growth. Diagrams of skeletal growth fields in a bivalve (*1*) and a cryptocystidean (lepralioid) cheilostomate bryozoan (*2*). Broad arrows in each diagram indicate the direction of expansion (marginal growth) of the skeletal field. The diagram of the cheilostomate shows only the very distal edge of the field in order to allow sufficient magnification to show wall thickening directions (narrow arrows). In the cheilostomate, the skeletal growth of the underside of the frontal is terminated at the time of ascus formation. Because the frontal-thickening and zooecial-lining deposits are discontinuous, demonstration of contemporaneous growth increments in those deposits is difficult.

parts within and among individual zooecia at different positions along that gradient. In cheilostomates, skeletal deposition rates are often quite rapid, and physiological changes resulting in difference in secretory function (hence different skeletal ultrastructures) tend to move rapidly over the secretory epithelium of any given wall. Therefore, boundaries between ultrastructural types may sometimes be nearly equivalent to growth surfaces. Also, except for the planar spherulitic ultrastructure on exterior walls (Fig. 111, 112) or the distally oriented spherulites of interior-walled aragonitic cheilostomates (Fig. 113,*1–3*; SANDBERG, 1973, figs. 3, 4), skeletal accretion is not reflected by growth banding at an angle to the zooecial wall. Therefore, growth increments may be quite clear in ultrastruc-

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FIG. 109. Frontal thickening.——*1,2. Adeona* sp., locality unknown; *1,* transverse section, etched, of zoarial branch at junction between axial thickening and lateral "normal" zooecia, sinuous lateral intercalary cuticles (C) extend all the way through the frontal despite extreme thickening of frontal shields of the occluded axial zooecia, frontal composed of numerous organic-bounded units of spherulitic aragonite (compare Fig. 114,*2–5*), note the zooecial linings (ZL) deposited only in the lower part of each zooecial interior, ×140 (bar = 100 μm); *2,* lower magnification view of specimen in *1,* note extreme thickening of frontal shields of the axial zoöecia in the dendritic thickening (D) as well as blisterlike kenozooid chambers (K) in that frontal thickening, ×25 (bar = 200 μm); both BMNH 1920.12.10.1.——*3. Adeonella atlantica* BUSK, rec., Nightingale Is., near St. Helena, S. Atl.; frontal shield; note accretionary layers and organic-bounded aragonite units; transv. sec., BMNH 1887.12.9.725, ×220 (bar = 50 μm).——*4. Adeona* sp., rec., locality unknown; detail of upper end of *1*; note sinuous intercalary cuticle and organic boundaries of aragonite units; ×400 (bar = 20 μm).

tures that have crystal orientations perpendicular to the growth surface (Fig. 113,*4*; 114,*1,3*). However, if there is only lamellar structure (Fig. 115,*2*; 116,*1,2*), then the location of growth increments (contemporaneously grown surfaces) is equivocal.

A further problem in demonstration of contemporaneity in bryozoan skeletons is that, unlike the condition in molluscan shells, some ultrastructurally distinctive skeletal units (e.g., superficial frontal layers, **zooecial linings**) are not present initially in a cheilostomate zooecium. Furthermore, in mollusks an epithelial cell lying along a radial expansion vector passing through an adductor scar will pass through all or essentially all skeletal secretory regions. In contrast, in cheilostomate secretory epithelia each cell's function and possible skeletal products are limited by its location within the zooid. In calcitic or bimineralic species, only the calcitic framework portion of the skeleton is continuous along basal surfaces for all zooecia and, as upward projections, into the lateral, transverse, and frontal walls of the zooecia. Other skeletal units, whether calcite or aragonite, occur as localized, discontinuous deposits, most commonly on the frontal exterior or on

FIG. 111. Growth surfaces of exterior walls.——*1. Petraliella bisinuata* (SMITT), rec., Albatross Sta. D2405, Gulf of Mexico; basal wall, distal indicated by arrow; note distally radiating fans of acicular calcite crystals and intermittent zones of very strong and very subdued accretionary banding; etched exterior, USNM 209448, ×1,100 (bar = 10 μm).——*2. Posterula sarsi* (SMITT), rec., Gulf of St. Lawrence; surface of calcified inner layer of ovicell just distal to orifice of fertile zooid, distal toward top; curved line near the bottom (arrow) marks line of emergence of ovicell as an exterior-walled lobe; BMNH 1911.10.1.1360A–B, ×1,150 (bar = 10 μm).——*3. Megapora ringens* (BUSK), rec., Shetland Is.; basal wall; planar spherulitic ultrastructure in rosettes radiating from scattered sites of initial calcification; etched exterior, BMNH 1911.10.1.630, ×1,180 (bar = 10 μm).——*4. Onychocella angulosa*? (REUSS), rec., locality unknown; basal wall; see comments on *3*; exterior, BMNH 1911.10.1.140, ×1,850 (bar = 5 μm).——*5. Arachnopusia unicornis* (HUTTON), rec., N.Z.; detail of planar spherulitic ultrastructure on exterior surface of inner calcified layer of ovicell; arrow indicates distal direction; BMNH 1886.6.8.4,5, ×4,900 (bar = 2 μm).

FIG. 112. *(See p. 254.)*

FIG. 113 (p. 255). Spherulitic structure in aragonitic and calcitic walls.——*1,3,4. Mamillopora cupula* (SMITT), rec., Gulf of Panama; *1,* detail of a single aragonite spherulite, note initial poorly etched core (organic rich?), lateral compromise boundaries between adjacent spherulites, distally expanding acicular crystals, and transverse accretionary banding, ×3,200 (bar = 2 μm); all USNM 184151; *3,* lateral wall, distal to right, spherulitic aragonite radiating from rows of rather evenly spaced centers of calcification to produce pattern very like trabecular structure of aragonite in scleractinian corals, etched oblique long. sec., ×1,325 (bar = 5 μm); *4,* distal wall, distal to left, calcification of transverse wall, in contrast to that in most cheilostomates, one-sided, with aragonite spherulites beginning at proximal side and growing distally, long. sec., ×1,300 (bar = 5 μm);——*2. Flabellopora arculifera* (CANU & BASSLER), rec., Albatross Sta. D5315, Philip.; zooecial lining projecting basally from frontal shield just inside orifice; note numerous, very finely spaced accretionary bands and coarse spherulitic calcite; frontal direction toward bottom of photograph, etched transv. sec., USNM 209437, ×2,550 (bar = 5 μm).

FIG. 114. *(See p. 256.)*

FIG. 115 (p. 257). Lamellar ultrastructure.——*1–3. Metrarabdotos tenue* (BUSK), rec., Caroline Sta. 68, off NE. Puerto Rico;, *1,* basal interior, large rhombic crystals with accretionary bands and incipient screw dislocation, ×6,100 (bar = 2 μm); *2,* frontal wall, showing only a few of the very numerous calcite lamellae that make up superficial frontal thickening (growth surface of this ultrastructure shown in Fig. 102,*1,2*), long. sec., ×4,200 (bar = 2 μm); *3,* detail of *2,* note subunits in crystals of lamellae, ×16,800 (bar = 1 μm); all USNM 209434.——*4–6. Labioporella calypsonis* COOK, rec., Konakrey, Senegal; *4,* frontal shield interior, fractured at very low oblique angle to surface, subunits of large rhombic-hexagonal crystals that make up lamellae emphasized by heavy etching of this specimen, ×5,100 (bar = 2 μm); *5,* another part of same wall surface, ×10,200 (bar = 1 μm); *6,* detail of *5,* ×20,400 (bar = 0.5 μm); all BMNH 1964.9.2.31.

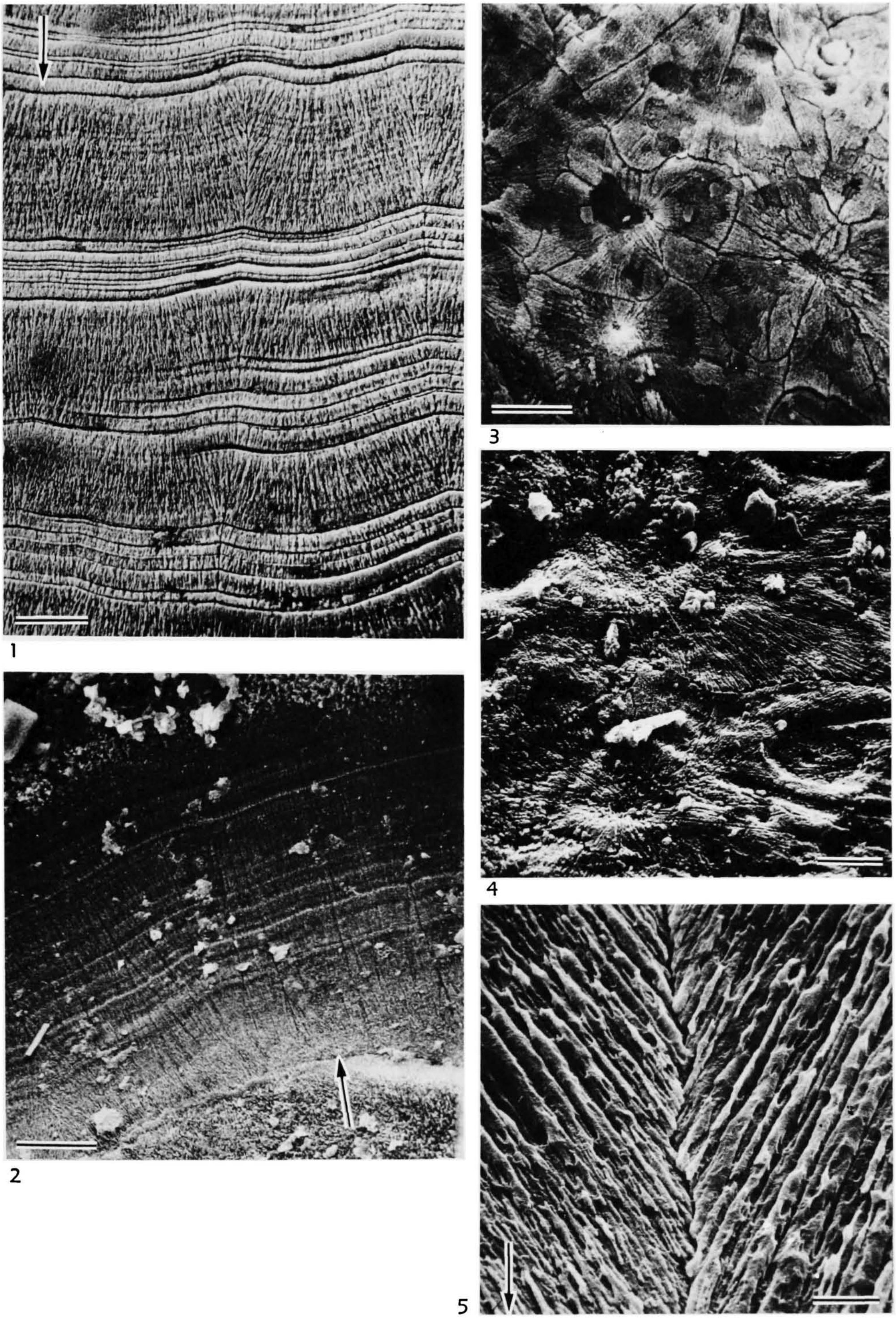


FIG. 111. *(For explanation, see facing page.)*

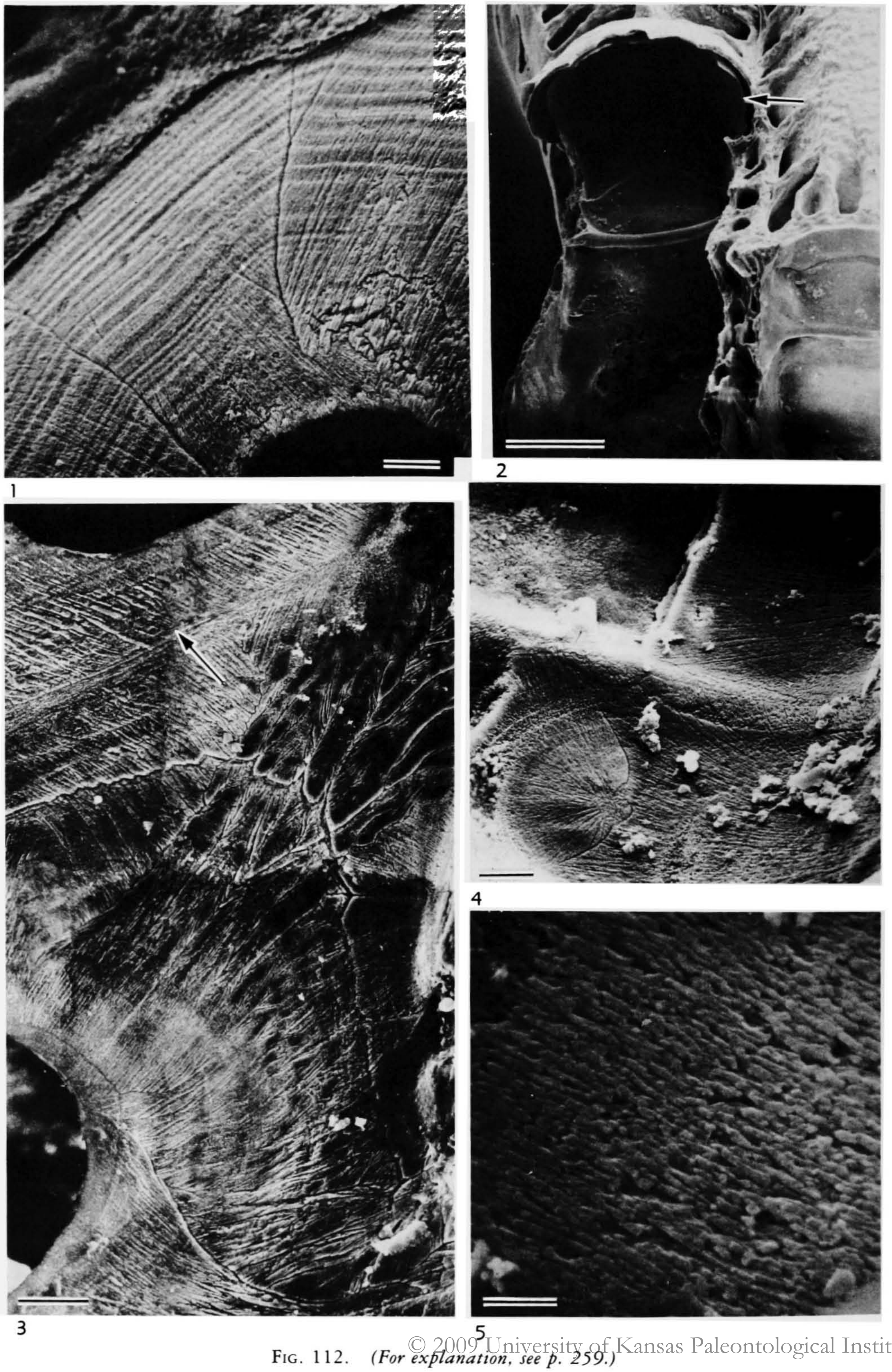


FIG. 112. *(For explanation, see p. 259.)*

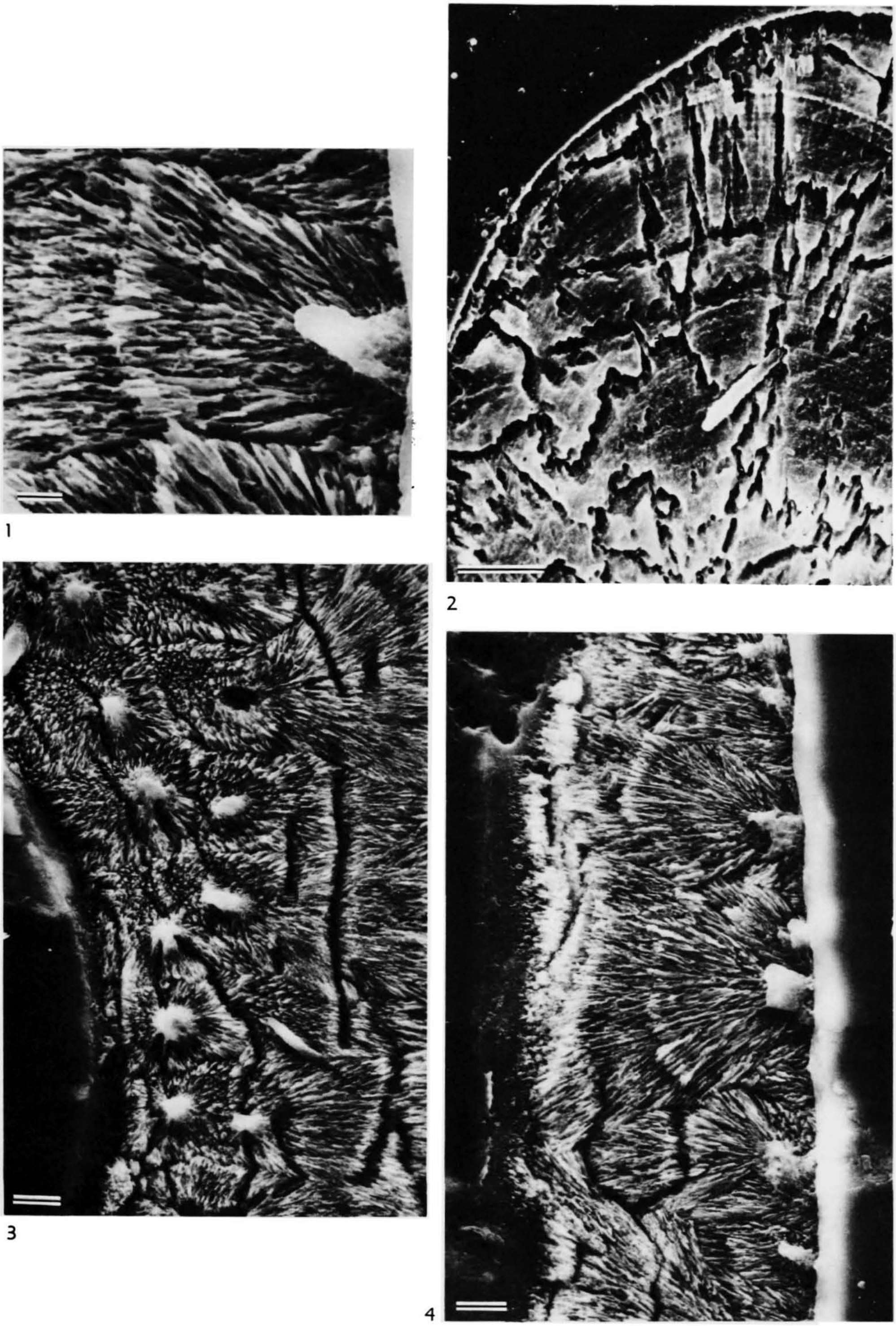


FIG. 113. *(For explanation, see p. 252.)*

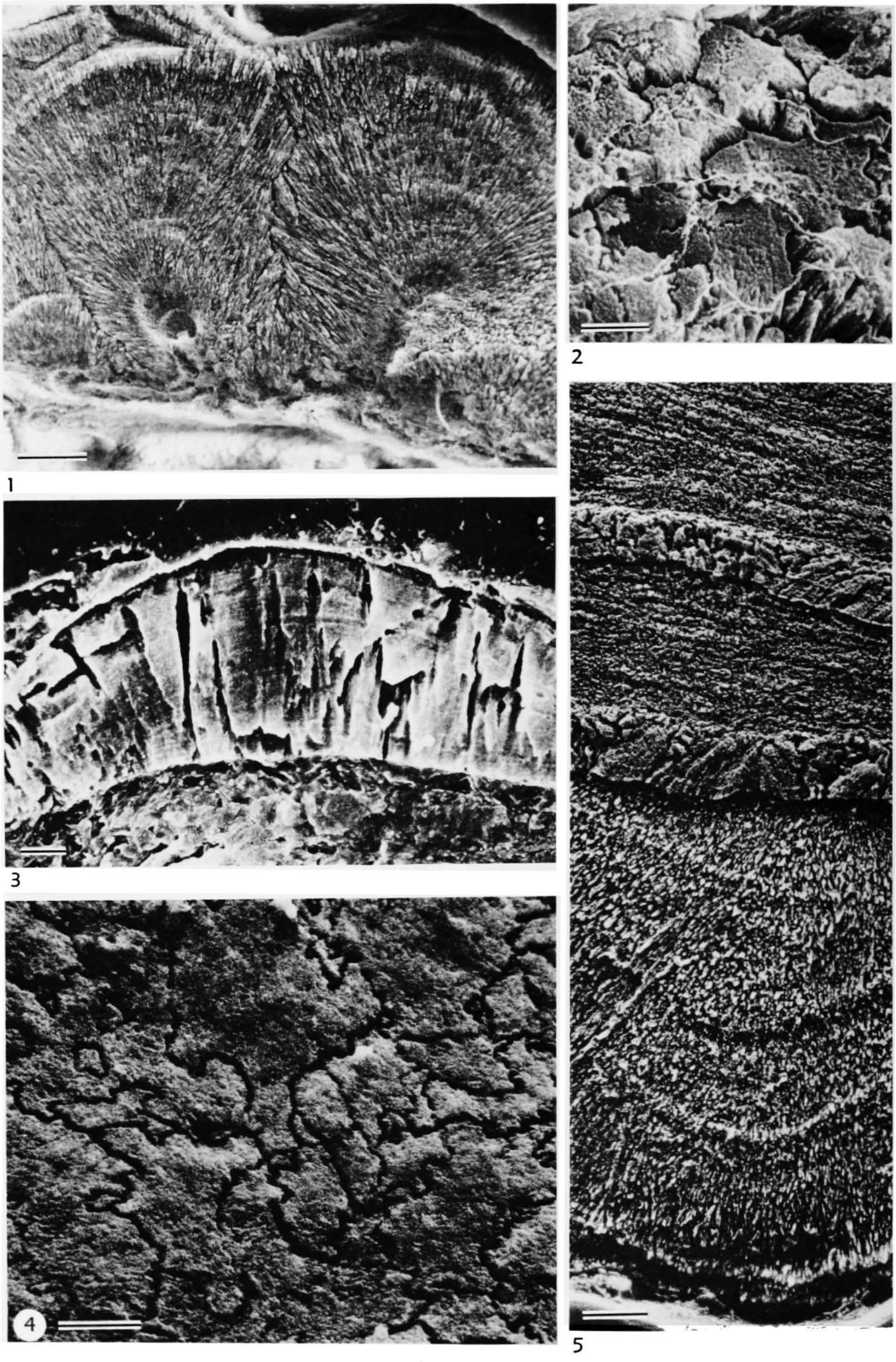


FIG. 114. *(For explanation, see p. 259.)*

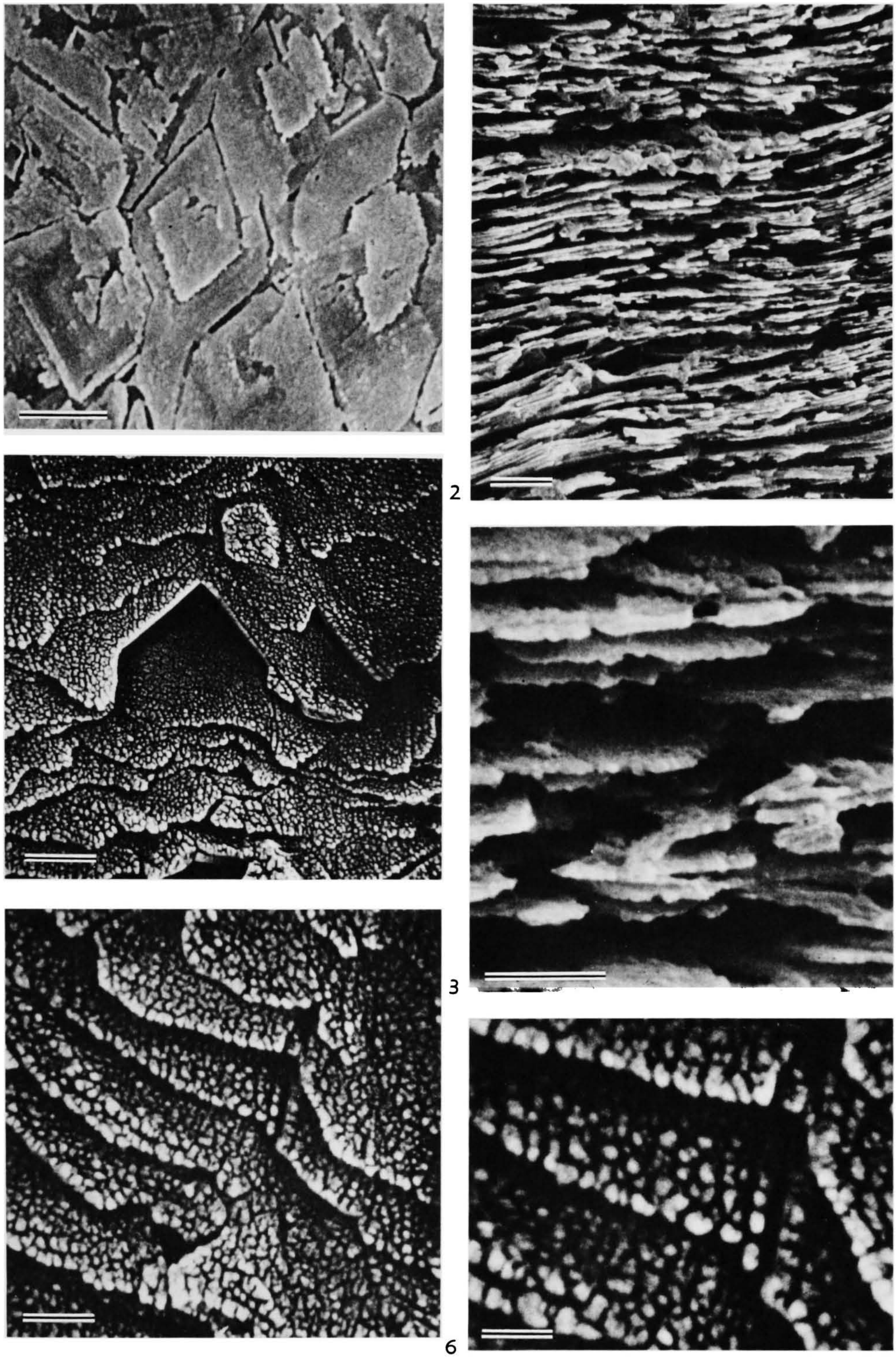


FIG. 115. *(For explanation, see p. 252.)*

FIG. 116. *(For explanation, see facing page.)*

the zooecial interior below the compensation device, less commonly on basal exteriors (of interior-walled forms). Totally aragonitic skeletons tend to be ultrastructurally uniform (acicular crystals in spherulitic arrays) throughout, although differences in spherulite orientations can indicate differences in direction of wall growth (Fig. 113,*1–3*; 117,*1–4*; 118,*1–3*).

Because different ultrastructural types have different expressions of growth increments, and because of discontinuity of skeletal units between and even within zooecia (e.g., units present only on frontal exterior, only on zooecial interior), it has not yet been possible to correlate the products of an instant of skeletal deposition in different parts of a colony or even among the various parts of a single zooecium. Tagging with radioisotopes (^{45}Ca or ^{14}C) and use of sectioning and microautoradiography should provide the data needed for such correlation.

In some cheilostomates (e.g., *Metrarabdotos*) it appears there may be some simul-

FIG. 112 (p. 254). Exterior walls in ovicells and peristomes.——*1,2. Posterula sarsi* (SMITT), rec., Gulf of St. Lawrence; *1,* upper exterior surface of outer calcified layer of ovicell with planar spherulitic ultrastructure growing back proximally (toward bottom) and medially, superficial frontal thickening layers of distal zooecium encroaching over ovicell in upper left, ×1,575 (bar = 5 μm); *2,* frontal view of an ovicelled zooecium with frontal wall and part of the ovicell broken away, arrow marking lumen between inner and outer calcified layers of ovicell, ×140 (bar = 100 μm); both BMNH 1911.10.1.1360A,B.——*3. Eurystomella bilabiata* (HINCKS), rec., Pacific Grove, Cal.; basal exterior of two adjacent zooids; stripes of planar spherulitic ultrastructure grow in toward central basal window of each zooecium; lateral junction between zooecia marked by arrow; BMNH 1964.1.2.1, ×1,500 (bar = 10 μm).——*4. Megapora ringens* (BUSK), rec., Shetland Is.; planar spherulitic ultrastructure near proximal edge of inner calcified layer of ovicell, distal toward left; BMNH 1911.10.1.630, ×780 (bar = 10 μm).——*5. Reteporella myriozoides* BUSK, rec., Challenger Sta. 148, Possession Is., Indian O.; etched surface of a peristome, distal toward upper left; crystals of planar spherulitic ultrastructure very nearly parallel and less elongate than in some other species; BMNH 1887.12.9.516, ×1,050 (bar = 10 μm).

FIG. 113. *(See p. 255.)*

FIG. 114 (see p. 256). Spherulitic structure in aragonitic and calcitic walls.——*1. Hippoporidra senegambiensis* COOK, rec., Konakrey, Senegal; frontal shield; spherulitic arrays of acicular aragonite start at scattered centers and meet at roughly planar compromise boundaries; etched long. sec., BMNH 1970.8.10.24, ×1,000 (bar = 10 μm).——*2. Adeona* sp., rec., locality unknown; etched section perpendicular to growth direction of spherulitic arrays of an aragonite wall; note organic membranes; BMNH 1934.2.10.20, ×4,850 (bar = 20 μm).——*3. Flabellopora arculifera* (CANU & BASSLER), rec., Albatross Sta. D5315, Philip., frontal shield; crudely laminated initial calcite wall covered, on basal side, by a zooecial lining of spherulitic calcite with many, close-spaced accretionary bands; frontal surface toward bottom, etched transv. sec., USNM 209437, ×3,120 (bar = 20 μm).——*4. Micropora* sp., rec., Albatross Sta. D2856; lower (basal) surface of a cryptocyst constructed of spherulitic calcite; spherulitic arrays separated by convoluted interlocking boundaries; USNM 209438, ×2,450 (bar = 50 μm).——*5. Tubiporella magnirostris* (MACGILLIVRAY), rec., Port Philip Head, Australia; lower part of a basal wall of an interior-walled form; crudely laminated calcite of basal wall interlayered near its lower limit with two spherulitic calcite layers, the second of which is followed by a spherulitic aragonite superficial layer on the basal exterior surface; etched transv. sec., BMNH 1927.8.4.24, ×975 (bar = 10 μm).

FIG. 115. *(See p. 257.)*

FIG. 116. Lamellar walls.——*1. Labioporella calypsonis* COOK, rec., Konakrey, Senegal; distal part of cryptocyst, distal toward bottom; note continuity of layers around distal end of frontal as well as in more massive central portions of wall; the somewhat more massive skeletal layers near middle of wall composed of fine, transverse, lathlike subunits; etched long. sec., BMNH 1964.7.2.31, ×2,200 (bar = 5 μm). ——*2. Membranipora grandicella* (CANU & BASSLER), rec., Albatross Sta. D5315, Philip.; cryptocyst, distal toward bottom (see Fig. 122,*2* for lower magnification view); note continuity of layers out of upper end of transverse vertical wall and around distal end of cryptocyst; thin, central poorly laminated portion was well developed distally before inception of concentric lamellae; cuticle incorporated into calcified wall extends well down below frontal surface above vertical transverse wall; etched long. sec., USNM 209441, ×750 (bar = 10 μm).

taneous edgewise growth (Boardman & Towe, 1966) of numerous lamellae in a narrow zone at the very distal growing edge of the skeleton. This is suggested by the occurrence of multiple lamellae at a rather thick but apparently unbroken edge of a well-preserved modern colony of *Metrarabdotos*. More commonly, distal ends of skeletal walls, in growing colonial margins of most cheilostomates studied, feather out to quite thin edges. The progressive, very broad, distally thinning zones over which lamellae accrete are evident in longitudinal sections of some embedded colonies (Fig. 119,*3,4*).

In the most broad sense, skeletal lamellae grow at their edges. New lamellae often arise as screw dislocations (Fig. 103,*3,4*), as seed crystals scattered on a narrow to broad zone or step (Fig. 102,*1–3*), or a combination of the two (Fig. 102,*4,6*; 115,*1*). Seed crystals grow at their edges until they impinge on adjacent crystals (Fig. 102,*3,4*) of the same lamellar "step" and form a solid layer, the "tread" of the lamellar step (Fig. 102,*3*). In some forms, lamellae arise as distally growing, superimposed steps formed by sheets of flat blades (Fig. 119,*1,2*). The width of the lamellar tread may be narrow relative to the total zooecial skeletal width (as in the bladed structure) or may extend over most of the secretory surface that is producing the lamellae (as in the laterally accreting, seed crystal structure). What has been called edgewise growth is effectively a more extreme form of **lamellar growth** than the latter. In it, numerous lamellar steps with very narrow "treads" are crowded into a narrow growth zone. The different parts of lamellae in **lamellar ultrastructure** are of different ages; the magnitude of the difference relates to the steepness of the lamellar "staircase." Thus edgewise growth in bryozoan skeletons is more like the narrow-zone development of the nacreous layer in gastropods (Wise, 1970), which has a very much shorter "tread" than do the broad nacre "steps" in bivalves (Wada, 1972; Wise, 1969).

Types of lamellar growth are clearly affected by the shape of crystals that compose the layers, i.e., equant crystals growing from numerous scattered centers or elongate and bladelike crystals advancing at their distal ends. One should much more reasonably expect the type of edgewise growth discussed by Boardman and Towe (1966) in forms with bladelike crystals (Fig. 119,*1,2*), than in those where there is seeding of scattered equant crystals over a large area (Fig. 102,*1–4*), as in bivalve nacre.

The planar spherulitic ultrastructure, which

Fig. 117. Spherulitic aragonitic walls.——*1–5*. *Cleidochasma porcellanum* (Busk), rec., Albatross Sta. 2405, Gulf of Mexico; *1,* frontal shield, spherulitic aragonite of two orientations meeting along an irregular boundary to right of center, several marked accretionary bands occurring near upper frontal surface, etched transv. sec., ×2,200 (bar = 5 μm); *2,* detail of *1,* ×5,400 (bar = 2 μm); *3,* low magnification view of same frontal shield, note tendency for greater wall thickening marginally, ×1,100 (bar = 10 μm); *4,* frontal exterior view, ×50 (bar = 200 μm); *5,* etched vertical section along sutured lateral zooecial boundary, interfingering of zooecial walls as well as accretionary banding of frontally growing aragonite spherulites well shown, ×550 (bar = 20 μm); all USNM 209439.

Fig. 118. *(See p. 262.)*

Fig. 119 (see p. 263). Foliated and lamellar ultrastructure.——*1,2*. *Tessarodoma boreale* (Busk), rec., Shetland Is.; *1,* frontal shield exterior growth surface, distal toward top; lathlike growth similar to foliated structure in bivalves and some structures shown in cyclostomates by Brood (1972), ×3,150 (bar = 2 μm); *2,* detail of adjacent wall, ×7,900 (bar = 1 μm); both BMNH 1911.10.1.841.——*3,4*. *Schizoporella errata* (Waters), rec., Gharadaqa, Red Sea; *3,* distal margin of colony, note extent (more than two zooecial lengths) of basal wall produced by multizooidal bud distal of last transverse wall, long. sec., ×50 (bar = 200 μm); *4,* detail of *3,* distal indicated by arrow, note that any lamination traced distally comes closer to basal exterior surface, effectively paralleling growth surface of distally thinning multizooidal zone shown in *3,* near top of wall, plastic has pulled away, disrupting some carbonate and organic layers, ×900 (bar = 10 μm); both BMNH 1937.9.28.18.

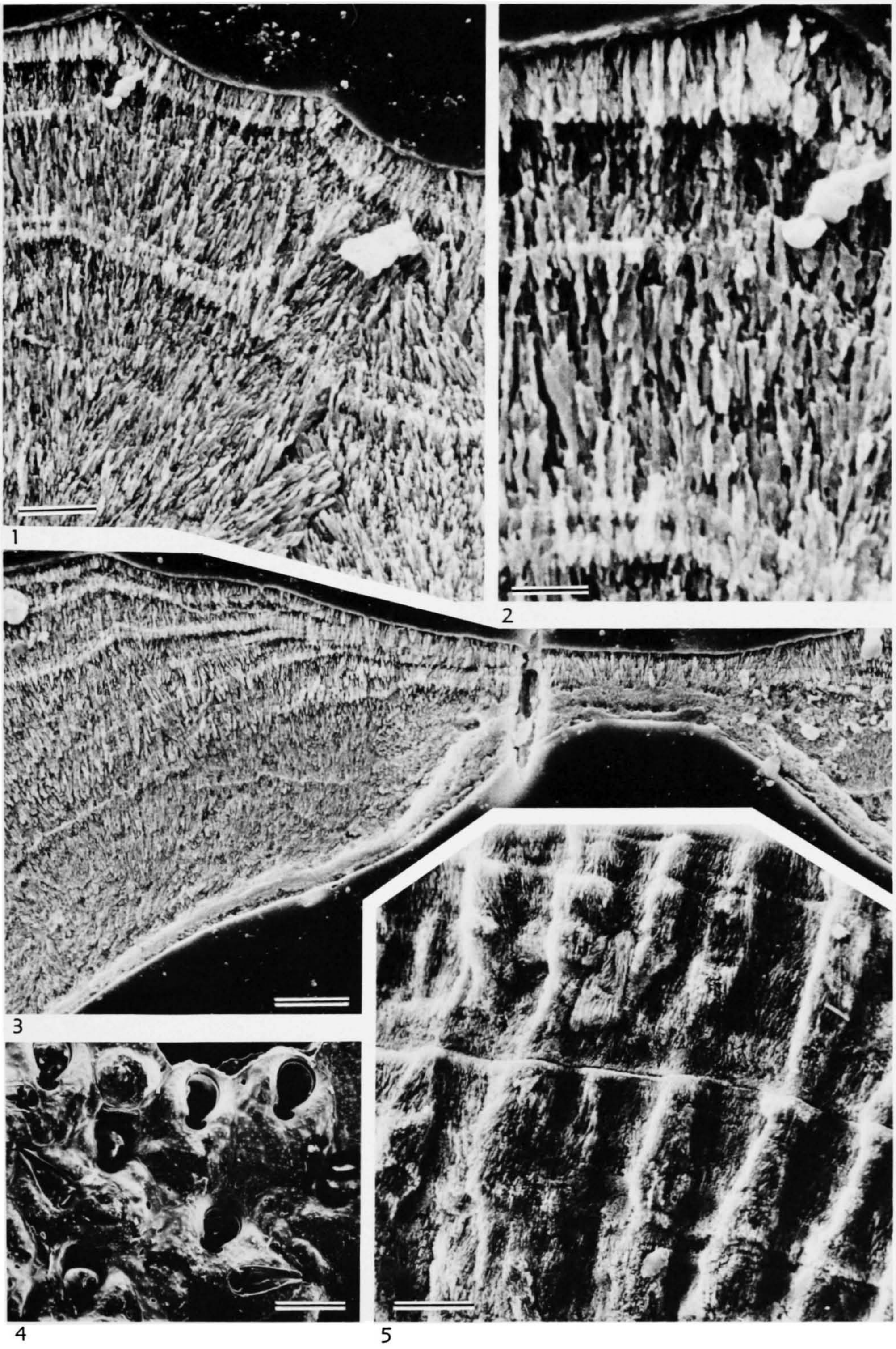


FIG. 117. *(For explanation, see facing page.)*

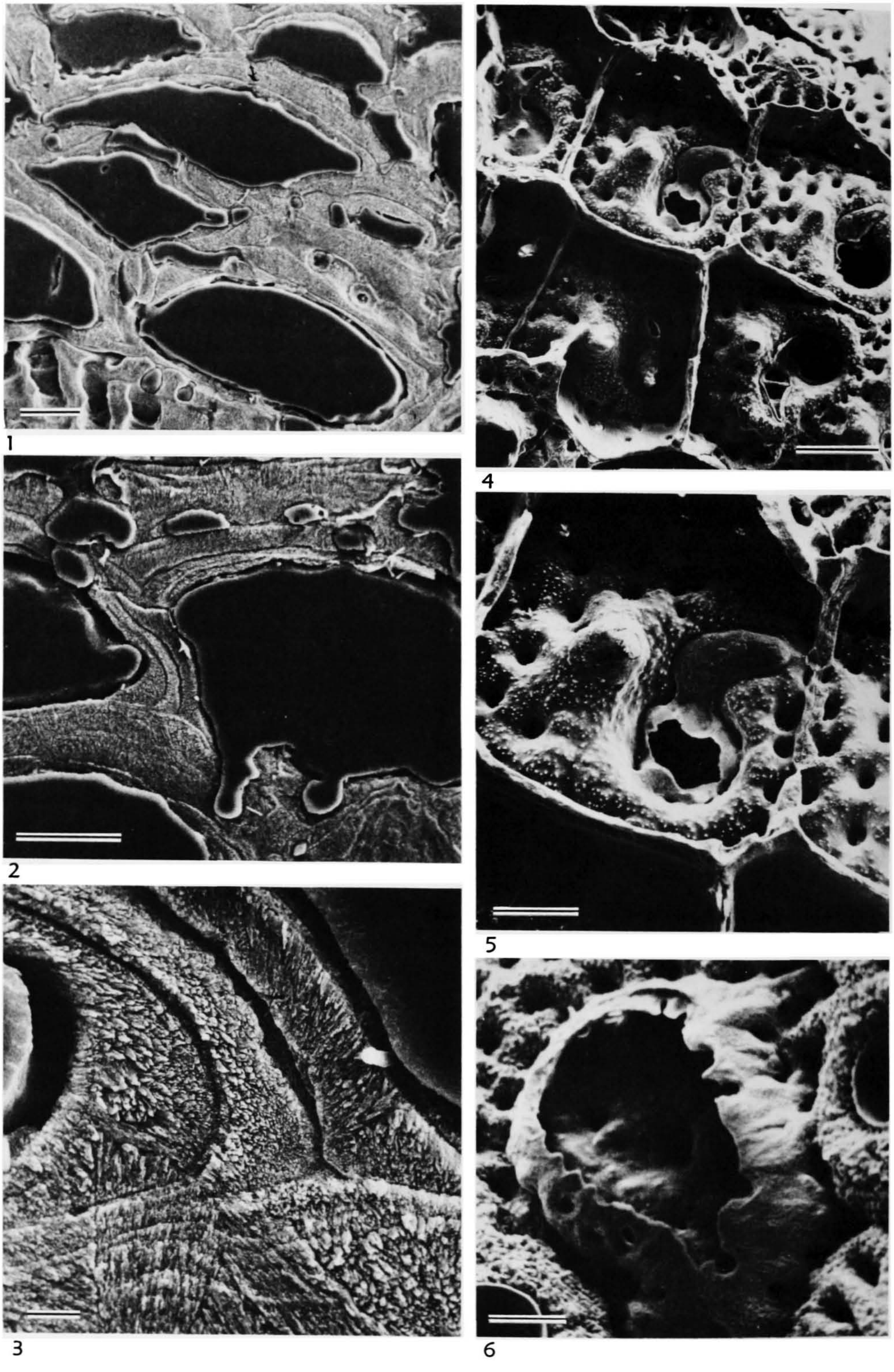


FIG. 118. *(For explanation, see p. 265.)*

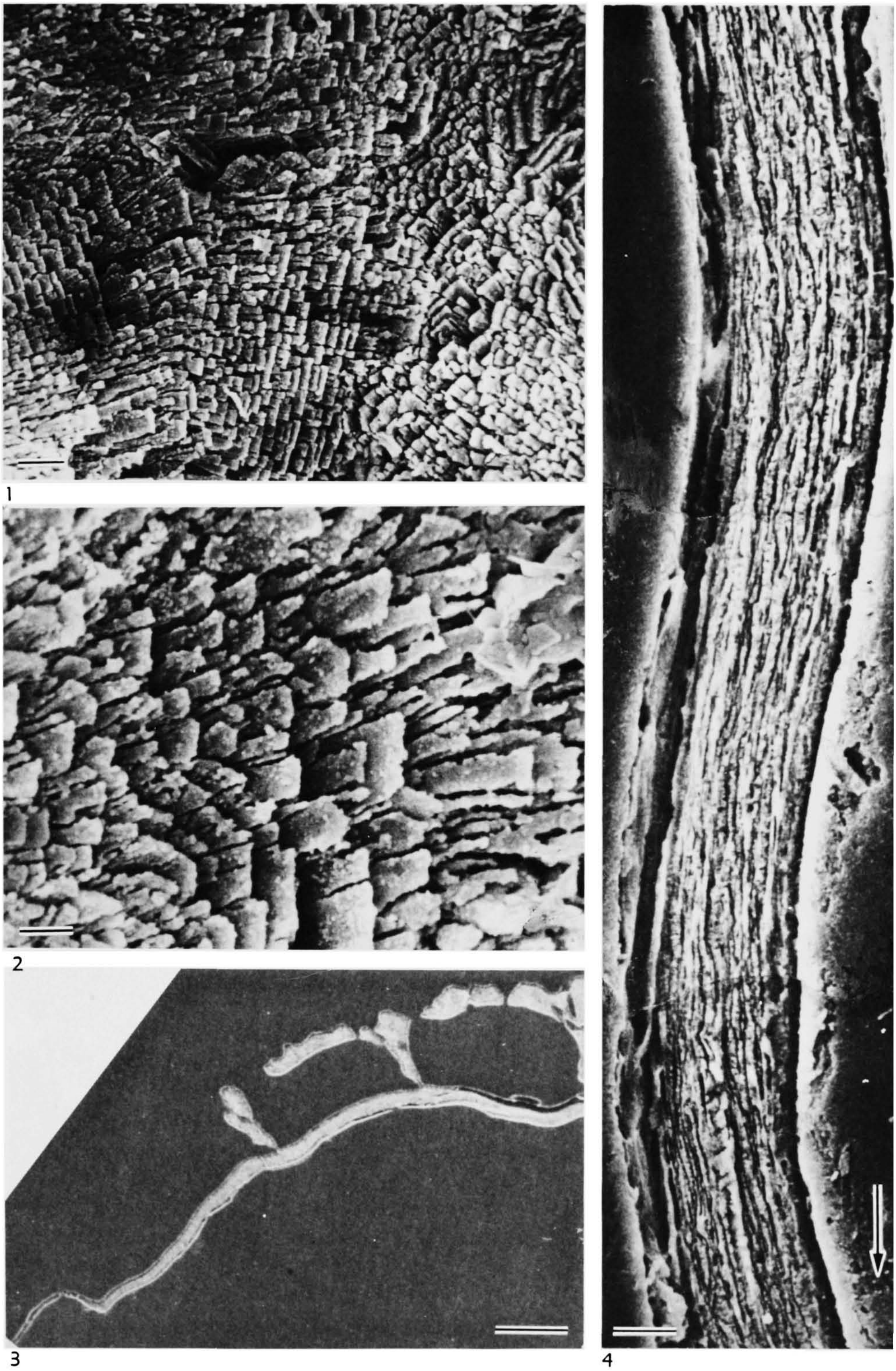


FIG. 119. *(For explanation, see p. 260.)*

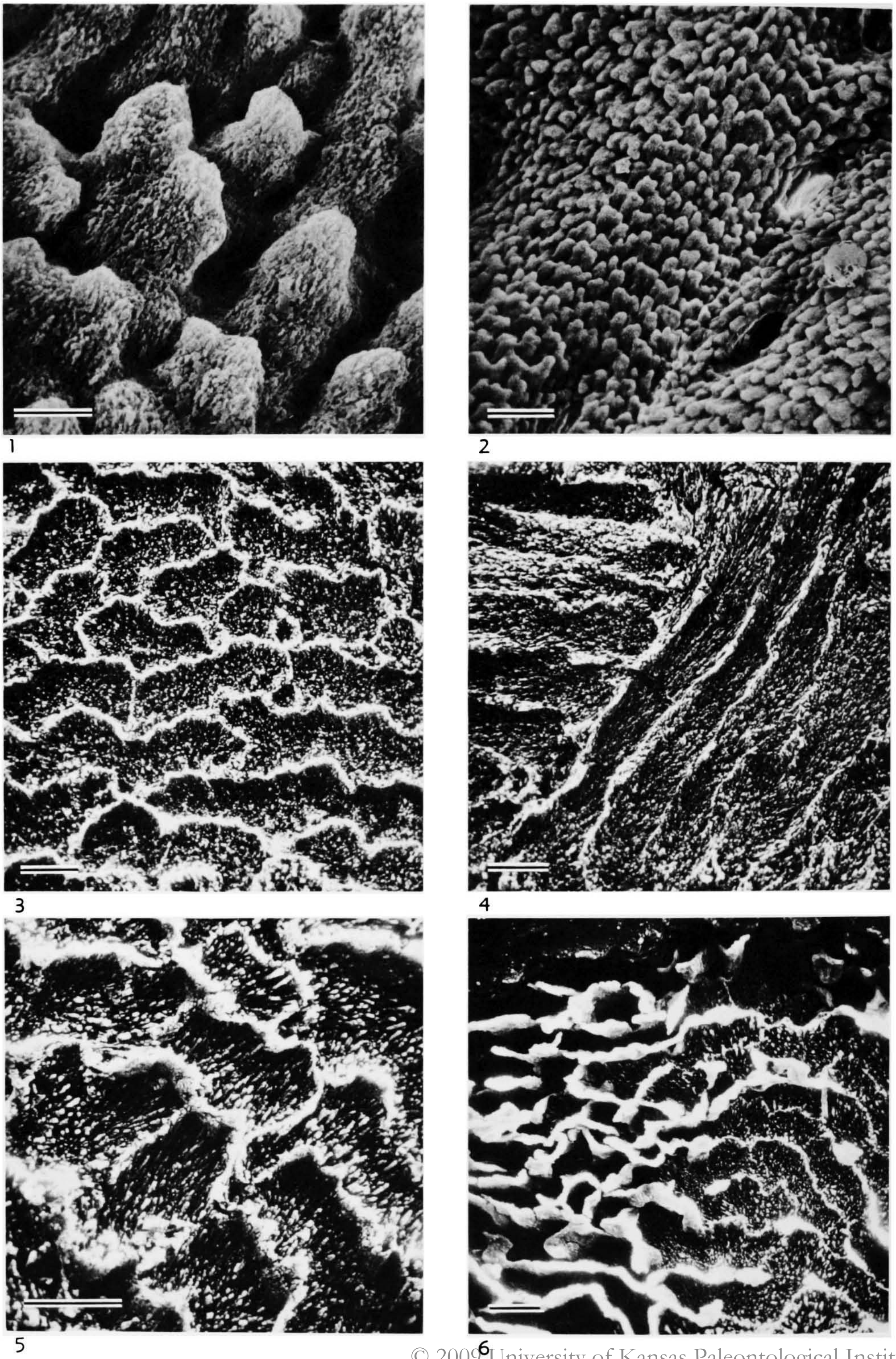


FIG. 120. *(For explanation, see facing page.)*

is the initial calcification of exterior walls against cuticle (Sandberg, 1971), gives clear evidence, in its accretionary banding, of the difference in time of deposition of the various parts of that thin initial skeletal layer.

Bryozoan workers have long noted the inception of deposition (along the proximal and lateral margins of each zooecium) of a superficial frontal calcification, which then progresses distally and toward the zooecial midline.

In an allusion to a temporal succession of skeletal units, the terms "primary," "secondary," and sometimes such higher order terms as "tertiary" have been used in the literature to designate particular ultrastructural units. Even in the relatively simpler system of stenolaemate skeletons the temporal connotations of "primary" and "secondary" are misleading. Although "primary" skeleton may be deposited at the growing tip before any "secondary" skeleton (Hinds, 1975), skeletal rods of "primary" material are deposited contemporaneously throughout the entire time of "secondary" material deposition in some forms (Tavener-Smith, 1969, 1973; Gautier, 1973) (Fig. 108).

In the cheilostomates, meaningful application of such terms with temporal connotations as "primary" and "secondary" becomes even more difficult because of the greater diversity and complexity of skeletal subunits and growth modes in cheilostomate skeletons. For example, cheilostomate skeletons may be either all calcite, all aragonite, or bimineralic. Furthermore, not only are there two distinct mineralogies present, but also a diversity of ultrastructural types. This ultrastructural variety is particularly true for calcite, although recent work (Sandberg, 1976 and unpublished) indicates greater ultrastructural diversity exists for aragonite than was previously thought. Also, the skeleton of any given species is commonly made up of three ultrastructural types, sometimes four, five, or perhaps more types. An opposite problem is that, in some aragonitic forms, except for a poorly developed outer planar spherulitic layer, the entire skeleton is constructed of a single ultrastructure.

Cheilostomate skeletons may, like stenolaemate skeletons, be produced by any one of a broad spectrum of growth modes ranging from only interior walls (except for ancestrular attachment surface) to all exterior walls (except for pore plates), with a variety of

Fig. 118 (see p. 262). Frontal budding.——*1–3. Hippoporidra senegambiensis* (Carter), rec., S. of Tema, Ghana; *1,* numerous superimposed, frontally budded zooecia, transv. sec., ×170 (bar = 50 μm); *2,* detail of adjacent area, note absence of lateral cuticles, ×300 (bar = 20 μm); *3,* detail of *2,* note blisterlike nature of new frontal zooecium and spherulitic aragonite. ×1,475 (bar = 5 μm); all BMNH 1970.8.10.24.——*4,5. Schizoporella floridana* (Osburn), rec., W. coast of Fla.; *4,* frontal view of region with developing, frontally budded zooecia, note all vertical walls are doubled and overlie vertical walls of lower zooecia, ×60 (bar = 100 μm); *5,* detail of *4,* note occluded orifice, ×120 (bar = 100 μm); both USNM 184158. ——*6. Porella compressa* (Sowerby), rec., Sound of Mull, Scot.; frontal view of developing, frontally budded zooecium; note thin walls and ultrastructural difference from adjacent superficial calcification of older zooecia; BMNH 1888.6.9.45, ×120 (bar = 100 μm).

Fig. 119. *(See p. 263.)*

Fig. 120. Compartmentalized spherulitic aragonite walls.——*1,2. Adeonellopsis distoma* (Busk), rec., Madeira; *1,* outer growth surface of frontal shield, etched, wall constructed of numerous parallel, fingerlike projections of spherulitic aragonite, ×2,250 (bar = 5 μm); *2,* lower magnification view of area of *1,* note reverse orientation of aragonite lobes in lower right, ×370 (bar = 200 μm); both BMNH 1911.10.1.927. ——*3,4. Adeonella atlantica* Busk, rec., Nightingale Is., near St. Helena, S. Atl.; *3,* frontal shield, showing aragonite lobes with organic envelopes, note shape similarity to pillow lava, etched transv. sec., ×1,675 (bar = 5 μm); *4,* etched section parallel to long axis of some aragonite lobes in frontal shield, compare orientation of individual aragonite needles to those in *3,* ×1,675 (bar = 5 μm); both BMNH 1887.12.9.725.——*5,6. Adeona* sp., rec., locality unknown; *5,* aragonite lobes in frontal shield, etched transv. sec., ×2,825 (bar = 5 μm); *6,* outer portion of frontal shield, note heavy organic partitions between aragonite lobes, etched transv. sec., ×1,400 (bar = 5 μm); both BMNH 1920.12.10.1.

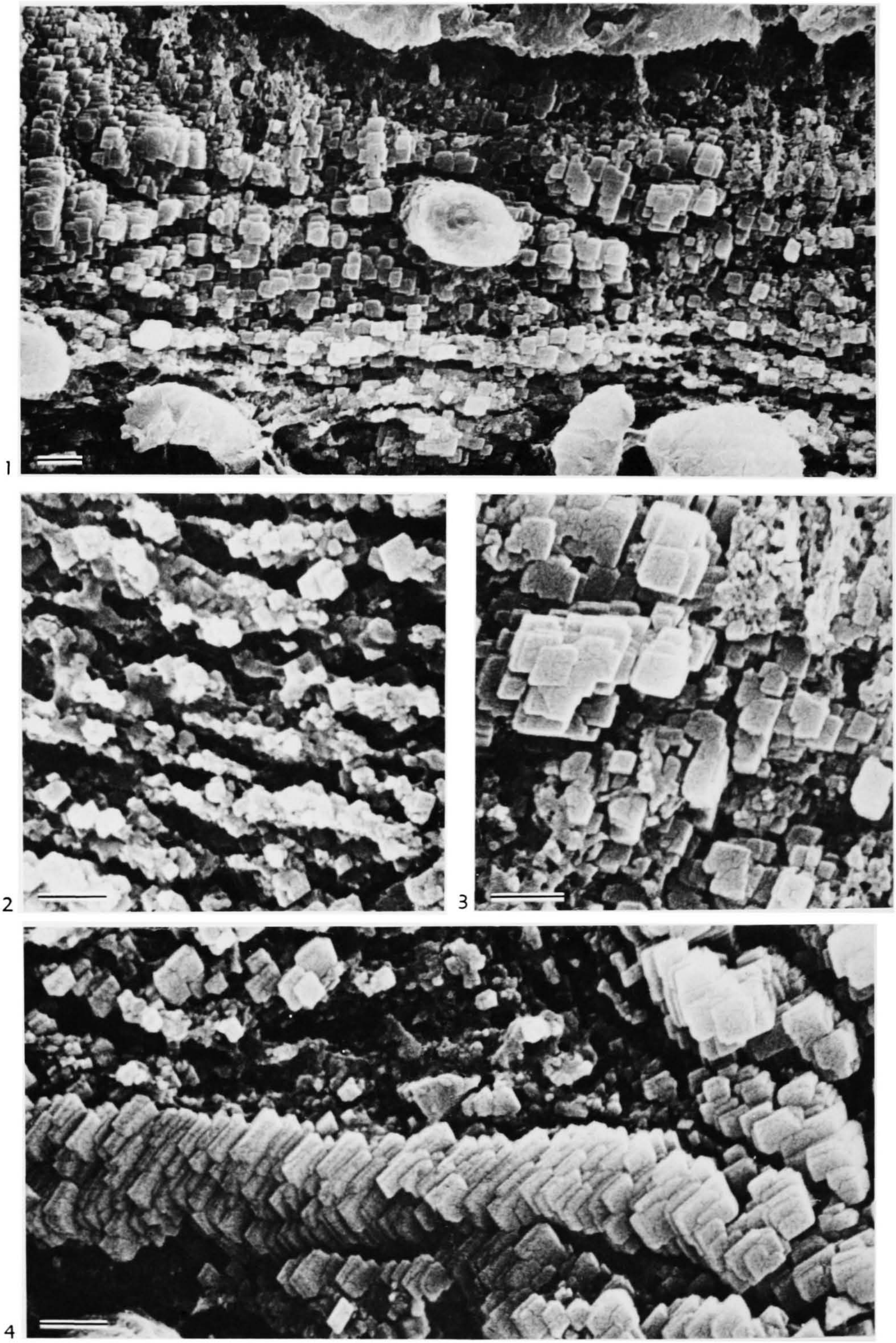


FIG. 121. *(For explanation, see facing page.)*

intermediate modes.

The skeletal succession of some cheilostomates may include repetitions of one or more ultrastructural units. This does not refer to the commonly observed identity of ultrastructure in morphologically equivalent parts in successive zooecia. Rather it is the recurrence, within the wall of a single zooecium, of an ultrastructural type already present in the previously deposited succession in that same wall (Fig. 114,*5*). This recurrence is comparable to the repetition of myostracal layers in some bivalves (Taylor, Kennedy, & Hall, 1969).

The mineralogic and ultrastructural diversity tabulated above reflects the greater range of variations in skeletal makeup known among cheilostomates than among stenolaemates.

The distinctive ultrastructural-mineralogic units of any individual cheilostomate skeleton are clearly sequential. There is little problem in any part of the skeleton in determining a "local stratigraphic section" in that skeleton and applying a sequential terminology (such as "primary," "secondary," "tertiary") to the observed units in that local section. However, great difficulty and uncertainty exists in making any inference of equivalence (correlation) of skeletal units among skeletons of different cheilostomes. Is "secondary" in one form with four ultrastructural units the same as "secondary" in a form with only three? Note that this is a separate issue from the question of contemporaneity of deposition in different parts of a zooecium or zoarium.

One could apply the terms "primary" and "secondary," respectively, to the initial structural framework of the zooecium, and the elaborations or thickenings added to it. This usage is similar to that of Cheetham, Rucker, and Carver (1969), who used the terms primary and "superficial." Except possibly for this structural approach, the use of such terms as primary, secondary, tertiary should be avoided, especially for designation of individual, ultrastructurally distinctive units. Such terms imply the existence, among skeletons of diverse taxa, of a sort of stratigraphic equivalence of units that simply cannot be demonstrated.

MINERALOGY AND ULTRASTRUCTURAL TYPES IN CHEILOSTOMATE SKELETONS

MINERALOGY

Skeletons of cheilostomate bryozoans are composed of calcite, aragonite, or both (Lowenstam, 1954; Schopf & Manheim, 1967; Rucker, 1967; Rucker & Carver, 1969; Sandberg, 1971; Poluzzi & Sartori, 1973, 1975). Calcite skeletons of living cheilostomates contain more $MgCO_3$ (3 to 12 mole percent, mean about 8 mole percent and most species between 6 and 9 mole percent; see Poluzzi & Sartori, 1973, 1975; Schopf & Manheim, 1967; Lowenstam, 1963, 1964b) than do skeletons of living cyclostomates (all calcitic). Cheilostomate skeletons (or skeletal parts) composed of aragonite contain little $MgCO_3$, but their Sr/Ca ratios are at or near that of seawater (Lowenstam, 1964a,b; Schopf & Manheim, 1967; Dodd, 1967).

In organisms with bimineralic carbonate skeletons, including cheilostomates, the two

Fig. 121. Dendritic calcite structures.——*1–4. Umbonula ovicellata* (Hastings), rec., Gairloch, NW. Scot.; *1,* frontal shield, distal to left, elliptical and curved features in center and lower edge are plastic fillings of endolithic algal borings, crystals quite uniformly rhombic, etched long. sec., ×1,000 (bar = 7.5 μm); *2,* detail of another area of section, note organic matrix sheets, ×4,000 (bar = 2.5 μm); *3,* detail of *1,* ×4,000 (bar = 2.5 μm); *4,* detail of another area of section, crystals in lower region forming an elongate dendritic array, ×4,000 (bar = 2.5 μm), all BMNH 1963.3.6.8.

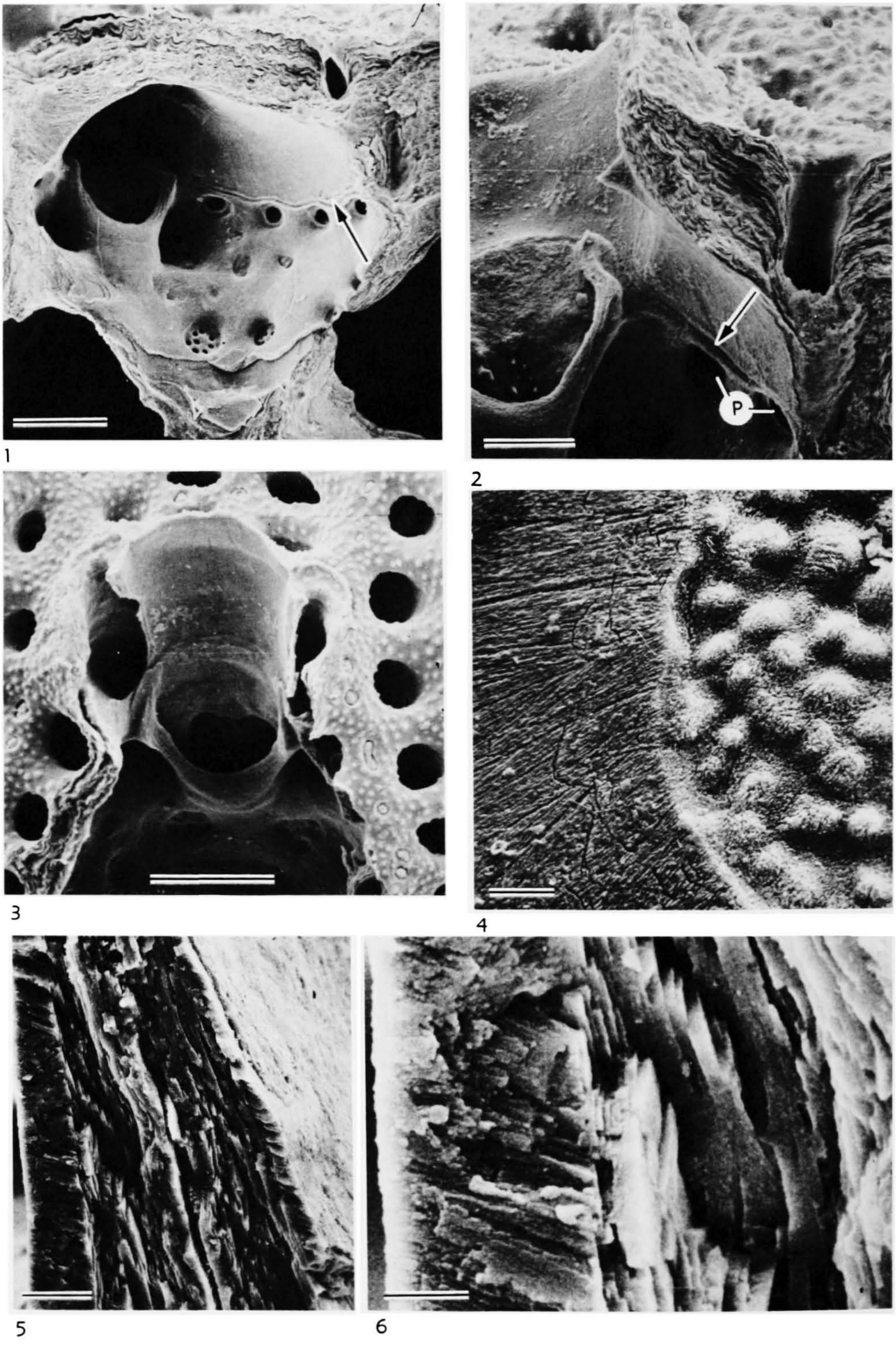


FIG. 122. *(For explanation, see facing page.)*

$CaCO_3$ **polymorphs** form discrete "microarchitecturally separate elements" (Lowenstam, 1954). In bimineralic cheilostomates the basic structural box of the zooecial skeleton is calcite; aragonite is added as elaborations or reinforcements whose position and degree of development vary considerably among taxa. Commonly, aragonite occurs as superficial layers on the frontal exterior surface only (see Fig. 125,*1*) (Cheetham, Rucker, & Carver, 1969; Sandberg & others, 1969), even in **cryptocystideans.** Neither bimineralic nor aragonitic **gymnocystideans** (*sensu* Banta, 1970; Sandberg, 1976) have been encountered. In some zoarial forms in which basal skeletal walls beyond the ancestrula are interior walls (some **lunulitiform colonies,** Greeley, 1969; Håkansson, unpublished; some **petraliiform colonies,** Sandberg, 1976), aragonite may also occur or even only occur as superficial basal thickenings. Only one example of aragonitic zooecial lining in a bimineralic species has been reported (Sandberg, 1976). In bimineralic adeonids and adeonellids, calcite may be clearly present in the basal and lateral walls, probably (but not yet certainly observed) in the lower part of the frontal; aragonite makes up the vast bulk of the frontal and even lateral and transverse walls of those bimineralic skeletons.

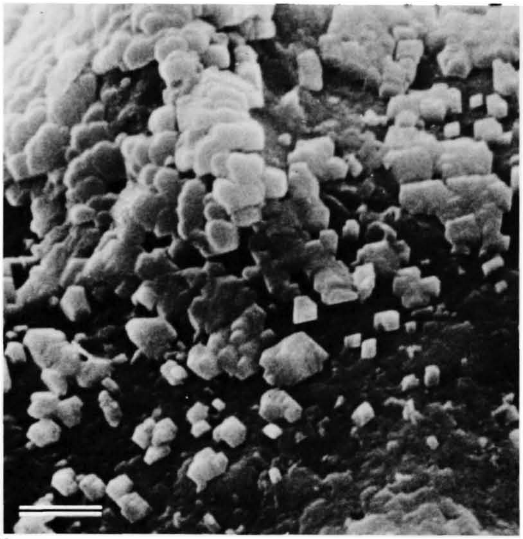
ULTRASTRUCTURAL TYPES

The predominant ultrastructural types in cheilostomate skeletons can be broadly characterized as lamellar and spherulitic. The crystal morphologies are largely mineralogically controlled. However, in contrast to the situation found in bivalves, in which most ultrastructures are aragonite (Kobayashi, 1969, 1971), calcite forms most ultrastructures in cheilostomate bryozoan skeletons.

The individual $CaCO_3$ crystals in cheilostomate skeletons have a wide range of observed morphologies. These include such distinctive types as very elongate needle-shaped or lath-shaped crystals elongate in the *c*-axis direction and thin rhombic or hexagonal crystals flattened in a plane perpendicular to the *c*-axis. Those latter, planar crystals commonly make up the lamellar skeleton units and may exhibit spiral growth steps (screw dislocations) (Fig. 102,*4–6*; 103,*3,4*) as a result of lattice defects (Wise & deVilliers, 1971; Wada, 1972). Tavener-Smith and Williams (1972, fig. 106, 139) noted such spiral growth, but appear to have too broadly applied the term "spiral growth" to include various arrangements of minute polycrystalline arrays (Tavener-Smith & Williams, 1972, fig. 31, 54).

There is some uncertainty (as discussed by

Fig. 122. Interior-exterior wall boundaries and calcite wall ultrastructures.——*1–3. Metrarabdotos tenue* (Busk), rec., Caroline Sta. 68, off NE. Puerto Rico; *1,* transverse fracture section; scalloped double line (arrow) along right lateral wall marks attachment of membranous frontal, exterior epifrontal wall above, areolar pores below, and rather tubular oral shelf distally (Y-shaped in this view); also note multiporous septulae and numerous layers of frontal wall, ×135 (bar = 100 μm); *2,* detail of fractured section of frontal, line of attachment of membranous frontal (arrow) extending above areolar pores (P) and around distal margin of oral shelf; above that line and continuing out peristome, wall bears planar spherulitic ultrastructure, ×260 (bar = 50 μm); *3,* frontal view of zooecium with frontal broken out, longitudinal stripes of planar spherulitic ultrastructure faintly visible on distal wall of peristome, ×175 (bar = 100 μm); all USNM 209434.——*4. Megapora ringens* (Busk), rec., Shetland Is.; detail of kenozooid in frontal view; exterior wall (gymnocyst) with planar spherulitic ultrastructure to left, interior wall (cryptocyst) with tuberculate thickening to right; curved line between marking outer edge of both membranous frontal and hypostegal coelom; BMNH 1911.10.1.630, ×950 (bar = 10 μm).——*5,6. Watersipora subovoidea* (d'Orbigny), rec., locality unknown; *5,* fractured transverse section, unetched, of lateral walls of adjacent zooecia; walls composed of mainly lamellar calcite, but with zooecial linings of massive, apparently spherulitic calcite, ×1,900 (bar = 5 μm); *6,* detail of *5,* ×6,000 (bar = 2 μm); both BMNH 1970.6.1.32.



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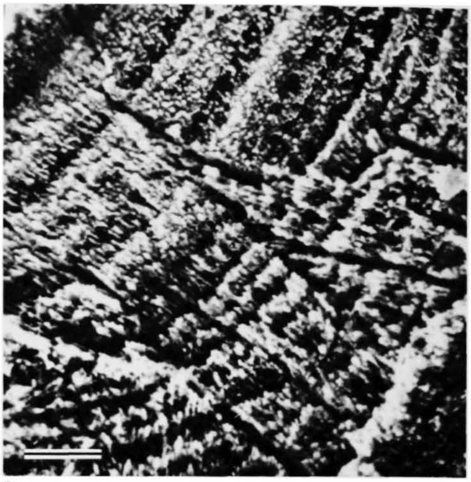

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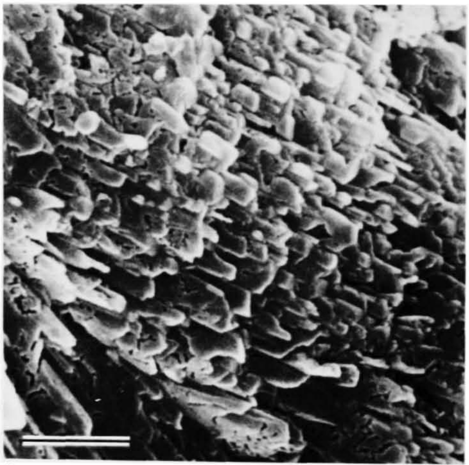

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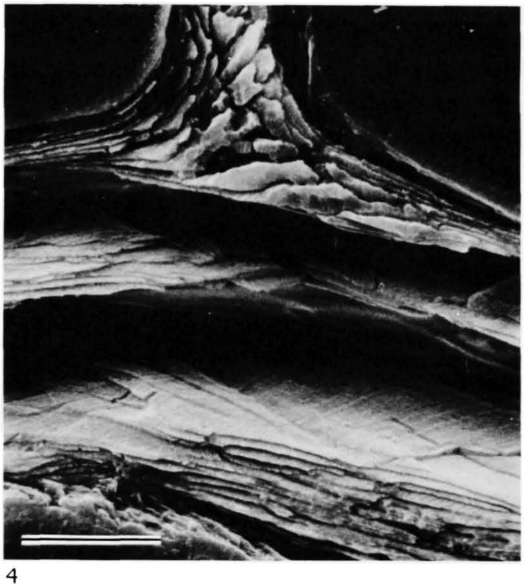

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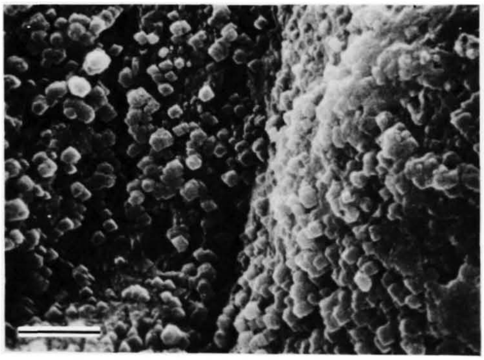

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FIG. 123. *(For explanation, see facing page.)*

Towe & Cifelli, 1967, p. 744–745; Towe, 1972, p. 2–4) as to what constitutes "a crystal." Certainly, in cheilostomate skeletons there are some "crystals" that, after strong etching, appear to be composed of many aligned "subcrystal units" (Fig. 115).

The shapes of individual skeletal crystals in bryozoans (as well as other organisms) are related to mineralogy, amount and distribution of organic matrix, rate of carbonate deposition, and other factors. There is a general similarity in those controls that transcends even phylum boundaries. For example, very similar spherulitic arrays of acicular aragonite occur in bryozoans, mollusks, scleractinian corals, and sclerosponges. In contrast, the effects of some factors may vary among taxa. Broad rhombic lamellar crystals with screw dislocations are only aragonite in gastropods and bivalves and only calcite in bryozoans and brachiopods, despite great morphologic similarity of all those crystals.

Organic matrix can be quite abundant in cheilostomate skeletal carbonate, whether as distinct intercrystalline sheets, separating and surrounding individual crystals or regions of crystals (Fig. 103,*2*; 109,*3,4*; 114,*2*; 120,*3–6*), or as a more diffuse intracrystalline network visible only after extensive etching (Fig. 103,*6*). In some instances, as in the more tabular aragonite (Fig. 103,*5*), the distribution of intercrystalline organic matrix seems strongly to affect the carbonate crystal shape.

In earlier published polarized-light studies of cheilostomate skeletons and in my limited number of such observations, the *c*-axis orientation of skeletal crystals has generally been easy to determine. The *c*-axes are usually aligned parallel to the wall surface in longitudinal stripes of planar spherulitic ultrastructure and perpendicular to the wall surface in most lamellar or **transverse spherulitic ultrastructures.** A detailed comparative study of optic orientation and crystal morphology and arrangement would be most beneficial for a clearer understanding of skeletal structure, particularly of the seemingly irregular or homogeneous units.

Individual crystals of some cheilostomate skeletal units may be quite striking (Fig. 119,*1,2*; 121) but nevertheless may resemble crystals in skeletons of other phyla. Therefore, the main value that skeletal ultrastructure may have in ontogenetic or phylogenetic reconstructions is not in the individual crystals, but rather in the aggregate units of crystals or successions of units. Examples of these aggregate units are the planar or lenticular lamellae, the planar spherulitic fans, and the conical or palisade spherulitic arrays. There are a number of less clearly organized (or at least less clearly understood) aggregates of crystals. These ultrastructures are poorly ordered arrays, usually involving minute, equant crystals for which preferred orientation individually or in aggregate is not evident. Similar ultrastructure in bivalves has been referred to as "homogeneous." Al-

Fig. 123. Ultrastructures of wall surfaces and sections.——*1. Membranipora grandicella* (Canu & Bassler), rec., Albatross Sta. D5315, Philip.; frontal shield (cryptocyst) exterior, distal toward top, USNM 209441, ×5,250 (bar = 2 μm).——*2.* Sertellid sp., rec., locality unknown; calcite zooecial lining layers on proximal side of basal-transverse wall junction; competitive, interfering growth of spherulitic calcite arrays clearly shown; etched long. sec., BMNH 1892.1.28.112, ×5,100 (bar = 2 μm).——*3. Tubiporella magnirostris* (MacGillivray), rec., Port Phillip, Vict., Australia; detail of basal exterior surface with lobes of acicular aragonite crystals, crystals here the more massive laths; BMNH 1887.6.27.1, ×6,800 (bar = 2 μm).——*4. Micropora* sp., rec., Albatross Sta. D2856; basal-transverse wall junction, distal toward right; note broad lathlike crytals in basal wall, separated because of embedding-plastic shrinkage; USNM 209442, ×300 (bar = 20 μm).——*5. Reteporella myriozoides* Busk, rec., Challenger Sta. 148, Possession Is., SW. Indian O.; frontal shield exterior surface; rhombic calcite crystals seeded over entire wall surface, forming layers by lateral accretion; BMNH 1887.12.9.516, ×5,250 (bar = 2 μm).——*6. Ogivalia gothica* (Busk), rec., Challenger, Prince Edward Is.; frontal shield interior surface, etched; calcite crystals here stubby rods, but in some nearby wall areas more flattened and rhombic; BMNH 1887.12.9.358, ×3,800 (bar = 2 μm).

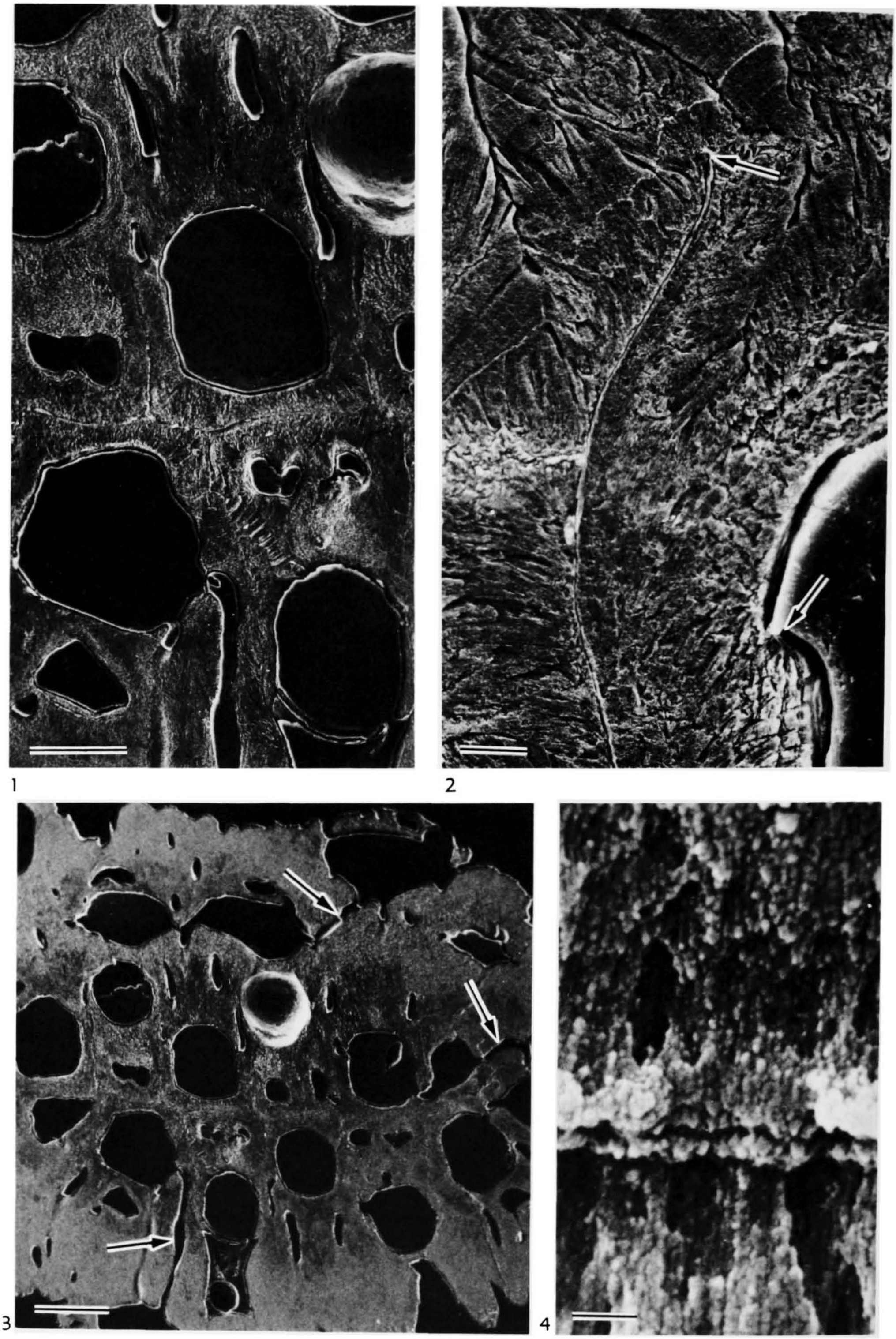

FIG. 124. *(For explanation, see facing page.)*

though some of the molluscan (and bryozoan) ultrastructures may approach a truly homogeneous texture, the term really reflects not a distinct ultrastructural type, but rather a complex of as yet poorly understood fine textures that have been beyond the resolution limit of the light microscope.

It is probably best not to perpetuate, as general categories, the "parallel" and "transverse" groups proposed earlier (Sandberg, 1971). The difference between lamellar ("parallel") and spherulitic ("transverse") ultrastructures can be totally a function of organic sheet development with no change in crystal morphology or orientation. This was particularly well shown by Mutvei (1972) for the cephalopod *Nautilus*. Furthermore, even in the "parallel" lamellar ultrastructure, the tabular crystals may sometimes be composed of "transverse" lath or needlelike subcrystals (Fig. 116,*1*; 122,*5,6*; Erben, 1974).

It is important to recognize that much of the distinction between the ultrastructural categories previously proposed for cheilostomate skeletons is a matter of degree of dominance of textural details either parallel to or perpendicular to the wall surface. With the exception of the planar spherulitic layer and skeletons of some interior-walled forms, the skeletal units are accreting over broad areas parallel to the wall surface. Textural features that are oriented parallel to the wall include discrete tabular or lenticular units separated by diffuse or distinct organic sheets (lamellar ultrastructure) and accretionary banding (most commonly seen as distal increments on crystals growing generally *transverse* to the wall). The main textural component perpendicular to the wall surface is that of crystals elongate in that growth direction. Those acicular or bladed crystals most commonly are arranged in spherulitic bundles transverse to the wall. Massive units common as zooecial linings provide an example of a possible arbitrariness in the terminology. Those massive units tend to be composed of spherulitic ultrastructure, but have accretionary banding. Depending on which of those components is most evident, the massive unit could be called either "parallel" or "transverse." Consequently those terms, although useful for orientational and descriptive purposes, should not be used as names of specific distinctive ultrastructural groups.

INDIVIDUAL CRYSTALS AND CRYSTAL AGGREGATES IN CALCITE AND ARAGONITE

Aragonite in cheilostomate skeletons was earlier (Sandberg, 1971) known only as acicular crystals, mainly in transverse, usually spherulitic arrays (Fig. 114,*1*; 117,*1–3,5*; Sandberg, 1971, pl. 3, fig. 1–8; pl. 4, fig. 1–3). Such spherulitic aragonite arrays comprise the entire skeleton (above an aragonite planar spherulitic layer) in some cheilostomates. Recent SEM study has shown that more blocky aragonite can occur if there are closely spaced organic sheets (Fig. 103,*5*) transverse to the direction of spherulite growth. Furthermore, acicular aragonite commonly has been found as planar spherulitic ultrastructure against cuticle in exterior walls (Sandberg, 1971, pl. 3, fig. 3).

Fig. 124. Frontal loss of intercalary cuticles.——*1–4. Porella compressa* (Sowerby), rec., Sound of Mull, Scot.; *1,* intercalary cuticles extend along basal surfaces of primogenial layer and up between lateral calcified walls to only slightly above upper end of interior zooecial cavity, overlying, frontally budded zooecia lack cuticle and are irregularly arranged, etched transv. sec., ×140 (bar = 100 μm); *2,* detail of a frontal-lateral junction, intercalary cuticle overgrown (upper arrow) by extrazooidal frontal thickening with distinct accretionary banding and spherulitic structure, shelf on inner lateral wall surface (lower arrow) marks upper end of maximum interior thickening of lateral wall and perhaps also lower edge of ascus, etched transv. sec., ×925 (bar = 10 μm); *3,* lower magnification view of area of *1,* note continuation of areolar pores through frontal thickening to frontally budded zooecia (arrows), ×55 (bar = 200 μm); *4,* detail of spherulitic structure in *2,* radiating arrays composed of minute aligned calcite crystals, ×18,500 (bar = 0.5 μm); all BMNH 1888.6.9.45.

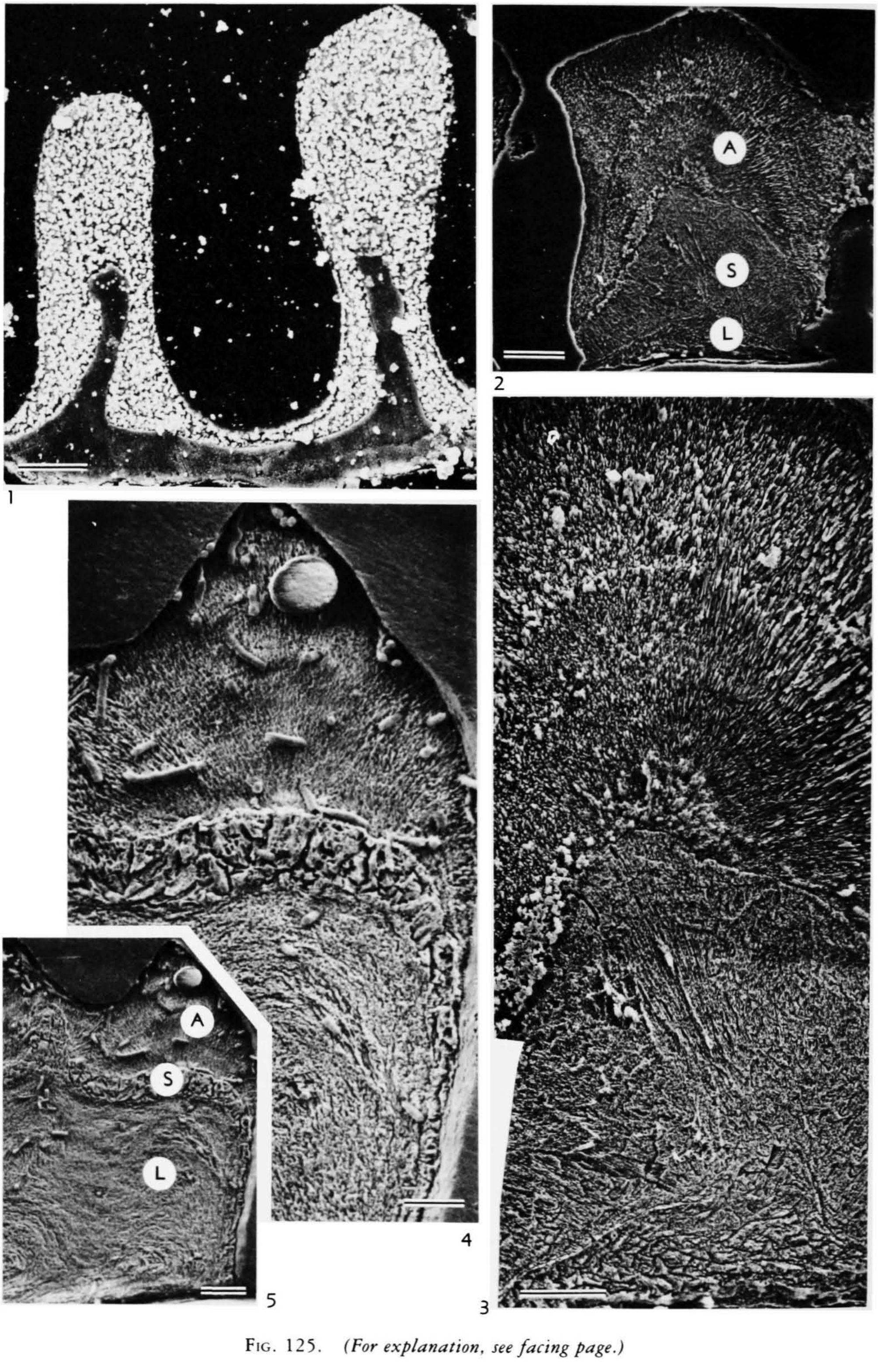

FIG. 125. *(For explanation, see facing page.)*

Calcite in cheilostomate skeletons is much more diverse in crystal morphology, but most ultrastructures are basically lamellar or spherulitic (note comparable groupings in bivalve shells as discussed by Taylor, 1973). Individual crystal morphologies and the aggregate arrangements for calcite in cheilostomate skeletons include:

1. Rhombic or hexagonal crystals, flattened in a plane perpendicular to the *c*-axis, are commonly quite large and often show screw dislocations (Fig. 102; 115,*1*). These crystals make up much of the lamellar ultrastructural units. Marginal growth of the individual crystals may leave distinctive accretionary banding (Fig. 102,*3*). Closely stacked or dendritic arrays of this general crystal type make up some of the lenticular or crudely laminated skeletal units, as well as some of the irregular, massive units (Fig. 121,*1–4*; 123,*1,5*).

2. In a few cheilostomates, broad calcite lamellae either show no clear individual crystal units (Fig. 123,*4*; not studied in polarized light) or have large, usually thin, bladelike crystals with indications of accretion at the end of the blade (Fig. 119,*1,2*). The latter crystals are similar to some bladelike crystals in stenolaemate bryozoan and brachiopod skeletons and represent a form of edgewise growth.

3. Some irregular massive or lenticular skeletal units are made up of a mixture of the flattened rhombic crystals discussed above and small truncated, rod-shaped crystals. These rods are parallel within individual arrays, but occur in diverging arrays that suggest a form of spherulitic growth (Fig. 123,*3,6*).

4. In the planar spherulitic layers occurring against cuticle, calcite crystals are most commonly acicular, rarely flattened laths (Fig. 111), and generally arranged in wedge- or fan-shaped arrays. In those arrays, individual crystals may stand out clearly or be subordinate in clarity to larger, usually triangular or trapezoidal aggregates of crystals (Fig. 111,*1,2*; 112,*1,3*; 122,*4*). These generalities of crystal orientation and appearance hold whether the calcification that produced the planar spherulitic ultrastructure occurred at an advancing linear front or radially from scattered centers of crystallization (Fig. 111,*3,4*).

5. It was noted above that spherulitic arrays transverse to the wall are the most common skeletal unit in aragonite. Similar spherulitic units are also quite common in calcite, but are made of crystals with a far greater variety of individual shapes. Acicular crystals of calcite comparable in size and shape to those that commonly form the planar spherulitic layer on exterior walls also make up some of the transverse spherulitic units (Fig. 123,*2*). In addition, such spherulitic calcite units may be made up of needlelike columns of very minute, equant crystallites (Fig. 124,*4*). In other cheilostomates the spherulitic arrays are composed of massive, crudely conical calcite masses with crenulate, interlocking boundaries (Fig. 114,*2–5*; 125,*4*). Such arrays are almost certainly the source of the pattern called "cell-mosaic" by Levinsen (1909) and Sandberg (1971) and

Fig. 125. Bimineralic walls.——*1. Metrarabdotos unguiculatum* (Canu & Bassler), rec., Albatross Sta. D2405, Gulf of Mexico; frontal shield, treated with Feigl solution; precipitate (Ag and MnO$_2$) selectively formed on superficial aragonite, leaving lower calcite unit etched but unstained; long. sec., USNM 184156, ×900 (bar = 10 μm).——*2,3. Pentapora foliacea* (Ellis & Solander), rec., Cornwall; *2*, frontal shield, initial, calcite portion composed of a lower, laminated unit (L) and an upper, spherulitic unit (S), which is, in turn, surmounted by a superficial spherulitic aragonite unit (A), long. sec., ×450 (bar = 20 μm); *3*, detail of *2*, ×1,250 (bar = 10 μm); both BMNH 1911.10.1.1561.——*4,5. Tubiporella magnirostris* (MacGillivray), rec., Port Philip Head, Australia; *4*, frontal shield, upper portion of wall penetrated by numerous borings (now plastic-filled), etched transv. sec., ×850 (bar = 10 μm); *5*, lower magnification view of same wall; lower, poorly laminated calcite portion (L) overlain by thin spherulitic calcite unit (S) and thicker, superficial aragonite unit (A), ×340 (bar = 20 μm); both BMNH 1927.8.4.24.

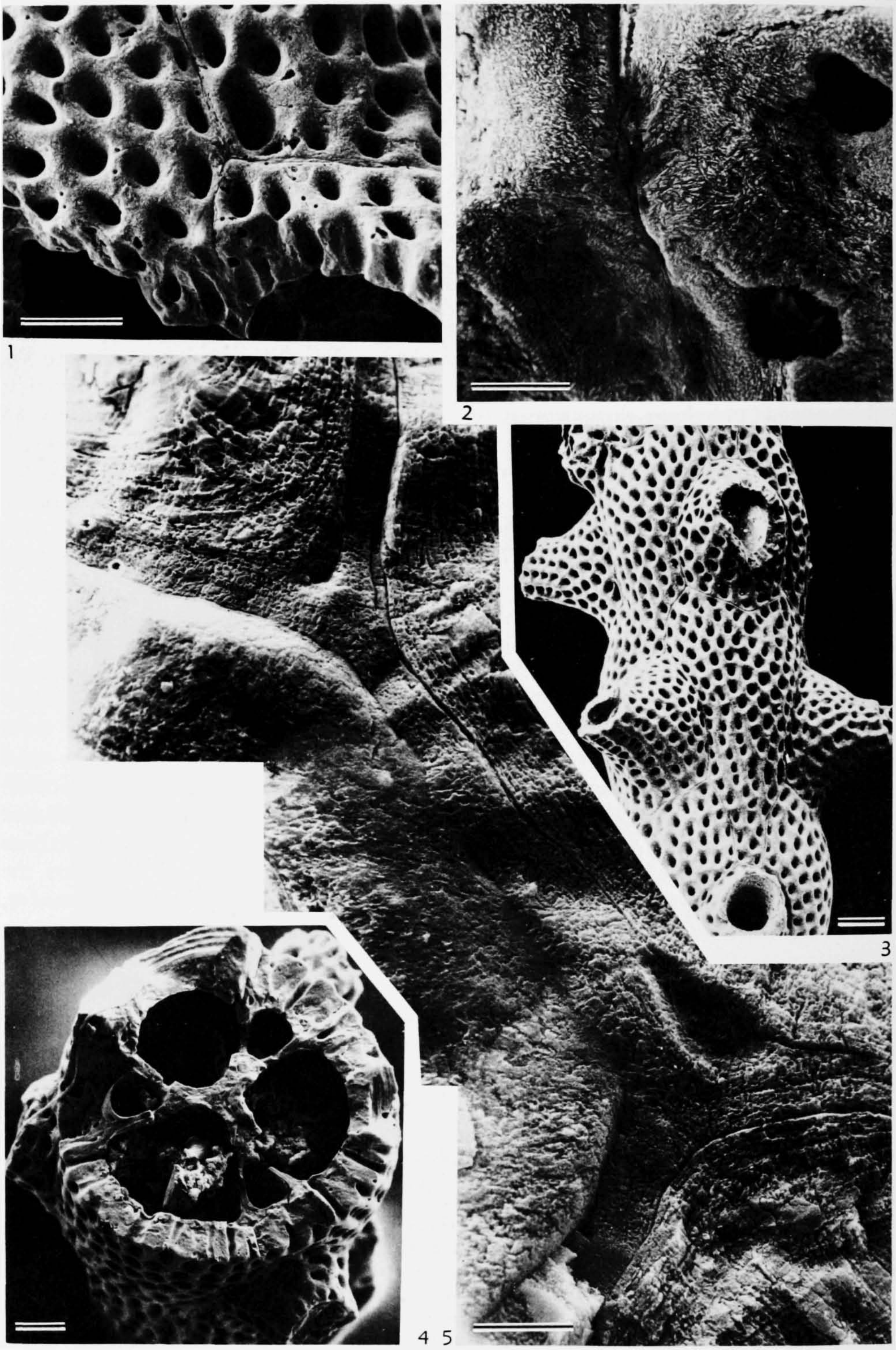

FIG. 126. *(For explanation, see facing page.)*

not actual, single-cell secretory zones (see also SANDBERG, 1976). In some such skeletal units the calcite appears to be in quite large crystals; etching reveals no substructure other than accretionary banding (Fig. 113,*4*; 114,*3*). In others, the etching shows a very fine, granular or acicular substructure that may be related to the arrangement of intracrystalline organic matrix. In some massive layers there occur calcite crystals that are arrayed as laths at an angle to the wall surface, sometimes in roughly conical groupings (Fig. 122,*6*; SANDBERG, 1971, pl. 2, fig. 9). These crystals are clearly flattened and appear to be growing by terminal extension toward the adjacent coelomic space with some intercalation of new crystals between in the conical arrays.

Spherulitic calcite commonly occurs in zooecial linings (Fig. 114,*2,3*; 122,*5,6*; 126,*5*) as well as superficial thickenings, especially in frontal shields. In those frontal shields, the spherulitic calcite is often followed by spherulitic aragonite (Fig. 125,*2–5*). In some cheilostomates, spherulitic aragonite alone may compose the superficial thickening of the frontal shield (Fig. 103,*1*; SANDBERG, 1971, pl. 4, fig. 1, 2).

Organic matrix occurs most commonly as intercrystalline networks, sheaths around individual crystals, or as bounding sheets at the outer surface of exterior walls or between some ultrastructural units. In some few groups there may be developed an intermediate level of organic matrix as envelopes compartmentalizing regions of an ultrastructural unit. For example, in adeonids the transverse spherulitic aragonite, which makes up most of the skeleton, is subdivided into long, fingerlike units by tubular organic sheaths. Within each sheath, numerous, minute aragonite needles are arranged with their long axes generally parallel to the long axis of the enclosing organic tube (Fig. 120,*3–5*). These organic-walled, fingerlike skeletal units appear to originate by distal prolongation of the numerous lobelike skeletal projections on the frontal exterior surface (Fig. 120,*1,2*).

CORRELATION OF ULTRASTRUCTURE AND SKELETAL GROWTH MODES

ULTRASTRUCTURAL RECOGNITION OF EXTERIOR AND INTERIOR SKELETAL WALLS

The recognition, on the basis of skeletal features, of ontogenetic development patterns and major taxonomic groups among cheilostomates depends heavily on the ability to differentiate calcified interior and exterior walls (SILÉN, 1944a,b), especially in the frontal region. Combining the various definitions of SILÉN (1944b, p. 436), BANTA (1970, p. 39), BOARDMAN and CHEETHAM (1973, p. 131), and BOARDMAN, CHEETHAM, and COOK (this revision): **exterior skeletal walls** are those walls which calcify against cuticle and which occur in body walls that (in their precalcified, membranous state) expanded the

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FIG. 126. Frontal intercalation of cuticle.——*1–5. Margaretta tenuis* HARMER, rec., Albatross Sta. D5134, Philip.; *1,* fractured frontal shield, etched, distal toward top, note lines of cuticle intercalation in lateral (running vertically through figure) and transverse positions, ×140 (bar = 100 μm); *2,* detail of *1,* intersection between line of lateral cuticle intercalation and transverse fracture, showing that cuticle is a near-surface phenomenon in frontal shield and does not extend down into lateral walls, ×1,400 (bar = 10 μm); *3,* exterior view of internode, distal toward top, note superficial cuticulate boundaries both proximal and distal to each peristome, as well as laterally, ×35 (bar = 200 μm); *4,* transverse fractured section, etched, of a zoarium, ×70 (bar = 100 μm); *5,* detail of *4,* axis of zoarial segment at triradiate junction (lower right), figure shows massive zooecial lining deposits of four zooecia surrounding thinner, initial skeletal layers, significantly, these initial layers are not subdivided by intercalary cuticles, ×1,400 (bar = 10 μm); all USNM 209446.

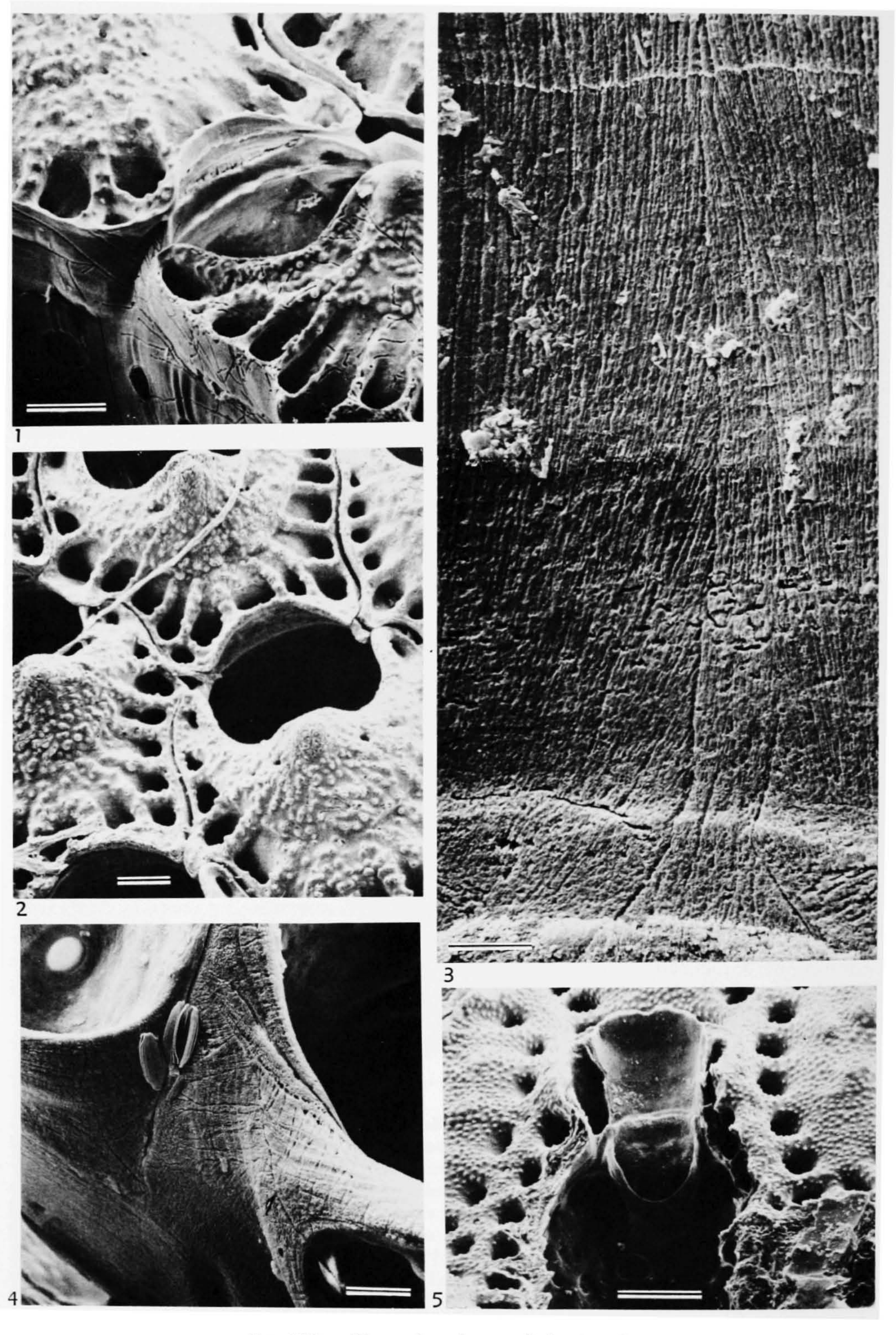

FIG. 127. *(For explanation, see facing page.)*

coelomic volume of the colony. **Interior skeletal walls**, in the same terms, are walls that grow off the inner surface of exterior skeletal walls (or other interior skeletal walls) by apposition and partition preexisting coelomic volume of the colony. In the absence of observations on preserved distal colony edges or on living colony growth (obviously not possible with fossils), such differentiation must be based on some skeletal record of the growth mode. In the case of contiguous exterior walls (e.g., lateral walls of two adjacent lineal series) the presence of doubled intercalary cuticles (in dead modern material) or of a sharp central break between the two walls (in fossils) is indicative of exterior walls. However, that criterion does not work for single, noncontiguous exterior walls, such as those in the frontal region. The ultrastructure of interior and exterior skeletal walls is distinctive and provides an excellent supplement to morphological criteria for wall differentiation. Superimposed lamellae or accretionary bands on both sides of a cheilostomate skeletal wall reflect the presence of secretory epithelia on both sides and therefore the origin of that wall as an interior wall. In contrast, initial calcification adjacent to cuticle in an exterior wall is an array of planar spherulites (Fig. 111; 112,*1,3–5*; 127,*3,4*; 128). Such planar spherulitic ultrastructure (see discussion in SANDBERG, 1971, 1973, 1976) is produced by calcification at a linear front advancing over a surface (the exterior cuticle). The spherulitic ultrastructure is visible on exterior walls of cheilostomates because it is left exposed on the outer surface of the skeletal wall by the one-sided skeletal growth away from cuticle. Planar spherulitic ultrastructure characterizes cuticulate exterior walls in skeletons of not only cheilostomate but also cyclostomate bryozoans (SÖDERQVIST, 1968; TAVENER-SMITH & WILLIAMS, 1972; BROOD, 1973). Similar ultrastructure has been found on the underside of coral tabulae and dissepiments (WELLS, 1969; BARNES, 1970; SORAUF, 1971, 1974), which, although not cuticulate, are formed by one-sided growth with calcification advancing on a linear front.

The existence of a distinctive ultrastructure on exterior walls in cheilostomate skeletons is of great significance in the interpretation of genesis of frontal shields and other walls, ovicells, spines, and other calcified features. Its presence or absence can usually be determined easily by SEM study of surfaces of specimens freed from sedimentary matrix. However, techniques for recognition of that planar spherulitic ultrastructure in sections must be developed before it could be of general use for study of solidly embedded cheilostomates or of ancient stenolaemates, which commonly occur in dense crystalline limestone.

Similar ultrastructure may occur in stenolaemates on the undersides of diaphragms, which calcify from one side only. However, because of the difference in zooecial shape and growth mode in cheilostomates, such one-sided, later ontogenetic, proximal partitions evidently do not occur. Even in stenolaemates, the interior wall nature of the dia-

FIG. 127. Cormidial apertures, exterior walls in peristomes, and transverse walls.——*1,2. Umbonula ovicellata* (HASTINGS), rec., Gairloch, NW. Scot.; *1,* oblique frontal view of zooecial aperture, zooecial row along left removed, exposed lateral walls showing planar spherulitic ultrastructure and numerous borings (algal?), note formation of peristome by distal zooid, ×120 (bar = 100 μm); *2,* frontal view, note sides of secondary orifice formed in part by lobes of superficial calcification by zooids of adjacent lateral rows, ×80 (bar = 100 μm); both BMNH 1963.3.6.8.——*3. Metrarabdotos tenue* (BUSK), rec., Caroline Sta. 68, off NE. Puerto Rico; detail of distal wall of peristome with stripes of planar spherulitic ultrastructure oriented distally (toward top); USNM 209434, ×2,400 (bar = 5 μm).——*4. U. ovicellata,* same data as *1*; detail of transverse-lateral wall junction, distal toward upper left; line of cuticle incorporation into upper transverse wall partly obscured by diatoms; planar spherulitic ultrastructure showing direction of growth of various wall regions; BMNH 1936.3.6.8, ×460 (bar = 20 μm).——*5. M. tenue,* lower magnification view of specimen in *3*; distal peristome wall is the cuticle-bounded proximal end of frontal shield of distal zooecium; ×120 (bar = 100 μm).

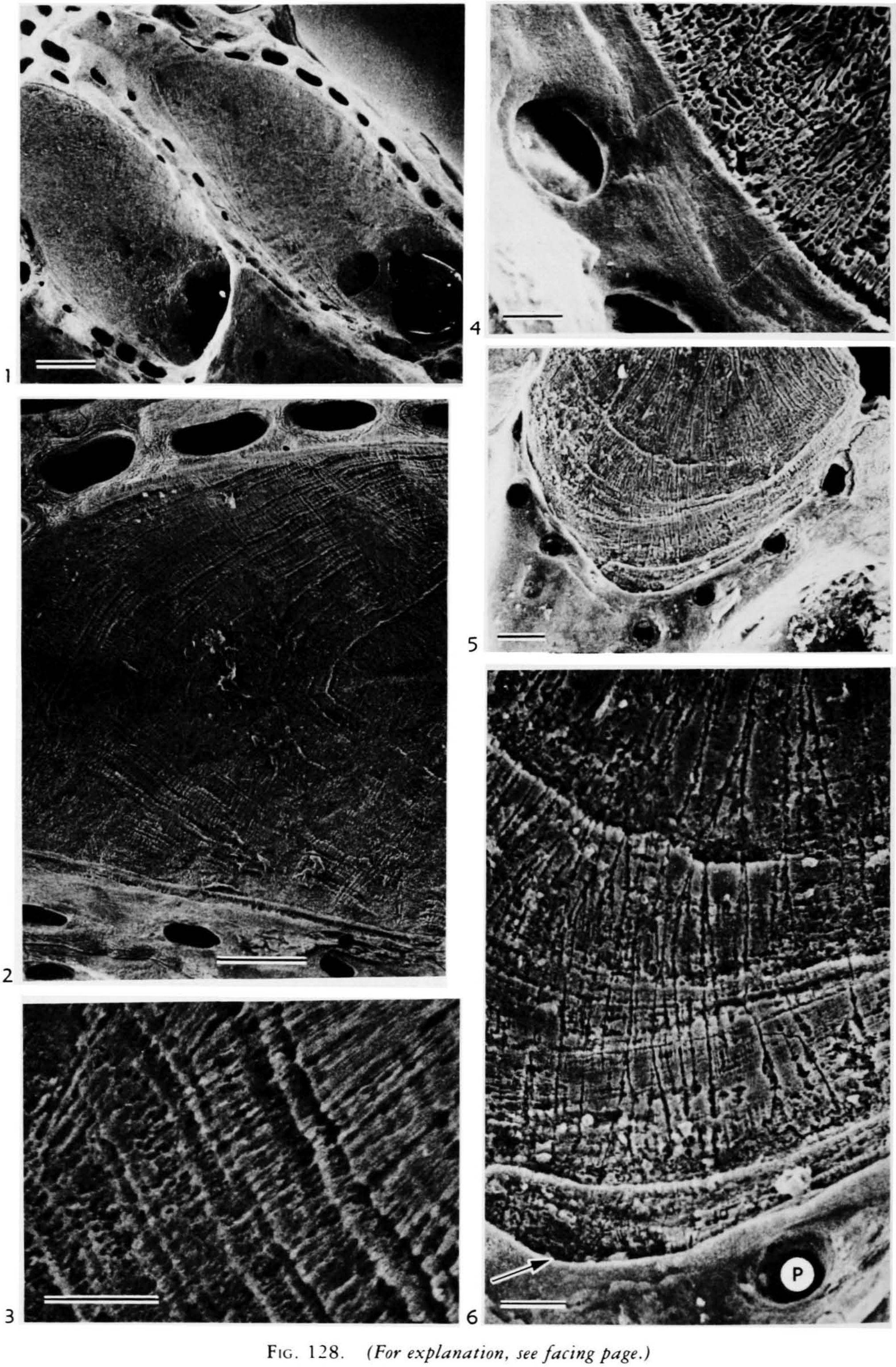

FIG. 128. *(For explanation, see facing page.)*

phragms is discernible by study of topological relationships between a diaphragm and surrounding walls.

When planar spherulitic ultrastructure is composed of longitudinal stripes, the accretionary lineations often form a scalloped curve (Fig. 111,*1*; Sandberg, 1971, pl. 2, fig. 1, 2, 4). On flat or convex surfaces the scalloped curve is convex in the distal growth direction. The situation may be different on such concave surfaces as the undersides of umbonuloid frontal shields (Fig. 128,*2,6*). Because the growth front on such concave walls is continually decreasing in radius of curvature as it advances toward the zooecial midline, there is a tendency toward distal narrowing of the arrays of planar spherulitic ultrastructure, and sometimes even distally concave scalloped growth lines. Growth front curvature, together with the distal bifurcation and expansion of spherulitic arrays, may be used to determine the direction of growth, even in small areas (or even fragments). The ability to recognize growth direction is significant in the reconstruction of earlier ontogenetic stages from mature zooecia. For example, the planar spherulitic ultrastructure in the region of the upper transverse wall and the secondary orifice of umbonuloids lends itself very well to a chronicling of the ontogeny of calcified structures in that region (including orifices that are **cormidial**, i.e., the joint product of more than one individual in the colony) (Fig. 122,*1–3*; 127).

It must be realized that, even in the simplest exterior wall construction, any calcified wall that might form is not expanding the coelomic volume. Rather it develops in a calcification zone that lags slightly behind the front of cuticle intussusception, where the coelomic expansion is occurring (see Schneider, 1957, 1963). Nevertheless, it is the intimate association of carbonate skeleton and the outermost bounding cuticle that demonstrates the exterior wall origin of such skeletal walls in cheilostomates. As discussed above, such exterior walls characteristically have, as their outermost carbonate unit, planar spherulitic ultrastructure. From that ultrastructure (with a few cautions mentioned below) we can recognize the exterior walls.

It should be emphasized that the cuticle-calcified wall association referred to here is the one developed penecontemporaneously at the distally advancing margin of wall growth. It does not refer to the possible later contact of cuticle with an already calcified wall, such as apparently occurs on the undersides of some frontal shields during ascus invagination.

Exterior walls commonly give rise to interior walls by apposition, but that first wall can never become an interior wall. It will always have an exterior cuticulate surface on one side, even if the wall is subsequently overgrown by skeletal layers of another part of the colony, for example, ovicells. However, it is relatively common for individual skeletal walls to have both interior and exterior wall portions. This is not surprising, because the operational difference between those two major wall types is deposition in

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Fig. 128. Frontal exterior walls.——*1–3. Posterula sarsi* (Smitt), rec., Gulf of St. Lawrence; *1,* basal view of several zooecia, etched, with basal walls broken away, distal toward lower right, ×80 (bar = 100 µm); *2,* detail of upper zooecium in *1,* distal toward right, note marginal areolae, line of membranous frontal attachment, and accretionary banding and distally oriented crystals of planar spherulitic ultrastructure on basal (exterior) surface of epifrontal shield, ×260 (bar = 50 µm); *3,* detail of *2,* ×1,650 (bar = 10 µm); BMNH 1911.10.1.1360A,B.——*4. Umbonula ovicellata* (Hastings), rec., Liverpool Bay, Eng.; detail of areolar pores, line of membranous frontal attachment and, in upper right, stripes of planar spherulitic ultrastructure, etched; BMNH 1936.12.30.380, ×425 (bar = 20 µm).——*5, 6. Metrarabdotos tenue* (Busk), rec., Caroline Sta. 68, off NE. Puerto Rico; *5,* basal view of a zooecium, etched, with basal wall broken away, distal toward upper right, ×130 (bar = 50 µm); *6,* detail of *5,* planar spherulitic ultrastructure begins immediately at line of membranous frontal attachment (arrow), above areolar pore (P), note numerous instances of competitive growth interference and accretionary bands of varying intensity, ×500 (bar = 20 µm); both USNM 209434.

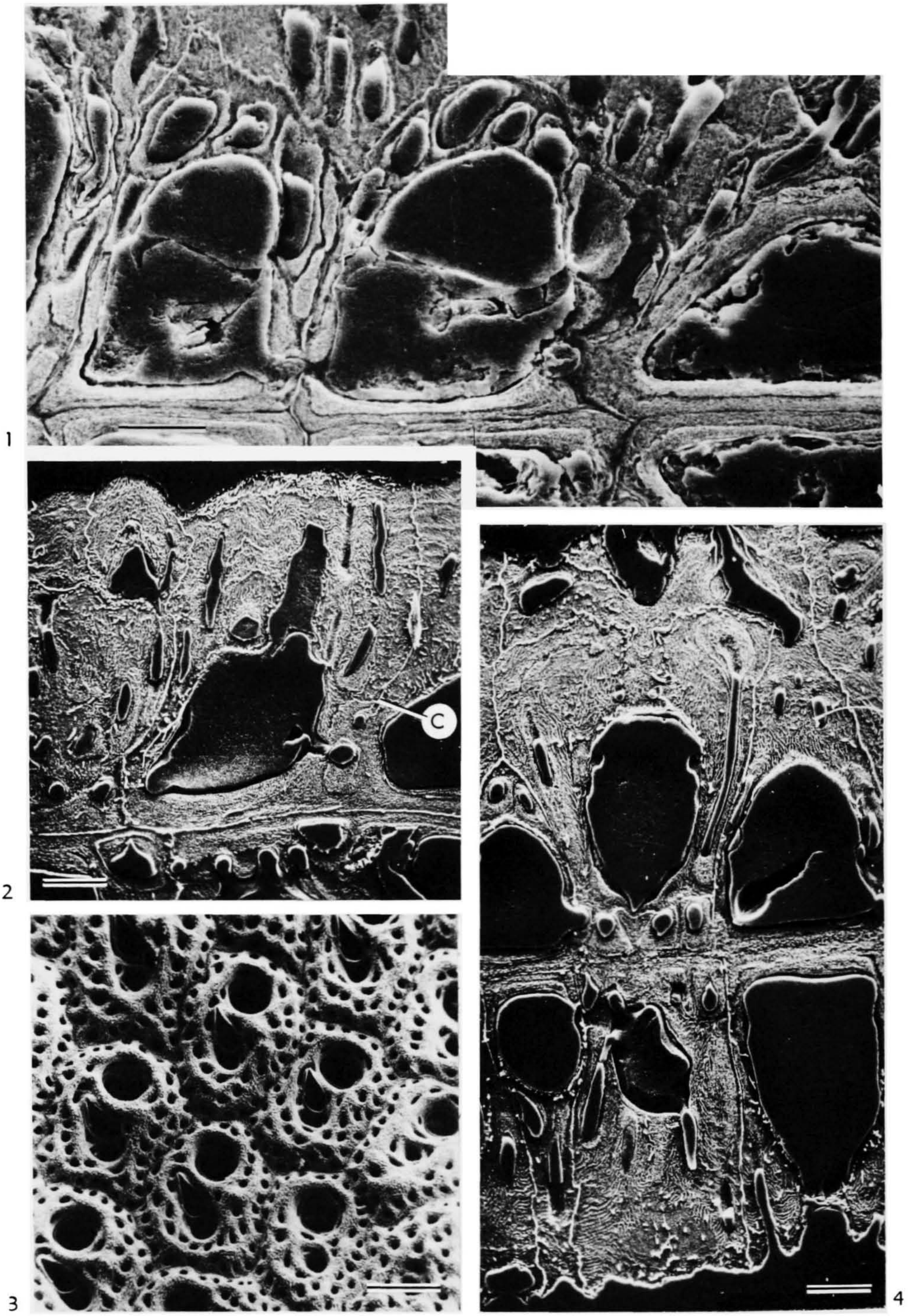

FIG. 129. *(For explanation, see facing page.)*

contact, or not in contact, with cuticle. Various growth patterns or positions of wall development are naturally in contact (or not) with cuticle, and a single wall may go through both stages. This occurs most commonly in the transverse vertical wall. The lower central part, often most of the wall, is an interior wall, grown by apposition off the inner surface of the basal wall. The upper part of the wall impinges on the frontal cuticle and continues upward growth, incorporating cuticle and producing a doubled exterior wall region with intercalary cuticle (Fig. 129,*2*). Most commonly that upper exterior wall part of the transverse wall is short relative to the total height of the wall (Fig. 116,*2*). However, it increases as frontal thickening occurs, and in some forms, such as the adeonids, comprises the bulk of the transverse wall. In those adeonids, the interior wall portion of the transverse wall is narrow relative to the total zooecium. As a result, near the lateral walls, intercalary cuticle extends through the transverse wall from frontal to basal surfaces (Fig. 129).

Several examples of ontogenetic transitions from interior to exterior walls are known in frontal walls. The frontal shield of an umbonuloid ascophoran originates as a cryptocystal extension (thus an interior wall) off the inner surface of the lateral and transverse walls below the membranous frontal wall (Fig. 130). The figure construction of Tavener-Smith and Williams (1970, fig. 35) is accurate, although they called the initial, marginal part of the umbonuloid frontal shield a gymnocystal wall, as did Cook (1973b). As that initially cryptocystal wall grows upward and medially, it ultimately meets the membranous frontal wall, attaches to the outermost frontal cuticle and extends to produce an epifrontal fold with cuticle and skeleton on its lower surface and a hypostegal coelom (which is extending the colonial coelomic space) above. In that process, the umbonuloid frontal shield becomes an exterior wall, calcifying (with planar spherulitic ultrastructure) against cuticle (Fig. 122,*1*; 128).

When extreme frontal thickening of cryptocystidean frontal shields occurs, the colonial coelom expands upward and calcification against cuticle occurs marginally (laterally, proximally, distally). The central portion of the frontal thickening was deposited below an upwardly advancing hypostegal coelom. However, at the vertical boundaries of the zooecium, the carbonate was secreted in contact with the cuticle just below an upward-moving front of cuticle intussusception (see Banta, 1972, fig. 3). This exterior-walled growth pattern is analogous to the distal extension of exterior basal and vertical walls at the colony margins in the "standard" cheilostomate pattern. Adding zooecial cavities in this upwardly growing skeletal succession would produce the frontally-budded lineal series of zooecia discussed by Banta (1972) (Fig. 118,*4,5*). In some cheilostomates frontal budding occurs as thin-walled, blisterlike zooecia without extensive frontal thickening (Fig. 118,*6*).

"STANDARD" GROWTH MODE FOR CHEILOSTOMATE SKELETONS

Most discussions of skeletal wall genesis in cheilostomates have implicitly or explicitly

Fig. 129. Frontal thickening.——*1–4. Adeona* sp., rec., locality unknown; *1,* lower part of three zooecia, distal to right, cuticles in transverse walls come down to join basal wall cuticles, note also zooecial lining deposits, especially on basal and lower vertical walls, etched long. sec., ×220 (bar = 50 μm); *2,* zooecium, distal to right, note considerable frontal wall thickening and that intercalary cuticle in vertical wall proximal to zooecium extends to basal wall, but in vertical wall distal to that zooecium, below point C, does not, etched long. sec., ×85 (bar = 100 μm); *3,* frontal exterior view of part of a colony, distal toward top, transverse wall boundaries with intercalary cuticle like that of lateral wall boundaries, ×50 (bar = 200 μm); *4,* colony branch, etched transv. sec., ×90 (bar = 100 μm); all BMNH 1920.12.10.1.

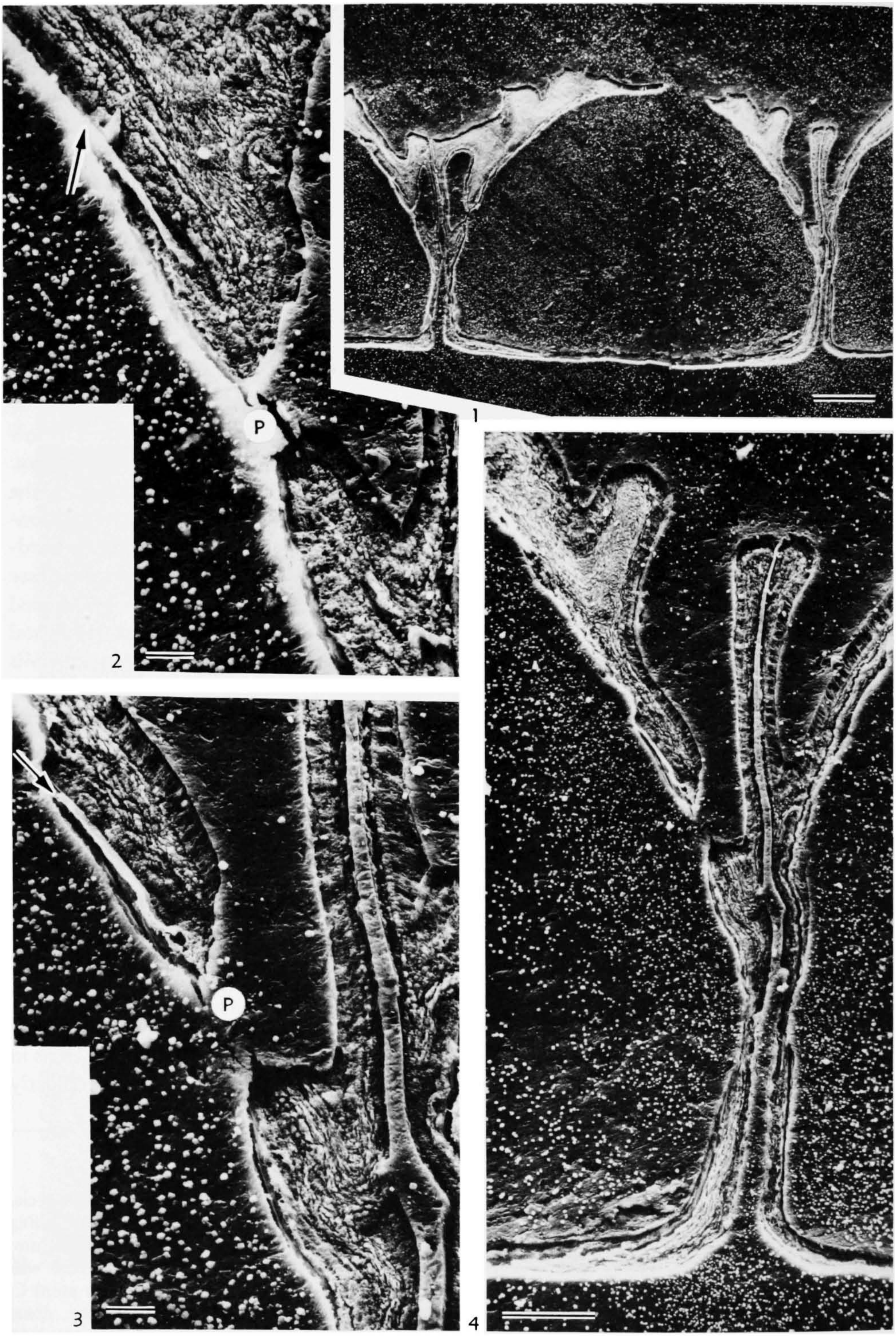

FIG. 130. *(For explanation, see facing page.)*

made use of what may be called the "standard" pattern of cheilostomate skeletal development. This pattern is the most common one among cheilostomates and is characterized by predominantly exterior-walled skeletal growth. That is, the calcified walls are cuticulate (exterior walls) laterally, basally, and frequently frontally, but noncuticulate (interior walls) distally (in the transverse wall) and in some frontal shields (see Silén, 1938, 1944a,b; Banta, 1969, 1970; Ryland, 1970).

However common it may be, this "standard" pattern clearly does not fit all cheilostomates. Recent studies have shown that it lies near the middle of a broad spectrum of cheilostomate skeletal growth modes which ranges from types with nearly all exterior walls to types with nearly all interior walls. It has been noted (Boardman & Cheetham, 1973, p. 163) that interior walls in cheilostomates may be limited to pore plates between zooecia (e.g., *Pyripora* and similar uniserial forms, Thomas & Larwood, 1956, 1960). At the other end of the spectrum, there appear to be more forms with interior-walled skeletons than was earlier realized. Banta (1968, 1969, 1970, 1972), Håkansson (1973), and Sandberg (1973, 1976) have pointed out diverse cheilostomates in which interior walls comprise most or all of the zoarium except for the basal surface of the ancestrula or the multiple primary zooids (Håkansson, 1973; Maturo, 1973). This interior-walled growth is particularly common in discoidal or linguiform zoaria (cupuladriids, conescharellinids, mamilloporids: Håkansson, 1973; Sandberg, 1973), some petraliiform zoaria (Sandberg, 1976), and some erect forms (cellariids and *Myriapora*: Banta, 1968, Sandberg, 1973; *Euthyrisella,* Harmer, 1902). The earlier inclusion of the sertellid *Triphyllozoon* as an example of this growth mode (Sandberg, 1973, p. 308) appears to be an error based on misinterpretation of the cuticle distribution.

Skeleton construction in the majority of cheilostomates appears to follow the intermediate, "standard" pattern. Those "standard" cheilostomates may be grouped on the basis of relative spatial arrangement of features in the frontal region. Those features include the cuticle, secretory epithelia, initially and subsequently calcified portions of the wall, hydrostatic mechanism, and coelomic spaces.

Knowledge of cuticle distribution in vertical walls of cheilostomate skeletons is thus important in deducing wall type and growth mode. One might expect simple inspection of the frontal surface of the zooecia to produce this information. However, because cheilostomates often deposit superficial thickenings of the frontal, that is often not the case, especially where zooecia in ontogenetically earlier stages are not preserved. It is common for secondary thickening to take the form of an extrazooidal, colonial calcification in which the cuticles that exist in vertical walls (usually only in lateral walls) become detached from the frontal cuticle and are buried beneath the resulting extrazooidal wall (Fig. 124,*1,2*). Inspection of frontal exteriors of such forms would fail to reveal the exterior wall nature of the vertical (usually lateral) walls.

Fig. 130. Cross sections of exterior frontal walls.——*1–4. Umbonula ovicellata* (Hastings), rec., Gairloch, NW. Scot.; *1,* zooecium, adjacent zooecia partially separated along lateral wall intercalary cuticles, embedding plastic filling intervening space, areolar pore on right open (and plastic-filled) all the way to frontal surface in plane of section, etched transv. sec., ×90 (bar = 100 μm); *2,* detail of region of areolar pore (P) of left adjacent zooecium in *1,* note incorporation of cuticle (arrow) into calcareous wall, above arrow lower surface of wall bears planar spherulitic ultrastructure, ×680 (bar = 10 μm); *3,* detail of right areolar pore of central zooecium in *1,* see comments on *2,* ×680 (bar = 10 μm); *4,* intermediate magnification view of right zooecial boundary in *1,* note continuous cuticulate boundary between vertical walls and thin but distinctive superficial frontal layer wrapping around upper frontal surface, ×260 (bar = 50 μm); all BMNH 1963.3.6.8.

Not only may cuticles be buried, but intercalary cuticles that do not extend down through the skeleton may be added near the frontal surface. Most commonly an upward growing interior transverse wall attaches to the frontal cuticle and produces a transverse intercalary cuticle during subsequent frontal thickening. This development also results from frontal thickening, but, in this case, the frontal cuticle has become embedded in the frontal skeletal wall. The frontal surfaces of such forms suggest the presence of cuticles in lateral and even transverse vertical walls (Fig. 126,*3*). However, as vertical sections of some such specimens show (Fig. 126,*1*,*2*), the vertical walls lack cuticle except at the frontal surface. Results of this study, using *Margaretta tenuis* HARMER, showed superficial cuticulate zooecial boundaries at the zoarial surface but an absence of intercalary cuticles in lateral walls within the zoarium (Fig. 126,*1*,*5*). However, observations of other species of that same genus (CHEETHAM & COOK, this revision; CHEETHAM, unpublished) revealed well-developed or intermittent intercalary cuticles throughout the lateral walls. Thus, at present it appears that one should not ascribe much taxonomic value to this character.

GENERAL FEATURES OF THE CLASS PHYLACTOLAEMATA

By Timothy S. Wood

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Within the large and diverse group of animals known as Bryozoa there occur several dozen species whose unique morphology, development, and ecology indicate a long independent evolutionary history. In 1856, Allman established for these species the distinct class Phylactolaemata (*phylasso,* guard + *laimos,* throat) named for the small liplike lobe of tissue overhanging the mouth. Easily recognized by the horseshoe-shaped lophophore in all but one genus, the phylactolaemates are also distinguished by an exclusively freshwater habitat, a relatively large polypide (Fig. 131), a muscular body wall, free encapsulated buds (statoblasts) and an unusual ciliated colony progenitor, which develops from the zygote.

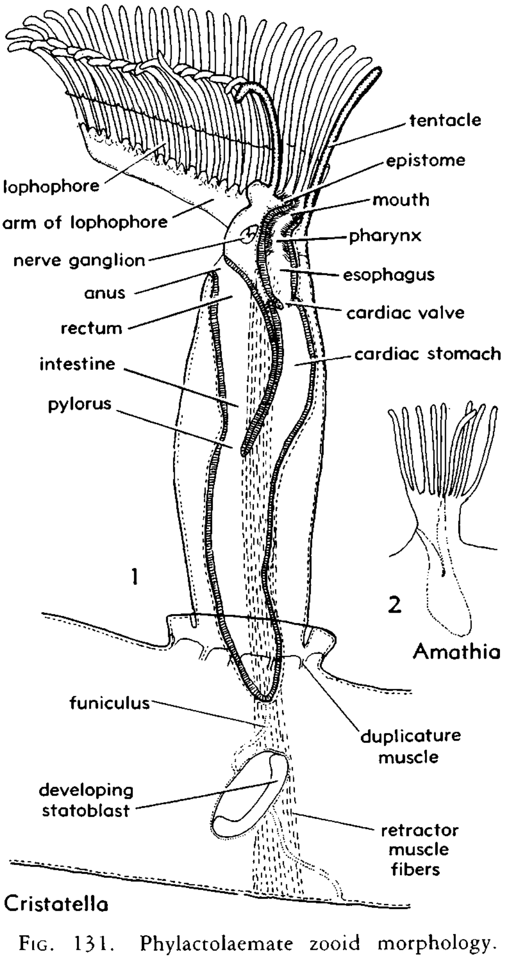

Fig. 131. Phylactolaemate zooid morphology.——*1.* Transverse section of zooid of *Cristatella mucedo* Cuvier (after Brien, 1960).——*2.* Zooid of the ctenostomate *Amathia convoluta* Lamouroux drawn to the same scale as *1.*

Though easily overlooked, phylactolaemate colonies are often dominant among organisms attached to substrates under water. They occur in nearly every clean body of fresh water where there exists suitable submerged substrate of wood, stone, vegetation or firm synthetic material. Before the practice of sand filtration in public waterworks, enormous quantities of these colonies chronically clogged the water mains of such cities as Boston, Hamburg, and Rotterdam (Whipple, 1910; Kraepelin, 1886; DeVries, 1890). Most species, however, occur in shallow bodies of standing water, and it is not unusual to find colonies of four or five different species inhabiting the same small pond. Both *Plumatella emarginata* Allman and *Fredericella sultana* (Blumenbach) may flourish in flowing water (Bushnell, 1966), although neither has obvious adaptations to a lotic habitat. With few exceptions, phylactolaemates grow within a temperature range of 15° to 26°C. A record high temperature of 37°C was recorded by Bushnell (1966) for living colonies of *Plumatella repens* (Linné) and *P. fruticosa* Allman at a shallow lake margin. Only *Fredericella sultana* is perennial in temperate latitudes, surviving under ice at temperatures close to freezing. Toxicity bioassays and field observations indicate a sensitivity of many species to low concentrations of certain industrial and domestic pollutants (Bushnell, 1974). Rogick and

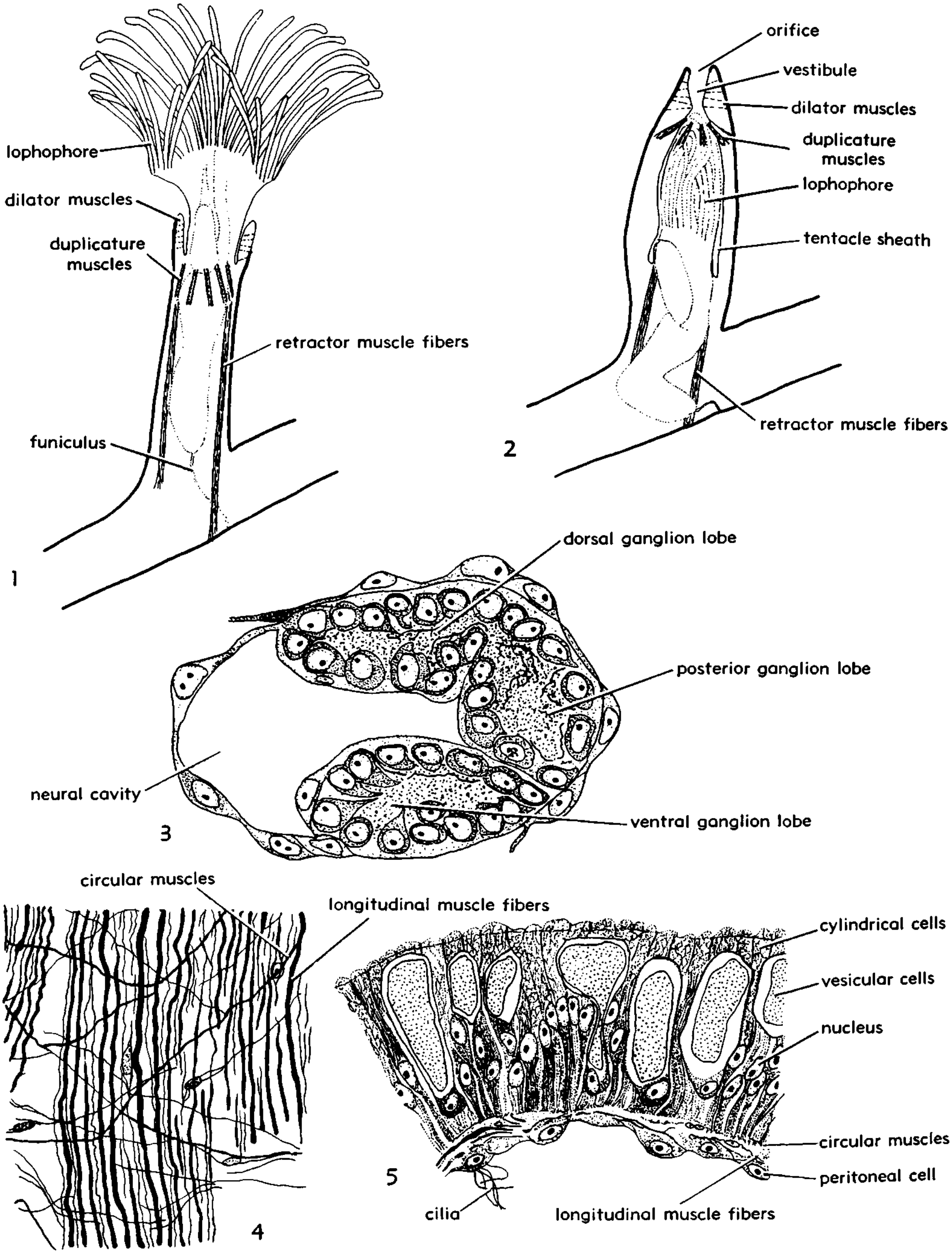

FIG. 132. Phylactolaemate zooid anatomy.——*1.* Intercoelomic muscles of *Plumatella casmiana* OKA with polypide in feeding position.——*2.* Intercoelomic muscles of *P. casmiana* with polypide in retracted position.——*3.* Sagittal section of nerve ganglion in *Lophopus crystallinus* (PALLAS) (after Marcus, 1934).——*4.* Surface view of zooecial muscles beneath epithelium in *Lophopodella carteri* (HYATT) (after Rogick, 1937).——*5.* Cross section of portion of zooecium in *Cristatella mucedo* CUVIER (after Brien, 1960).

Brown (1942), nevertheless, collected *Plumatella repens* from a Puerto Rican stream contaminated with livestock wastes.

ZOOID MORPHOLOGY

In a schematic sense the phylactolaemate colony is a vessel of coelomic fluid in which are suspended many independently moving organ systems performing major physiological functions. Each active unit, known as a polypide, communicates directly to the colony wall through muscle fibers, a funiculus, and a common peritoneum. The polypide and its adjacent colony wall are customarily combined in the term "zooid," defined as the individual member of a colony. Such a unitary concept, however, is awkward when applied to the phylactolaemate Bryozoa where septa are infrequent in many species and the colony may be little more than a sac of communal polypides. For lack of specific identity between a polypide and a section of colony wall it is useful to distinguish these parts and to use "zooid" only in reference to an individual in a more abstract sense.

Colony wall.—The phylactolaemate colony wall is a histologically complex structure composed of well-defined tissue layers beneath an externally secreted integument (Fig. 132,*5*). Although details may vary considerably among species and even in different areas of the same colony, the basic pattern may be generalized. In *Pectinatella* the nonliving outer material is a gelatinous deposit consisting largely of water, but according to Kraepelin (1887) also containing some protein, chitin, and other organic materials. The dendritic colonies of *Plumatella* and *Fredericella,* however, develop a firm cuticle composed mainly of chitin (Hyman, 1958). Prior to chitin secretion, young zooids usually have a sticky exterior which allows them to adhere to the substrate or each other and to collect a thin crust of particles from the ambient water. The presence of a slightly raised longitudinal keel has some diagnostic value in species identification.

Beneath this nonliving material lies a single **epithelial layer** consisting of two cell types (Fig. 132,*5*). The columnar cylindrical cells form a uniform surface and are apparently involved in secretion of the outermost material (Brien, 1953). The larger vesicular cells contain fatty deposits that led Marcus (1934) to suggest a role in food storage. At the anterior budding region of the zooids, a distinct layer of undifferentiated cells underlies the epithelium. These are apparently totipotent for either cylindrical or vesicular cells, and transitional forms have been described by Brien (1960).

An interesting feature of the colony wall is the presence of thin **circular** and **longitudinal muscle layers** below the epithelium (Fig. 132,*4,5*). Circular muscle fibers, presumably derived from peritoneum, are able to execute limited orienting movements of the zooid.

The innermost tissue is a thin peritoneum bearing scattered tracts of cilia, particularly in the anterior portions of the zooids. The cilia beat continuously, driving coelomic fluid in random eddies among the polypides. This coelom was long thought to be separated from the two coelomic spaces of the epistome and lophophore. Together these were considered respectively homologous to the **metacoel, protocoel** and **mesocoel** of other lophophorates, and were named accordingly; however, Brien (1960) believes that all three cavities are continuous and can be characterized histologically only by their ciliation. The distinguishing terminology remains tentatively in use.

Polypide.—The polypides of a phylactolaemate colony are basically **monomorphic**. Each is autonomous with a lophophore of ciliated tentacles, a recurved digestive tract, and a single funiculus joining the gut caecum to nearby peritoneum (Fig. 131,*1*; 133,*4*). In addition, a dorsal nerve ganglion and mus-

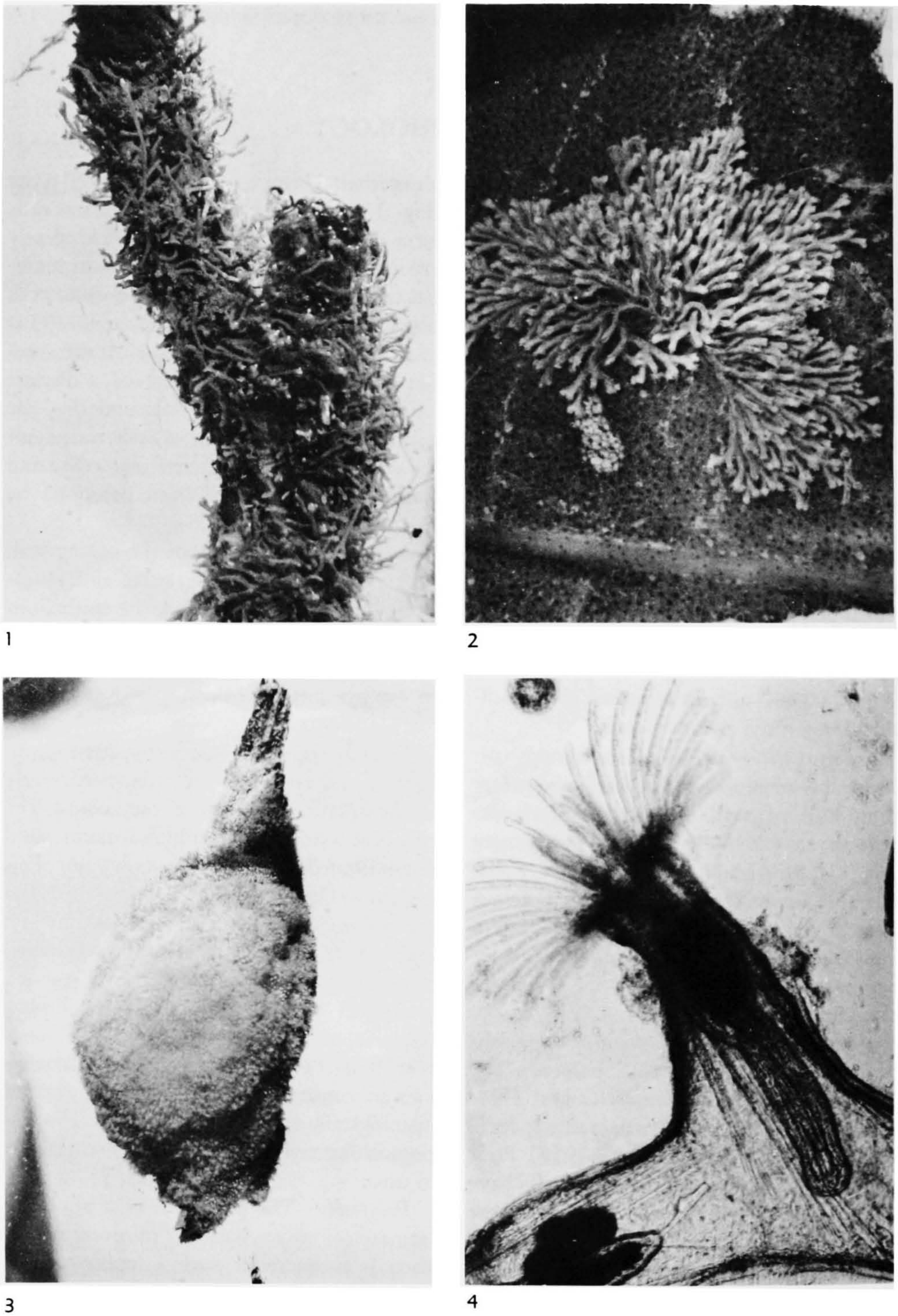

FIG. 133. *(For explanation, see facing page.)*

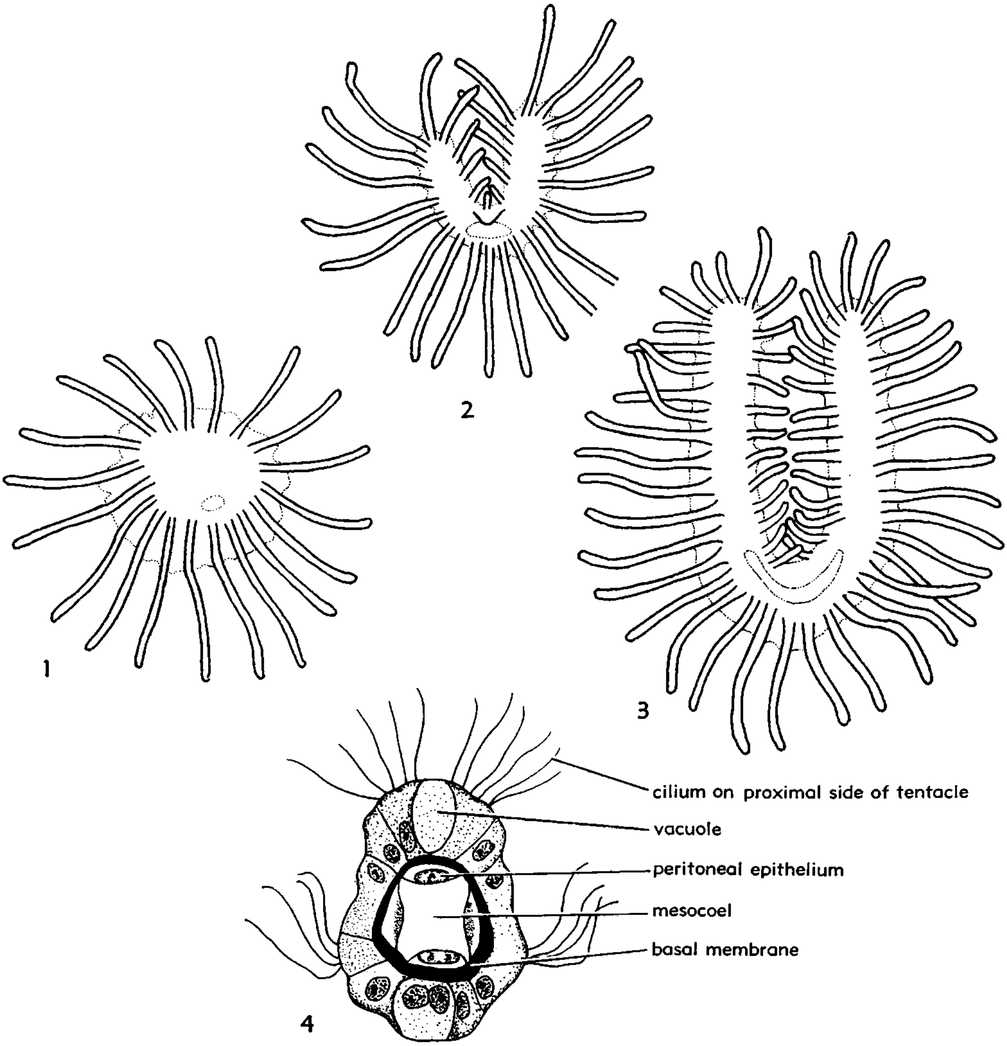

Fig. 134. Structure of the phylactolaemate lophophore.——*1. Fredericella sultana* (Blumenbach), anterior view of the lophophore showing circular conformation.——*2. Plumatella casmiana* Oka, anterior view of the lophophore showing moderate dorsal inflection.——*3. Pectinatella magnifica* (Leidy), anterior view of the lophophore showing pronounced dorsal inflection.——*4.* Tentacle cross section in *Lophopodella carteri* (Hyatt) (after Rogick, 1937).

culature is associated with movements of the polypide.

Lophophore.—In species of *Fredericella* the lophophore is reminiscent of Gymnolaemata, a small bell-shaped structure formed by 20 or so tentacles arranged in a circle around the mouth. In all other species, however, the ring of tentacles is inflected dorsally to produce

Fig. 133. Phylactolaemate colony form.——*1.* Colony of *Fredericella sultana* (Blumenbach) growing on a submerged twig, ×3.0.——*2.* Colony of *Plumatella casmiana* Oka growing on underside of floating leaf of *Nelumbo lutea,* ×3.0.——*3.* Colony of *Pectinatella magnifica* (Leidy) from the underside of a floating log, ×0.5.——*4.* Polypide of *P. casmiana* showing lophophore, gut caecum, and retractor muscles; the funiculus is clearly visible extending from the polypide on the left, ×50.0.

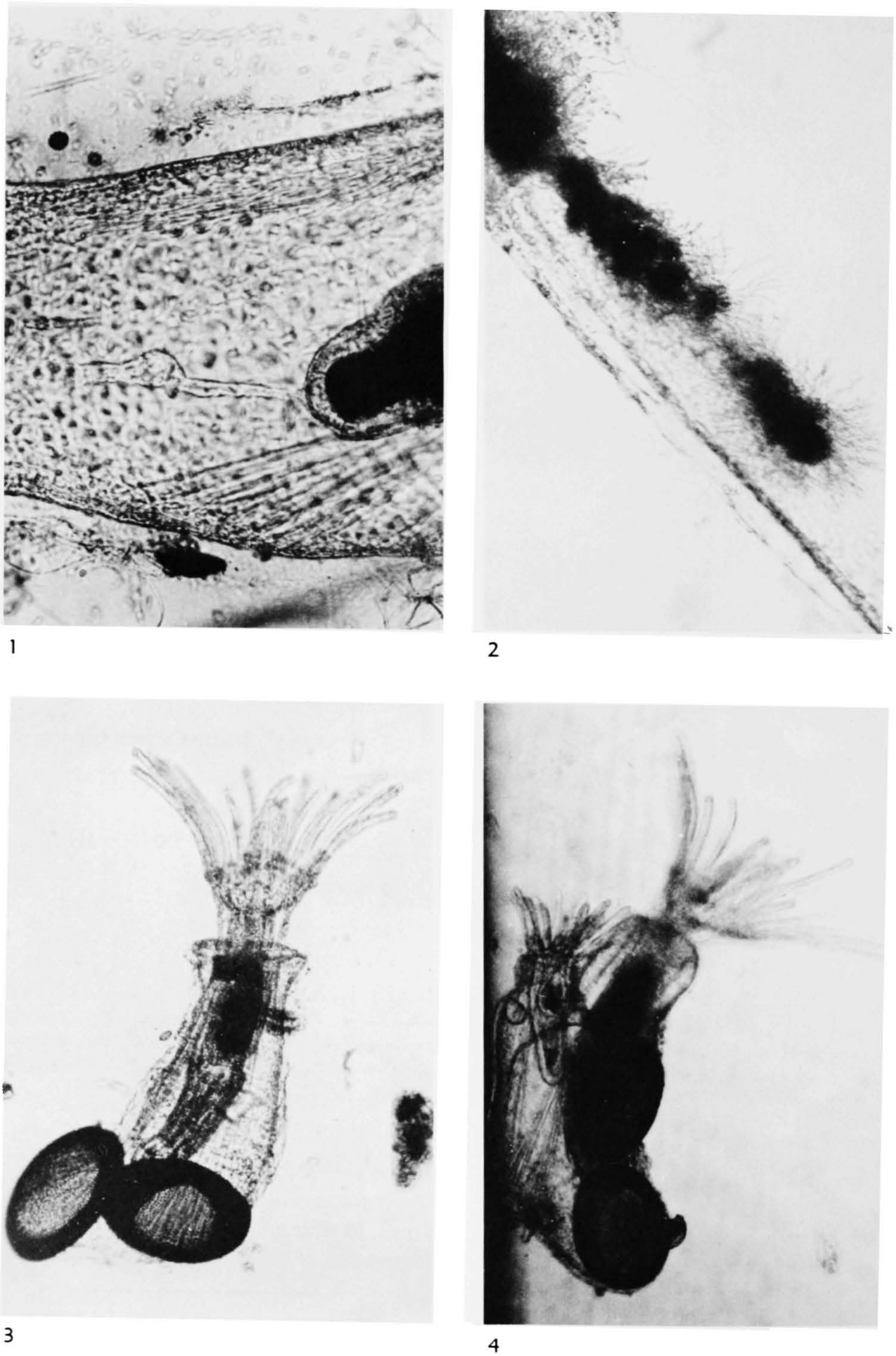

FIG. 135. *(For explanation, see facing page.)*

the characteristic horseshoe shape with two arms projecting freely on either side of the mouth. Species with the deepest inflection carry the greatest number of tentacles (Fig. 134,*1,3*). On *Pectinatella gelatinosa* OKA polypides, over 100 tentacles have been reported (TORIUMI, 1956). Tentacles of the outer series are longer than those of the inner, and a membrane connects all of them near the base. The projection of tentacles on both sides of each arm creates a narrow central groove in which food particles are collected and passed along to the mouth. Thus, a horseshoe-shaped lophophore operates differently from one of circular design and the two may differ in function and efficiency.

In all species the continuous mesocoel of the lophophore extends for the length of each hollow tentacle. Tentacles are roughly triangular in cross section (Fig. 134,*4*), and bear one medial and two lateral tracts of cilia (MARCUS, 1934; ROGICK, 1937). Stiff hairlike projections extending laterally between tentacles are easily seen in living specimens but have not been described from prepared sections. Longitudinal muscle fibers and several tentacular nerves allow tentacles to respond individually to impinging particles. Zooids of *Plumatella emarginata* have been observed to bring the tips of tentacles together repeatedly and trap protozoa near the mouth region. In *Plumatella casmiana* OKA the tentacles of individual zooids occasionally maintain a curious rhythmic flicking movement of several pulses per second (VIGANÒ, 1968).

Digestive tract.—The recurved digestive tract varies only slightly from the gymnolaemate plan. Unique to the Phylactolaemata is a triangular flap of tissue known as an epistome, which overhangs the mouth (Fig. 131,*1*). By means of muscle fibers within its coelomic interior, the epistome moves about actively, and although it never closes the mouth it can alter the shape of the mouth opening. Most likely the function of this structure is chemosensory.

The mouth is a **stomodaeal cavity** that leads to a strongly ciliated vestibule, the pharynx, in which particulate food is collected and tumbled about (Fig. 131,*1*). A nonciliated esophagus opens periodically to receive a cluster of particles and push it through the cardiac valve into the stomach. Slow peristaltic contractions originating at the caecum move slowly along the **cardiac stomach** and thoroughly mix the food. A little at a time, food is eased through an unciliated pylorus into the so-called intestine, where it is packed into a dense mass and expelled through the anus as a fecal pellet. Although MARCUS (1926) testified to pH gradients in various parts of the digestive tract, the observations of living rotifers in fecal pellets of *Lophopodella* indicate suprisingly mild—or at least selective—enzymatic activity (ROGICK, 1938). Phylactolaemates are known to ingest quantities of bacteria, but the possibility of intracellular digestion of these and other minute organic particles has never been seriously explored.

Funiculus.—A single funiculus spans the metacoel from the stomach caecum to a certain point on the body-wall peritoneum, according to species (Fig. 131,*1*; 135,*1*). It is a tubular strand of tissue incorporating small muscle fibers, and it is the major site of spermatogenesis and asexual production of statoblasts. These critical roles will be discussed later in some detail.

Intracoelomic muscles.—Retraction and protrusion of the polypide is effected by coordinated action of several distinct sets of muscles (Fig. 132,*1,2*). Most conspicuous of these are two bundles of retractor fibers originating

FIG. 135. Phylactolaemate reproduction.——*1.* Funiculus extending from the gut caecum of *Plumatella casmiana* OKA showing the earliest stage of statoblast formation, ×150.——*2.* Sperm developing along the funiculus in *Fredericella sultana* (BLUMENBACH), ×250.——*3.* Ancestrula of *P. casmiana* recently emerged from a statoblast; the two statoblast valves are clearly evident, ×50.——*4.* Parietal budding in a young colony of *P. casmiana*; note the new duplicate bud to the left of the smaller polypide, ×50.

posteriorly on the colony wall, extending laterally along the polypide, and inserting at various points from the esophagus to the lophophore. Sudden contraction of these muscles jerks the polypide into the colony interior, carrying with it a thin membranous portion of the zooecial tip that turns inward to become a tentacle sheath (Fig. 132,*2*). Anteriorly the sheath opening is constricted by a sphincter, beyond which lies a small chamber called the vestibule. Prior to polypide eversion the sphincter relaxes and small muscle fibers dilate the vestibule. Bundles of duplicature muscle fibers, radiating from the tentacle sheath to the colony wall, slowly contract against coelomic pressure, widening the space through which the lophophore must pass. Almost simultaneously the retractor muscles relax and allow the polypide to emerge, pushed by the pressure of coelomic fluid. The tentacle sheath everts and the duplicature muscles now relax and become taut, serving as fixator ligaments to halt the polypide's outward progression. The lophophore opens, cilia beat, and feeding resumes.

Nervous system.—Every polypide in a colony has a nerve ganglion located dorsally in the mesocoel of the lophophore between the mouth and the anus. It is essentially a vesicle delimited by a thin nucleated membrane enclosing large dorsal, ventral, and posterior ganglionic lobes. Each lobe has a central fibrillar region and a periphery of ganglion cells (Fig. 132,*3*). A large tract from each side of the ganglion passes dorsally into the nearest lophophore arm, accompanied for the proximal third of its length by an extension of the neural vesicle. The tracts bifurcate into right and left branches to innervate internal and external rows of the tentacle sheath, and then branch out as a plexus between the epidermal and muscular layers of the colony wall. Other nerves from the ganglion provide a network of presumably bipolar cells along the entire digestive tract. The epistome is well innervated, supporting the suggestion of a sensory function. Specialized sensory cells occur on the tentacles, intertentacular membrane, epistome, and in the unsclerotized epithelium at the zooid tip.

The most detailed accounts of the phylactolaemate nervous system are those of Gerwerzhagen (1913) and Marcus (1934), working with *Cristatella* and *Lophopus,* respectively. There are yet many aspects to be clarified, including innervation of retractor muscles and the question of interzooidal nervous communication.

PARIETAL BUDDING OF ZOOIDS

Bryozoan colonies grow in size by the addition of new zooids, and colony morphology is to a large extent determined by patterns of sequential budding. Among most gymnolaemate species the budding process generally begins with the formation of a septum across the parental zooid, creating an additional small sac in which the new polypide is to develop. Phylactolaemates, however, like the living cyclostomes, reverse this sequence: the new polypide appears first and gradually draws away from the parental zooid as the colony wall elongates or enlarges.

A long succession of investigators have observed and interpreted the budding process in *Cristatella* (Davenport, 1890), *Pectinatella* (Oka, 1891), *Plumatella* and other genera (e.g., Kraepelin, 1887, 1892; Brien, 1936, 1953). The **primordium** originates from a cluster of dedifferentiated epithelial cells on the ventral body wall of a parental zooid (Fig. 136). Their mass bulges into the metacoel, pushing ahead of it a thin covering of peritoneum. A central cavity appears and from it develop two narrow dorsal and ventral invaginations that elongate, and eventually converge and fuse to form a continuous U-shaped tube (Fig. 136). This becomes the digestive tract, with the future cardiac valve at the point of fusion. Oka (1891) described a somewhat modified series of events for *Pectinatella gelatinosa,* but the effect is the same.

Meanwhile, as the developing bud elongates, a narrow strand of peritoneum separates from the ventral side, remaining attached to the colony wall at one end and to the distal part of the bud at the other (Fig. 136). Eventually this strand develops a hollow interior and becomes the funiculus. A third invagination now pinches off from the original central cavity, forming a small vesicle that becomes the nerve ganglion lying close to the pharynx. From points behind and in front of the ventral mouth opening, small fingerlike projections appear and extend laterally as tentacles of the two arms of a lophophore. This places the anus beyond the dorsal row of tentacles and orients the mouth squarely between the lateral arms. When the bud is fully formed, an orifice is created by a rupture in the body wall, and the diminutive polypide protrudes and begins feeding immediately.

Painstaking observation by Brien (1953) revealed a fascinating hierarchy of three bud primordia occurring on every mature zooid (Fig. 136). The so-called **main bud** is largest of the three and is always the first in line of succession. Close beside it ventrally lies a minute **duplicate bud** (Fig. 135,*4*), and on the dorsal side toward the parental zooid is a small **adventitious bud.** As the main bud develops into a new polypide the following adjustments are made: the duplicate bud becomes a main bud to the new polypide, the adventitious bud becomes a main bud to the parental polypide, and new duplicate and adventitious primordia appear in appropriate new locations.

The combination of stimuli required to initiate bud development is unknown. Occasionally the zooids of laboratory-reared colonies, while appearing perfectly healthy, will cease budding and eventually die without being replaced, even though good bud primordia are present. In other cases a colony may suddenly enter a growth phase in which new generations of zooids develop every day for several days. In *Plumatella casmiana* it has been shown that in old colonies a main bud primordium may apparently be stimulated to develop by the death of its parental zooid (Wood, 1973). These aspects of polypide budding deserve further study.

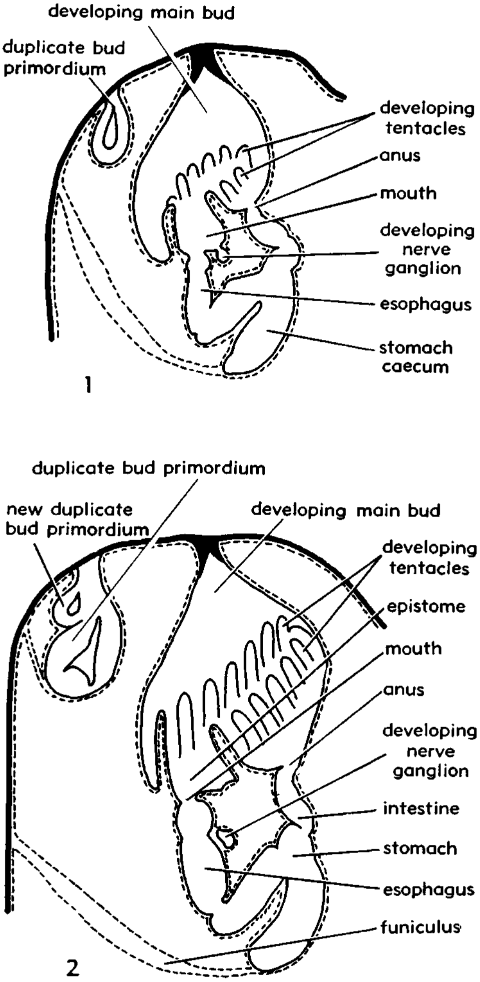

Fig. 136. Late stages of phylactolaemate zooid budding (after Brien, 1960).——*1.* Developing main bud with small saclike duplicate bud.——*2.* Further development and appearance of new duplicate bud primordium.

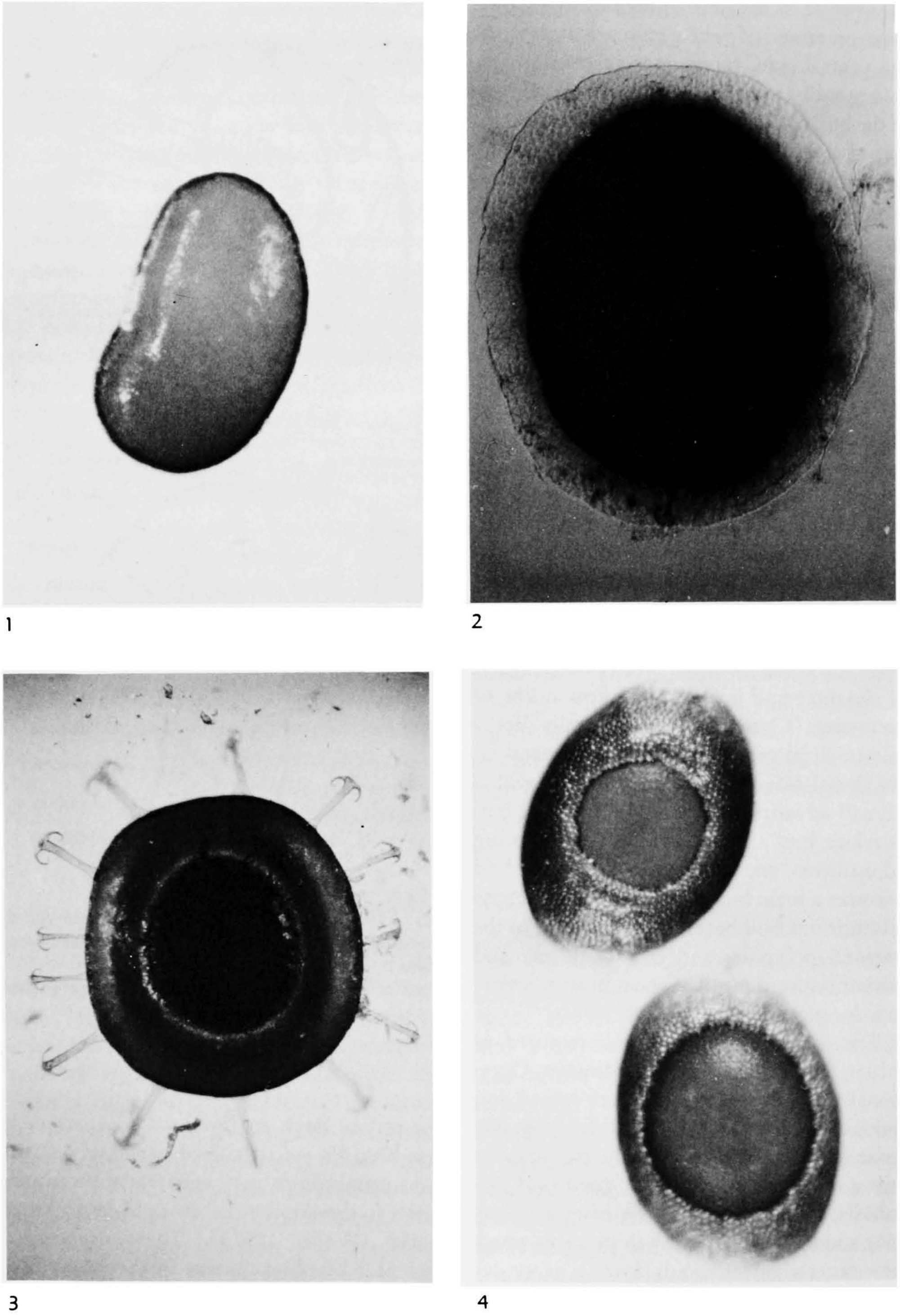

FIG. 137. Phylactolaemate statoblasts.——*1.* Piptoblast of *Fredericella sultana* (BLUMENBACH), ×100. ——*2.* Sessoblast of *Plumatella emarginata* ALLMAN, ×180.——*3.* Floatoblast of *Pectinatella magnifica* (LEIDY), ×50.——*4.* Dorsal (upper) and ventral (lower) sides of floatoblasts of *Plumatella repens* (LINNÉ), ×65.

STATOBLASTS

The temperate freshwater habitat has an inconstant environment, fluctuating in temperature, pH, dissolved oxygen, nutrients, turbidity, water level, and in other chemical and physical conditions. For all but a few stream-tolerant organisms there is seldom a water route by which individuals can escape suboptimal conditions of a pond or lake and disperse to other locations. It is not surprising, therefore, that most invertebrate species living in fresh water have in their life histories a dormant resistant stage that may serve both as a disseminule and as a mechanism for surviving periods of unfavorable conditions. Certain adult rotifers, nematodes, and tardigrades can withstand prolonged dehydration (CROWE, 1971). Thick-walled cryptobiotic eggs occur among many aschelminths and crustaceans, and protozoan cysts are common. Sponges and bryozoans, the two groups of exclusively colonial organisms in fresh waters, both produce highly resistant structures by asexual processes unknown among their marine relatives. The sponge gemmule is an accumulation of food-filled amoebocytes enclosed in a spherical thick-walled capsule (LEVEAUX, 1939). The bryozoan statoblast is a discoid envelope of chitin containing large yolky cells and an organized germinal tissue capable of becoming a single polypide ancestrula for a new colony (Fig. 135,*3,4*; 137). Statoblasts can endure severe environmental stress and will survive freezing in both dried and undried conditions. ODA (1959) was able to germinate statoblasts of *Lophopodella carteri* (HYATT) that had been dried for over six years.

The development of statoblasts has been traced by many workers including KRAEPELIN (1892), BRAEM (1890), OKA (1891), and more recently by BRIEN (1954). The important role of the funiculus begins soon after its initial appearance alongside the developing bud. Dedifferentiated cells of epithelial origin migrate from the parental zooecium into the tubular funiculus, forming a loose axial strand. As the funiculus elongates it shifts its distal position away from the developing bud. The axial cells slowly proliferate near the concave side facing the polypide bud, while a few muscle fibers appear opposite them. This sets the stage for statoblast production, which may follow immediately, but often occurs some time later or not at all. Among rapidly growing colonies of *Plumatella repens,* however, statoblasts begin to form on the funiculi of developing polypides that have not yet emerged from the colony interior.

The environmental or physiological conditions favoring statoblast production are unknown. The first sign of activity is a small bulge to one side of the funiculus where axial cells arrange to form a vesicle, and yolk-filled funicular cells accumulate on its proximal side (Fig. 135,*1*; 138,*1,2*). As the cell mass mushrooms away from the side of the funiculus it remains covered with a thin layer

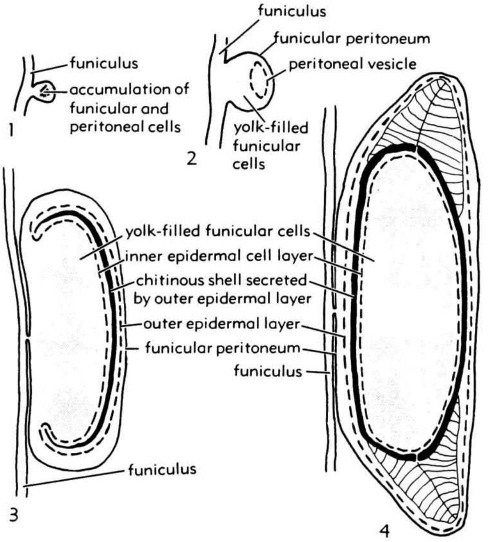

FIG. 138. Statoblast development in *Plumatella fungosa* (PALLAS) (based on Brien, 1954).——*1.* An accumulation of yolk-filled funicular cells surrounding peritoneal cells.——*2.* Appearance of vesicle lined with peritoneal epithelium.——*3.* Radial growth of peritoneal vesicle around yolky mass.——*4.* Formation of external chitinous structures.

of funicular peritoneum. The vesicle enlarges, flattens to a two-layered disc and spreads out along the surface to enclose the large accumulation of yolky cells (Fig. 138,*3*). The inner epidermal layer now is destined to give rise to a new polypide. The outer cells become columnar and begin secreting a chitinous protective shell on all sides. Those cells along the margin may become particularly large and surround themselves with thin walls of chitin (Fig. 138,*4*). They then lyse and are replaced by a gas, giving the statoblast a peripheral area that provides buoyancy. The completed capsule has a marginal suture along which two halves will separate when the new polypide is ready to emerge (see BUSHNELL & RAO, 1974, for excellent scanning micrographs of statoblasts). When fully formed the statoblast is released from its peritoneal envelope on the funiculus and remains free in the metacoel. In certain species it may be discharged through a temporary pore of a living zooid (MARCUS, 1941; VIGANÒ, 1968), although usually statoblasts are released upon disintegration of the colony. The number of statoblasts produced by a single polypide varies according to species. BUSHNELL (1966) reported as many as twenty per polypide of *Plumatella repens,* whereas *Pectinatella, Cristatella,* and *Lophopus* typically form only one. Where multiple statoblasts occur they arise in close succession in a proximodistal gradient along the funiculus.

As a rule, statoblasts do not germinate immediately, but enter a dormant or quiescent state, lasting from several days to many months. The major studies of statoblast dormancy are somewhat contradictory regarding the factors that trigger germination (BROWN, 1933; ODA, 1959; MUKAI, 1974). Variability is apparently introduced by differential ages of the statoblasts, their specific developmental histories, and exposure to varying regimes of temperature, light, moisture, and water chemistry. In an excellent review of this subject, BUSHNELL and RAO (1974) suggested that considerable species differences exist and that much experimental work has yet to be done.

Gross morphological features of the statoblast are often important for diagnosis of phylactolaemate species. Recent scanning micrographs by BUSHNELL and RAO (1974) and WIEBACH (1975) show excellent surface details on statoblasts of a few species. Those statoblasts with a peripheral pneumatic **annulus** are produced in all genera but *Fredericella,* and are called **floatoblasts** (Fig. 137,*3,4*). In genera such as *Pectinatella* and *Cristatella* these are equipped with marginal hooks (Fig. 137,*3*), which seem to suggest dispersal by catching onto bird plumage. BROWN (1933), however, is probably correct in his belief that they serve more to prevent the washing away of dormant statoblasts from favorable substrates. Hooks are absent from the floatoblasts of *Plumatella* species (Fig. 137,*4*), but the holdfast function is retained by a second type of statoblast called a **sessoblast** (Fig. 137,*2*). These are generally larger than *Plumatella* floatoblasts and lack the buoyant annulus. Generally formed simultaneously with floatoblasts, they appear in the zooecial tubes nearest to the substrate and are firmly cemented directly to the substrate along with an underlying portion of the body wall. Long after the colony has disintegrated these sessoblasts remain attached, appear in linear patterns of small black dots on rocks or submerged logs. Curiously, the sessoblast seems to form directly against the colony wall rather than the funiculus, but despite the careful attention given to every other aspect of phylactolaemate development, sessoblast origins remain obscure.

A remarkable species is *Plumatella casmiana,* which produces at least three different morphological types of floatoblasts in addition to the sessoblast (WIEBACH, 1963). One of these, called a **leptoblast,** bypasses diapause and may complete polypide development while still within the parental colony. Upon release through a vestibular pore, the leptoblast germinates almost immediately (VIGANÒ, 1968).

In *Fredericella,* generally considered the most primitive of all phylactolaemates (LACOURT, 1968), statoblasts have neither hooks nor a buoyant annulus, nor are they cemented to a subtrate (Fig. 137,*1*). They may, in fact, never be released at all but instead held firmly within the narrow tubular zooecium. To distinguish these structures from the cemented sessoblasts with which they are so often confused, Eveline Marcus (1955) proposed the name **piptoblast.** Since it is never liberated, the piptoblast can serve only the function of maintaining a population through suboptimal conditions. It is fragmented portions of the upright zooecial branches that serve as disseminules in this species (Wood, 1973).

SEXUAL REPRODUCTION

Sexuality is an enigma in the Phylactolaemata, for it appears to have little real function. As a means of reproduction it is vastly out-performed by the asexual development of statoblast colonies. Its potential for genetic recombination is blocked by the apparent habit of self-fertilization (Braem, 1897; Marcus, 1934). Nevertheless, sexual activity has been observed in all major species, occurring at various seasons of the year in colonies both large and small. If sexuality is a vestigial process in the Phylactolaemata there is at least no evidence that it faces negative selection. Published information, however, is scanty and incomplete, and further investigation of the process is definitely needed.

Colonies are **monoecious,** producing both eggs and sperm, although typically only a few of the zooids in a colony participate in gametogenesis. Sperm develop in clusters from peritoneal tissue on the funiculus (Fig. 135,*2*) or, in the case of *Cristatella,* on mesodermal strands of tissue spanning the metacoel (Braem, 1890). They differ from the sperm of Gymnolaemata, having a shorter head, a helical mass of mitochondrial material in the middle region, and more cytoplasm in the tail (Franzén, 1970). They are released into the coelomic fluid and apparently never leave the colony. Eggs arise from a short invagination of peritoneum between the parental polypide and its adventitious bud. The invagination, constituting an ovary, becomes somewhat pedunculate and typically contains 20 to 40 eggs in various stages of maturity (Fig. 139,*1*). Only one egg among these is ever fertilized, the rest detaching from the zooid wall and eventually disintegrating. Meanwhile, an invagination of elongated cells from the zooecial wall occurs beside the ovary opposite the adventitious bud. This grows to become an embryo sac, involving all tissue

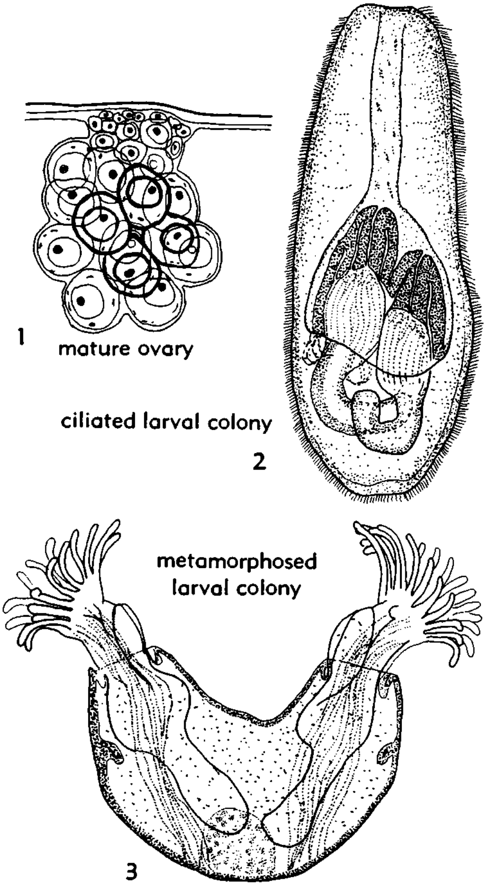

Fig. 139. Phylactolaemate sexual reproduction.——*1.* Mature ovary of *Plumatella fungosa* (Pallas) (after Brien, 1960).——*2.* Ciliated larval colony of *P. fungosa* (after Brien, 1954).——*3.* Metamorphosed larval colony of *P. fungosa* (after Brien, 1960).

layers from the metacoel to the colony exterior. The fertilized egg will not undergo further changes until it enters the embryo sac. Such entry has not been witnessed.

In the embryological events that follow, the zygote undergoes **holoblastic cleavage** and forms an elongate **blastula** whose cells become arranged in two distinct layers. At one pole of the embryo 2 to 4 small polypides develop in a fashion similar to parietal budding, and a fold of body wall grows up as a **mantle** from the middle of the embryo nearly to cover the new polypides. A mass of cilia completely cover the embryo colony, and a rupture of the embryo sac releases the entire structure to the ambient water.

The so-called larva (Fig. 139,*2*) has at its leading aboral pole an accumulation of nervous tissue described by MARCUS (1926), and from this end it probes potential substrates for a period up to 24 hours. Preliminary experiments by HUBSCHMAN (1970) with *Pectinatella* larvae indicate an importance of particle size in substrate selection and a distinct preference for natural over manufactured surfaces. Upon contact with a suitable substrate, the larva attaches with a glandular secretion from the aboral pole, the mantle fold pulls back, and the new polypides emerge and begin feeding (Fig. 139,*3*).

COLONY MORPHOLOGY

Despite the small number of phylactolaemate species, there is an impressive variety in colony morphology within the class, ranging from strongly tubular to essentially globular. The massive gelatinous colonies of *Pectinatella magnifica* (LEIDY) have been reported with diameters as large as 0.6 m (GEISER, 1937), with many thousands of polypides crowded together over the surface (Fig. 133,*3*). By contrast, *Fredericella sultana* (BLUMENBACH) often exists as a stringy tangle of tubules and widely separated polypides (Fig. 133,*1*). Other species may have been very flattened colonies closely adhering to the substrate in a crustose mat (Fig. 133,*2*). In every case, zooids throughout a colony are essentially identical in morphology and in the manner in which they form new buds, and nearly all polypides arise from positions ventral to the parental zooid. Any slight differences in morphology between the ancestrula and subsequently budded zooids are generally temporary and are almost certainly environmentally induced. Also, while ancestrula tissues may be expected to contain initially more yolky food reserves than those of subsequent zooids, there is nothing more to suggest an astogenetic gradient. However, we can recognize at least four conditions influencing morphology of the colony as a whole: differential interzooidal growth, varied time interval between successive buds, directional orientation of buds, and the density of zooids.

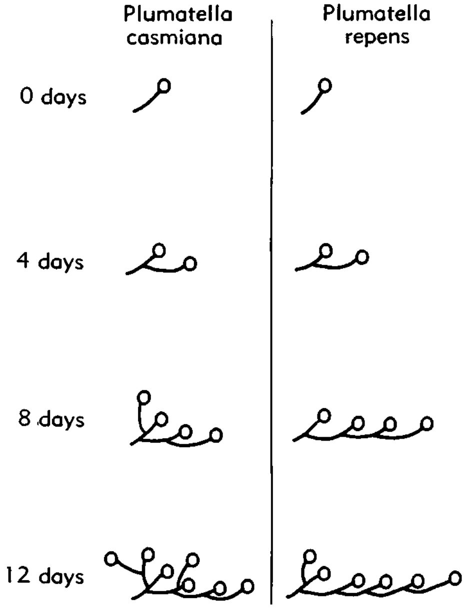

FIG. 140. Phylactolaemate budding patterns; comparison of *Plumatella repens* (LINNÉ) and *P. casmiana* OKA, based on mean data from 265 zooids in natural populations occurring together (after Wood, 1973).

Differential interzooidal growth.—Elongation of tubular branches draws new polypides away from the parental zooids, resulting in very open, dendritic colonies. In *Fredericella sultana* this growth is so pronounced that the branches cannot maintain continuous contact with the substrate throughout their length, and hence they tend to be largely free. Luxuriant colonies of this species form dense spongy tufts several centimeters thick, which may occur on the surface of lake sediments away from any solid substrate. By contrast, compact tubular parts of certain *Hyalinella* colonies have so little linear growth that several polypides may all seem to emerge from a slightly enlarged portion of the metacoel.

Varied time interval between successive buds.—The polypides of *Plumatella repens* and *P. casmiana* are morphologically very similar, yet colonies of the former are usually open and reptant while those of the latter are often dense and compact. Wood (1973) considered this dichotomy to be largely the result of different time intervals between successive bud production. Observations of 265 colonies showed a mean lapse of 7.7 days between the appearance of first and second buds of a zooid in *P. repens.* In *Plumatella casmiana* the interval is only 3.7 days. Moreover, the first bud in *Plumatella repens* emerges at a mean zooid age of 2.7 days, whereas *P. casmiana* zooids are generally 3.5 days old before their first bud is feeding. The effect of these temporal differences is a dense colony in one species and a more open or reptant one in the other (Fig. 140). There is some evidence that the compactness of *Plumatella casmiana* provides some protection from damage by midge larvae.

Directional orientation of buds.—In the families Plumatellidae and Fredericellidae, where zooids are mainly tubular, new buds arise directly ventral to the parental zooid. Whether they eventually bend to the left or right appears largely a matter of chance. A significant departure from this randomness is shown by the gelatinous colonies of Pectinatellidae and Cristatellidae, in which successive buds generally arise on alternate sides of the ventral sagittal plane. The effect is a colony whose shape is specific and predetermined according to species, such as the fan shape of *Lophopus* and the linear configuration of *Cristatella.*

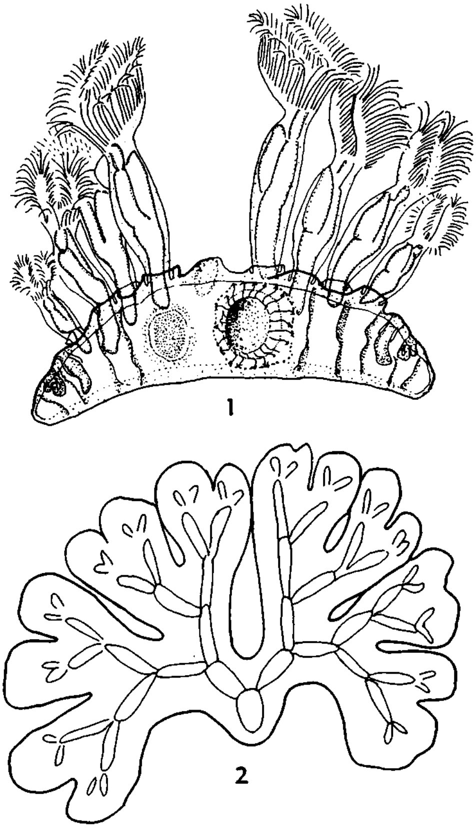

Fig. 141. Directional orientation of phylactolaemate buds.——*1.* Transverse section of *Cristatella mucedo* Cuvier showing progression of young to old zooids from lateral edges toward the midline (after Brien, 1954).——*2.* Schematic surface view of *Lophopus crystallinus* (Pallas) colony showing fan shape (after Marcus, 1934).

Colony growth in *Lophopus crystallinus* (Pallas) has been detailed by Brien (1954). The colonies are small, soft and transparent, seldom having more than 12 polypides. All polypides are oriented in the same direction, and all share a common saclike body cavity. The colony ancestrula, emerging from a statoblast, produces two daughter zooids in succession to the right and left of the ventral sagittal plane. Each of these in turn buds two zooids, and the process repeats itself as the colony spreads into a fan shape (Fig. 141,*1*). Before long, lobulations develop and the sinuses between them deepen to fragment the colony into smaller sections.

In *Cristatella mucedo* CUVIER the statoblast ancestrula gives rise to as many as five daughter zooids, both lateral and medial to the ventral sagittal plane (KRAEPELIN, 1887). These in turn produce zooids until the colony is heart-shaped with its cleft on the dorsal side of the first zooid. Budding is most active at the two upper lobes, and these gradually spread apart to become poles of an elongated colony. At this point the oldest zooids occupy a medial position in the colony and the youngest occur along the lateral edges (Fig. 141,*2*). Between these on both sides is a budding zone in which the ventral sides of all polypides face the periphery and new buds orient to the parental zooid exactly as in *Lophopus*. As a row of new zooids forms along the lateral edges, the older medial zooids become senescent and are resorbed into the colony, so that while the colony may grow longer it does not become any wider.

Density of zooids.—In most species each zooid may produce 2, 3 and occasionally as many as 5 daughter zooids. With no predetermined limits to growth it often happens that zooids normally adherent to the substrate exhaust the available two-dimensional space and can only grow vertically from the surface. This often occurs around small sticks and submerged branches where space is limited. A similar situation is faced by young colonies developing simultaneously from a dense accumulation of statoblasts. The result is a thick spongelike mat of contiguous vertical zooids that may give the colony surface a honeycomb appearance (BUSHNELL & WOOD, 1971). In *Plumatella fungosa* (PALLAS) this growth form is typical of the species.

PHYLOGENETIC CONSIDERATIONS

In 1741 when ABRAHAM TREMBLEY discovered the first known phylactolaemate colony, he assumed it to be closely related to colonial hydroids. The systematics of freshwater bryozoans has been a challenge to investigators ever since. With uniform polypide morphology and considerable phenotypic plasticity, the phylactolaemates offer few morphological features for species identification. Key diagnostic characters, based entirely on external anatomy, presently include statoblast dimensions, tentacle number, and certain details of the colony wall. All of these have been shown to be quite variable within a single population. Numerous taxonomic schemes have been proposed for phylactolaemate Bryozoa, notably those of ALLMAN (1856), JULLIEN (1885), KRAEPELIN (1887), VANGEL (1894), ROGICK (1935), TORIUMI (1956), and LACOURT (1968). Only TORIUMI has clarified the status of certain species by the laboratory rearing of colonies, and this approach deserves further attention.

It can hardly escape notice that, when properly arranged, phylactolaemate species exhibit three simultaneous morphological trends. A general decrease in interzooidal distance is accompanied by increased complexity of statoblasts and a rise in the number of tentacles borne by each lophophore. This is not to imply a monophyletic lineage, however; LACOURT (1968) proposed, in fact, a rather complex systematic scheme with at least three major divisions. Nevertheless, beginning with the Fredericellidae, the morphological gradients from simple to complex are distinct and provide support for the following assumptions:

1. Phylactolaemate evolution has brought about increased confluence among zooids, to the point that polypides are grouped together in open coelomic chambers. At the same time, chitinous sheathing exterior to the colony wall (*Fredericella, Plumatella*) has been replaced

by a gelatinous material of variable thickness (*Hyalinella, Pectinatella, Lophopodella*).

2. The simple unadorned statoblast of *Fredericella* must be considered primitive. Buoyant and cemented statoblasts represent a progressive step in *Plumatella* species, succeeded by the multifunctional spinous structures of *Pectinatella, Cristatella,* and *Lophopodella.*

3. An increase in the number of tentacles on the lophophore apparently confers certain advantages, perhaps in feeding or gaseous exchange, and is interpreted as representing phylogenetic advancement. Providing space for additional tentacles requires that the lophophore become deflected inwardly. Thus the horseshoe shape, often incorrectly cited as a vestige of primitive bilateralness, is barely evident in the Fredericellidae, but attains its greatest development in the more recently evolved Pectinatellidae and Cristatellidae (Fig. 134,*1*).

Phylactolaemate relations with other bryozoan groups are by no means obvious, although it is reasonable to suppose that the class represents an ancient lineage with an origin early in bryozoan evolution. The relatively large monomorphic zooids, the retention of three body regions (protosome, mesosome, metasome), and the muscular colony wall all point to this conclusion. Several authors have suggested that ancestral phylactolaemates preceded the gymnolaemates on the basis of morphological similarities between certain members of the former group and the phoronids (e.g., CORI, 1941; MARCUS, 1958; HYMAN, 1959; DAWYDOFF & GRASSE, 1959; BRIEN, 1960). However, NIELSEN (1971) described morphogenic inconsistencies that he believed to make such a close relationship unlikely. Further suggestive evidence for the precedence of phylactolaemate Bryozoa was offered by JEBRAM (1973b) in the observation that all species bud in an oral direction. This can be most easily explained by assuming the origin of phylactolaemates from a sessile or semisessile ancestor, development of an orally directed budding pattern, and subsequent reversal of budding polarity. This would permit an erect serial type of growth, conferring certain advantages to the colony which helped realize the spectacular adaptive radiation in gymnolaemate species, while phylactolaemates remained at a phylogenetic dead-end.

With the curious habitat isolation between phylactolaemate and gymnolaemate Bryozoa, both groups have become highly modified. One is left with the rather safe hypothesis that both groups share with the extinct Trepostomata a common Precambrian ancestor (BUGE, 1952). The virtual lack of fossil information on such ancient geneology warrants little further speculation on this point.

GLOSSARY OF MORPHOLOGICAL TERMS

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Terms and definitions are as used in this volume and include variant usages by volume authors. This glossary is not complete for the phylum. Additional terms and definitions will be included in volumes to follow as revisionary work proceeds.

This glossary does not distinguish recommended terms or their usages, for it is not meant to be authoritative. We do not believe that terms or their definitions should be fixed. Morphologic concepts are progressive approximations of full biologic understanding. Therefore, definitions should be constantly revised as knowledge of biologic relationships increases. Unthinking acceptance of a definition can lead to failure to ask critical questions, and progress is retarded. As understanding improves, concepts are modified or discarded and new concepts added. Terms applied to those concepts are more numerous than the concepts themselves and even more subject to change.

Definitions followed by one or more authors' names or by figure numbers in parentheses are as specifically used or cited by those authors in this volume. Definitions not followed by authors' names or figure numbers are as used or cited in the papers by Boardman, Cheetham, and Cook. Synonyms are those cited by authors in this volume or used by them as defined terms.

For some terms in this glossary, there are additional usages common in the literature but not included by any author in this volume. An example is the use of aperture for the opening in the skeleton of an anascan cheilostomate occupied by the membranous part of the zooidal frontal wall.

abandoned chamber. In stenolaemates, abandoned part of zooidal chamber generally sealed off by basal diaphragm (Fig. 142, 146).

acanthopore. Synonym of style or stylet in stenolaemates.

acanthorod. Synonym of style or stylet in stenolaemates.

acanthostyle. (a) In stenolaemates, a type of stylet; core a well-defined, smooth rod of nonlaminated calcite, sheath laminae usually strongly deflected toward zoarial surface, and sheath lamellar bundle wide. Acanthostyles usually larger than paurostyles (Fig. 219,*9*; 270,*1*) (Blake). (b) Rod-shaped calcite structure in zooecial walls or in extrazooidal vesicular tissue; core of hyaline calcite, may have sheath of cone-in-cone laminae if located in laminated wall or tissue; protrudes at zoarial surface as spine (Fig. 248,*3b*) (Utgaard). (c) Synonym of style or stylet in stenolaemates.

accretionary banding. Banding transverse to direction of growth of skeletal wall, of part of wall, or of individual crystal, resulting from addition of distinct growth increments (Fig. 102,*3*; 109,*3*; 111,*4*).

adventitious bud. In phylactolaemates, small bud primordium on dorsal side of main bud toward parental polypide; becomes main bud to parental polypide as original main bud develops into new polypide (Wood).

adventitious polymorph. In gymnolaemates, polymorph that communicates with just one other zooid; generally smaller than, and in extreme form almost structural appendage of, that zooid (Fig. 84,*1–3*).

aktinotostyle. Type of stylet in cryptostomates; core constructed of laminae that are medially arched toward zoarial surface, laterally deflected to form spines; contains scattered nonlaminated granules and, rarely, a continuous nonlaminated rod may be present in core; sheath laminae weakly to strongly directed toward zoarial surface; sheath lamellar bundle narrow (Fig. 219,*7*; 270,*3*).

anascan. Cheilostomate in which autozooids have hydrostatic system including largely to partly exposed flexible part of frontal wall and, consequently, no ascus (Fig. 72,*1–4*).

anastomosing colony. Branching erect colony in which branches join and rebranch to form open network (Fig. 15,*1*) (Utgaard).

ancestrula. (a) Zooid formed by metamorphosis of larva to found colony in stenolaemates and most gymnolaemates; generally differs in size and other morphologic characters from other zooids in colony; compare primary zooid. (b) In phylactolaemates, first zooid formed from a statoblast to found colony (Wood).

annulus. Outer epidermal layer of statoblast of phylactolaemates that encircles protective capsule containing germinal mass; can be air-filled and with or without marginal hooks, causing statoblast to float (floatoblast), or can form an adhesive encrusting layer (sessoblast) (Wood).

apertural muscle. One of either of two pairs of muscles, occlusor muscles of operculum or diaphragmatic dilator muscles, of cheilostomate autozooid (Lutaud).

aperture. In stenolaemates, terminal skeletal opening of zooid (Fig. 25, 26).

articulate colony. In stenolaemates, erect colony with jointed branches; node or joint consists of noncalcified, thick cuticular material in life (Utgaard).

ascophoran. Cheilostomate in which autozooids have hydrostatic system including ascus beneath continuous protective frontal shield developed as cryptocyst, gymnocyst, or umbonuloid shield (Fig. 68,*1,2*; 69,*1,2*).

ascus. Exterior-walled, flexible-floored sac beneath frontal shield of autozooid in ascophoran cheilostomates; encloses water-filled chamber opening at or near orifice to function in hydrostatic system; derived by infolding of part of frontal wall beneath gymnocyst or cryptocyst, or by overarching of frontal wall by umbonuloid shield and associated structures (Fig. 68,*1d,e*; 69,*1b,c*; 78,*1a*).

astogenetic differences. Differences in morphology unique to zooids comprising asexual generation and therefore restricted to zones of astogenetic change in colony.

astogeny. Course of development of sequence of asexual generations of zooids and any extrazooidal parts which together form colony.

atrial bag. Part of polypidian vesicle attached to frontal wall of developing zooid, from which tentacle sheath is formed by slight constriction separating it from digestive lumen (Fig. 91,*2*).

autozooid. (a) Zooid having at some stages of ontogeny protrusible lophophore, with or without feeding ability. (b) Usual, common zooid containing feeding organs in colony; capable of carrying out all life functions in monomorphic colony (Utgaard; Blake; Karklins).

autozooidal polymorph. Autozooid differing from ordinary feeding zooids in size, shape, tentacle number, or other feature, which may or may not be reflected in any skeletal parts present, but retaining protrusible lophophore with or without feeding ability (Fig. 69,*1c*).

avicularium. In cheilostomates, autozooidal or more commonly heterozooidal polymorph having equivalent of orificial wall relatively larger and more intricately reinforced than those of ordinary feeding autozooids, to form mandible (Fig. 71,*2,3*; 81,*3*).

axial bundle. In Rhabdomesina, cluster of axial zooecia differentiated as distinct axial structure (Fig. 283).

axial zooecium. In Rhabdomesina, elongate polymorph that parallels zoarial axis for part or all of its length. Those that diverge from axis become typical autozooecia (Blake).

basal attachment. In Ptilodictyina, proximal part of zoarium consisting of encrusting base adnate to substrate and connecting segment that develops distally into zoarium (Fig. 223,*2*).

basal bud. In gymnolaemates, bud arising from basal wall of parent zooid, as on reverse surface of unilaminate erect colony branch and in some uniserial erect colony branches.

basal canal. Circumoral lacuna of lophophore into which internal lacunae of all tentacles open (Fig. 96).

basal diaphragm. In stenolaemates, diaphragm that acts as floor of living chamber (Fig. 2, 37).

basal disc. In stenolaemates, encrusting proximalmost part of ancestrula; direct development of metamorphosis of the larva (Fig. 25, 26).

basal layer. Synonym of skeletal part of encrusting colony wall in stenolaemates.

basal plate. Synonym of basal platform in cheilostomates.

basal platform. Multizooidal skeletal layers of basal zooidal walls in cheilostomates.

basal window. Uncalcified subcentral portion of exterior basal zooidal wall in encrusting cheilostomate colony (Fig. 69,*1d*).

basal zooecium. Small polymorph on basal surface of some Ceramoporidae (Fig. 145).

basal zooidal wall. In stenolaemates and gymnolaemates, exterior or interior zooidal supporting wall, opposite and generally parallel to orificial wall; can be absent in zooids budded above encrusting base in some erect and some multilaminate encrusting colonies.

beak. Pointed, rounded, or lobate skeletal rim on which mandible of cheilostomate avicularium occludes and to which it may or may not conform in length and shape (Fig. 70,*3b*; 84,*1,2*).

bifoliate colony. In stenolaemates, erect colony in which two layers of zooids bud back to back from interior multizooidal median wall (Fig. 30,*1,3a,4*).

bilaminate colony. In cheilostomates, colony with erect branches consisting of two layers of zooids with separate but adjacent, commonly exterior basal walls; flexible or rigid, depending on degree of calcification (Fig. 70,*1a*).

bimineralic skeleton. Cheilostomate zoarium or zooecium having some layers composed of calcite and others of aragonite (Fig. 67,*1c*; 68,*1e*).

biological interference. Effect exerted by organism on mineralogy, crystal morphology, and other properties of its skeleton, which make those properties different from equivalent properties of actually or potentially coprecipitated inorganic carbonates (Sandberg).

bisexual. Zooid or colony that produces both male and female gametes.

blastema. Undifferentiated part from which organ develops or tissues proliferate (Lutaud).

blastula. Single-layered embryonic stage produced by cleavage of zygote (Steen, 1971).

body cavity. Space enclosed by zooidal, multizooidal, or extrazooidal walls containing zooidal organs or other structures suspended in body fluid.

body wall. (a) Wall enclosing the body cavity of a colony and its parts, including zooids, parts of zooids, multizooidal parts, and any extrazooidal parts; consists of inner cellular peritoneum, outer cellular epidermis, and outermost noncellular layers, including cuticular, gelatinous, or skeletal material, or a combination; in phylactolaemates, includes layers of longitudinal and circular muscles between epidermis and peritoneum. (b) Wall of zooid or bud, consisting of inner cellular peritoneum, outer cellular epithelium, and at least in exterior walls outermost cuticle with or without underlying skeleton; in fully developed zooids, with nerve layer (diffuse peripheral endings or plexus) between epidermis and peritoneum (Fig. 89).

boring. External mold of ctenostomate colony immersed in calcareous substrate; produced by chemical penetration during colony growth (Fig. 85,*3*).

branch midrib. Protruding, central, compound range wall in center of branch in some bifoliate fistuliporines (Fig. 210,*2c*).

brood chamber. (a) In stenolaemates, zooidal or extrazooidal coelomic chamber in which eggs develop into larvae (Fig. 52). (b) In most gymnolaemates, water-filled space partly enclosed by body walls of one or more polymorphs, within which embryos are held during development, generally one at a time, topologically outside body cavity of colony (Fig. 69,*1c*; 70,*2*).

brown body. (a) In stenolaemates and gymnolaemates, encapsulated mass of degenerating cells from lophophore, gut, some muscles, and some other nonskeletal parts of zooid varying in different groups; either retained in zooidal body cavity or expelled after regeneration of feeding and digestive organs (see Fig. 40,*3b*). (b) Synonym of brown deposit (Karklins).

brown deposit. In stenolaemates, granular deposit of iron oxide or pyrite presumably representing fossilized remains of organic material which were either functional organs or brown bodies of degenerated states in life (Fig. 40,*1,5*; 43,*3*; 46,*1,4a*).

bud. (a) In stenolaemates and gymnolaemates, newly developing, asexually produced zooid, initiated as body walls. (b) In phylactolaemates, newly developing, asexually produced zooid, initiated as statoblast or polypide (Wood).

budding. Asexual reproduction of zooids.

budding pattern. In stenolaemates, shapes of buds and their relative positions on supporting structures.

$CaCO_3$ polymorph. Either of two forms of $CaCO_3$, calcite or aragonite, which constitute cheilostomate skeletons (Sandberg).

caecum. Blind prolongation of stomach portion of digestive tract in which food remains for some time (Fig. 91; 95,*4*).

canaliculus. Large style in Actinotrypidae that inflects autozooecial wall, producing ridge in zooecial chamber parallel to zooecial length, each with a septumlike appearance (Fig. 194, 195).

cardia. Curved tubular part of digestive tract into which esophagus opens; in some ctenostomates (and one cheilostomate) differentiated into gizzard and stomach portions (Fig. 91; 95,*4*).

cardiac stomach. In phylactolaemates, tubular part of stomach between cardiac valve and caecum (Fig. 131,*1*).

carina. Protruding median ridge on surface of zoarium of Goniocladiidae formed by protruding vertical mesotheca (Utgaard).

carnosan. Ctenostomate in which autozooids bud directly from other autozooids, or alternate in groups with groups of kenozooids (Fig. 66,*1–3*).

celluliferous side of colony. Synonym for frontal side in stenolaemates.

cerebral ganglion. Nerve center lying in oral constriction between base of lophophore and esophagus on anal side of polypide (Fig. 96; 100,*2*).

circular muscle layer. Outer of two thin muscle layers in body wall of phylactolaemates between peritoneum and epithelium (Fig. 132,*4,5*).

closure. Synonym of frontal closure in cheilostomates.

coelom. Body cavity lined with peritoneum.

collar. Pleated membranous structure attached to diaphragm of ctenostomate zooid; contained within vestibule when lophophore is retracted and exposed at frontal surface when lophophore is everted (Fig. 66,*2a,3*).

colony. Morphologic and functional unit that interacts with the environment as a complete organism, consisting of one or more kinds of physically connected zooids, multizooidal parts, and in some colonies extrazooidal parts, all assumed to be genetically uniform.

colony control. Process influencing growth and functions of zooids to make then differ morphologically and functionally from solitary animals because of membership in colony.

colony wall. In phylactolaemates, body wall composed of outer noncellular cuticle or gelatinous layer, epithelial layer, longitudinal and circular muscle layers, and inner peritoneum (Wood).

columnar epithelium. Mitotically active epithelium of body wall of bud or of more restricted area of proliferation, capable of secreting cuticle (Fig. 87,*1*).

common bud. Synonym for confluent budding zone in stenolaemates.

communication organ. Complex of interdigitating cell types, together with cuticular or calcareous pore plate, which form exclusive means of communication between principal body cavities of fully developed gymnolaemate autozooids, between parts of some zooids, and between zooids and extrazooidal parts (Fig. 68,*1d,e*).

communication pore. (a) In stenolaemates, pore in interior wall through which physiological communication among zooids or between zooids and extrazooidal parts is assumed (Fig. 35,*4*; 46,*3*). (b) In gymnolaemates, single or one of several minute pores in pore plate traversed by cells of communication organ.

compensating sac. Synonym of ascus in cheilostomates.

compound skeletal wall. Skeletal wall calcified on edges and both sides, therefore necessarily an interior wall. Most vertical walls in stenolaemates.

condyle. One of pair of bilaterally arranged skeletal protuberances on which operculum of autozooid or mandible of avicularium is hinged in some cheilostomates; in asymmetrical avicularia of some cheilostomates can be single (Fig. 81,*3b*).

confluent budding zone. In stenolaemates, coelomic budding space and enclosing exterior walls connecting body cavities of a few to many buds or combinations of buds and zooids (Fig. 25, 26).

confluent multizooidal budding zone. In stenolaemates, confluent budding zone that originates outside of zooidal boundaries opposite endozone and which contains only buds at distal ends or edges of colony (Fig. 25, 26).

confluent zooidal budding zone. In stenolaemates, confluent budding zone that originates within outer coelomic space of zooids opposite exozone, or in some taxa opposite distal endozone (Fig. 54,*3,4*).

connecting segment. In Ptilodictyina, part of zoarial attachment between encrusting base and regularly developed distal part of zoarium (Fig. 223,*2*).

core. In stenolaemates, one of two structural elements forming stylets; formed either of laminated or nonlaminated skeletal material or a combination of both; generally separated from sheath laminae by growth discontinuity (Blake).

cormidial orifice. In cheilostomates, skeletal support for zooidal orifice which is joint product of more than one zooid (Fig. 122,*1–3*; 127).

cortex. In stenolaemates, main portion of zooecial wall adjacent to zooecial boundary (Utgaard).

costa. One of usually paired spines fused medially and commonly intermittently laterally to form costal shield of cribrimorph cheilostomate zooid.

costal shield. Discontinuous frontal shield or part of frontal shield of cheilostomate zooid, formed by unfused or intermittently fused spines overarching uncalcified part of frontal wall (Fig. 71,*1–3*).

cribrate colony. In stenolaemates, sheetlike or frondose colony with flattened, anastomosing branches separated by fenestrules (Utgaard).

cribrimorph. Cheilostomate with autozooids having costal shields composed wholly or in part of spines fused medially, and most commonly intermittently along lengths (Fig. 71,*1–3*).

cryptocyst. Continuous frontal shield or part of frontal shield of cheilostomate zooid, formed by calcification of interior wall grown into body cavity subparallel to and beneath frontal wall; completely calcified or with uncalcified spots covered by cuticle or plugged with cellular and noncellular material; in anascans, commonly with lateral notches or openings for passage of parietal muscles; in ascophorans, with marginal or submarginal communication organs connected to underlying principal body cavity of zooid (Fig. 67,*1a–e*; 72,*1,3*).

cryptocystidean. Anascan or ascophoran cheilostomate with autozooids having frontal shields (cryptocysts) formed by calcification of interior body walls grown into body cavities subparallel to and beneath frontal walls (Sandberg).

cuticle. Noncellular organic outer layer of body wall secreted by columnar epithelium of bud (Fig. 87); composed of mucopolysaccharides in glycoproteinic frame, hardened by a tanning process.

cyphonautes larva. In gymnolaemates, ciliated larva with bivalved cuticular shell; most commonly planktotrophic, but in some cheilostomates having nonfunctional digestive tract (Fig. 85,*4*).

cystiphragm. In stenolaemates, lateral skeletal partition extending from zooecial wall into chamber and curved inward to form cyst or collar that extends partly or entirely around zooidal chamber (Fig. 30,*1*; 46,*7*).

cystoidal diaphragm. In stenolaemates, transverse skeletal structure formed by two diaphragms in contact only part way across zooecial chamber to form an enclosed compartment between them (Fig. 264).

cystopore. Synonym of vesicular tissue in stenolaemates.

dactylethra. In stenolaemates, defined originally as an aborted, shortened polymorph; interpreted here to be a degenerated feeding zooid closed by terminal diaphragm (Fig. 48,*6–8*).

dendrite. Short, usually branched process of nerve cell that conducts impulses to cell body (Steen, 1971).

dendritic thickening. In some erect bilaminate cheilostomates, extreme skeletal thickening along axes of colony branches formed by thickened frontal shields of axial autozooids and overlying kenozooids (Fig. 109,*2*).

dendroid colony. In stenolaemates, erect branching colony with branches circular in cross section and most zooids budded from vertical walls of other zooids.

diaphragm. (a) In stenolaemates, membranous or skeletal partition that extends transversely across entire zooidal chamber (Fig. 31,*5*; 36,*1*). (b) In gymnolaemate autozooid, muscular ring of body wall forming attachment between inner end of vestibular wall and outer end of tentacle sheath; commonly connected to vertical walls of zooid by diaphragmatic dilator muscles (Fig. 66,*3*).

diaphragmatic dilator muscle. One of generally bilaterally paired muscles that traverse body cavity of gymnolaemate autozooid to insert on muscular diaphragm at connection between vestibular wall and tentacle sheath (Fig. 66,*3*).

digestive epithelium. Cellular lining of digestive tract derived from secondary invagination of epithelium of body wall (LUTAUD).

dilator muscle. One of commonly multiple, radially or bilaterally arranged muscles that traverse body cavity of gymnolaemate autozooid to insert on diaphragm (diaphragmatic dilator muscle) or vestibular wall (vestibular dilator muscle) for dilation during lophophore protrusion.

direct nerve. One of two nerve strands composing each of twin peripheral nerves following tentacle sheath toward orifice and frontal wall.

distal bud. In gymnolaemates, bud arising from distal side of vertical wall of parent zooid to continue growth in principal growth direction of parent, as in most encrusting and erect colonies (Fig. 76,*1b*; 77,*1a*; 80,*1,2*).

distal direction. Principal direction of growth of colony or of major part of colony, away from founding zooid or zooids (ancestrula, multiple primary zooids, statoblast ancestrula, or preexisting colony fragment); can be subparallel or subperpendicular to principal growth directions of zooids.

distal hemiseptum. In stenolaemates, hemiseptum projecting from distal zooidal wall or mesotheca.

distolateral bud. In gymnolaemates, bud arising from distolateral side of vertical wall of parent zooid to initiate growth in direction slightly diverging from principal growth direction of parent, as in most encrusting and erect colonies (Fig. 75,*1a*).

divaricator muscle. One of pair of muscles that traverse body cavity of cheilostomate avicularium to insert near fixed margin of mandible, and of some cheilostomate autozooids to insert near fixed margin of operculum, both of which are opened by their action.

double-walled colony. Synonym of free-walled colony in stenolaemates.

duplicate bud. In phylactolaemates, minute bud primordium lying close beside main bud ventrally; becomes main bud to new polypide (Fig. 135,*4*).

duplicature muscle fiber. In phylactolaemates, one of bundles of muscle fibers that widen anterior end of tentacle sheath through which lophophore passes during protrusion, and serve as fixator ligaments for protruded polypide (Fig. 132,*1,2*).

ectocyst. Variously used to correspond to cuticular layer of body wall or also to include epidermis, cuticle, and skeleton (LUTAUD).

ectoderm. Embryological term sometimes applied to epidermis in bryozoans (Fig. 87).

edgewise growth. Skeletal growth in which calcification of walls occurs by simultaneous addition of calcite to edges of crystals at growing ends of walls; wall laminae may be at any angle to growth lines (Fig. 29,*1,2*).

embryonic fission. In tubuliporates, asexual division of primary embryo into secondary, and in some species, tertiary embryos, presumably all with the same genetic makeup.

encrusting colony. (a) Colony in which most zooids are attached to substrate by their basal walls. (b) In gymnolaemates, colony in which each autozooid of unilaminate colony or of basal layer of multilaminate colony is attached to substrate by all of its basal wall (tightly encrusting), or by protruding parts of its basal wall or kenozooids budded from its basal wall (loosely encrusting).

encrusting wall of colony. In stenolaemates, basal wall of colony adjacent to substrate (Fig. 25; 26; 28; 30,*5a,b*).

endocyst. Variously used to include both epidermis and peritoneum, or peritoneum alone (LUTAUD).

endoplasmic reticulum. Organelle consisting of fine, branching, anastomosing tubules, spaces, or isolated vesicles present in cytoplasm of most cells (STEEN, 1971).

endozone. In stenolaemates, inner parts of zooids of a colony, characterized by one or a combination of growth directions at low angles to colony growth direction or colony surface, thin vertical walls, and relative scarcity of intrazooidal skeletal structures (Fig. 10, 11).

entosaccal cavity. In stenolaemates, that part of zooidal body cavity within membranous sac (Fig. 2).

epidermis. Epithelium of body wall; secretes cuticle and, in stenolaemates and cheilostomates, underlying deposit of calcium carbonate (skeleton) within organic matrix (Fig. 2) (LUTAUD).

epifrontal fold. Double-walled fold of exterior body wall and contained body cavity overarching membranous frontal wall in umbonuloid cheilostomates (SANDBERG).

epistome. Small, movable, liplike lobe of tissue and contained coelom overhanging the mouth of a phylactolaemate zooid (Fig. 131,*1*).

epithelial layer. In phylactolaemates, single layer consisting of two cell types, columnar cells that secrete outermost noncellular material of colony wall, and vesicular cells containing fatty deposits (WOOD).

epithelium. Outer cellular layer of zooid body wall (epidermis) and internal cellular layer lining lumen of alimentary tract (digestive epithelium) (Fig. 87; 88,*1*).

erect colony. Colony that extends into water from relatively small encrusting base or rootlets.

esophagus. (a) In phylactolaemates, nonciliated part of digestive tract between pharynx and cardiac valve (Fig. 131). (b) Used, in part, as synonym of pharynx (LUTAUD).

eustegal epithelium. In free-walled stenolaemates, epithelium that secretes exterior cuticle (Fig. 142, 143).

excurrent chimney. Localized current created by the feeding action of adjacent zooids which carries excess water and any rejected particles away from colony surface (Fig. 25).

exilazooid, exilazooecium. In stenolaemates, generally small polymorph originating in outer endozone or exozone between feeding zooids with few or no basal diaphragms so that living chamber space is available for possible organs (Fig. 48,*5*).

exosaccal cavity. In stenolaemates, that part of zooidal body cavity between membranous sac and body wall (Fig. 2).

exozone. In stenolaemates, outer parts of zooids of colony, characterized by one or more combinations of growth directions at high angles to colony growth directions or colony surfaces, thick vertical walls, and concentrations of intrazooidal skeletal structures (Fig. 10, 11).

explanate colony. Erect, sheetlike or frondose colony, in some with lobate extensions (KARKLINS).

exterior skeletal wall. In cheilostomates, skeletal wall that calcifies against cuticle and occurs in a body wall that, in its precalcified, membranous state, expanded coelomic volume of colony (SANDBERG).

exterior wall. Body wall that extends body of zooid and of colony; includes outermost cuticular or gelatinous layer (Fig. 1).

external muscle. Muscle, such as retractor or parietal, which extends across body cavity from body wall to lophophore or digestive tract, or to other body wall (Fig. 99).

extrazooidal part. Protective or supportive colony structure which, once developed, remains outside zooidal boundaries throughout the life of a colony; in phylactolaemates, the exterior colony body walls and adjacent body cavity transitional with exterior zooidal vertical walls and body cavities.

extrazooidal skeleton. In cheilostomates, skeletal layers of extrazooidal body walls produced by coalescence of body walls originally bounding hypostegal coeloms of zooids or formed concurrently at growing extremities with budding of zooids (Fig. 70,*1b*).

feeding zooid. A zooid that at some ontogenetic stage(s) possesses a protrusible lophophore, a digestive tract, muscles, a nervous system, and funicular strands capable of functioning to provide nourishment to itself and to any connected nonfeeding zooid or other nonfeeding part of colony; may include some or all zooids within a colony.

Feigl's solution staining. Mineralogical staining technique by which location of aragonite within cheilostomate skeleton can be recognized by selective precipitation of silver and MnO_2 on aragonite (Fig. 125,*1*).

fenestrate colony. Erect colony in which branches form a reticulate pattern (Fig. 15,*1,3*; 60,*1*).

fenestrule. One of the open spaces between branches of fenestrate colonies (Fig. 60,*1*).

fibrillation. Arrangement of myofilaments in muscle fibers (LUTAUD).

firmatopore. Type of kenozooecium consisting of slender, proximally directed tubule on reverse side of zoarium in tubuliporates (BASSLER, 1953).

fixed-walled colony. In stenolaemates, colony in which orificial walls of feeding zooids are fixed directly to apertures so that confluent outer body cavities between zooids are eliminated (Fig. 26).

flask-shaped chamber. In stenolaemates, chamber defined by skeletal funnel cystiphragm within zooidal living chamber (Fig. 46,*6,7*).

flexibly erect colony. In gymnolaemates, erect colony in which zooids and any extrazooidal parts present are uncalcified (ctenostomates) or lightly calcified (some cheilostomates), thus permitting extensive motion in moving water (Fig. 13,*2*; 66,*1*).

floatoblast. Statoblast with peripheral pneumatic annulus, having or lacking marginal hooks (Fig. 137,*3,4*).

fragmentation. Asexual reproduction of colony by direct growth from zooid or group of zooids broken from preexisting colony (compare hibernaculum, statoblast).

free-living colony. Cheilostomate or ctenostomate colony without general attachment to substrate; commonly partly mobile on or in unstable sea-bottom sediments by means of specialized polymorphs (Fig. 14,*4*).

free-walled colony. In stenolaemates, colony that is loosely covered by membranous exterior walls not attached at apertures of feeding zooids so that confluent outer body cavities connecting zooids are produced (Fig. 25).

frondose colony. In stenolaemates, erect colony with branches flattened into leaflike shapes and zooids budded from vertical walls of other zooids (UTGAARD).

frontal budding. In gymnolaemates, budding from frontal wall or associated structure, such as hypostegal coelom of parent zooid, to produce autozooids in some multilaminate encrusting colonies and some free-living colonies; or to produce adventitious polymorphs in many kinds of colonies (Fig. 69,*1b,2*; 79,*2*).

frontal closure. In cheilostomates, calcified frontal and orificial walls of autozooid that were membranous when lophophore was functional, but became permanently sealed; commonly retains traces (scars) of cuticular operculum and parietal muscle insertions (Fig. 76,*2,3*; 80,*4*).

frontal membrane. Flexible, membranous part of frontal wall of cheilostomate autozooid (Lutaud).

frontal shield. Protective and supportive skeletal structure on frontal side of retracted organs of cheilostomate autozooid, grown as part of frontal wall or as part of exterior body wall overlying, or interior body wall underlying frontal wall (Fig. 65,*2–7*).

frontal side of colony. In stenolaemates and gymnolaemates, side of unilaminate colony that contains orifices of feeding zooids (Fig. 28, left sides of *1b* and *6*; 76,*1–5*; 78, right side of *1a*).

frontal structure. In gymnolaemate autozooid, relationship of frontal wall and, where present, of frontal shield to hydrostatic system.

frontal wall. (a) In fixed-walled stenolaemates and all gymnolaemates, an exterior zooidal wall attached to and wholly or partly supporting the orificial wall; provides front side to zooid more extensive than orificial wall alone (Fig. 1, 4). (b) In gymnolaemates, bounds frontal side of zooid at least in early ontogenetic stages, but commonly is modified by partly calcified supportive and protective structures in cheilostomates (Fig. 65,*1–7*).

funicular strand. Cellular tissue traversing the body cavities of zooids, buds, and extrazooidal parts of gymnolaemate colonies to connect feeding organs and communication organs to body walls; produces sperm in male or hermaphrodite autozooids (Fig. 68,*1e*).

funiculus. (a) System of strands of spindle-shaped cells that are continuous with peritoneum of digestive tract and body wall, extend across body cavity and along body wall between pore plates, are attached to special club-shaped cells through communication pores of pore plates in body walls, and thus extend from zooid to zooid throughout colony (Fig. 4; 87,*2*) (Lutaud). (b) In phylactolaemates, tubular strand of tissue incorporating small muscle fibers spanning metacoel from caecum to peritoneum of colony wall (Fig. 142,*1*) (Wood).

funnel cystiphragm. In stenolaemates, skeletal structure within zooidal living chamber which defines flask-shaped or funnel-shaped chamber, interpreted to be walls of intrazooidal polymorph (Utgaard) or calcified parts of membranous sac or orificial-vestibular wall of feeding zooid (Boardman) (Fig. 46,*6,7*).

funnel-shaped chamber. Synonym of flask-shaped chamber in stenolaemates.

fused-wall colony. Synonym of fixed-walled colony in stenolaemates.

giant bud. In gymnolaemates, unpartitioned distal end of lineal series two or more zooid lengths in extent, formed by lag in formation of interior transverse walls relative to growth of exterior walls of multizooidal origin (Lutaud).

gizzard. In some ctenostomates (and one cheilostomate), spheroidal to elongate inner portion of cardia with epithelial surface supporting few to many, pointed or rounded plates or teeth.

glycoprotein. One of group of protein-carbohydrate compounds, such as mucin (Steen, 1971).

Golgi apparatus. Organelle, well developed in cytoplasm of secretory cells, consisting of a set of flat formations of endoplasmic reticulum (Lutaud).

gonozooecium. In stenolaemates, inflated polymorph that provides brood chamber in which eggs develop into larvae (Fig. 52,*8*).

granular microstructure. In cystoporates, skeletal microstructure characterized by subquadrate crystallites; generally dark-colored in thin section (Utgaard).

granular-prismatic microstructure. In cystoporates, skeletal microstructure characterized by blocky to prismatic crystallites elongated perpendicular to epithelium that secreted skeleton; generally light-colored in thin section (Utgaard).

growing tip. Proliferating distal extremity of colony, colony branch, or lineal series of zooids, characterized by columnar, mitotically active epithelium and undifferentiated peritoneal layers (Fig. 89,*1,4*).

growth habit. General form or shape in which a colony grows, and its relationship to the substrate; examples are a unilaminate encrusting colony or a conical free-living colony.

gymnocyst. Continuous frontal shield or part of frontal shield of cheilostomate zooid, formed by calcification of exterior frontal wall; completely calcified or with uncalcified, cuticle-covered spots (Fig. 69,*1,2*; 71,*1,2*).

gymnocystidean. Ascophoran cheilostomate with autozooids having gymnocysts as their frontal shields (Sandberg).

hemiphragms. In stenolaemates, shelflike skeletal projections in zooidal living chamber, which alternate in ontogenetic series from opposite sides of zooecia; hemiphragms in any one zooid commonly comparable in morphology (see Fig. 40,*5*).

hemisepta. In stenolaemates, shelflike skeletal projections in zooidal living chambers, generally on proximal walls or in one or two pairs in alternate positions on proximal and distal sides of zooecia. Proximal and distal hemisepta commonly different in morphology in zoaria of Paleozoic age (Fig. 32,*1*; 267,*1*).

hemispherical colony. In stenolaemates, colony of approximately hemispherical shape in which zooids bud from encrusting colony wall and vertical walls of other zooids, and in some taxa from intracolony overgrowths.

heterostyle. Type of stylet in cryptostomates; core of lenses of nonlaminated calcite separated by bands of laminae continuous with sheath laminae; sheath laminae weakly to strongly directed toward zoarial surface; sheath lamellar bundle narrow (Fig. 219,*5*; 270,*2*).

heterozooid. In gymnolaemates, a polymorph with nonprotrusible or no lophophore, and therefore no apparent feeding ability, musculature different from that of autozooids or lacking, and specialized organs present or lacking (Fig. 70,*1c,3*).

hibernaculum. Encapsulated bud in some gymnolaemates, with fusiform to irregular stiffened cuticular cover containing yolklike material and partly developed feeding and digestive organs capable of germinating to produce first zooid of new colony, either attached to or detached from dead parent colony; formed as inswellings or outswellings of body wall of parent zooid.

hollow ramose colony. In stenolaemates, erect branching colony in which zooids bud from cylindrical axial colony walls (Fig. 36,*4b*; 54,*1*).

holoblastic cleavage. Mitotic division of zygote to form blastula consisting of cells approximately equal in size (Steen, 1971).

hydrostatic system. System for protruding lophophore in gymnolaemate autozooid, consisting of flexible part of frontal wall, or infolded sac derived from it, and attached parietal muscles.

hypostegal coelom. (a) Part of body cavity of cheilostomate zooid separated from principal body cavity by ingrowth of body wall to form cryptocyst, or extended from principal body cavity enclosed in double-walled outfold to form umbonuloid shield; remains confluent with principal body cavity or is connected to it only by communication organs (Fig. 67,*1b*; 68,*1b,d*; 71,*1*). (b) Synonym of outer coelomic space in free-walled stenolaemates.

hypostegal epithelium. In free-walled stenolaemates, epithelium that secretes extrazooidal skeleton (Fig. 143).

hypostegia. Synonym of hypostegal coelom in cheilostomates.

immature region. Synonym for endozone in stenolaemates.

inferior hemiseptum. Synonym of distal hemiseptum in stenolaemates (Karklins).

initial layer of skeleton. Layer of cryptocyst or umbonuloid shield in cheilostomate zooid first deposited by proliferating epidermal cells, commonly of different microstructure or mineral composition from superficial skeletal layers (Fig. 67,*1c*; 68,*1d*).

inner epithelium. In free-walled stenolaemates, epithelium that secretes skeleton, including both zooidal epithelium, which secretes zooidal skeletal walls, and hypostegal epithelium, which secretes extrazooidal skeleton (Fig. 142, 143).

integration. Extent to which zooids in combination with any extrazooidal parts differ morphologically from solitary animals because of colony control of growth and functions.

intercalary cuticle. Cuticle composed of outermost layers of lateral walls of contiguous lineal series of zooids in gymnolaemate colony (Fig. 116,*1*).

interior skeletal wall. In cheilostomates, skeletal wall that grows off inner surface of exterior skeletal wall or other interior skeletal wall by apposition and partitions preexisting coelomic volume of colony (Sandberg).

interior wall. Body wall that partitions preexisting body cavity into zooids, parts of zooids, or extrazooidal parts; may or may not include cuticular or gelatinous layer (Fig. 1).

interray. Area between rays of monticular zooecia in star-shaped monticules, generally composed of extrazooidal vesicular tissue in cystoporates (Utgaard).

intertentacular organ. In some gymnolaemates, elongate protuberance of body wall on distal side of lophophore beneath tentacle bases bearing terminal pore through which fertilized eggs are released to develop generally into planktotrophic larvae.

interzooidal budding. In stenolaemates, budding that occurs outside of living chambers of zooids, so that one bud cannot be related to single parent zooid.

interzooidal communication organ. In gymnolaemates, communication organ that connects one zooid to another.

interzooidal growth. In phylactolaemates, growth of colony wall between newly budded polypides and parental polypides (Wood).

interzooidal polymorph. In gymnolaemates, polymorph intercalated in budding series to communicate with two or more zooids, in space smaller than those occupied by ordinary feeding zooids (Fig. 71,*2,3*).

intracoelomic muscle. Synonym of external muscle.

intracolony overgrowth. Overgrowth of encrusting zooids onto colony surface, initiated from adjacent surviving zooids (Fig. 36,*1*).

intracuticular skeleton. In cheilostomates, skeletal layers that lie between noncellular organic sheets or within noncellular organic networks continuous with cuticles of uncalcified exterior walls.

intrazooidal budding. In stenolaemates, budding that occurs within the living chamber of a single parent zooid.

intrazooidal communication organ. In cheilostomates, communication organ that connects hypostegal coelom to principal body cavity of the same zooid.

intrazooidal polymorphism. In stenolaemates, sequential development of two different kinds of zooids in same living chamber (Fig. 49,*6,7*).

intrinsic body-wall muscles. Circular and longitudinal muscle layers in body walls of phylactolaemates.

jointed erect colony. In cheilostomates, erect colony in which zooids and any extrazooidal parts present are well calcified except at more or less regular intervals along branch lengths, thus permitting motion in moving water (Fig. 14,*1*).

keel. (a) In stenolaemates, flat median portion of zooid wall between sinuses in recumbent part of endozone (Fig. 56). (b) Synonym of carina in some stenolaemates. (c) In phylactolaemates, a longitudinal medial ridge extending along the recumbent tubular portions of a colony (Wood).

kenozooid. (a) In stenolaemates, any polymorph lacking lophophore and gut, muscles, and orifice. (b) In gymnolaemates, polymorph lacking orificial wall or its equivalent, lophophore, alimentary canal, and, in most, muscles (Fig. 66,*1,2*).

lamellar growth. Skeletal growth involving many parallel to subparallel layers or lamellae. A lamella grows either by advancement of bladelike crystals at the distal end or by marginal increase and impingement of scattered seed crystals on a broad-to-narrow zone or step to form solid layer; different parts of each lamella are of different ages (Sandberg).

lamellar ultrastructure. In cheilostomates, broad group of skeletal ultrastructures consisting of planar or lenticular aggregates of commonly tabular crystals of calcite forming layered units (lamellae) oriented parallel to wall surfaces; aggregates separated by diffuse or distinct organic sheets (Fig. 115,*2*).

lanceolate colony. In Ptilodictyina, erect, unbranched, bifoliate colony with proximally tapering zoarial segment (Fig. 242,*1e*).

larva. (a) Sexually produced, motile, ciliated immature individual from which most colonies of stenolaemates and gymnolaemates are developed by metamorphosis and growth; in stenolaemates, the larva is incapable of feeding, and is developed by fission of brooded embryos; in gymnolaemates, the larva is either capable of feeding (planktotrophic) and generally developed without brooding, or incapable of feeding (lecithotrophic) and developed from a brooded embryo. (b) In phylactolaemates, a brief motile phase composed of one or more fully-developed polypides enclosed in a ciliated mantle, the product of sexual reproduction (Wood).

lateral skeletal projections. Skeletal structures in living chambers of stenolaemates that occupy positions opposite feeding organs; including hemisepta, hemiphragms, ring septa, mural spines, and skeletal cystiphragms.

lateral wall. One of pair of vertical walls of gymnolaemate zooid, elongated generally subparallel to principal direction of zooid growth to give length, and together with transverse wall, depth to body cavity of zooid; most commonly developed as exterior wall extending body of colony in series of lineally budded zooids; in cheilostomates, includes skeletal layers (Fig. 70,*1–3*).

lecithotrophic development. In gymnolaemates, production by brooding of naked ciliated larva lacking digestive tract and subsisting entirely on nutrient supplied by maternal zooid; larva has variable but short motile stage before metamorphosis.

lepralioid. Ascophoran cheilostomate in which autozooids have frontal shields formed as cryptocysts (Sandberg).

leptoblast. Floatoblast that germinates almost immediately after release from parent colony (Wood).

ligament. Muscle fibers embedded in collagen with tubular peritoneal envelope (Lutaud).

lineal growth. Formation of zooidal line by successive development of new zooids from proximal portion of bud by growth of transverse partitions separating zooids from proliferating distal portion of bud (Fig. 89,*1*).

lineal series. In gymnolaemates, single line of connected zooids sequentially related by direct asexual descent; bounded basally, laterally, and frontally by exterior walls of multizooidal origin, through which communication organs generally are formed to connect with zooids in adjacent lineal series (Fig. 76,*1b,2,3*; 77,*2*; 80,*2*).

lipid. Organic compound insoluble in water but soluble in organic solvents, and upon hydrolysis generally yielding fatty acids (Steen, 1971).

living chamber. In stenolaemates, outermost part of zooidal body cavity in which major organs are housed when lophophore is retracted (Fig. 37).

longitudinal direction. Direction parallel to colony growth direction.

longitudinal muscle layer. Inner of two thin muscle layers in body wall of phylactolaemates between peritoneum and epithelium (Fig. 132,*4,5*).

longitudinal partition. In gymnolaemates, common double wall consisting of contiguous lateral walls of adjacent zooidal series growing together and kept together by reciprocal pressure and adherence of cuticular and skeletal layers; formed by peripheral indentation of exterior wall at growing tip (Fig. 89,*2–4*).

longitudinal ridge. Short, vertical plate perpendicular to mesotheca in some bifoliate Fistuliporina; a multizooidal skeletal structure (Utgaard).

longitudinal section. (a) In stenolaemates, section oriented so that zooids are cut parallel to their entire length. (b) In gymnolaemates, section oriented so that zooids are cut parallel to length and perpendicular to width.

longitudinal wall. In Ptilodictyina, compound skeletal wall between laterally adjacent zooecia that is structurally continuous for variable distances in general colony growth direction (Fig. 228).

lophophoral fold. Part of polypidian vesicle from which lophophore is formed, by development at constriction between atrial bag and digestive lumen and infiltration of peritoneal layers (Fig. 91,*2*).

lophophore. Part of the body wall beginning at inner end of vestibule and ending at mouth, including tentacle sheath and tentacles; comprises the feeding organ of a feeding zooid and a specialized organ of some nonfeeding polymorphs.

lophophore neck. Elongate movable cylindrical structure formed by everted tentacle sheath carrying tentacle crown far beyond orifice of gymnolaemate autozooid.

lunarial core. In cystoporates, one central hyaline projection or several subcylindrical spinelike hyaline projections in the lunarium, which serve as centers of growth of the lunarial deposit (UTGAARD).

lunarial deposit. Synonym of lunarium in stenolaemates.

lunarium. In cystoporates, microstructurally distinct or thicker part of autozooecium or large monticular zooecium; on proximal or lateral side of zooecium and projecting above zooecial aperture or peristome as a hood; commonly with shorter transverse radius of curvature than remainder of zooecial wall (Fig. 144).

lunulitiform colony. In cheilostomates, free-living colony of discoidal to conical shape (SANDBERG).

macula. In stenolaemates, cluster of a few polymorphs, extrazooidal skeleton, or a combination; clusters more or less regularly spaced among feeding zooids, commonly forming prominences, less commonly flush or depressed areas on colony surfaces (Fig. 59).

main bud. Largest of three bud primordia occurring on every mature zooid in phylactolaemates; first to form new polypide (Fig. 135,*4*).

mandible. Orificial wall equivalent in avicularium of cheilostomates, opened and closed by greatly augmented divaricator and occlusor muscles (Fig. 70,*1c*; 71,*3*; 81,*3a*).

mantle. Ciliated fold of colony wall nearly covering one to four small polypides of sexually produced colony progenitor in phylactolaemates; lost after release from parent colony and settlement (WOOD).

marginal zooecium. In Ptilodictyina, zooecium of polymorph at lateral margins of bifoliate zoarium, commonly without endozone (Fig. 230,*2*).

massive colony. In stenolaemates, colony of irregular shape in which zooids bud from the encrusting colony wall, from vertical walls of other zooids, and in some taxa, from intracolony overgrowths.

maternal zooid. In gymnolaemates, autozooid with or without feeding ability which extrudes eggs, generally one at a time, into brood chamber through pore in lophophore wall below and between distal pair of tentacles (Fig. 72,*1–4*).

mature region. Synonym for exozone in stenolaemates.

median granular zone. In Ptilodictyina, middle layer of mesotheca with granular microstructure (Fig. 227–229).

median lamina. Synonym for median wall in stenolaemates.

median rod. In Ptilodictyina, long rodlike extrazooidal skeletal structure oriented longitudinally in median granular zone of mesotheca (Fig. 227, 231, 235).

median tubule. Synonym of median rod in stenolaemates.

median tubuli. In stenolaemates, aligned pustules or mural lacunae in laminated skeleton (BLAKE).

median wall. In stenolaemates, erect colony wall parallel to colony growth direction, interior and multizooidal, from which zooids bud back-to-back to form bifoliate colony (Fig. 30,*1,3a,4*).

membranous sac. In stenolaemates, membrane that surrounds digestive and reproductive system of zooid, dividing body cavity into two parts, the entosaccal cavity within sac, and the exosaccal cavity between sac and zooidal body wall (Fig. 2).

mesenchyme. All tissues derived from embryonic mesoderm, including connective tissues, parietal peritoneal network, funiculus, and muscles (LUTAUD).

mesocoel. Body cavity of second division of deuterostome body; assumed to correspond to cavity within and at base of tentacles in Bryozoa (STEEN, 1971).

mesoderm. Embryological term sometimes applied to peritoneum in bryozoans.

mesopore. Synonym of mesozooecium in stenolaemates (see mesozooid).

mesotheca. Synonym of median wall in stenolaemates.

mesozooid, mesozooecia. In Paleozoic stenolaemates, space-filling polymorph in exozone between feeding zooecia; closely tabulated out to distal end so that no room available for functional organs (Fig. 42,*3*).

metacoel. Body cavity of third division of deuterostome body; assumed to correspond to principal body cavity of zooid in Bryozoa (STEEN, 1971).

metamorphosis. An extensive external and internal reorganization of a larva to produce a founding zooid (ancestrula) or multiple founding zooids (primary zooids) of most stenolaemate and gymnolaemate colonies.

metapore. In Rhabdomesina, slender tubular opening in exozonal wall, oriented approximately perpendicular to zoarial surface (Fig. 262, 286). Metapores generally originate at base of exozone;

with diaphragms in few species.

microenvironmental variation. Differences within colony in morphology of zooids or extrazooidal parts, which cannot be inferred to express ontogeny, astogeny, or polymorphism; may be irregular or gradational and related to crowding, irregularities in substrate, encrustation, turbulence, breakage, boring, or sedimentation.

microvilli. Minute cylindrical processes forming striated or brush borders of epithelium (LUTAUD).

midray partition. Compound vertical wall along center of monticular ray or cluster of zooecia in cystoporates; may be multizooidal, extrazooidal, or both (Fig. 171,*1c*).

minutopore. Synonym of mural tubula in cystoporates.

mitochondrion. One of minute spherical, rod-shaped or filamentous organelles present in all cells and of primary importance in metabolic activities (STEEN, 1971).

mixed nerve. Nerve formed by conjunction of motor and sensory fibers (LUTAUD).

monila. In stenolaemates, concentric thickening of zooecial wall; resulting in beadlike appearance in longitudinal or transverse section (UTGAARD).

monoecious. Hermaphrodite; producing both female and male sex cells, as colonies and some zooids in Bryozoa (STEEN, 1971).

monomineralic skeleton. Cheilostomate zoarium having all skeleton present composed exclusively of either calcite or aragonite (Fig. 70,*1b*; 72).

monomorphic colony. Colony in which one kind of zooid occurs in the zone of astogenetic repetition.

monomorphic polypides. Independent organ systems of one morphologic kind throughout zone of astogenetic repetition in a phylactolaemate colony (WOOD).

monomorphic zooids. Zooids of one morphologic kind throughout zone of astogenetic repetition in a gymnolaemate colony.

monticule. In stenolaemates, generally applied to cluster of polymorphs which makes a prominence on colony surface; also synonym of macula in stenolaemates.

morular cell. Cell filled with cluster of refringent spherules, found in peritoneal network and in funicular strands (Fig. 87,*1*; 88,*3*).

mucopolysaccharide. One of a series of complex organic compounds consisting of mixtures of glycoproteins and polysaccharides (STEEN, 1971).

multifoliate colony. In stenolaemates, erect colony with more than three mesothecae radiating from colony or branch center, each mesotheca supporting feeding zooids in bifoliate pattern (UTGAARD).

multilaminate colony. In cheilostomates, encrusting, generally nodular colony, commonly with irregular erect protuberances, consisting of two or more superposed layers of zooids produced by frontal budding, intracolony overgrowth, or a combination (Fig. 13,*3,4*; 79,*2*).

multiserial budding. In gymnolaemates, budding in which lineal series are regularly and most commonly continuously in contact, zooids in adjacent series are regularly connected by communication organs through exterior walls, and adjacent series form more or less coordinated growing edge for major part of colony (Fig. 80,*1,2*).

multizooidal bud. Synonym of giant bud in gymnolaemates.

multizooidal budding zone. In cheilostomates, distal region of colony with laterally confluent body cavity, within which all vertical walls of zooids arise as interior walls to partition zooid body cavities from each other.

multizooidal layer. Noncellular, cuticular or skeletal layer of body wall continuous from zooid to zooid and into buds or budding zones in gymnolaemate colonies (Fig. 69,*1d*).

multizooidal part. Part of a colony, such as continuous wall layers of zooids, buds, or budding zones, which is grown outside existing zooidal boundaries but becomes part of zooids as colony develops.

mural lacuna. Synonym of pustule in stenolaemates.

mural spine. In stenolaemates, small skeletal spine extending into zooidal chamber from skeletal wall or diaphragm (Fig. 41,*1–4*).

mural style. In Ptilodictyina, small rodlike skeletal structure consisting of superposed flexed segments of zoarial laminae; rarely containing discontinuous minute core; may project as minute spine above zoarial surface (Fig. 227, 235).

mural tubula. In cystoporates, small calcite rod in wall cortex, generally perpendicular to wall and zooecial boundary (UTGAARD).

muscle layer. In phylactolaemates, one of two adjacent layers of muscles, longitudinal and circular, lying between epithelial and peritoneal layers of colony wall to function in lophophore protrusion (WOOD).

myocyte. Embryonic cell of mesodermal origin that develops into a muscle fiber.

myoepithelial cell. Contractile ectodermal cell with intracellular striated muscles (LUTAUD).

nanozooid. In tubuliporates, polymorph with single tentacle, muscular system, reduced alimentary canal, and membranous sac (Fig. 49,*5–7,9*).

nematopore. In tubuliporates, slender tubular kenozooecium opening on reverse side of zoarium with tubes directed in obliquely distal direction (BASSLER, 1953).

noncelluliferous side of colony. Synonym for reverse side of colony in stenolaemates.

obverse side of colony. Synonym for frontal side of colony in stenolaemates.

occlusor muscle. One of pair of bilaterally arranged muscles, in series with parietals, which traverse body cavity of gymnolaemate zooid to insert on operculum or mandible and function in closing (Fig.68,*1e*).

ontogenetic variation. Differences in morphology of zooids or extrazooidal parts arising from changes during course of zooidal or extrazooidal development; recognizable in stenolaemate or gymnolaemate colony as increases in size or complexity among zooids or extrazooidal parts along proximal gradient from growing extremities toward founding zooid or zooids.

opercular scar. Trace of cuticular operculum preserved in frontal closure of cheilostomate autozooid.

operculum. (a) Presumably hinged, skeletal covering of zooecial aperture in melicerititid tubuliporates (Fig. 36,*2–4*). (b) In gymnolaemates, distally directed, flaplike fold of orificial wall, reinforced by cuticular or calcified margins, axes, or general surface, which by means of attached occlusor muscles closes orifice when lophophore is retracted (Fig. 66,*2a*; 68,*1d*; 72,*1*).

opesia. (a) Opening defined by inner margin of cryptocyst, serving as passageway for lophophore in some anascan cheilostomates. (b) Membranous area of frontal wall defined by inner margin of cryptocyst (LUTAUD).

orifice. Porelike or puckered opening within, or slitlike opening on margin of orificial wall, through which the lophophore is protruded and retracted (Fig. 2).

orificial wall. (a) Exterior, terminal or subterminal zooidal wall that bears or defines orifice and is attached through orifice to the vestibular wall; it may be attached to or free from supporting zooidal walls (Fig. 2). (b) In stenolaemates, a single, membranous, exterior, generally terminal body wall that covers the skeletal aperture and includes a simple circular orifice through which the tentacles protrude (Fig. 25, 26). (c) In gymnolaemates, a body wall that defines or contains the orifice through which the lophophore of an autozooid is protruded; commonly a single flaplike fold, reinforced to form operculum, at or near distal end of a frontal wall with which it is structurally and developmentally continuous; in most cheilostomates, synonymous with operculum (Fig. 66,*2a,3*).

outer coelomic space. In free-walled stenolaemates, coelomic space between outer skeletal surface and exterior membranous wall (Fig. 25).

ovicell. (a) In cheilostomates, structure consisting of body walls, some or all of which are calcified, enclosing brood chamber; commonly placed at or near distal end of maternal zooid (Fig. 72,*1–3*). (b) Synonym of gonozooid in stenolaemates.

parallel fibrous ultrastructure. Synonym of planar spherulitic ultrastructure in cheilostomates (SANDBERG).

parietal muscle. (a) One of commonly multiple, usually bilaterally paired muscles that traverse body cavity of gymnolaemate zooid to insert on flexible part of frontal wall or floor of ascus, generally to function in hydrostatic system (Fig. 66,*2b*; 70,*1a*). (b) One of two sets of external muscles in anascan cheilostomate zooid (LUTAUD).

parietodepressor muscle. Parietal muscle (b) originating on lateral wall and inserting on flexible frontal wall, and therefore a synonym of parietal muscle (a) in gymnolaemates (Fig. 99).

parietodiaphragmatic muscle. Parietal muscle (b) originating on lateral wall and inserting on diaphragm, and therefore a synonym of diaphragmatic dilator muscle in gymnolaemates (Fig. 99).

parietovaginal muscle. One of muscular ligaments extending from muscle fibers of tentacle sheath to base of distal transverse wall of gymnolaemate autozooid (Fig. 99).

PAS test. Cytological technique by which location of polysaccharides within cell can be determined (STEEN, 1971).

paurostyle. Type of stylet in cryptostomates; core irregular, may be weakly differentiated rod of nonlaminated material; sheath laminae weakly deflected toward zoarial surface; sheath lamellar bundle narrow. Paurostyles usually smaller than acanthostyles (Fig. 219,*4*; 270,*1*).

periancestrular budding. In gymnolaemates, budding to produce zooids surrounding ancestrula, either radially from ancestrula, or more commonly by wrapping of distolaterally and proximolaterally budded lineal series around proximal end of ancestrula (Fig. 75,*5,7*; 79,*1*).

perigastric cavity. Synonym of principal body cavity of zooid.

perimetrical attachment organ. In stenolaemates, circular, collarlike membrane, attached at inner perimeter to tentacle sheath, at outer perimeter both to outer end of membranous sac and to skeletal body wall (Fig. 43,*1*; 45,*2–4,5b*).

peripharyngeal ganglion. Prolongation of cerebral ganglion around oral orifice, lying between basal canal of lophophore and epithelium of pharynx (Fig. 96; 100,*2*).

peripheral nerve. Any nerve serving extrapolypidian organs and wall (Fig. 100, 101).

peristome. (a) In stenolaemates, an outward tubular extension or rim of zooidal body wall beyond general surface of colony; either extension of interior vertical wall in free-walled colony (Fig. 39,*2*), or exterior frontal wall in fixed-walled colony (Fig. 28,*6*; 54,*3*). (b) In ascophoran cheilostomates, tubular outfold of body wall and contained body cavity together surrounding operculum and orifice at inner end, with calcified wall of exterior origin facing inward around orifice; can be produced entirely by one zooid or have components from adjacent zooids; opening of ascus can be inside or outside peristome (Fig. 67,*1d,e*; 68,*1d,2*; 82,*3a,b*).

peritoneum. (a) Inner cellular layer of body wall lining body cavity in both bud and fully developed zooid, continuing into tentacles and around digestive tract, and consisting of various cellular categories (Fig. 88,*2*). (b) In phylactolaemates, thin innermost layer of colony wall, bearing scattered tracts of cilia that drive coelomic fluid among polypides (Wood).

petraliiform colony. In cheilostomates, encrusting unilaminate colony loosely attached by protruding parts of basal walls of autozooids or by basally budded kenozooids (Sandberg).

phagocyte. Cell having ability to engulf particles (Steen, 1971).

pharynx. Strongly ciliated part of digestive tract into which mouth opens (Fig. 2; 4; 96; 131,*1*).

pinnate growth habit. In stenolaemates, erect colony in which lateral branches grow in same plane from opposite sides of main axial branch.

piptoblast. Statoblast lacking both annulus and marginal hooks, often adhering to the colony wall by small keel-like projections on the basal valve, not released from parent colony (Fig. 137,*1*).

pivotal bar. Complete skeletal rim on which fixed edge of mandible is hinged in some cheilostomate avicularia (Fig. 71,*2*; 84,*2*).

planar spherulitic ultrastructure. Skeletal ultrastructure consisting of essentially two-dimensional, wedge- or fan-shaped arrays of acicular or rarely flattened laths of calcite or aragonite, formed in cheilostomates as first calcification against cuticle in exterior walls (Fig. 111).

planktotrophic larva. In gymnolaemates, ciliated larva generally produced without brooding, possessing functional digestive tract, and having lengthy motile phase before metamorphosis.

pleated collar. See collar.

polyembryony. Synonym of embryonic fission in tubuliporates.

polymorph. In stenolaemates and gymnolaemates, a zooid that differs distinctly in morphology and function from ordinary feeding zooids at same stage of ontogeny and in same asexual generation within a colony; may be a feeding or nonfeeding zooid specialized to perform sexual, supportive, connective, cleaning, defensive, or other functions; minimally includes body cavity and enclosing body walls.

polymorphic colony. Colony with more than one kind of zooid in zone of repetition (Utgaard).

polymorphism. Repeated, discontinuous variation in morphology of zooids in colony; may be recognized in many stenolaemate and gymnolaemate colonies in the same generation of a zone of astogenetic change or among any zooids at the same ontogenetic stage in a zone of astogenetic repetition.

polypide. (a) Feeding organ of zooid, internally budded and periodically renewed from cellular layers of body wall; includes lophophore and digestive tract (pharynx, esophagus, cardia, stomach and caecum, pylorus, rectum), tentacle sheath, and cerebral ganglion (Fig. 91). (b) Major organs of autozooid contained in membranous sac of tubuliporate bryozoan (Utgaard). (c) In phylactolaemates, independently moving organ system performing major physiological functions, suspended with other polypides in common vessel of coelomic fluid (Fig. 133,*4*).

polypidian bud. Newly developing digestive tract and feeding organs, originating as cluster of epithelial cells on distal side of growing transverse partition to invaginate into body cavity, together with surrounding subepithelial layers, to form first polypide of developing zooid (Fig. 90,*4*).

polypidian vesicle. Double-layered polypidian bud, with central cavity lined by undifferentiated internal epithelium formed early in development of polypide (Fig. 92,*1*).

polysaccharide. One of a group of complex carbohydrates, which upon hydrolysis yields more than two molecules of simple sugars (Steen, 1971).

pore chamber. Part of body cavity of gymnolaemate zooid partly separated by interior wall continuous with portion of zooidal wall containing communication organ (Fig. 69,*1f*; 76,*1b*).

pore plate. Part of communication organ in gymnolaemates formed as thin calcareous or cuticular part of body wall of zooid or extrazooidal part, bearing one or more minute pores through which cells of special form project; grown as interior wall, but can be continuous with, and provide communication through either interior or exterior walls (Fig. 68,*1d,e*).

postmandibular area. Membranous part of frontal wall equivalent of cheilostomate avicularium, on which mandibular divaricator muscles insert; commonly separated from beak by partial or complete skeletal rim on which fixed edge of mandible is hinged (Fig. 71,*3*; 81,*3a*).

primary bud. One of buds arising as hollow outward expansions of cellular layers from distal and lateral areas of body walls of ancestrula (Lutaud).

primary direction of encrusting growth. In stenolaemates, general direction along substrate of encrusting growth of ancestrula and first generations of colony (Fig. 25, 26, right of disc; also see Fig. 52,*2*).

primary wedge of encrusting zooids. In stenolaemates, ancestrula and first generations of colony that all grow in same general direction along substrate (Fig. 52,*2*).

primary zone of astogenetic change. Zone of astogenetic change forming proximal part of colony, beginning with founding zooid or zooids (ancestrula, statoblast ancestrula, or multiple primary zooids), commonly continuing distally through a few generations, and followed distally by primary zone of astogenetic repetition (see zone of astogenetic change).

primary zone of astogenetic repetition. Zone of astogenetic repetition following primary zone of astogenetic change distally and commonly consisting of numerous generations of zooids (see zone of astogenetic repetition).

primary zooid. Ancestrula, or one of two or more simultaneously partitioned zooids formed after metamorphosis of larva to found colony in some cheilostomates; commonly smaller and otherwise morphologically different from subsequently budded zooids (Fig. 79,*4*).

primordium. First accumulation of cells comprising identifiable beginning of developing organ or structure (STEEN, 1971) (compare blastema).

principal body cavity. In gymnolaemate autozooid, body cavity generally enclosed by basal, vertical, and orificial walls, and frontal wall, cryptocyst (and adjacent inner cellular layer), or ascus floor; occupied almost fully by retracted organs and muscles, except in degenerated stages (Fig. 66,*3*; 68,*1b*; 69,*1b*).

protocoel. Body cavity of first, most anterior of three divisions of deuterostome body; assumed to correspond to cavity of epistome in phylactolaemates (STEEN, 1971).

proximal bud. In gymnolaemates, bud arising from proximal side of vertical wall of parent zooid to initiate growth in direction opposite to principal growth direction of parent, as in repair of injury (Fig. 76,*1a*).

proximal direction. Direction opposite to distal, toward founding zooid or zooids of colony.

proximal hemiseptum. In stenolaemates, hemiseptum projecting from proximal zooidal wall.

proximolateral bud. In gymnolaemates, bud arising from proximolateral side of vertical wall of parent zooid to initiate growth in direction greatly diverging from principal growth direction of parent, as in parts of encrusting colonies (Fig. 75,*5,6*).

pseudocoel. Body cavity lined at least in part by epidermis.

pseudopore. Pore that penetrates all or part of skeletal layer but not cuticle in many exterior walls (Fig. 26; 35,*4*).

pustule. In stenolaemates, small equidimensional skeletal structure consisting of crinkled segments of skeletal laminae (Fig. 246,*1a*).

pylorus. Ciliated part of digestive tract into which stomach portion of cardia opens and in which remnants of digestion are agglutinated with mucins into a whirling mass (Fig. 2; 95,*1*).

ramose colony. Synonym of dendroid colony in stenolaemates.

range of zooids. Zooids aligned in direction of colony growth.

range partition. In Ptilodictyina, elongate structure of extrazooidal stereom between zooecial ranges (Fig. 229,*2*; 236,*1,2*).

range wall. In cystoporates, wall parallel to colony growth direction between ranges of zooids; discontinuous or relatively continuous; extrazooidal or partly extrazooidal and partly multizooidal in origin (Fig. 209; 210,*1*).

ray. In cystoporates, cluster of monticular zooecia radiating from center of star-shaped monticule (Fig. 171,*1c*).

rectal pouch. Part of digestive tract into which pylorus opens, and which ends at anus (Fig. 91).

rectum. In phylactolaemates, so-called intestine in which fecal pellets are formed and passed through anus (Fig. 131,*1*).

regenerative budding. In cheilostomates, budding from within zooecial walls of broken zooid (Fig. 76,*1a*).

retractor muscle. (a) One or more bundles of muscle fibers originating on basal or vertical zooidal walls or on colony wall, and inserting on base of lophophore and pharyngeal or cardiac regions of digestive tract; retracts tentacles and introverts tentacle sheath (Fig. 2–4). (b) In phylactolaemates, two bundles of muscle fibers originating on colony wall and inserting on polypide at various points from esophagus to lophophore (Fig. 131,*1*; 133,*4*).

reverse side of colony. In stenolaemates, back side of erect unilaminate colony; side opposite to that on which feeding zooids open (Fig. 28,6, right side of colony).

rigidly erect colony. In cheilostomates, erect colony in which zooids and any extrazooidal parts present are well calcified, generally increasingly so toward proximal encrusting base, thus permitting little motion in moving water (Fig. 13,*1*; 14,*2*; 83,*1*).

ring septum. In stenolaemates, centrally perforated skeletal diaphragm in zooidal living chamber (Fig. 40,*2*).

rosette. Cellular apparatus of communication organs of the funicular system, made of club-shaped cells across pores (LUTAUD).

sagittal section. Median longitudinal section in gymnolaemates (LUTAUD).

screw dislocation. Spiral growth steps induced by lattice defects in thin rhombic or hexagonal crystals that make up lamellar skeletal unit; in cheilostomates, thus far seen only in calcite skeletons (Fig. 102,*4–6*; 103,*3,4*).

secondary direction of encrusting growth. In stenolaemates, general direction of growth of wedge of zooids along substrate opposite to that of ancestrula and first generations (see left side of Fig. 25).

secondary wedge of encrusting zooids. In stenolaemates, wedge of zooids that buds from downfold of encrusting colony wall resting on upper surface of primary wedge, and that grows in general direction opposite to primary direction of colony growth (see Fig. 25, left side).

septula. Synonym of communication organ.

septum. (a) In stenolaemates, newly-formed compound, interior, body wall of bud (UTGAARD). (b) Synonym of canaliculus in Actinotrypidae. (c) Synonym of interior wall (LUTAUD).

sessoblast. Statoblast cemented through colony wall to substrate, usually with rudimentary annulus, but lacking marginal hooks or spines (Fig. 137,*2*).

sexual zooid. In gymnolaemates, autozooid in which eggs, sperm, or both are developed, with or without skeletal expression of this function in cheilostomates; can have or lack feeding ability (Fig. 69,*1c,2*).

sheath laminae. In stenolaemates, one of the two structural elements forming stylets; sheath laminae concentrically enclose the core of a stylet and are directed toward the zoarial surface. Sheath laminae are continuous with those of the remainder of zoarium, differing only in orientation (BLAKE).

simple skeletal wall. In stenolaemates, skeletal wall calcified on edges and one side only, either exterior or interior.

simple-walled colony. Synonym of fixed-walled colony in stenolaemates.

single-walled colony. Synonym of fixed-walled colony in stenolaemates.

sinus. In stenolaemates, groove on either side of keel in zooid wall in recumbent part of endozone, which accommodates inner end of next younger zooid in rhombic zooidal arrangement (Fig. 56).

skeleton. In stenolaemates and cheilostomates, calcareous layers of body wall and any connected calcareous structures deposited by epidermis on its external side opposite peritoneum and body cavity, and therefore exoskeletal throughout zoarium.

soft-part polymorph. Cheilostomate zooid differing from ordinary feeding zooids in having sexual features, membranous structures for brooding embryos, or elongate tentacles for producing exhalant water currents, which are apparently not reflected in differences in skeletal parts.

solid ramose colony. Synonym of dendroid colony in stenolaemates.

spherulitic ultrastructure. In cheilostomates, group of skeletal ultrastructures consisting essentially of either two-dimensional wedge- or fan-shaped arrays oriented parallel to wall surfaces (planar spherulitic ultrastructure), or three-dimensional conical or palisade arrays oriented transverse to wall surfaces (transverse spherulitic ultrastructure); arrays of acicular to bladelike or blocky calcite or aragonite crystals (Fig. 111; 113,*1–3*).

spine. In cheilostomates, tubular to flattened outpocketing of calcified exterior body wall and contained body cavity, commonly in groups overarching uncalcified part of frontal wall of autozooid to form costal shield, or margining orificial wall distally and laterally to form peristomelike structure (Fig. 72,*2,3*).

spine base. In cheilostomates, collarlike skeletal remnant of attached end of spine (Fig. 77,*2*).

statoblast. Free encapsulated bud in discoid envelope of chitin, with large yolky cells and organized germinal tissue capable of giving rise to polypide to start most phylactolaemate colonies; formed on funiculus of parent zooid by migration of epithelial cells (Fig. 135,*3*).

statoblast ancestrula. First zooid produced by germination of statoblast to found new phylactolaemate colony (Fig. 135,*3*).

stereom. In stenolaemates, extrazooidal skeletal deposits, consisting of either dense skeleton or vesicle roof skeleton (Fig. 201,*1b*; 205).

stolon. In stoloniferous ctenostomates, tubular kenozooids or extensions of autozooids from which autozooids are budded.

stoloniferan. Ctenostomate in which one or more autozooids are budded from a single kenozooid generally of elongate tubular form (Fig. 85,*3*).

stomodaeal cavity. Anterior part of gut lined with ectoderm infolded to form mouth (STEEN, 1971).

striae. In Ptilodictyina, small skeletal ridges consisting of tightly arched skeletal laminae projecting above general zoarial surface (Fig. 224,*2a*).

style. (a) In stenolaemates, general term for rodlike skeletal structure approximately parallel to adjacent zooecia, which forms spinose projection on zoarial surface (Fig. 51,*1–8*). (b) Synonym of stylet.

stylet. (a) In stenolaemates, any member of class of rodlike skeletal structures, oriented approximately perpendicular to zoarial surface and parallel to zooecia (BLAKE). (b) Synonym of style.

subcolony. In stenolaemates, grouping within colony of zooids and any extrazooidal structures, which may or may not be skeletally identifiable, but which carries on most or all functions of whole colony (Fig. 59,*1–3*).

subsequent zone of astogenetic change. Zone of astogenetic change following primary or subsequent zone of astogenetic repetition distally; develops asexually from zone of astogenetic repetition and therefore lacks ancestrula (see zone of astogenetic change).

subsequent zone of astogenetic repetition. Zone of astogenetic repetition following subsequent zone of astogenetic change distally (see zone of astogenetic repetition).

superficial layer of skeleton. One of commonly multiple layers successively deposited on frontal side of advancing initial skeletal layer of cryptocyst or umbonuloid shield in cheilostomate zooid, commonly increasing thickness of frontal shield several-fold; commonly different in microstructure or mineral composition from initial layer (Fig. 67,*1c*; 68,*1d*).

superior hemiseptum. Synonym of proximal hemiseptum in stenolaemates (Karklins).

supporting walls. Body walls of zooids that support orificial walls; includes basal walls, vertical walls (lateral and transverse walls of gymnolaemates), and frontal walls.

tangential section. In stenolaemates, section just under surface of colony oriented so that zooids are cut at approximate right angles near outer ends.

tentacle. One of a row of tubular extensions of body wall and contained body cavity that surrounds the mouth in a circular or bilobed pattern; in feeding zooids, ciliated to produce water currents that concentrate food particles near mouth (Fig. 2, 4).

tentacle crown. Tentacles of a zooid in expanded feeding position.

tentacle sheath. Part of body wall that is introverted to enclose tentacles in their retracted position and everted to support tentacles in their protruded position; boundary with vestibular wall is generally the sphincter muscle, forming diaphragm in gymnolaemates (Fig. 2–4).

tentacular atrium. Cavity enclosed by retracted tentacle sheath, containing tentacles (Fig. 92,*2*).

tergopore. Type of kenozooecium on reverse side of zoarium, with polygonal aperture in some tubuliporates (Bassler, 1953).

terminal diaphragm. In stenolaemates, membranous or calcified diaphragm near zooecial aperture that seals living chamber from surrounding environment. Calcified terminal diaphragms are either exterior (tubuliporates and ceramoporines) or interior (most Paleozoic stenolaemates) (see Fig. 27; 34; 42; 43,*3*).

transverse partition. Interior wall separating successive zooids in zooidal lines, formed from invaginated fold of cellular layers in middle of which skeletal lamina is secreted (Fig. 90,*1*).

transverse section. (a) In stenolaemates, section oriented so that recumbent or inner ends of zooids are cut transversely. (b) In gymnolaemates, section oriented so that zooids are cut parallel to width and perpendicular to length.

transverse spherulitic ultrastructure. In cheilostomates, skeletal ultrastructure consisting of three-dimensional conical or palisade arrays of acicular to bladelike or blocky calcite or aragonite crystals oriented transverse to wall surfaces (Fig. 113,*1–3*).

transverse wall. One of pair of vertical walls of gymnolaemate zooid, oriented generally subperpendicular to principal direction of zooid growth; together with lateral walls gives depth to body cavity of zooid; most commonly developed at least in part as interior wall completely separating body cavities of zooids within lineal series; in cheilostomates, includes skeletal layers (Fig. 68,*1,2*).

trifid nerve. Three-branched peripheral motor nerve, with branches to insertion of retractor muscle, esophagus, and along tentacle sheath to direct nerve (Fig. 100,*2*).

trifoliate colony. In stenolaemates, erect colony with three mesothecae radiating from colony or branch center, each supporting feeding zooids in bifoliate pattern (Utgaard).

tunnel. Elevated, branched anastomosing ridge on colony surface in Rhinoporidae; a curved roof covers branched tunnel-like space that possibly was brood space (Fig. 192).

umbonuloid. Ascophoran cheilostomate in which autozooids have frontal shields formed by calcification on basal side of epifrontal fold (umbonuloid shield) (Sandberg).

umbonuloid shield. Continuous frontal shield or part of frontal shield of cheilostomate zooid, formed by calcification of inner wall of exterior double-walled fold and contained body cavity, overarching flexible part of frontal wall from its proximal and lateral margins to face flexible part of frontal wall; attached to vertical walls by interior wall segments pierced by pores of marginal communication organs connecting hypostegal coelom to underlying principal body cavity of zooid, and in some by additional uncalcified, cuticle-covered openings (Fig. 68,*1,2*; 70,*1,3*).

unilaminate colony. Encrusting or erect colony consisting of a single layer of zooids opening in approximately the same direction.

uniserial budding. In gymnolaemates, budding in which lineal series rarely and irregularly come in contact, communication organs are absent or rare between zooids in adjacent series, and each lineal series forms more or less independent growing tip of colony (Fig. 76,*1–5*; 77,*1,2*).

uniserial colony. In stenolaemates, encrusting colony in which zooids bud in single row in direct parent-descendant relationship (Fig. 31,*1,2*).

unisexual. Zooid or colony that produces either male or female gametes but not both.

vertical plate. In cystoporates, platelike compound wall, generally parallel to colony growth direction; commonly extrazooidal but may be in part multizooidal (Fig. 196,*2*).

vertical wall. (a) One of zooidal supporting walls that is entirely or in part at high angle to basal and orificial walls, giving depth, length, or both to zooidal body cavity; can be exterior, interior, or a combination, and if interior, complete or incomplete (Fig. 1, 10, 11). (b) In gymnolaemates, a lateral or transverse wall of zooid.

vesicle. In Fistuliporina, blisterlike, boxlike, or less commonly tubelike element of extrazooidal vesicular tissue bounded by calcified walls and roof; space in vesicle presumably contained no soft tissue (Utgaard).

vesicle roof. In Fistuliporina, flat or curved skeletal component of vesicle on distal or frontal side of a vesicle; simple interior wall (Utgaard).

vesicle wall. Straight to curved lateral sides of vesicle, generally simple, interior wall, may be compound in a few genera (Utgaard).

vesicular cell. Cell occupied by voluminous vesicular inclusion, found in peritoneal network and in funicular strands, and partly consumed in development of digestive tract and feeding organs (Fig. 87,*1*; 88,*4*).

vesicular tissue. Extrazooidal skeletal structures in Fistuliporina composed of adjacent and superimposed vesicles (Fig. 143).

vestibular dilator muscle. One of commonly multiple, radially arranged muscles that traverse body cavity of gymnolaemate autozooid to insert on vestibular wall.

vestibular wall. That part of the body wall surrounding the vestibule and connecting tentacle sheath to orificial wall (Fig. 2, 3).

vestibule. (a) Variable space through which lophophore passes in protruding and retracting (Fig. 2; 3; 132,*2*). (b) In cryptostomates, that part of zooecial chamber between aperture and either hemisepta or boundary between exozone and endozone.

vibraculum. Type of avicularium in cheilostomates, with mandible elongated beyond beak and commonly slung between asymmetrical condyles (Lutaud).

vicarious polymorph. In gymnolaemates, polymorph intercalated in budding series to communicate with two or more zooids, in space subequal to or larger than those occupied by ordinary feeding zooids (Fig. 81,*3,4*).

zoarium. In stenolaemates and cheilostomates, the skeleton of a colony, consisting of zooecia together with any connected multizooidal and extrazooidal skeleton.

zone of astogenetic change. Part of colony in which zooids show morphologic differences from generation to generation in more or less uniform progression distally, ending with pattern capable of endless repetition of one or more kinds of zooids.

zone of astogenetic repetition. Part of colony in which zooids show one or more repeated morphologies from generation to generation distally in pattern capable of endless repetition.

zooecial compartment. Body cavity of zooid (Lutaud).

zooecial lining. (a) In stenolaemates, distinct skeletal layer lining zooidal chamber, generally laminated, with laminae parallel to chamber surfaces. (b) In cheilostomates, skeletal layer structurally continuous around inner surface of vertical and commonly basal walls of zooid.

zooecial wall. (a) Skeletal wall of zooid. (b) Body wall of zooid including skeletal layers and underlying soft cellular layers (Lutaud).

zooecium. (a) In stenolaemates and cheilostomates, the skeleton of a zooid, consisting of calcareous layers of zooidal walls and any connected intrazooidal calcareous structures. (b) In phylactolaemates, consisting of any nonliving secreted parts of the body wall (Wood).

zooid. (a) One of the physically connected, asexually replicated morphologic units which, together with multizooidal parts and any extrazooidal parts present, compose a colony; it may separately perform major colony functions with systems of organs or other internally organized structures, much like a solitary animal, or it may be a polymorph consisting minimally of body cavity and enclosing body walls. (b) In phylactolaemates, polypide and its adjacent colony wall (Fig. 133,*4*).

zooidal autonomy. Extent to which zooids are comparable morphologically to solitary animals.

zooidal bend. In stenolaemates, region of zooid where growth direction turns outward to colony surface; in outer endozone or inner exozone (Utgaard).

zooidal boundary. (a) Outermost extent of body walls of zooid. (b) In stenolaemates, boundary generally referred to along vertical walls between zooid and contiguous zooids or contiguous extrazooidal structures; most commonly indicated by abutting laminae from contiguous walls, organic-rich partitions, granular zones, or centers of bilateral symmetry where boundaries not indicated microstructurally (Fig. 2). (c) In gymnolaemates, boundary between zooid and contiguous zooids, extrazooidal parts, or the environment, especially along vertical walls; most commonly marked by combination of outermost cuticles of contiguous exterior lateral walls and parts of transverse walls and microstructural differences or centers of symmetry in interior parts of transverse walls.

zooidal control. Process influencing growth and functions of zooids to make them comparable morphologically and functionally to solitary animals in spite of membership in colony.

zooidal pattern. In stenolaemates, three-dimensional shapes and interrelationships of zooids within colony.

THE ORDERS CYSTOPORATA AND CRYPTOSTOMATA

OUTLINE OF CLASSIFICATION

The following outline of the orders Cystoporata and Cryptostomata summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each suprageneric group. A single number refers to genera; where two numbers are given, the second indicates subgenera in addition to the nominate subgenus.

Order Cystoporata, 90. *Ord.-Perm.*
Suborder Ceramoporina, 10. *M.Ord.-L.Dev.*
  Ceramoporidae, 10. *M.Ord.-L.Dev.*
Suborder Fistuliporina, 80. *Ord.-Perm.*
  Anolotichiidae, 7. *Ord., M.Dev.*
  Xenotrypidae, 2. *?L.Ord., M.Ord.-M.Sil.*
  Constellariidae, 2. *M.Ord.-U.Ord., ?L.Sil.*
  Fistuliporidae, 29. *Sil.-Perm.*
  Rhinoporidae, 2. *L.Sil.-M.Sil.*
  Botrylloporidae, 1. *M.Dev.*
  Actinotrypidae, 3. *L.Miss., Perm.*
  Hexagonellidae, 14. *L.Dev.-U.Perm.*
  Cystodictyonidae, 11. *M.Dev.-L.Perm.*
  Etherellidae, 2. *Perm.*
  Goniocladiidae, 7. *Miss.-Perm.*

Order Cryptostomata, 78; 2. *Ord.-Perm.*
Suborder Ptilodictyina, 38. *Ord.-Perm.*
  Ptilodictyidae, 8. *M.Ord.-L.Dev.*
  Escharoporidae, 6. *M.Ord.-L.Sil.*
  Intraporidae, 2. *M.Dev.-U.Dev.*
  Phragmopheridae, 1. *U.Carb.*
  Rhinidictyidae, 10. *L.Ord.-M.Sil.*
  Stictoporellidae, 3. *L.Ord.-M.Sil.*
  Virgatellidae, 2. *M.Ord.*
  Family Uncertain, 6.
Suborder Uncertain, 1.
Suborder Rhabdomesima, 39; 2. *Ord.-Perm.*
  Arthrostylidae, 17. *L.Ord.-L.Perm.*
  Rhabdomesidae, 7. *U.Sil.-U.Perm.*
  Rhomboporidae, 6; 1. *?U.Dev., L.Miss.-U.Perm.*
  Bactroporidae, 1. *M.Dev.*
  Nikiforovellidae, 4. *?L.Dev., M.Dev.-U.Perm.*
  Hyphasmoporidae, 3; 1. *L.Carb.-U.Perm.*
  Family Uncertain, 1.

RANGES OF TAXA

The stratigraphic distribution of orders, superfamilies, and families of Bryozoa recognized in this volume of the *Treatise* is indicated graphically in Table 4, which follows (compiled by JACK D. KEIM).

TABLE 4. *Stratigraphic Distribution of the Cystoporata and Cryptostomata*

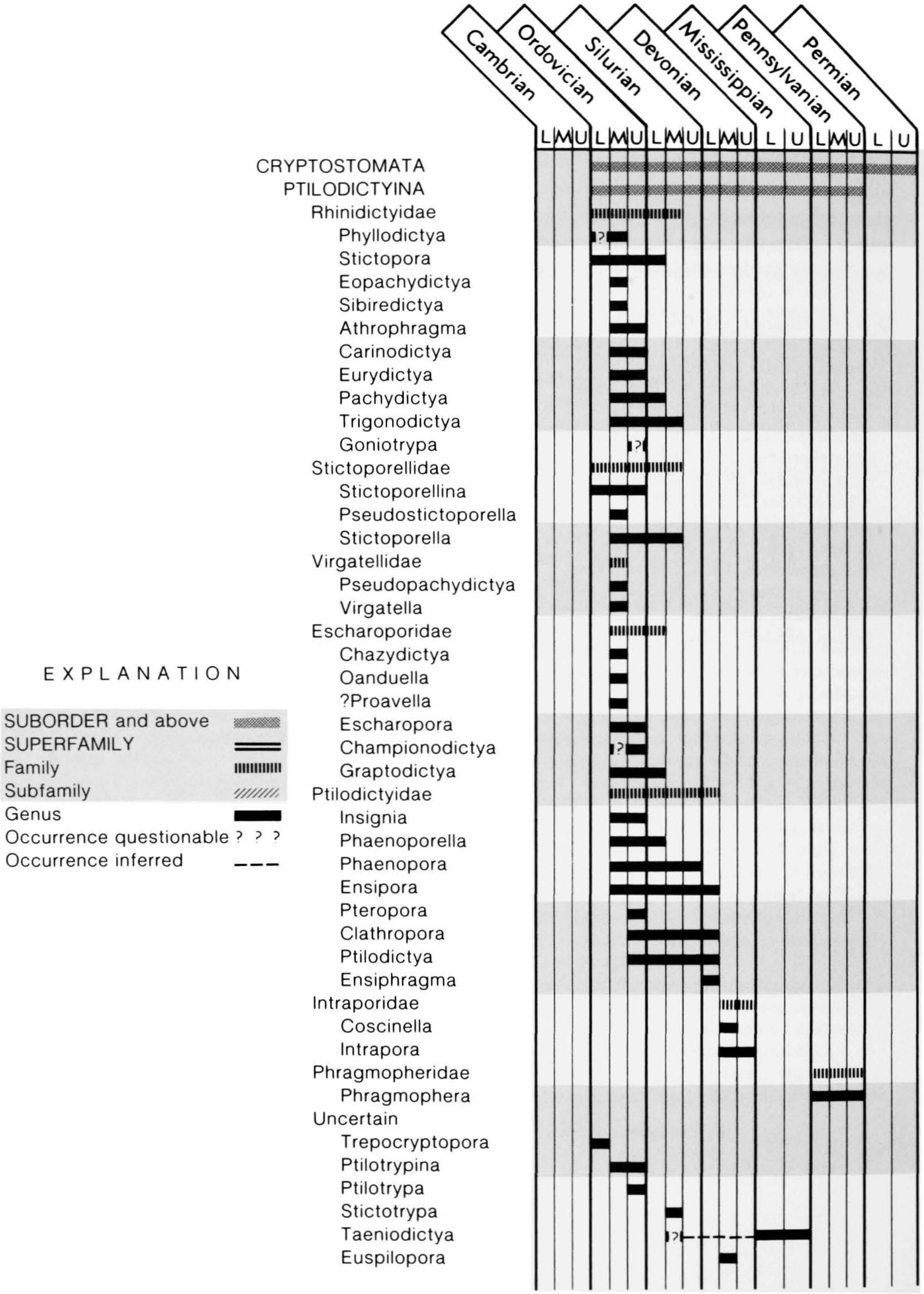


TABLE 4. (*Continued.*)

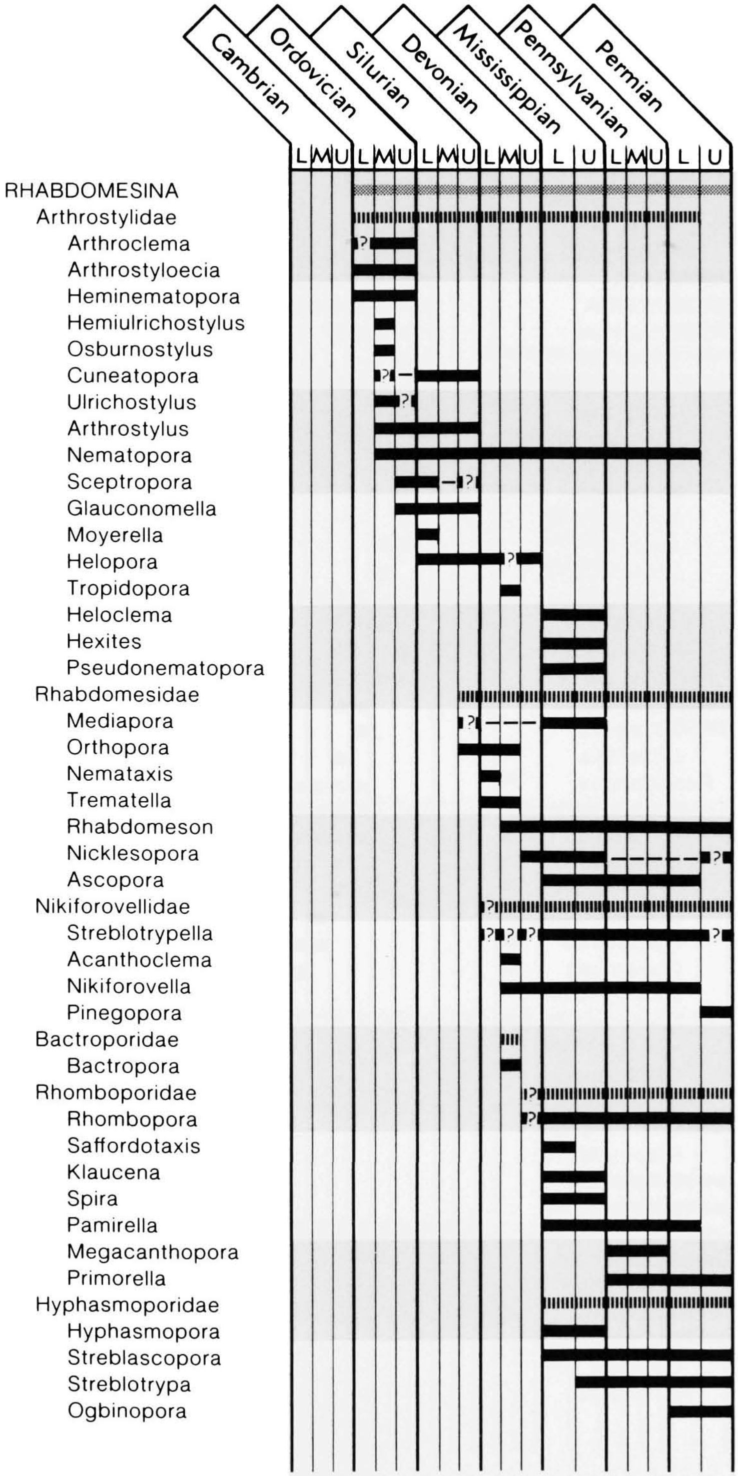


TABLE 4. (*Continued.*)

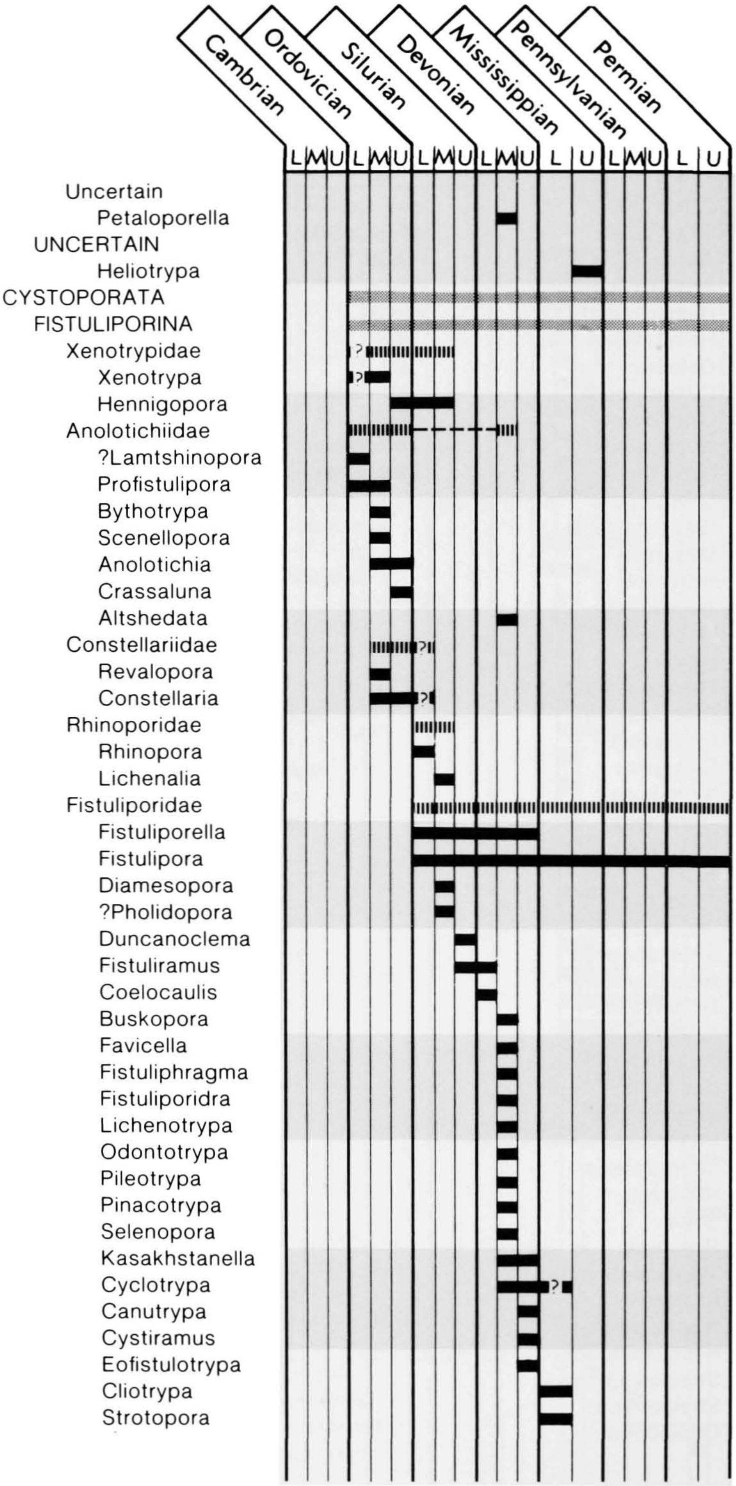
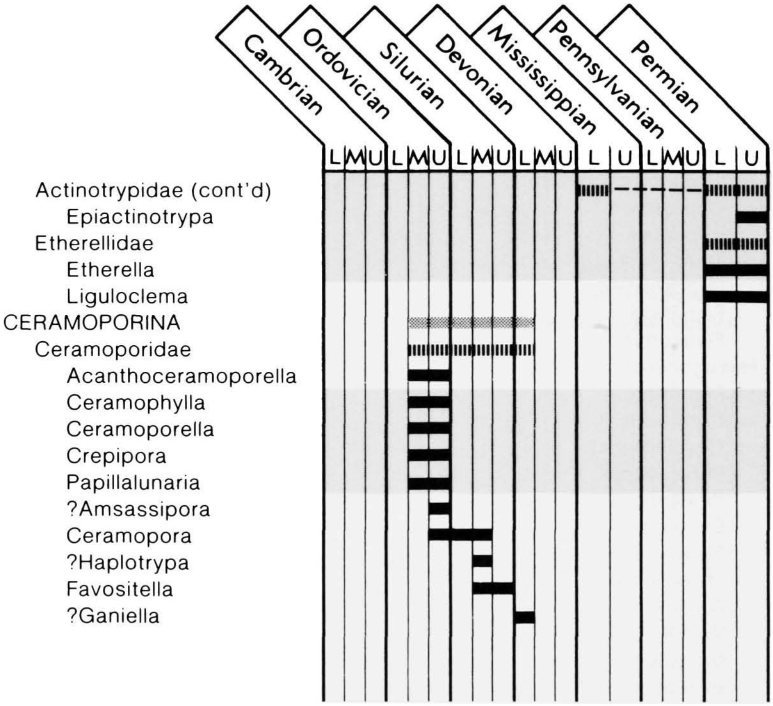


TABLE 4. (*Continued.*)

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U
Fistuliporidae (cont'd)							┅	┅	┅	┅	┅	┅	┅	┅	┅	┅	┅	┅	┅
Cheilotrypa													━	━					
Eridopora														━					
Metelipora															━?	━?	━?	━	
Dybowskiella																		━	━
Fistulocladia																		━	━
Fistulotrypa																		━	━
Hexagonellidae										┅	┅	┅	┅	┅	┅	┅	┅	┅	┅
Prismopora										━	━	━	━	━	━	━	━	━	━
Ceramella											━								
Coscinotrypa											━								
Phractopora											━								
Scalaripora											━								
Evactinopora													━	━					
Fistulamina													━	━					
Meekopora													━	━					
Glyptopora														━					
Volgia															━	━	━		
Meekoporella																	━	━	
Evactinostella																		━	
Coscinium																		━	━
Hexagonella																		━	━
Botrylloporidae											┅								
Botryllopora											━								
Cystodictyonidae											┅	┅	┅	┅	┅	┅	┅	┅	
Acrogenia											━								
Ptilocella											━								
Semiopora											━								
Stictocella											━								
Taeniopora											━								
Thamnotrypa											━								
Dichotrypa											━?	–	━	━					
Cystodictya											━	━	━	━					
Sulcoretepora													━	━					
Lophoclema															━	━	━		
Filiramoporina																		━	
Goniocladiidae													┅	┅	┅	┅	┅	┅	┅
Goniocladiella													━	━					
Aetomacladia													━	━	━	━	━	━	━
Goniocladia													━	━	━	━	━	━	━
Ramiporalia													━	━	━	━	━	━	━
Ramiporella													━?━	━?━	━	━	━	━	━
Ramiporidra													━?━	━?━	━	━	━	━	━
Ramipora																		━	━
Actinotrypidae													┅	–	–	–	–	┅	┅
Actinotrypa													━						
Actinotrypella																		━	

TABLE 4. (*Continued.*)



PALEOBIOLOGY AND TAXONOMY OF THE ORDER CYSTOPORATA

By John Utgaard

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GENERAL MORPHOLOGY

Cystoporates are extinct, marine, double-walled bryozoans displaying a wide variety of growth habits and belonging to the class Stenolaemata. They typically have long conical or tubular autozooecia with basal diaphragms, although some have short autozooecia without diaphragms. The growth direction of the autozooecia changes and diverges from the growth direction of the colony, producing an endozone and an exozone. Basal layers, where observed, are of simple construction (Fig. 142) and are exterior walls that presumably were covered by an outermost layer of cuticle. Interior vertical zooecial walls are compound. However, in many genera of the suborder Fistuliporina, particularly in the Fistuliporidae, the lateral and distal sides of an autozooecium are composed of superimposed vertical parts of extrazooidal vesicular tissue (vesicle walls), so that part of the autozooid is bounded by a simple interior wall (Fig. 143, 153). This is a rare, if not unique, feature in double-walled bryozoans.

Another unusual feature, found in most Fistuliporina, is the partial to complete isolation by extrazooidal vesicular tissue of new autozooecia budded on either the basal layer or mesotheca. The presence of these new autozooids, isolated from their neighbors, suggests colony-wide control of budding rather than direct parent-daughter autozooecial budding. In many fistuliporines, new autozooecia are budded on top of extrazooidal vesicular tissue in the exozone.

Cystoporates in the suborder Fistuliporina are characterized by large amounts of extrazooidal vesicular tissue (=cystopores) and stereom. Vesicular tissue is almost invariably composed of simple interior skeletal deposits (Fig. 143) secreted only from the upper or outer side. Available evidence suggests that vesicular tissue housed no viable soft parts and served as a buttress between isolated or partly isolated zooecia. Stereom is fairly dense skeletal material produced by essentially continuous deposition or contiguous deposit of vesicle roofs without intervening vesicle walls or chambers.

Most genera in the Cystoporata have a lunarium, which projects above the general zoarial surface (Fig. 144) and above the rim or the peristome, if present, of the autozooecial orifice. The lunarium consists of a microstructurally distinct or thicker deposit developed throughout the exozone of the autozooecium. It is located on the proximal side of each autozooecium or rotated to the left or right lateral side (see Fig. 205). Lunaria are known in such post-Paleozoic, double-walled tubuliporates as *Lichenopora,* in which the membranous sac occupies the proximal half of the living chamber, next to the lunarium.

Most genera of the suborder Ceramoporina evidently had two means of interzooidal communication, via coelomic fluid in the hypostegal coelom, as in other double-walled tubular bryozoans, and via communication pores in the compound skeletal zooecial walls (Fig. 142). Pores in the zooecial walls apparently are restricted to ceramoporines among Paleozoic tubular bryozoans. Contrary to many published reports, I have seen no undoubted communication pores in members of the suborder Fistuliporina. Evidently their only means of interzooidal communication was via coelomic fluid in the hypostegal coelom.

Some genera of the Fistuliporina, partic-

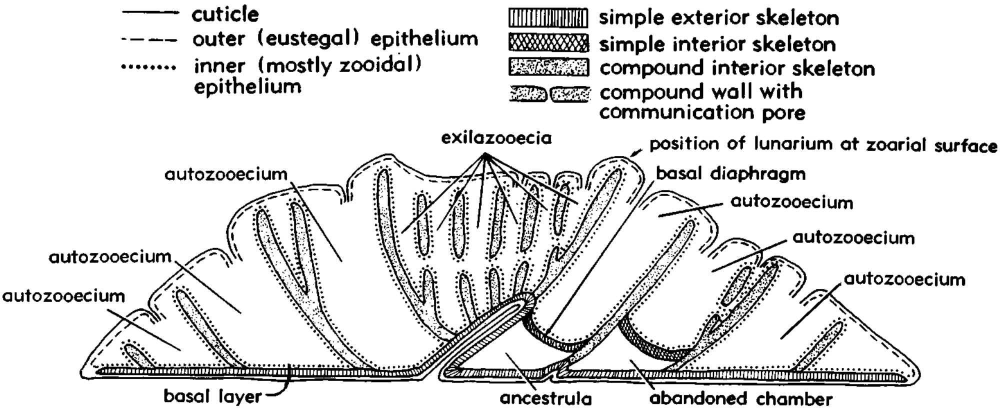

FIG. 142. Cystoporate morphology. Longitudinal section through hypothetical double-walled ceramoporine (after Utgaard, 1973). Simple skeletal walls include the basal layer and basal diaphragms in autozooecia. The basal layer folds back upon itself on the left side of the ancestrula. Some exilazooecia (right-center) are shown with a terminal-vestibular membrane, as if they had an extrusible polypide; others (left-center) are shown with an imperforate terminal membrane. Communication pores are shown in exilazooecial walls. Autozooecial walls also have communication pores, but the section is through the lunarial deposit on the proximal side of each zooecium, and this deposit is imperforate.

ularly the cystodictyonids, etherellids and goniocladiids, are monomorphic. Many fistuliporines have polymorphic colonies and most are dimorphic, with larger monticular zooecia in addition to the normal autozooecia. A few fistuliporines have intermonticular autozooecia with expanded subspherical outer ends termed **gonozooecia**. Their morphology and development in a colony suggests that these zooids were polymorphs, possibly involved with production of eggs and brooding of embryos. One monomorphic goniocladiid has a subspherical expansion in the vesicular tissue that possibly served as a brood space. Most genera of the Ceramoporina are trimorphic and have normal autozooecia, large monticular autozooecia, and exilazooecia, which are small, tubular zooids (formerly called mesopores or cystopores) developed in the exozone (Fig. 142). One ceramoporine has, in addition, **basal zooecia** (Fig. 145) and displays the greatest degree of polymorphism in the Cystoporata. Funnel cystiphragms and flask-shaped chambers in many Cystoporata suggest that intraautozooecial polymorphism may be widespread in the order.

AUTOZOOIDS

RECOGNITION OF AUTOZOOIDS IN THE CYSTOPORATA

Autozooids are the normal individuals in a colony (BORG, 1926a, p. 188), which perform all the usual body functions (RYLAND, 1970, p. 29). At one or more stages in their ontogeny, autozooids have a protrusible lophophore (BOARDMAN, 1971, p. 2). Using the definition of zooid as an individual member of a colony, minimally consisting of body wall enclosing a coelom and connected by the body wall to other members of a colony (BOARDMAN, CHEETHAM, & COOK, this revision), and evidence from microstructure, budding, and colony construction, several kinds of zooecia in the Cystoporata could have been autozooecia.

In the Fistuliporina, the choice is narrowed to one or usually no more than two kinds of zooecia. Some fistuliporines are monomorphic in both intermonticular and monticular areas; all zooecia can be considered to be autozooecia that housed feeding organs.

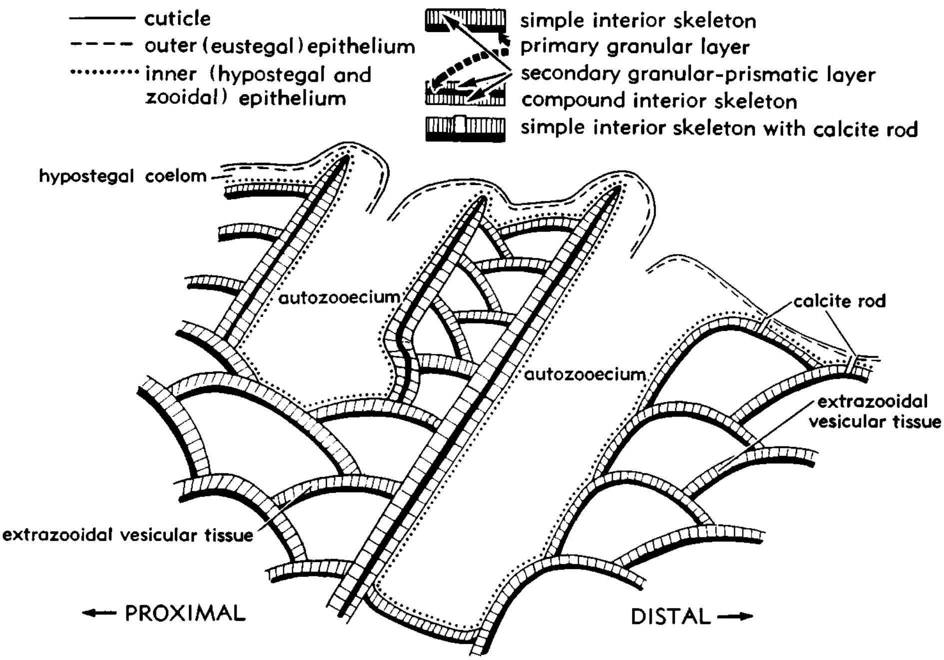

FIG. 143. Cystoporate morphology. Longitudinal section through hypothetical fistuliporine based on observed sections but showing double-walled construction (after Utgaard, 1973). The autozooecium on the left was formed by septa produced on old vesicular tissue by folding of the inner (hypostegal) epithelium. It has a peristome and compound walls. The autozooecium on the right has a compound wall on the lunarial side, which is proximal (left side in figure), but the distal side is composed of superimposed vertical simple walls of extrazooidal vesicular tissue. It has no peristome and the inner, zooidal epithelium curves up and out to continue as the inner (hypostegal) epithelium below the hypostegal coelom. Walls and roofs of the vesicles or vesicular tissue can be composed of the inner granular primary layer alone or the primary layer and a secondary granular-prismatic layer. Outer cuticle is shown attached to the calcite rod of small acanthostyles or tubuli in the vesicle roofs.

Most fistuliporines have intermonticular autozooecia that are slightly smaller than the otherwise similar monticular zooecia (see Fig. 180,*1b*); both types probably housed feeding organs. The intermonticular autozooecia are considered to be the common kind of autozooecia and the monticular zooids to be polymorphs (UTGAARD, 1973, p. 324). A few fistuliporines have zooecia with expanded outer ends on the colony surface; these are probably autozooecia modified to serve a brooding function.

The polymorphic colonies of the Ceramoporina have as many as four different kinds of zooecia. All are possible autozooecia. Only two of these types are common to all ceramoporines: the large intermonticular zooecia and the slightly larger monticular zooecia. The intermonticular zooecia probably housed feeding organs because they compare in size, number, and position with autozooecia of monomorphic fistuliporines. As with the Fistuliporina, the larger monticular zooecia probably also housed autozooids. Smaller zooecia on the frontal or nonbasal surface of some ceramoporine colonies possibly are another kind of autozooecium, a kind of polymorph that is called an exilazooecium. Rare basal zooecia, found so far only in some colonies of *Ceramopora,* were probably not autozooecia.

Inferred autozooecia in the Cystoporata are comparable in relative size, shape, position of origin, extent of living chamber,

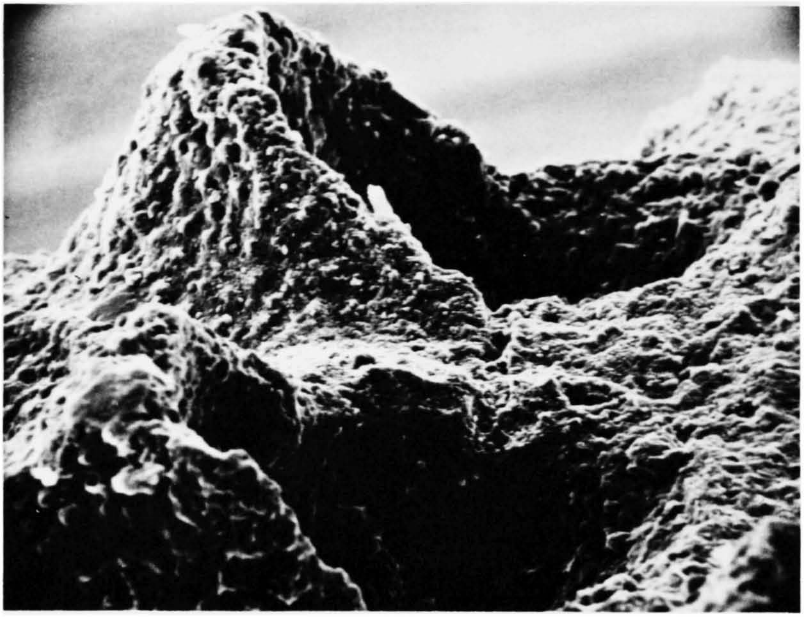

FIG. 144. Cystoporate morphology. *Cheilotrypa hispida* ULRICH, Glen Dean Ls., Miss. Sloans Valley, Ky. Lunarium on the proximal side of an autozooecium; note the small protrusions on the proximal side (left), which are the surface expression of minute calcite rods in tubuli in the thick lunarial deposit. Scanning-electron photograph, SIUC 3001, ×260.

intrazooecial structures, distribution in the colony, and similarity to probable ancestrula with inferred autozooecia in the Trepostomata (BOARDMAN, 1971) and autozooecia in the Tubuliporata (BORG, 1926a, 1933).

LUNARIA

Most genera in the Cystoporata have a lunarium on the proximal side of each autozooecium and on each large monticular zooecium. Lunaria are not present in exilazooecia, basal zooecia, or in extrazooidal vesicular tissue. The lunarium projects above the general surface of the zoarium (Fig. 144) and above the rim or peristome of the autozooecial orifice in unworn specimens. In most genera, zooecia are radially arranged around monticular centers with lunaria on the sides of zooecia nearest monticular centers (see Fig. 183,*1c,d*). In some bifoliate forms, lunaria rotate to the right- or left-lateral side of autozooecia in the exozone (see Fig. 205,*1b*).

The lunarium, cut transversely in tangential thin sections or acetate peels, generally has a shorter radius of curvature than the remainder of the zooecial orifice (see Fig. 159,*1b,c,e*). In some genera the ends of lunaria project into zooecial cavities (see Fig. 174,*1e,f*; 180,*2a,b*) and greatly modify shapes of skeletal living chambers. In other cystoporates the radius of curvature of the lunarium is approximately the same as that of the distal side of the zooecium, regardless of whether the aperture is elongated in the proximal-distal direction (see Fig. 158,*1c*), or is approximately circular. In some, the lunarium is small or spinelike (see Fig. 183,*2a*; 188,*1b*).

Lunaria appear in early ontogenetic stages of autozooecia and are distinct skeletal structures that generally can be seen in longitudinal and transverse thin section as well as in tangential section. Lunarial deposits in many genera are continuous, extending from outer endozones or inner exozones to zoarial sur-

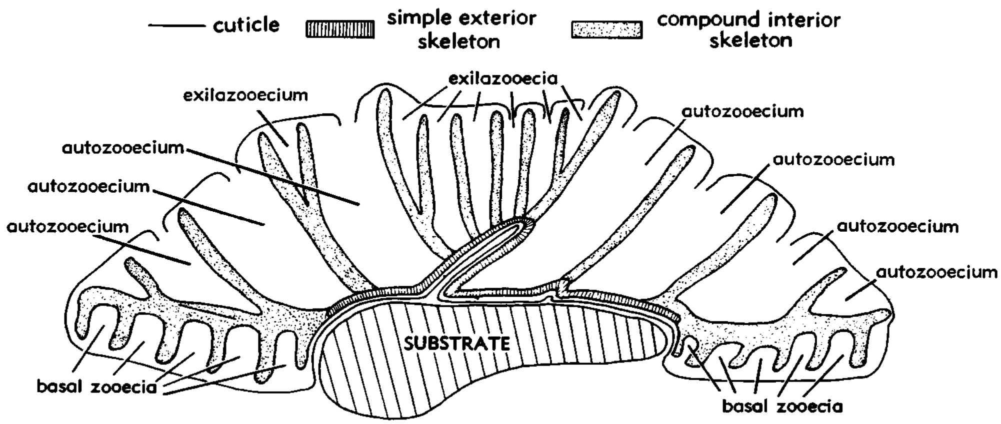

FIG. 145. Cystoporate morphology. Longitudinal section through hypothetical double-walled *Ceramopora* with a celluliferous base (after Utgaard, 1973). Epithelia are omitted. The celluliferous base contains relatively short, narrow, diaphragmless polymorphs called basal zooecia. Probably lacking polypides, they opened into the hypostegal coelom on the free basal margins of the colony, beyond the encrusted substrate. Their walls are compound. Only the basal layer in the ancestrula and adjacent to the encrusted substrate is a simple wall.

faces (see Fig. 158,*1a,e*; 160,*1e,i*). In a few genera, such as *Anolotichia* (see Fig. 164), the structure of lunarial deposits changes markedly near zoarial surfaces. In most cystoporates, the structure of the lunarium is relatively uniform throughout its length. Lunaria commonly increase in size in the exozone in the growth direction of the autozooecium. Thus, in cystoporates with lunaria and exozones, the lunaria are developed and visible externally in well-preserved specimens. Microstructures and ultrastructures of lunarial deposits are not uniform within the order Cystoporata or even within some families.

Borg (1965) and Utgaard (1968a) reported lunaria in post-Paleozoic hornerids and lichenoporids. Boardman (1971) described the position of the membranous sac in a lichenoporid as being on the proximal (lunarial) side.

AUTOZOOECIAL LIVING CHAMBERS

In modern tubuliporates the living chamber is that part of a zooid lined by zooidal epithelium, and it houses the functional organs of the zooid, if any are present. Skeletal remains of living chambers in autozooids of cystoporates as well as trepostomates (Boardman, 1971, p. 5) can be studied in unworn specimens or beneath protective overgrowths. Estimating the minimum extent of a living chamber by trying to trace "time lines" of skeletal deposition from a basal diaphragm into and along the autozooecial wall to the zooecial boundary is difficult in trepostomates (Boardman, 1971, p. 5), and is virtually impossible in cystoporates. In the Fistuliporina the wall laminae are obscure or walls have a granular and granular-prismatic microstructure. In the Ceramoporina, this method could be successful, but wall laminae apparently were deposited in bundles in the form of partial cylinders and not as complete cylinders lining the zooecium, as was usual in trepostomates. Minimum length of a living chamber can be estimated from studying relatively unabraded specimens, but the best estimate comes from studying living chambers preserved beneath overgrowths (Boardman, 1971, p. 5).

Autozooecial living chambers in the Cystoporata.—Nearly all living chambers in the cystoporates are either modified cone-cylinder shapes with the smaller, modified cone-shaped inner end on the basal layer or mesotheca and the larger, cylindrical portion in the exozone; or cylinders with a nearly flat basal diaphragm. The length of these living chambers ranges from approximately two autozooecial diameters to about seven. In *Botryllopora,* which has comparatively narrow living chambers, they may be as much as nine times as long as wide. Most living chambers in the cystoporates are approximately three to five times as long as wide.

Cross-sectional shapes of inner ends of living chambers of the modified cone-cylinder type may be hemispherical, mushroom-shaped, subcircular, triangular, or subtriangular. Many bifoliate fistuliporines have right- and left-handed autozooecia that join mesothecae at teardrop- or club-shaped contacts (see Fig. 205,*1f*; 207,*1e*). Cross-sectional shapes of living chambers in exozones may be circular to elliptical. These basic shapes may be modified depending upon the radius of curvature of the lunarium, whether or not the ends of the lunarium project into the autozooecial cavity, or the presence of canaliculi, large septalike styles that inflect autozooecia (see Fig. 194,*1d,e*; 195,*1c,2b*). In many cystoporates the lunarium encloses part of a round to elliptical cylinder-shaped space on the side of and paralleling a larger round to elliptical space enclosed by the remainder of the autozooecial walls (see Fig. 159,*1c*; 180,*2a–c*). Possible polypide remnants in this smaller cylinder suggest that the lunarium formed a groove in which the polypide was located.

In a few constellariids, the basal structures of living chambers may be curved or cystoidal diaphragms or a combination of cystoidal diaphragms and flat diaphragms. In these forms, the living chamber generally has a bisected funnel shape and a smaller cross-sectional area in its inner portion and is cylindrical in its longer, outer portion. The deepest part of the living chamber is on the proximal side of the autozooecium, next to the lunarium if one is present.

In many bifoliate and a few encrusting species of fistuliporines, a proximal hemiseptum partly divides the living chamber into a modified conical inner portion and a cylindrical outer portion. Species of *Strotopora, Cliotrypa* and *Fistuliphragma* have alternating hemiphragms, which are triangular and platelike or curved spines, and which protruded into the living chamber.

Basal diaphragms and abandoned chambers.—As an autozooecium grows and the living chamber reaches a certain length (which is not constant in a colony), a new basal diaphragm is formed in many cystoporates. Other cystoporates with relatively short autozooecia do not have basal diaphragms. Lengthening of the outer end of the autozooecia and, especially, formation of a new basal structure, are probably related to the degeneration-regeneration cycle in an autozooid. As in the trepostomates (BOARDMAN, 1971, p. 18), spacing of basal diaphragms in many cystoporates is such that **abandoned chambers** between successive basal diaphragms are usually much shorter than the living chamber in the same autozooecium. Length of the abandoned chambers in the cystoporates usually ranges from less than one to slightly more than three autozooecial diameters, and generally is less than two autozooecial diameters.

Formation of a new basal diaphragm probably involved proliferation of a new epithelium and peritoneum from the lateral walls of the zooid across the zooecium at a level closer to the surface of the colony than the preceding basal diaphragm. Brown bodies, some other cellular material, and coelomic fluids probably were left behind in the abandoned chamber. If the basal zooidal epithelium next to the basal diaphragm were drawn intact to a new position farther out in the autozooid, brown bodies or fossilized brown deposits would not be found in abandoned chambers, but they commonly are. In the cystoporates, basal structures are simple-walled in construction, being deposited by epithelium on the outer side. Except in some ceramoporines, where an abandoned chamber may be connected to the living chamber of an adjacent autozooecium or exilazooecium through communication pores in zooecial walls, living tissue was probably not present in abandoned chambers. Brown deposits encapsuled with membrane, diffuse brown deposits, and rare membranous linings found in abandoned chambers are probably the remnants of brown bodies, cellular material, coelomic fluid and membrane left behind in the abandoned chamber when a new basal zooidal epithelium was proliferated and a new basal skeletal diaphragm was formed.

In the cystoporates, as in the trepostomates (Boardman, 1971, p. 5), the new living chamber consisted of most of the old living chamber, minus the abandoned segment, and new space where new zooecial walls were secreted at the outer end of the autozooecium while the polypide was degenerated.

Terminal and subterminal diaphragms.—Among Paleozoic bryozoans, subterminal diaphragms, with reverse curvature indicating deposition from the inner side, are known only in some ceramoporines (Utgaard, 1968b, p. 1445–1446). They are common in autozooecia and some exilazooecia, especially in species of *Ceramoporella.* It is possible that some reversed subterminal diaphragms are compound, being calcified by the zooidal epithelium on the inside and the inner (hypostegal) epithelium on the outside (Fig. 146), but most appear to have been calcified from the inside only.

Borg (1933) reported terminal and subterminal diaphragms in autozooecia and kenozooecia in heteroporid tubuliporates. Considerable variation exists, within and among genera of heteroporids, in the abundance of terminal and subterminal diaphragms. Nye (1968, p. 112) reported pore-bearing terminal and subterminal diaphragms and imperforate intermediate diaphragms in some post-Paleozoic tubuliporates. Both the terminal and intermediate diaphragms have laminae flexed toward the inner end of the autozooecium where the diaphragm joins the zooecial walls, indicating at least partial deposition from the inner side. Pores have not been observed in the terminal and subterminal diaphragms in ceramoporines.

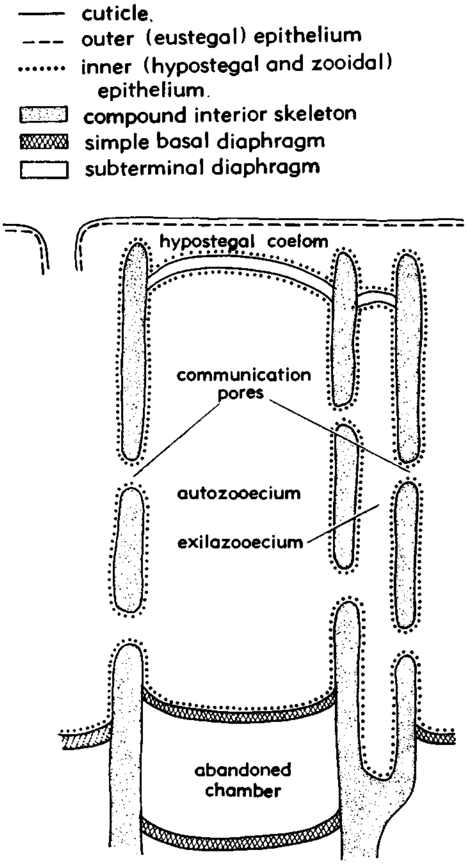

Fig. 146. Cystoporate subterminal diaphragms. Idealized diagram of living chambers in an autozooecium and an exilazooecium in the ceramoporine *Ceramoporella,* which are closed by a subterminal diaphragm (after Utgaard, 1973). The subterminal diaphragms clearly are mainly or entirely deposited from their inner side. The inner (hypostegal) epithelium below the hypostegal coelom could have had a part in secreting the subterminal diaphragms from the outer side. The abandoned chamber, between successive basal diaphragms, contained no viable tissue whereas the chambers below the subterminal diaphragms contained at least a living epithelium, a peritoneum, and coelomic fluid by virtue of their communication with adjacent zooids via communication pores.

Terminal and subterminal diaphragms have been observed in more than a dozen genera of the Fistuliporina. They are of simple construction (see Fig. 186,*1e*), but, unlike those in the ceramoporines, they were deposited by an inner or hypostegal epithelium below the hypostegal coelom on the outer side of the diaphragm. Pores have not been observed in these diaphragms in fistuliporines. Some membranous structures previously referred to as pellicles or opercula in the fistuliporines may be terminal or subterminal diaphragms (UTGAARD, 1973).

BORG (1933, p. 320) thought that the formation of terminal diaphragms was a part of the degeneration-regeneration cycle. It seems likely that the polypide would degenerate in a ceramoporine autozooid when the terminal or subterminal diaphragm was formed, especially if the subterminal diaphragm were formed in the region of the vestibule. It is possible that the inner part of a polypide could lie dormant, nourished through communication pores. The entire zooid probably would be abandoned to degenerate or decompose in a fistuliporine below a terminal or subterminal diaphragm, if the diaphragm lacked a pore. The presence of possible polypide remnants in large "abandoned" chambers (capped living chambers) below terminal diaphragms supports the inference that they underwent decomposition without complete degeneration to form a brown body.

Living chambers capped with terminal or subterminal diaphragms are much longer than normal abandoned chambers in the same colony and even in the same zooecium, indicating that terminal or subterminal diaphragms do not, as a matter of course, become the next basal diaphragm when a polypide is regenerated, as ULRICH (1890, p. 315–316) thought. It is possible that terminal diaphragms were produced during degeneration and were resorbed during regeneration in the degeneration-regeneration cycle. BORG (1933, p. 298, 302–303) reported resorption of the subterminal diaphragms in parts of the colonies of the tubuliporate *Heteropora.* However, the presence of some long, abandoned chambers, including those containing flask-shaped chambers, funnel cystiphragms, and partial funnel cystiphragms (see below), suggest possible capping by terminal diaphragms rather than the usual basal diaphragms. The relative rarity of obvious terminal diaphragms and longer-than-normal abandoned chambers suggests that they were not consistently part of a normal degeneration-regeneration cycle. In addition, membranous remnants possibly representing sacs of undegenerated polypides have been found in several living chambers capped by subterminal diaphragms.

Perforated apertural structures (opercula) have been reported in several genera of cystoporates. These need further study.

LATERAL STRUCTURES

Cystoporates display relatively few lateral intrazooecial structures as compared to some other stenolaemate bryozoans. Cystoporates lack skeletal cystiphragms. Only a few genera (see Fig. 176,*1a,d*; 183,*1e*; 191,*1c*) have spine- to platelike hemiphragms that alternate across the autozooecium. Formation of hemiphragms may have been related to a degeneration-regeneration cycle. Some of the bifoliate fistuliporines have a proximal or proximolateral hemiseptum (see Fig. 205,*1e*) at the zooecial bend. One genus, *Prismopora,* has a recurved distal hemiseptum at the zooecial bend region. A few fistuliporines have short, hyaline mural spines in longitudinal and horizontal rows in the exozone.

Funnel cystiphragms and partial funnel cystiphragms, lateral structures found in few cystoporates, are discussed below.

Hollow spherical cysts.—Hollow spherical calcareous cysts have been observed in autozooecia in nine species of cystoporates. BASSLER (1911, p. 86, 90) and UTGAARD (1968b, p. 1449) reported such structures from the Ordovician ceramoporine *Crepipora incrassata* BASSLER, and ULRICH (1890, p. 318) reported similar structures in a species of *Fistulipora* from the Devonian of New York. In addition, a survey of the thin-section collection at the U.S. National Museum of Natural History revealed similar cysts in the Ordovician ceramoporine *Crepipora venusta* (ULRICH), the Ordovician anolotichiid *Anolotichia ponderosa* ULRICH, an unidentified Devonian species of *Fistulipora,* an unidentified Permian fistuliporid, the Devonian fistuliporid *Cyclotrypa communis* (ULRICH), the Mississippian hexagonellid *Glyptopora elegans* (PROUT), and the Devonian cystodictyonid *Dichotrypa foliata* ULRICH.

The cysts are generally circular in cross section, although those in *Dichotrypa foliata* and the unidentified Devonian species of *Fistulipora* are ovate to elongate-ovate in cross section. The microstructure of the cysts is granular in those species with granular-prismatic walls and laminated in those species with laminated walls. They are generally attached to the autozooecial walls or basal diaphragms, or both, but a few appear to "float" in the autozooecial cavity if the plane of the section misses the site of attachment. The wall of the cysts generally is 0.01 mm thick or slightly less. The cysts generally range from 0.10 to 0.20 mm in diameter, though some of the elongate-oval ones are up to 0.30 mm in maximum dimension. In *Crepipora venusta,* several abandoned chambers contain clusters of from 3 to 9 smaller calcareous cysts, each about 0.05 mm in diameter. Their walls are fused, and several cysts are aggregated into a grapelike mass.

Some of the cysts are apparently empty but most contain a relatively small amount of brown granular material. The small cysts in grapelike clusters in *Crepipora venusta* are nearly filled with brown residue.

Most hollow cysts are in abandoned chambers. One hollow cyst has been observed near the distal end of a living chamber that is capped by a terminal diaphragm (*Dichotrypa foliata*), one is possibly in a living chamber (*Anolotichia ponderosa*) and one is in an open living chamber (*Glyptopora elegans*). In an unidentified fistuliporid from the Permian, the cyst is in an abandoned chamber immediately below an autozooecial living chamber that is modified by half of a funnel cystiphragm. Hollow cysts apparently can occur anywhere within an autozooecial living chamber.

ULRICH (1890, p. 318) suggested that the cysts in the tubuliporate *Ceriocava ramosa* D'ORBIGNY (ULRICH, p. 318, fig. 7e, f) from the Cretaceous of France and in the unidentified species of *Fistulipora* from the Devonian of New York were homologous with "true cystiphragms" in monticuliporid trepostomates. However, as CUMINGS and GALLOWAY (1915, p. 351–354, and fig. 17–22) determined, cystiphragms do not contain brown residue and their major functions seem to be to limit the size and impart a generalized shape to the autozooecial living chamber (CUMINGS & GALLOWAY, 1915, p. 354–355; BOARDMAN, 1971, p. 12). Unlike the relatively rare, subspherical to spherical hollow cysts, cystiphragms in monticuliporids generally occur in ontogenetic series and provide a living chamber that was relatively constant in shape during ontogeny (BOARDMAN, 1971, p. 12). The rare hollow cysts generally occupy half to four-fifths of the diameter of a small part of a living chamber and greatly modify the shape of that part of the living chamber. In addition, these cysts generally contain brown residue, and in this respect differ from cystiphragms.

BASSLER (1911, p. 86) called the cysts in *Crepipora incrassata* "rounded, ovicell-like structures" and further suggested (p. 90) that they ". . .would seem to bear most resemblance to the ovicells of the cyclostomatous bryozoans." The presence of a similar, hollow, calcareous cyst in an autozooecium of a modern species of *Hornera* that also has gonozooecia and brown bodies suggests that these structures in Paleozoic cystoporates were neither ovicells nor encysted brown bodies.

BOARDMAN (1960, 1971) and DUNAEVA (1968) reported similar, hollow cysts in the Devonian and Carboniferous trepostomates *Leptotrypella, Aisenvergia,* and *Volnovachia.* The hollow spheres in *Volnovachia,* illustrated by DUNAEVA (1968), are smaller

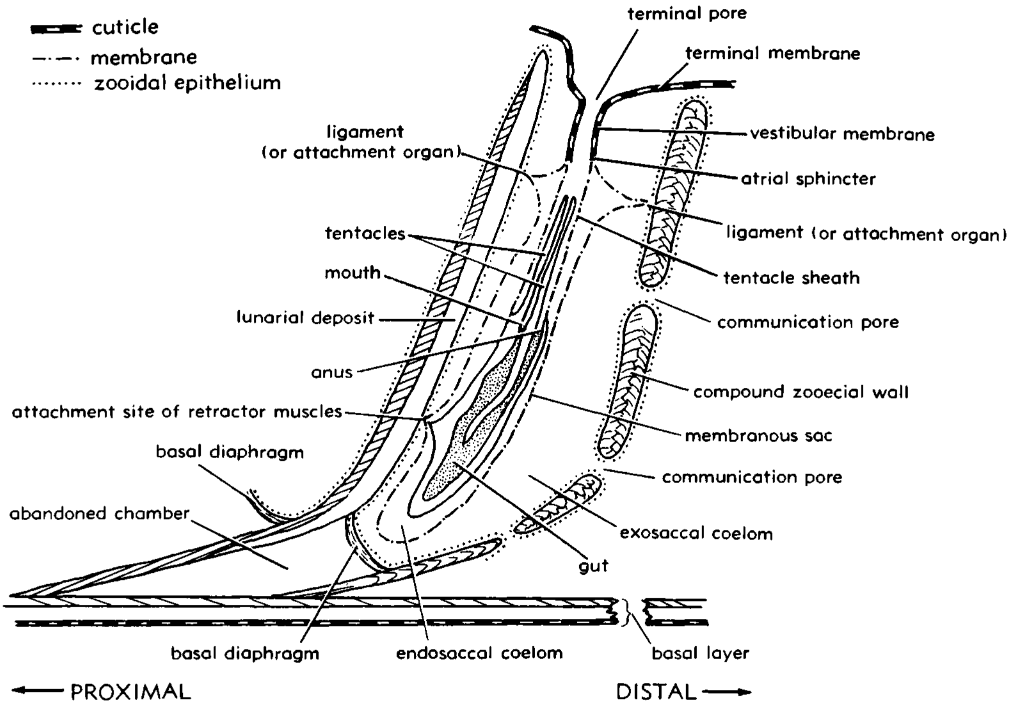

FIG. 147. Cystoporate functional morphology. Longitudinal section through a hypothetical model of a ceramoporine autozooid based on soft tissue of a recent lichenoporid tubuliporate (after Utgaard, 1973). Eustegal epithelium, peritoneum, and muscles that widen the vestibule are omitted from the drawing.

and more numerous than most of the cysts in the cystoporates. They are about the same size, though in larger numbers, than the cysts in *Crepipora venusta.* DUNAEVA (1968) suggested that the small spheres might be eggs. BOARDMAN (1971) suggested that they are encysted foreign bodies or perhaps even encysted brown bodies.

The size, shape, location, rarity, and associated brown material of hollow spherical cysts suggest that they were: (1) not homologous with monticuliporid cystiphragms that modified the size and shape of normal autozooecial living chambers; (2) not encysted brown bodies formed from the degeneration of a polypide; (3) not ovicells; (4) not eggs (at least not the cysts found in the cystoporates). One of BOARDMAN's suggestions (1971) seems to be the most likely proposed so far: that they are encysted foreign bodies. It seems most likely that the rare cysts were formed in autozooecial living chambers by an inpocketing of the zooidal epithelium that ranged in shape from hemispherical to spherical with one or more narrow skeletal connections to the autozooecial wall or basal diaphragm. Such an inpocketing could be the result of a local pathological stimulus or presence of a foreign body. The brown residue in most of the cysts suggests a pathologic stimulus or biological foreign body.

INTERPRETIVE FUNCTIONAL MORPHOLOGY OF CYSTOPORATE AUTOZOOIDS

Recent tubuliporates as a model.—Similarities in mode of growth led BORG (1926b, p. 596; 1965, p. 3) and BOARDMAN (in BOARDMAN & CHEETHAM, 1969; 1971, p. 6–7) to look for a growth model for Paleozoic tubular bryozoans in the post-Paleozoic double-walled tubuliporates. The evidence for a double-walled colony construction in tubular bryozoans and BORG's order Stenolaemata, which included the tubuliporates, trepostomates and cystoporates, led BOARDMAN (1971, p. 6) to recent tubuliporates as a logical first approximation for a model for zooid form and function in tubular bryozoans. A generalized autozooid, based on that of a lichenoporid tubuliporate is used here (Fig. 147) as a model for autozooids in the Cystoporata.

Evidence from Paleozoic cystoporates.—In addition to evidence from budding locations, microstructure, ultrastructure, and growth of the skeleton, the preservation of HCl-resistant organic matter in living chambers below overgrowths or terminal diaphragms gives some indication of the nature and extent of zooidal tissues. The nature of this preserved organic material suggests certain characteristics that cystoporate autozooids had in common with autozooids of trepostomates and tubuliporates. One of these is the degeneration-regeneration cycles.

Polypide remnants in cystoporates.—A very few fossilized cystoporate autozooecia contain long, tubular, brown deposits that range from interrupted patches of brown granular material to fairly complete tubular membranes (UTGAARD, 1973). These are found in living chambers below overgrowths or terminal or subterminal diaphragms, and probably represent polypide remnants rather than brown bodies from a degenerated zooid. In abandoned chambers of several zoaria containing the long, tubular brown deposits are compact brown deposits, more likely remnants of brown bodies (UTGAARD, 1973). The long, tubular, membraneous deposits suggest that at least those cystoporates had autozooids with a membranous sac.

A few of these tubular deposits occupy almost the whole width of the living chamber; most occupy only a part, some less than half, of the living chamber width (UTGAARD, 1973). Similar polypide and membranous sac placement is common in recent tubuliporates. Some of these organic remnants are closer to the proximal or lunarial side, at least toward their outer end, a situation found in zooids of recent *Lichenopora* (BOARDMAN, 1971).

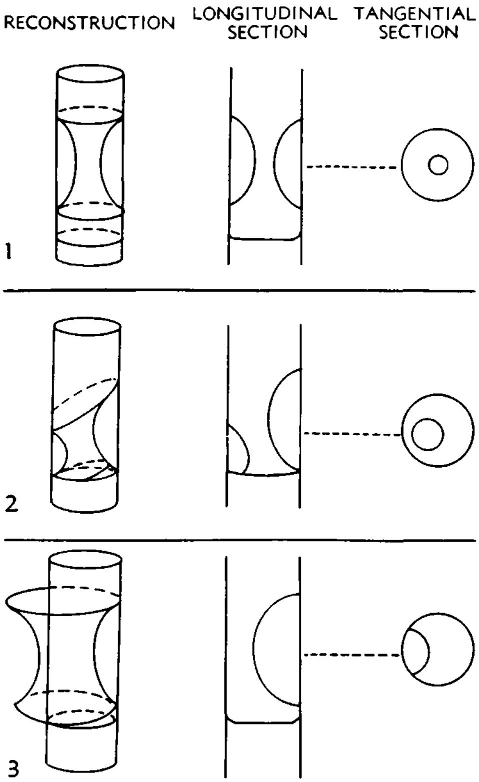

FIG. 148. Cystoporate flask-shaped chambers. Variations in shape and size of flask-shaped chambers as seen in longitudinal and tangential thin sections, produced by different inclinations and positions of the axis of a funnel cystiphragm (after Utgaard, 1973).——*1,* Axis of funnel cystiphragm centered on autozooecial axis and not inclined.——*2,* Axis of funnel cystiphragm inclined to axis of autozooecium.——*3,* Axis of funnel cystiphragm parallel to but offset from axis of autozooecium.

Organic linings of autozooecial chambers, possible membranous diaphragms, and enigmatic organic threads and cysts are rare in cystoporates (UTGAARD, 1973) and their possible extent and paleobiological importance are unknown.

FLASK-SHAPED CHAMBERS

The occurrence of complete and partial funnel cystiphragms, which form flask-shaped chambers in the Cystoporata, was summarized by Utgaard (1973). More variation in shape exists in flask-shaped chambers in the cystoporates (Fig. 148) than in trepostomates. The possibility that they are intraautozooecial polymorphs was discussed by Boardman (1971) and Utgaard (1973). Boardman and McKinney (1976) later suggested that they are calcified partitions reflecting the shapes of organs of the lophophore and gut of the feeding autozooids, calcified during a dormant, nonfunctional stage. If that were so, autozooecial living chambers would be greatly modified by their presence, and the resulting flask-shaped chambers presumably would have been sealed off and abandoned and would not have been occupied by succeeding, normal polypides. In some cystoporates, there is clear evidence that the flask-shaped chambers were occupied by a zooid with a polypide (Utgaard, 1973, p. 338–339). Funnel cystiphragms are found in ontogenetic series and some of the flask-shaped chambers contain fossilized brown bodies and polypide remnants indicating that they were occupied by a zooid with a polypide, probably a polymorphic one.

ZOOECIAL POLYMORPHS

EXILAZOOECIA

Exilazooecia are found in most genera of the Ceramoporidae but are not developed in the Fistuliporina. The term exilazooecium is a modification of the term "exilapore" (Dunaeva & Morozova, 1967, p. 87) originally used for mesopores in some Trepostomata that are relatively narrow and long and that lack or have only a few basal diaphragms spaced far apart. By the definition of zooid used in this work, there is little doubt that the exilazooecia in ceramoporines are zooecia of some smaller kind of zooid. Because the soft parts and function may never be known, the descriptive term "exilazooecium" is preferred to terms based on function, tissues, or organs, such as kenozooecium, nanozooecium, and heterozooecium. Exilazooecia in ceramoporines differ from mesozooecia and alveoli. The descriptive term "cystopore" does not fit these structures as well as the term "exilazooecia."

Exilazooecia in the Ceramoporidae.—Exilazooecia in the Ceramoporidae arise by formation of a septum (a compound wall) proximal to a semirecumbent autozooecial wall in the outer endozone or inner exozone (see Fig. 158,*1a*; 159,*1g*). Exilazooecia have never been observed to arise by formation of a compound wall on the basal layer or mesotheca. Exilazooecia extend from their locus of origin to the zoarial surface. They have a relatively long, narrow, tubular cavity with a rounded cross section. In some genera they are slightly more subangular and larger in cross section in the inner exozone and become progressively more circular and smaller toward the zoarial surface. Exilazooecia can be absent to abundant between autozooecia in intermonticular areas in the ceramoporines, and generally a cluster of exilazooecia forms the center of a monticule. They generally lack intrazooecial skeletal structures but basal diaphragms are present in some relatively long exilazooecia and subterminal diaphragms may be present, generally at the same level as subterminal diaphragms in adjacent autozooecia.

Exilazooecial wall microstructure is similar to that of autozooecia in the Ceramoporidae, that is, with broadly curved laminae and generally a broadly serrated boundary zone. The cortex is thinner and a zooecial lining is thin or absent in the exilazooecia. Exilazooecia do not have lunaria or lunarial deposits (Utgaard, 1968b, p. 1449). Acanthostyles may be present in exilazooecial walls (see Fig. 157,*1e,g*; 160,*1b*).

In genera of the Ceramoporidae that have communication pores, the pores are present in the exilazooecial walls as well as in the autozooecial walls. Pores may connect the cavities of adjacent autozooecia, adjacent exilazooecia, or contiguous exilazooecia and autozooecia. Communication pores commonly are fewer between exilazooecia than between autozooecia. In one Middle Ordovician *Acanthoceramoporella,* the communication pores are enlarged to huge gaps in the walls, and flat and curved basal diaphragms may extend across several autozooecia and exilazooecia (UTGAARD, 1973, p. 340).

Interpretive functional morphology of exilazooecia.—The presence of compound exilazooecial walls, zooecial linings, basal diaphragms, terminal diaphragms deposited from their inner side, and communication pores in exilazooecia indicate the presence of a secretory zooidal epithelium. Ceramoporines are double-walled bryozoans and coelomic fluid in the exilazooecia could communicate with the (presumably exosaccal) coelomic fluid in adjacent autozooecia and exilazooecia through the hypostegal coelom as well as through communication pores. When subterminal diaphragms without pores were formed, coelomic communication could still take place through communication pores in the zooecial walls (Fig. 146).

Encapsuled brown structures, reminiscent of brown bodies formed from degeneration of a polypide, have been reported (UTGAARD, 1968b, p. 1446) in exilazooecia in *Ceramophylla vaupeli* (ULRICH). These brown structures strongly suggest the presence of live tissue, in addition to the zooidal epithelium. Kenozooids in modern heteroporid tubuliporates (BORG, 1933, p. 362, 368) have a zooidal epithelium, peritoneum, coelomic fluid, and various cells in the coelomic fluid, but they do not degenerate to produce an encapsuled brown body because they do not have a polypide. Nanozooids in recent tubuliporates do have a reduced extrusible polypide and a membranous sac and do degenerate to form brown bodies (BORG, 1926a, p. 234, 236). Thus, some exilazooecia may have contained a modified polypide or other organs.

LARGE MONTICULAR ZOOECIA

The zooecia that immediately surround monticular centers in most cystoporates are slightly larger than common intermonticular zooecia, which are interpreted to have housed the normal feeding autozooids. The larger zooecia have comparable wall structure and thickness, living chamber length, abandoned chamber length, and intrazooecial skeletal structures, including funnel cystiphragms and flask-shaped chambers. The only differences they show with intermonticular autozooecia are a slightly larger diameter and the commonly radial arrangement of the lunarium and proximal side of the living chamber around the monticular center (see Fig. 183,*1c,d*). When they show radial arrangement, the lunarium is on the side nearest the monticular center. Intermonticular autozooecia also display radial arrangement of lunaria in many cystoporates. It seems likely that the larger monticular zooecia housed slightly larger feeding autozooids. The functional significance of the larger monticular autozooids is not yet clear, but it seems likely that they did not serve a reproductive or brooding function. Forms that have inferred gonozooecia also have large monticular zooecia.

BASAL ZOOECIA

Polymorphic basal zooecia are known only in some colonies of *Ceramopora imbricata* HALL (see Fig. 156,*1a*) (UTGAARD, 1969, p. 289). They develop in the free margins of encrusting colonies, beyond the encrusted part of the colony, which has a simple-walled basal layer. The basal polymorphs have relatively short, narrow cavities that are subcircular in cross section and most closely resemble exilazooecia in shape and size. They have compound walls and most likely opened into a basal, centripetal expansion of the hypostegal coelom that continued from the frontal surface of the colony, around the growing margin, to the peripheral part of the base of the colony (Fig. 145). There is no evidence, to date, of a possible modified polypide or membranous sac in these basal polymorphs, but their mode of growth suggests that they were lined by a secretory zooidal epithlium and contained coelomic fluid that was in communication with a hypostegal coelom.

GONOZOOECIA

Intermonticular autozooecia with expanded subspherical outer ends have been known for some time (Ulrich, 1890, p. 383) in a few cystoporates. To date, they have been found only in the Fistuliporidae and only in the genera *Strotopora* and *Cliotrypa.* Spaces in vesicular tissue, interpreted to be gonocysts, have been reported (Shulga-Nesterenko, 1933, p. 49).

In *Cliotrypa* and *Strotopora,* an autozooecium of normal living-chamber diameter opens into an enlarged chamber. Several of these gonozooecia are commonly developed at the same level in a colony (see Fig. 176, 191). Colonies that died with gonozooecial expansions at the surface display low, rounded hemispherical blisters, each with a small subcircular pore in no set location on the blister. Many are broken, presumably after death of the colony, and appear as large, hemispherical depressions with elevated rims. In section, the enlarged end of the gonozooecium is seen to cover adjacent extrazooidal vesicular tissue (see Fig. 191,*1b,e*) and, in some cases, adjacent autozooecia. Some adjacent autozooecia adjusted their direction of growth and grew around the expanded part of the gonozooecium (Utgaard, 1973, fig. 72). Calcified centripetal shelflike structures and curved plates have been reported (Utgaard, 1973, p. 341) in the enlarged part of some gonozooecia.

Older colonies may contain a zone of abandoned gonozooecial chambers and a younger zone of gonozooecia. Although unproved, these zooecial polymorphs were probably involved with egg production and the brooding of embryos. This conclusion is supported by the zonal, cyclical arrangement, the large chambers connected to normal-sized autozooecia, the pores opening through the surface of the large blisters, and the smaller number of gonozooecia compared to normal autozooecia.

EXTRAZOOIDAL SKELETAL STRUCTURES

Cystoporates in the suborder Fistuliporina are characterized by many extrazooidal skeletal structures, an unusual condition in bryozoans. The more important of these structures are described in the following discussion.

VESICULAR TISSUE AND STEREOM

The most prominent and widespread extrazooidal skeletal structures are vesicular tissue and stereom. Vesicular tissue or vesicles may originate on the budding surfaces (a basal layer or mesotheca), in the endozone, or in the exozone. Vesicles in some fistuliporines partly to completely isolate autozooecia and the distance of isolation may be narrow to wide (see Fig. 167,*1c*; 190,*3b,c*). Vesicle walls and roofs are almost invariably simple interior structures, deposited from the outside or frontal side by an epithelium under the colonial hypostegal coelom. Rarely, vesicle walls are compound; vesicle roofs are always simple. Commonly, the vesicle wall and roof merge into a single curved plate.

Vesicles display a considerable range in size and shape in fistuliporines. A few forms have narrow, long, tubelike vesicles. Many have vesicles with subequal height and width. Most fistuliporines have low, wide, blisterlike vesicles. Walls and roofs may be straight, producing boxlike or polygonal shapes (see Fig. 190,*3*), or curved, producing blisterlike shapes (see Fig. 184,*1d*) with polygonal to subcircular cross sections. Vesicles range from very small, generally less than one-quarter the zooecial diameter, to very large, being several times as wide as the autozooecium. Most are nearly half the diameter of an autozooecium. In many genera, vesicle height decreases outward in the outer endozone and exozone.

Zones of thick vesicle roofs are common within the exozone or at the zoarial surface in many genera, suggesting semicolony-wide control of deposition. In many fistuliporines, particularly those with bifoliate colony construction, vesicle roofs thicken and the space between successive vesicle roofs decreases to create an essentially continuous deposit of stereom. Stereom may occupy the outer exozone (see Fig. 198) or the entire exozone (see Fig. 209).

Available evidence suggests that vesicular tissue and stereom were deposited under colony-wide or semicolony-wide control and served as space filler and buttressing between autozooecia.

VERTICAL PLATES

Extrazooidal skeletal structures that are platelike and lie in planes generally parallel to the growth direction of autozooecia in the exozone are here termed **vertical plates**. They are relatively rare but several distinctive kinds have been observed in some cystoporates belonging to the suborder Fistuliporina.

Midray partitions.—A few genera have, surrounding monticules, radiating clusters or fascicles of autozooecia—rays—separated by **interrays** composed of vesicular tissue. Rays have compound vertical plates, termed **midray partitions**, along the center (see Fig. 171,*1c*; 193,*1a,c*). In some colonies of *Constellaria* (Cutler, 1973) hyaline material ("yellow tissue") forms a considerable portion of the midray partition. Where bordered by monticular ray zooecia, the midray partitions are, in part, multizooidal structures. In *Revalopora* (see Fig. 172,*1b*) the midray partitions may extend into the center of the monticule, where they are bordered by vesicles rather than by monticular zooecia. Such parts of midray partitions are extrazooidal in origin.

Vertical plates in intermonticular areas.—A few cystoporates have compound vertical plates in the exozone in intermonticular areas. Those in *Hexagonella* (see Fig. 196,*2a*) stand as elevated ridges forming polygons at the zoarial surface, and outline each monticule and its associated intermonticular autozooecia, emphasizing the subcolony aspect of monticules. Portions of some vertical plates border zooecial cavities and may be, in part, multizooidal structures.

Compound range walls.—Genera in the Cystodictyonidae generally have compound **range walls** that separate longitudinal ranges of autozooecia from their locus on the mesotheca to the zoarial surface. In the endozone, they are thin, compound walls that possibly developed early. The dark-colored primary layer in autozooecial walls and vesicles abuts the secondary, light-colored layer of the mesotheca. The primary, dark-colored layer of compound range walls commonly abuts the central, dark-colored primary layer in the mesotheca (see Fig. 209,*1c*), indicating that range walls developed earlier than adjacent autozooecial walls and vesicle walls. A part of the compound range wall may serve as the lateral wall of an autozooecium, and compound range walls can be, in part, multizooidal structures. The range walls may lose their distinctiveness in the exozone, as in *Dichotrypa* (see Fig. 207,*1e*), but commonly are thicker (being called libria), have branched dark zones (valvae) and tubules (see Fig. 210,*1e*), and can protrude on the zoarial surface as longitudinal ribs (see Fig. 210). The central compound range wall, termed the **branch midrib** (see Fig. 210,*2c*), or the central and contiguous lateral range walls (see Fig. 206,*2c*), may be thicker and higher and produce a marked bipartite or tripartite branch symmetry.

TUNNELS

Genera in the small family Rhinoporidae

have elevated, branched to anastomosing ridges on the zoarial surface (see Fig. 192,*1b,c*). They are poorly understood but apparently developed on vesicular tissue, are covered by a rounded roof, and are here called tunnels. Their function is not known but they may have been extrazooidal brood spaces.

MULTIZOOIDAL SKELETAL STRUCTURES

Multizooidal skeletal structures in the Cystoporata include basal layers, mesothecae, and low, longitudinal ridges developed on some mesothecae. Some vertical plates (see above) may be, in part, multizooidal.

Basal layers.—Encrusting, hemispherical and massive colonies of cystoporate bryozoans have a basal layer and presumably the initial, encrusting portions of all erect colonies had a basal layer too. The basal layer presumably had an outer, exterior cuticular portion, although none has been found preserved in cystoporates. The basal layer is a simple exterior wall, deposited by an epithelium on its inner side. Microstructure of basal layers differs among cystoporates and is discussed elsewhere.

Mesothecae.—A considerable number of cystoporates have bifoliate, trifoliate, or multifoliate colony construction and have mesothecae of variable thickness and microstructure. Also, mesothecae, though generally planar, may be undulatory, crenulated, or sharply folded.

Like the basal layer, the mesotheca served as the budding surface and as the bottom of the living chamber in most bifoliate, trifoliate, and multifoliate forms. Most of these forms have relatively short autozooecia. Median tubules or calcite rods were observed in the median portion of the mesotheca only in *Glyptopora* and *Aetomacladia.* They are generally absent in cystoporates with a mesotheca.

Vertical longitudinal ridges.—A few genera in the Hexagonellidae and Cystodictyonidae have low, longitudinal ridges on the mesotheca. They extend into the proximal part of the autozooecia and into vesicles (see Fig. 199,*1a,b*) and may be developed for a considerable distance, through several autozooecia and vesicles. They evidently were formed within linear folds of the basal epithelium, before vesicle and autozooecial walls were formed, but their function is not known.

SKELETAL MICROSTRUCTURE AND ULTRASTRUCTURE

Many workers have mentioned the "indistinct," "fibrous," "homogenous granular-fibrous," "granular," or "microporous" nature of skeletal walls in the Cystoporata, particularly in the fistuliporines. The cystoporates display a variety of skeletal microstructures that permits interpretive reconstruction of the depositing epithelium. Preliminary studies of the ultrastructure of cystoporates support some of the interpretations based on light-microscope studies, but additional studies of ultrastructure using electron microscopy are needed.

THE CERAMOPORINA

The ceramoporines primarily have a laminated skeletal microstructure with some skeletal elements of dense, light-colored, hyaline calcite. Laminae are here interpreted to have been deposited parallel to the secreting epithelium, like those in trepostomates (Boardman in Boardman & Cheetham, 1969, p. 211), and are considered to represent growth surfaces. The irregular discontinuous nature of the laminae, which was noticed in tangential sections by Ulrich

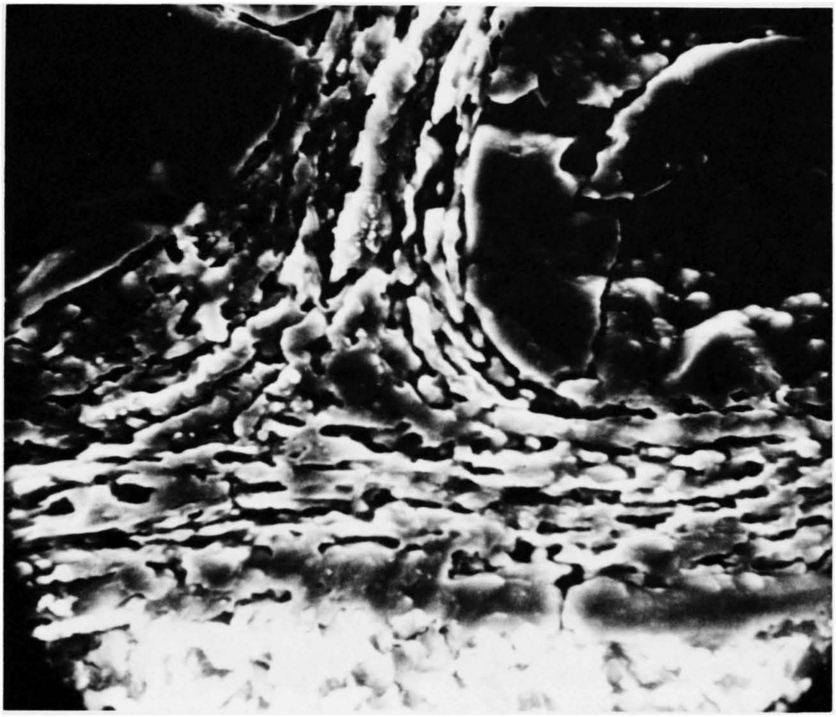

FIG. 149. Cystoporate skeletal structure. *Ceramophylla vaupeli* (ULRICH), McMicken Mbr., Eden F., U. Ord., Cincinnati, Ohio. Longitudinal section, etched, through basal layer (below) and autozooecial wall in endozone. Note large tabular crystallites in lower portion of basal layer, which has a hyaline appearance in thin sections, and smaller tabular crystallites in laminated upper portion of basal layer; also note tabular crystallites and distinct zooecial boundary in compound, longitudinally laminated autozooecial wall in the endozone. Scanning electron photograph, USNM 159859, ×1,050.

(1890, p. 311), suggests that skeletal material was not uniformly deposited in nested cylinders in the autozooecia. The larger discontinuous laminations are ultralaminae in bundles that feather out against the autozooecial cavity, suggesting that they were secreted now here, now there in an autozooecium. At any one time, new and slightly older laminae lined an autozooecial cavity. Autozooecial and exilazooecial walls are compound, the laminae on either side of the zooecial boundary being secreted by the epithelia of adjacent zooids. In inner endozones, compound walls are thin, have narrow zooecial boundaries, and may be longitudinally laminated. In outer endozones and in exozones, laminae are broadly curved in the growth direction of autozooecia, commonly have an irregularly intertonguing appearance, and zooecial boundaries may be narrow but commonly are wide, serrated zones.

Basal layers in encrusting and hollow ramose zoaria are simple, that is, deposited from only one side, and longitudinally laminate, with laminae parallel to the secreting epithelium. In many ceramoporines the basal layer consists of two parts: a lower or outer primary layer that is light colored and hyaline in appearance, with large tabular crystallites in at least one ceramoporine (*Ceramophylla vaupeli*; Fig. 149); and an upper or inner secondary layer with a distinct longitudinally laminated microstructure and ultrastructure. Presumably the primary layer was bounded by an external cuticle.

Mesothecae in bifoliate species of *Ceramophylla* have a compound, trilayered construction with a central, primary, hyaline

FIG. 150. Cystoporate skeletal structure. *Ceramoporella flabellata* (ULRICH), Corryville Mbr., Maysville Gr., U. Ord., Jefferson Lake, Ind. Transverse surface, etched, showing discontinuity between small, tabular crystallites in laminated zooecial wall and larger, more subtabular to granular crystallites in lunarial deposit in bottom center of figure. The lunarial deposit is laminated and has a large rib on its proximal side. Scanning electron photograph, SIUC 3002, ×650.

layer and outer, secondary laminated layers like the secondary basal layer of encrusting colonies.

Lunarial deposits in the Ceramoporidae have a dense, light-colored hyaline appearance under a light microscope, but indistinct, distantly spaced laminations are observable in some forms. One to several lighter colored, rod-shaped **lunarial cores** may extend longitudinally in a lunarial deposit and may extend above the general surface of the lunarium as knobs or spines (UTGAARD, 1968b, p. 1445). Indistinct laminations are concentric around the cores. Preliminary studies of the ultrastructure of the lunarial deposits reveal that some have a more granular, but still recognizably laminate ultrastructure (Fig. 150, 151), with slightly larger crystallites than the wall, and are compound. Some of the hyaline appearance may be due to a preferred orientation of the optical axes of the crystallites. Part of the lunarial deposit is secreted by zooidal epithelium on the distal side, where a thin, laminated zooecial lining may be later secreted, and part by epithelium on the proximal side of the lunarial deposit. Lunarial cores may be composed of crystallites that are coarser than those in laminated lunarial deposits (HEALY & UTGAARD, 1979, p. 184).

Acanthostyles with a dense, light-colored hyaline core surrounded by thin cone-in-cone laminae and spherical bodies of light-colored, dense hyaline calcite, surrounded by laminated wall material, are known from zooecial walls in two genera of Ceramoporidae (UTGAARD, 1968b, p. 1449, 1452). Their ultrastructure has not been investigated.

Basal diaphragms in zooecia in the Ceramoporina typically are simple. They are deposited by the zooidal epithelium on their upper side, and are laminated, with the laminae running parallel to the depositing epithelium. Terminal and subterminal diaphragms (UTGAARD, 1968b, p. 1445–1446; 1973, p. 328) have a dense hyaline microstructure, and their configuration indicates that they were deposited, primarily at least, from the inside. It is possible that they are compound, and were deposited from inside by the epithelium of a degenerated or resting zooid and from outside by the inner colonial epithelium beneath the hypostegal coelom. The ultrastructure of these diaphragms has not been investigated. The few funnel cystiphragms that have been found in ceramoporines are longitudinally laminated and simple, suggesting deposition by an epithelium lining the flask-shaped chambers or on one side of a membrane.

HEALEY and UTGAARD (1979, p. 185) have shown that communication pores in *Ceramophylla vaupeli* have a lining of laminae smaller than those in the zooecial walls. They indicate in addition that the skeleton of *Ceramophylla vaupeli* consists of ordinary, low-magnesium calcite, and has well-preserved original ultrastructure.

THE FISTULIPORINA

Fistuliporines display laminated, hyaline, granular, and granular-prismatic microstructures. Laminae are interpreted as having been deposited parallel to the secreting epithelium and essentially parallel to growth surfaces. Laminated skeleton is present in some basal layers, mesothecae, autozooecial walls, lunaria, vesicular tissue, stereom, basal diaphragms, terminal diaphragms, and funnel cystiphragms. All of these structures except autozooecial walls, lunaria, and mesothecae are of simple rather than compound construction. Laminated autozooecial walls are generally longitudinally laminate, and the laminae and zooecial boundary are indistinct. **Mural tubulae,** small calcite rods generally perpendicular to the wall surface, may be developed in autozooecial walls.

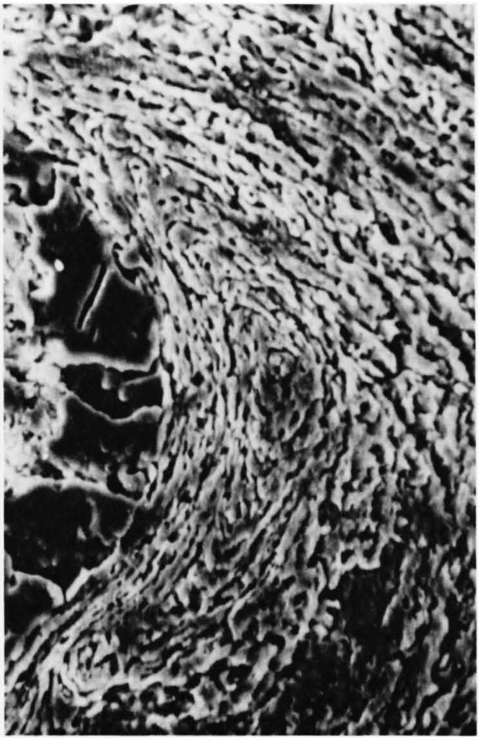

FIG. 151. Cystoporate skeletal structure. *Ceramophylla vaupeli* (ULRICH), McMicken Mbr., Eden F., U. Ord., Cincinnati, Ohio. Tangential section, etched, showing lunarial core with coarser crystallites, laminated lunarial deposit with tabular crystallites, and laminated autozooecial wall with tabular crystallites. Scanning electron photograph, USNM 159859, ×500.

Hyaline skeletal material is present in the lunarial deposits of some genera, in calcite rods (variously called acanthostyles, "acanthorods," "acanthopores," "minutopores," mural or median tubulae, and septa or canaliculi in the Actinotrypidae), and in calcite masses (yellow tissue in *Constellaria,* midray partitions in *Constellaria*). TAVENER-SMITH (1969b, p. 97; 1973), WILLIAMS (1971a), and HEALEY and UTGAARD (1979) have noted the granular ultrastructure of calcite rods or acanthostyles, which may be composed of large, irregular to rodlike crystallites. TAVENER-SMITH (1969b, p. 97) and WILLIAMS (1971a) have suggested that they served as attachment sites for muscles. They possibly

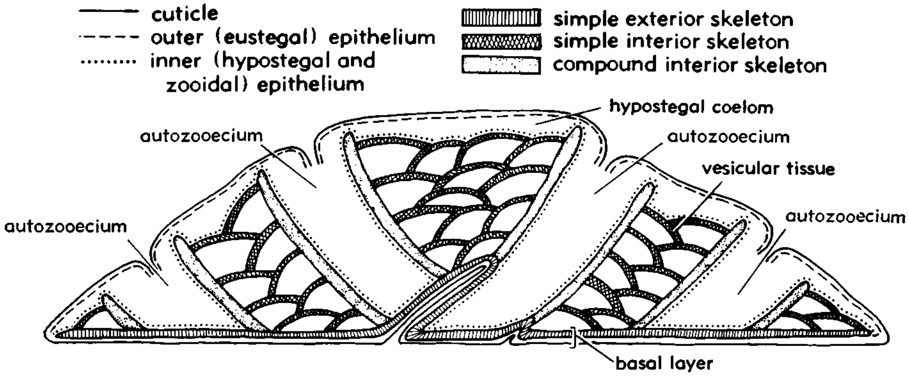

FIG. 152. Cystoporate skeletal structure. Longitudinal section through a hypothetical double-walled fistuliporine (after Utgaard, 1973). The basal layer is a simple exterior wall; all other walls are interior, that is, without an outer bounding membrane. Autozooecia have compound walls and the vesicular tissue is extrazooidal with simple walls secreted by the inner (hypostegal) epithelium immediately below the hypostegal coelom.

anchored the outer membrane of the double-walled colony (UTGAARD, 1973, p. 324).

Some fistuliporines have skeletal structures composed of a thick, primary, dark-colored granular layer. Many have a thin primary layer composed of granular or elongate crystallites and a thicker, secondary, light-colored granular-prismatic layer composed of granular, elongate, or prismatic crystallites with their long axis perpendicular to or nearly perpendicular to the secreting epithelium (HEALY & UTGAARD, 1979). This granular-prismatic microstructure has been interpreted as being secondary, due to recrystallization of the primary, presumably laminated, skeletal crystallites. Basal layers with this type of microstructure have a lower or outer primary layer, which may be thin and composed of fine dark granules. Presumably, a cuticle was secreted at the base of the colony and the primary granular layer was deposited on top of the cuticle (Fig. 152). In many forms, on top of this primary skeletal layer is the thicker secondary layer of granular-prismatic microstructure (Fig. 179,*1a*).

Mesothecae and vertical plates that divide a branch longitudinally or separate rows of autozooecia (compound range walls) are compound: a median primary layer that commonly is thin, dark, and granular is flanked by secondary layers that are lighter colored, commonly thicker, and are composed of granular-prismatic crystallites.

Autozooecial walls in Fistuliporina with granular microstructure are composed of dark granular material with no evident zooecial boundary. Those with granular-prismatic microstructure have a thin, dark, granular, primary layer containing the zooecial boundary, flanked by secondary, generally thicker, lighter colored, granular-prismatic layers secreted by zooidal epithelium and lining the autozooecial cavities of autozooecia that are in contact. More commonly, where an autozooecium is adjacent to vesicular tissue, the granular-prismatic layer adjacent to the vesicle was secreted by epithelium under the hypostegal coelom, which covered the outer rim of the peristome and extended down and onto the uppermost roof of the interzooidal vesicular tissue (Fig. 143). The secondary layer lining the autozooecial cavity is commonly thicker than the secondary layer formed on the outside of the peristome. The elongate and prismatic crystallites in the secondary layer generally are perpendicular to the zooecial boundary and the epithelium. In *Anolotichia* (UTGAARD, 1968a, p. 1039), elongate and prismatic crystallites fan out toward the zooecial aperture in rings of thickened autozooecial walls, somewhat similar to monilae in some trepostomates. The microstructure is reminiscent of orally diverging crystallites in the autozooecial walls in *Lichenopora*. In *Lichenopora*, however, the crystallites apparently are plates composing laminae diverging outwardly. In many fistuliporines the lateral and distal sides (but not the proximal or lunarial side) of some autozooecia lack a peristome and the zooidal epithelium sweeps in a gradual curve onto the last roof of extrazooidal vesicular tissue. In these autozooecia, part of the skeletal wall is made up of the vertical parts (or walls) of overlapping vesicles (Fig. 143). In tangential thin sections, these parts are commonly linear segments, each belonging to one vesicle. In longitudinal thin sections, these parts are serrated (Fig. 153). Such bounding walls are simple. They have a primary, dark, granular layer and, commonly, a secondary, light-colored granular-prismatic layer next to the zooidal epithelium. The secondary layer lining an autozooecial cavity may continue up into the secondary layer of a vesicle two or three vesicles toward the zooecial aperture (Fig. 153), indicating that the secondary layer may have been deposited considerably later than the adjacent primary layer.

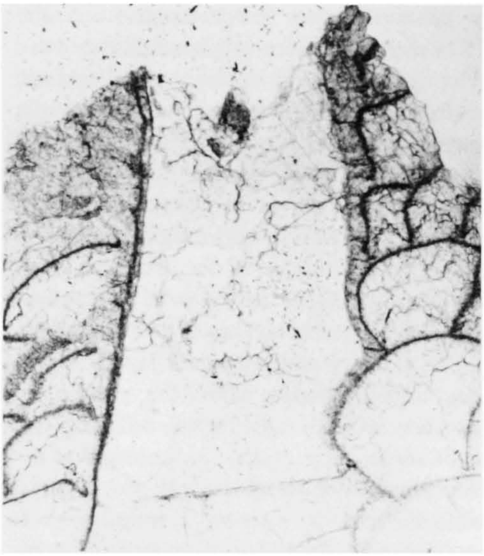

FIG. 153. Cystoporate autozooecial walls. *Meekopora clausa* ULRICH, Glen Dean Ls., Miss., Sloans Valley, Ky. Longitudinal section showing distal side of autozooecium (right) bounded by superimposed vertical vesicle walls. The light-colored, secondary, granular-prismatic layer is thicker in these vesicle walls than in the vesicle roofs to the right. SIUC 3000, ×100.

Lunarial deposits with granular-prismatic microstructure are of compound construction. The thin, dark, granular, primary layer of the lunarium may continue into the dark, granular, primary layer of the lateral and distal sides of the autozooecial walls (see Fig. 197,*1a*), or may terminate at the ends of the lunarial deposit adjacent to the zooecial cavity. In the latter case (see Fig. 180,*2b,c*), the dark granular primary layer and secondary layers of the lateral parts of the autozooecial wall unconformably abut the secondary proximal layer of the lunarial deposit. Commonly, the secondary layer of the lunarial deposit is relatively thin on the distal side of the lunarium adjacent to the zooidal epithelium, and has a granular-prismatic microstructure. The secondary layer on the proximal side of the lunarial deposit generally is thicker, has a granular-prismatic microstructure, and was lined by epithelium that generally sloped down off the lunarium and continued, below the hypostegal coelom, onto the outermost vesicle roof of the interzooidal vesicular tissue. Where autozooecia were adjacent, the epithelium on the proximal side of a lunarial deposit continued down into the zooidal epithelium of the adjacent autozooid.

In zoaria with a basal layer or mesotheca, new autozooecial walls were deposited as septa, which are unconformable on the basal layer or mesotheca (see Fig. 167,*1a*). The primary layer and the secondary layers, if present, of the autozooecial septa abut the basal structure. Elongate and prismatic crystallites in the secondary layers in the two structures are at right angles.

Extrazooidal vesicular tissue with granular or granular-prismatic microstructure is almost invariably simple. An inner, primary, relatively thin, dark, granular layer is always present and may constitute the entire vesicle. More commonly, it is covered by a thin to conspicuously thicker, light-colored, granular-prismatic layer. The skeleton of vesicular tissue must have been overlain and deposited by epithelium below the hypostegal coelom. In a few forms, for example, in *Lichenotrypa,* some vesicle walls form as septa on older vesicle roofs, and grow upward for a short distance before vesicle roofs are deposited between them. These short segments of vesicle wall are compound, with a central granular primary layer and lateral, secondary granular-prismatic layers.

The primary and secondary layers of vesicles unconformably abut the compound autozooecial walls (usually the secondary layers of autozooecial walls), indicating that the vesicles were deposited after the autozooecial walls. Further, the primary layer and, if present, the secondary layer of superjacent vesicles unconformably abut the upper surface of subjacent vesicles.

WILLIAMS (1971a), TAVENER-SMITH (1973), and TAVENER-SMITH and WILLIAMS (1972) suggested that all bryozoans with a calcified skeleton have a primary skeletal layer consisting of acicular crystals of calcite (rarely aragonite in some gymnolaemate bryozoans) and that all stenolaemates have a secondary layer that invariably consists of carbonate laminae, separated by protein sheets. These laminae consist of tablets commonly perpetuating screw dislocations or overlapping rows of fibers in spiral growth, typically the latter in the extinct orders. TAVENER-SMITH maintained (pers. commun., 1971), that the granular and granular-prismatic microstructures so common in fistuliporines are due to recrystallization. The gradual transition of crystals from the granular-prismatic layer into the obviously secondary sparry-calcite filling of zooecial and vesicle cavities, which is seen in some forms, seems to support the view that these microstructures are produced by recrystallization.

The following facts suggest that the granular and granular-prismatic microstructural types need further study. First, many fistuliporines consistently have granular and granular-prismatic skeletons, including the lunarial deposit (*Hexagonella, Dybowskiella, Crassaluna*), whereas others consistently have granular and granular-prismatic autozooecial walls and vesicles but hyaline lunarial deposits (*Fistuliphragma, Duncanoclema, Strotopora, Cliotrypa*). If the granular and granular-prismatic microstructure is recrystallized, then in specimens of the latter genera, only a part of the skeleton is recrystallized. Second, *Diamesopora subimbricatum* (HALL) from the Silurian, *Taeniopora exigua* NICHOLSON and *Canutrypa francqana* BASSLER from the Devonian, and *Cheilotrypa hispida* ULRICH from the Mississippian have granular-prismatic microstructure in the basal layer or mesotheca and in autozooecial walls and vesicles in the endozone, but have a laminated microstructure in the exozone. In the generally laminated exozone of *Canutrypa francqana,* distal cystlike structures consistently have a granular-prismatic microstructure. Third, BOARDMAN and CHEETHAM (1973, p. 147) reported that the Silurian tubuliporate *Diploclema sparsum* has interior walls that are well laminated but has simple exterior walls with a columnar structure (a primary granular and a secondary granular-prismatic layer).

It is unlikely that some skeletal layers would be consistently recrystallized and others would not, if in fact they invariably consisted of carbonate laminae, particularly if the layers were of the same composition. The consistency of the change from granular-prismatic microstructure in the endozone to laminated microstructure in the exozone suggests a real ontogenetic change in original skeletal ultrastructure or composition and not vagaries of recrystallization. At this time, it seems premature to assume that all stenolaemates had laminated secondary layers. It is possible that elongate, prismatic, or acicular crystals could have been primary crystallites deposited perpendicular to the secreting epithelium. WARNER and CUFFEY (1973, p. 23) also suggested this possibility. The granular-prismatic microstructure of many fistuliporines resembles that of originally laminated, high-Mg calcite that recrystallized to low-Mg calcite in a cheilostomatous bryozoan

(SANDBERG, 1975a). Thus, it possibly was produced by recrystallization of originally laminated calcite. HEALEY and UTGAARD (1979, p. 190–193) found evidence for this in *Cystodictya* where the laminated mesotheca, composed of granular to mostly tabular crystallites of high-Mg calcite arranged in laminae, locally displays granular and granular-prismatic ultrastructure and microstructure, probably as a result of local recrystallization.

Even if the granular and granular-prismatic microstructures were produced by recrystallization, the relationship between the two layers indicates continued thickening of the secondary, granular-prismatic layer after the primary granular layer was formed. The microstructures of different skeletal parts also strongly suggest unconformable relationships. These permit reconstruction of the order of deposition of different skeletal parts and of the changes in configuration of the secreting epithelium.

DOUBLE-WALLED GROWTH MODEL

BORG (1926b) described the double-walled nature of the lichenoporid and hornerid tubuliporates (see free-walled colonies, BOARDMAN, this revision) and suggested (p. 596) that the trepostomates had the same kind of body wall. BORG thought that it would be impossible to demonstrate this positively in fossils. Again, BORG (1926a, p. 482) stated that it was evident that the Trepostomata are more closely related to the double-walled tubuliporates than to the single-walled tubuliporates. ELIAS and CONDRA (1957, p. 37–38) alluded to the "sclerenchyma" in fenestrate cryptostomates and in trepostomates as apparently being deposited in the same manner as in *Hornera* and related tubuliporates, that is, by an ectoderm that stretched externally over the whole zoarium. Thus, they surmised that fenestrates had a double wall and proposed the new order Fenestrata, to be included with the orders Cyclostomata (here called Tubuliporata) and Trepostomata in BORG's class Stenolaemata. In a posthumous publication, BORG (1965, p. 3) stressed the relationship of the Fistuliporidae to the Lichenoporidae and the Trepostomata to the Heteroporidae and stated that he had succeeded in showing that they had a covering of soft tissue over the entire colony surface. TAVENER-SMITH (1968, p. 86, 88, 89; 1969a, p. 291) used the double-walled concept described by BORG as a basis for construction of a double-walled model for fenestellid growth. BOARDMAN (BOARDMAN & CHEETHAM, 1969, p. 209, 213) suggested that the double-walled concept of BORG could be extended to most fossil tubular bryozoans (notably the Trepostomata, Cryptostomata and Cystoporata) and later presented (BOARDMAN, 1971, p. 6–7) a more detailed account of the double-walled concept as applied to trepostomates. In addition BOARDMAN (1973) discovered the fossilized remnant of the external cuticle on the outer surface of a colony of a trepostomate from the Ordovician: the most direct proof yet of the double-walled nature of a Paleozoic bryozoan.

THE DOUBLE-WALLED CONCEPT AS A MODEL FOR THE CYSTOPORATA

The presence of new autozooecia budded in the exozone in virtually any part of the colony in many cystoporates, on old autozooecial walls or on extrazooidal vesicular tissue, is strong evidence that cystoporates are double-walled bryozoans with a cuticle surrounding the entire colony. In many fistuliporines, autozooecia are isolated or partially isolated at the basal layer by intervening extrazooidal vesicular tissue. The presence of these new autozooids, isolated from their neighbors, also suggests colony-wide budding control by an outer membrane, rather than direct parent-daughter autozooecial origins. In addition, autozooecial walls in most cystoporates are compound walls, as are interior walls of modern tubuliporates, secreted under an infolding of inner epithelium into a hypostegal coelomic cavity.

The relatively uniform level of the outer surface (exclusive of the basal layer) of cystoporate colonies suggests a colony-wide epithelium and colony-wide control of growth. The only projections are relatively short calcite rods (acanthostyles and tubulae), some vesicle walls, vertical plates, autozooecial peristomes, and lunaria. Projections of similar magnitude are known in modern double-walled lichenoporids and hornerids. Individual, isolated autozooecia do not project significant distances above the general surface of the colony in cystoporates as they do in some single-walled tubuliporates. Growth of interior walls continued at nearly the same rate over the entire frontal surface of the colony.

The nature of the extrazooidal vesicular tissue and stereom in the Fistuliporina strongly suggests a double-walled construction. First, there is no space of relatively constant volume and shape and commonly no space for zooids in the vesicular tissue. In only a few species did vesicle walls form before vesicle roofs. In most species, vesicle walls and roofs are essentially one, curved structural unit. Thus, vesicular tissue is extrazooidal and must have required physiological communication with feeding zooids for nutrients. Second, thick vesicle roofs or stereom at the zoarial surface or in abandoned zones in the exozone indicate deposition from one epithelium on the outside of vesicles. Third, most vesicle walls and all vesicle roofs are simple walls. Some workers have reported pores in vesicle roofs and walls, but such pores are extremely rare. The simple-walled nature of vesicles suggests that they contained no living tissue, at least no secretory epithelium, and were not zooids. For that reason they are not, as BORG (1965) suggested, structures similar to alveoli in lichenoporid tubuliporates. The development of autozooecial walls on the outer side of vesicle roofs in the exozone also indicates that an epithelium existed on the outer side of the vesicles. This epithelium would almost have to be nourished by a coelom that was, in turn, protected from the environment by an outer membrane.

A possible membrane remnant is preserved over the zooecial orifice and extends over the vesicular tissue beneath an overgrowth (UTGAARD, 1973, p. 323) on a colony of *Cheilotrypa hispida*.

Utilizing the double-walled concept of growth for the Cystoporata (Fig. 142, 143, 145, 152), it is probable that the inner epithelium (the zooidal and hypostegal epithelia of authors) secreted all of the calcareous skeleton. The outer (eustegal) epithelium secreted only the cuticular cover on the upper surface of the colony (the surface excluding the basal layer), including the terminal-vestibular membranes of the zooids.

ZOARIAL FORM AND LOCUS OF BUDDING

The Cystoporata display a wide variety of zoarial growth habits, including some that are unique as well as nearly all those exhibited by other tubular bryozoans in the orders Trepostomata, Cryptostomata, and Tubuliporata (BOARDMAN & CHEETHAM, 1969, p. 206). Zoarial growth form in various Paleozoic tubular bryozoans has been discussed by ULRICH (1890, p. 294–296) and ROSS (1964b, p. 932–934), among others, and a good summary of growth forms in the Fistuliporidae was presented by MOORE and DUDLEY (1944, p. 248–250, 258–264). BORG (1965), BOARDMAN and UTGAARD (1966), and MCKINNEY (1977b) discussed budding and three-dimensional packing of autozooecia in some Paleozoic tubular bryozoans. More work is needed on details of the location and geometry of budding or septa formation, the three-dimensional geometry of autozooecia, zooecial polymorphs and extrazooidal structures, and on the packing of the individual components (colony construction) and their relationship to zoarial growth form. As Boardman (Boardman & Cheetham, 1969, p. 216) pointed out, mere reference to the growth form without references to the internal architecture and budding patterns does not distinguish between colonies that may have similar growth habits but significantly different internal construction. For example, the cystoporate genera *Botryllopora, Ceramopora,* and *Fistulipora* and the post-Paleozoic tubuliporate *Lichenopora* can all assume a small, subcircular, discoidal growth form with an encrusting base and one central monticule with autozooecia radiating out from the center of the colony. This superficial resemblance in colony form masks important differences in the location and details of budding of autozooecia and exilazooecia and the geometry and packing of zooecia and any extrazooidal structures. Some information of this nature is available for the Cystoporata, and it is adequate to provide a general summary.

Encrusting sheetlike zoaria.—In encrusting sheetlike zoaria (see Fig. 157,*1b*; 159,*1a,d,g*; 181,*1a,b*), autozooecia originate by septal formation within a fold of epithelium on top of the calcified basal layer around the growing margin of the colony (Fig. 142, 152). In the Ceramoporina, autozooecia typically are narrower at the basal layer than in the exozone, are hemispherical in cross section at the basal layer, and display a keel and sinus (Boardman & Utgaard, 1966, fig. 2, 3) in the outer recumbent portion and at the zooecial bend (see Fig. 159,*1a,f*). Exilazooecia originate by septal formation in the outer endozone or inner exozone (see Fig. 158,*1a*; 159,*1a*) so that only autozooecia are in contact with the basal layer. A similar situation, where only autozooecia and not exilazooecia originate at the basal layer, is found in the order Trepostomata. In contrast, in the suborder Fistuliporina of the order Cystoporata, extrazooidal vesicular tissue can originate at the basal layer and partly to completely isolate the autozooecia (see Fig. 181,*1a,b*). Autozooecia may be narrow to full width and may have keels and sinuses. New autozooecia rarely develop except at the basal layer in most encrusting sheetlike zoaria in Cystoporata. In some zoaria of *Ceramopora,* where free margins extend beyond the encrusted substrate (Utgaard, 1969, p. 289–290), autozooecia originate lateral to the basal layer and above skeletal tissue associated with polymorphs in a celluliferous base (Fig. 145).

Fig. 154. Cystoporate autozooecial budding. *Fistulipora waageniana* Girty, Wu-shan Ls., Penn., near Daning Xian, China. Longitudinal section showing an autozooecium with a short, recumbent initial portion budded on top of extrazooidal vesicular tissue. USNM 61922, ×50

Hemispherical and massive zoaria.—In hemispherical and massive zoarial growth forms (see Fig. 161,*1c*; 163,1*a*; 170,*1c*) autozooecia originate at the growing periphery of the colony on the basal layer, as in encrusting sheetlike zoaria. In the Ceramoporina, they may also originate by septal formation on autozooecial walls over the entire upper surface of the colony (see Fig. 161,*1b*), so that new autozooecia are intercalated between older autozooecia in the exozone. The new autozooids reach a maximum diameter in a relatively short distance (two to three autozooecial diameters) above their point of origin. In addition, new autozooecia may also originate by septal formation on top of old extrazooidal vesicular tissue (Fig. 143, 154) in the Fistuliporidae.

Hollow ramose zoaria.—In hollow ramose zoaria in the Ceramoporidae, autozooecia originate by septal formation near the leading edge of the cylindrical basal layer. They generally have a narrow hemispherical outline and a keel and sinus in the zooecial bend region (see Fig. 160,*1g*). As in the encrusting sheetlike zoaria, only autozooecia are in contact with the basal layer. In thicker colonies, new autozooecia may originate between old autozooecia in the exozone, over the entire zoarial surface, by formation of new septa on autozooecial walls.

In Fistuliporidae with hollow ramose growth forms (see Fig. 175,*2c*; 177,*2d*; 179,*1c*), autozooecia originate at the growing edge of an irregular, tubular basal layer by formation of new septa on the basal layer. Unlike other growth forms in the Fistuliporina with a basal layer, autozooecia are not isolated at the basal layer by vesicular tissue, but vesicular tissue does partly isolate the autozooecia at the basal layer in encrusting overgrowths of some hollow ramose forms. In some forms with wide exozones, such as some *Dybowskiella,* new autozooecia may originate in the exozone by septa formation on old vesicular tissue. At the basal layer, autozooecia originate in linear series and generally are arranged rhombically in deep tangential sections in the outer endozone. Preliminary investigation suggests that significant differences in autozooecial geometry and packing exist in different genera. For example, species of *Diamesopora* have hemispherical to subtriangular autozooecial cross sections at the basal layer, with the base of the triangle resting on the basal layer (see Fig. 179,*1c*), whereas in *Cheilotrypa* the autozooecial cross section is mushroom-shaped to subtriangular with a flattened point of the triangle resting on the basal layer (see Fig. 175,*2a*). In many examples of *Cheilotrypa,* the hollow axial tube displays regularly spaced expansions and contractions (see Fig. 175,*2f,g*) and, in some, the hollow axial tube is present distal to a cylindrical encrusted object, such as a rhomboporoid bryozoan. Such variations in the hollow axial tube and autozooecial shape and packing suggest that there is more taxonomic diversity in hollow ramose growth forms than has previously been suspected and that species should not be uncritically referred to a genus merely because they have a hollow ramose growth form.

Solid ramose zoaria.—In solid ramose growth forms, new autozooecia originate between older autozooecia by formation of new septa on autozooecial walls at the growing tip of the colony. New septa are formed at the growing tip in what becomes the endozone, or axial region of the branch.

In some Ceramoporina (Utgaard, 1968b, p. 1448) with solid ramose zoaria, rather thick-walled autozooecia reach their full diameter in a distance of about one or two autozooecial diameters. Exilazooecia originate in the inner exozone.

In some solid ramose *Constellaria* (McKinney, 1975, p. 70, 71; 1977b, p. 323–326), new autozooecia originate in the corners of distally expanding polygons in an irregular to orderly fashion, the most orderly resulting in autozooecia that are triangular in cross section. Autozooecia in the endozone, particularly in *Constellaria,* generally have a larger diameter than they do in the exozone. Autozooecia narrow in the zooecial bend region and many new autozooecia are produced here by septal formation on old autozooecial walls. In addition, extrazooidal vesicular tissue, which may be present or absent in the endozone of ramose zoaria, is formed at the zooecial bend region so that autozooecia may be partially or completely isolated in the exozone by vesicular tissue. Autozooecia generally have a circular cross section in the exozone. In one species from the Baltic, identified as *Constellaria varia* Ulrich by Bassler (1911, p. 220), endozonal autozooecia are very large and flare toward the zoarial surface. They are crossed by diaphragms that are at nearly the same level in adjacent autozooecia, and in curved zones representing abandoned growing tips. Some new septa in the inner endozone and in the zooecial bend region are formed on these diaphragms (also see McKINNEY, 1977b, p. 320). Thus, in this form, monticular components, including zooids, are budded in the monticules in the exozone. In addition, one new zooecial septum has been observed forming on a diaphragm in an autozooecium in the exozone of a Middle Ordovician *Constellaria* from Kentucky (Fig. 155).

In Fistuliporidae that have solid ramose growth forms, new autozooecia are produced by septa formation on old autozooecial walls at the growing tip of the colony, which becomes the axial endozone. In the endozone, autozooecia have a cross-sectional shape that commonly displays a keel and sinuses on the distal and lateral sides and a rounded proximal side when the lunarium is developed. McKINNEY (1975, p. 70; 1977b, p. 320, pl. 8, fig. 2) has determined that in *Canutrypa,* new autozooecia originate in the trough of the keel of the parent autozooecium. Autozooecia are in complete contact or may be isolated by large, elongate blisters of extrazooidal vesicular tissue. New autozooecia can originate in wide exozones by new septa formation on old vesicular tissue.

Slender ramose zoaria of *Fistulocladia* have a cylindrical central endozone composed of narrow, tubelike vesicles with flat vesicle roofs and circular cross section. The central endozone has cyclical zones of stereom. Autozooecia are budded off the flanks of the central cylinder, where they are narrowly isolated by stereom, and are circular in cross section (see Fig. 186,*1c*).

Frondescent zoaria.—In frondescent growth forms—erect, leaflike **frondose colonies**—in some species of *Ceramoporella* (UTGAARD, 1968b, p. 1450–1451), new autozooecia originate at the growing tip, in the endozone, by formation of new septa on autozooecial walls. New autozooecia have a long endozonal portion where they parallel older autozooecia, and they reach their normal diameter in a distance of from two to four zooecial diameters. Autozooecia reach their maximum diameter in the inner endozone, where they have a cross-sectional shape that ranges from hemispherical to irregularly polygonal, but commonly with a rounded proximal side where the lunarium is developed. In the outer endozone, autozooecia display a crude rhombic packing, have sinuses and a keel, and a rounded proximal side where the lunarial deposit is situated. The few frondescent Ceramoporidae known so far display a marked reduction in autozooecial diameter from the inner endozone to the exozone and, for the most part, the autozooecia lose their rhombic arrangement in the exozone.

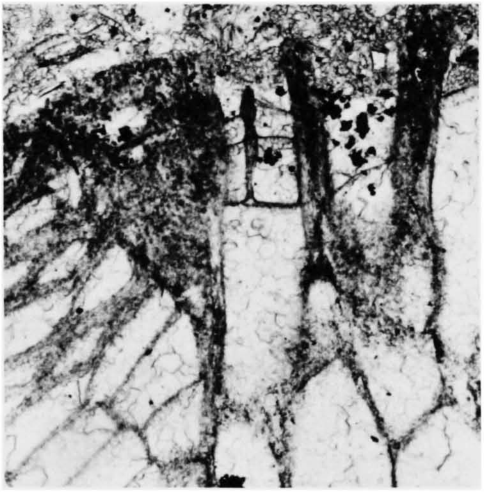

FIG. 155. Cystoporate autozooecial budding. *Constellaria* sp., M. Ord., Mason Co., Ky. Longitudinal section showing new compound zooecial wall produced by septum formation on a basal diaphragm; vesicular tissue to left. USNM 159858, ×100.

Frondescent Constellariidae are similar to ramose Constellariidae.

Bifoliate, trifoliate, and multifoliate zoaria.—In bifoliate zoaria of *Ganiella* and *Ceramophylla* (see Fig. 158,*1a,d*) in the Ceramoporidae, autozooecia originate at the growing margin of the mesotheca by formation of new septa on the mesotheca. As in the basal layer of encrusting sheetlike and hollow ramose zoaria, only autozooecia are in contact with the mesotheca of these bifoliate zoaria; autozooecia are narrow and hemispherical in cross section and a keel and sinuses are developed in the zooecial bend region.

The Fistuliporina display a wide variety of bifoliate, trifoliate, or multifoliate growth forms. Bifoliate zoaria generally are compressed in the plane of the mesotheca and include branched or unbranched frondose forms, **cribrate colonies** with anastomosing branches and large, subcircular fenestrules (Fig. 198,*1b*; 212,*2*), and straplike forms, the latter being regularly or irregularly branched or anastomosing, forming an **anastomosing colony**. One (see Fig. 206,*1b*) has an **articulate colony**, with flexible joints at dichotomous branchings. Trifoliate forms are narrow with parallel sides and can have regularly or irregularly developed trifoliate branches. Most branching is in the plane of the mesotheca; less commonly frondose bifoliate or narrow trifoliate forms have branches perpendicular to the mesotheca. Multifoliate colonies have a central multifoliate portion with radiating bifoliate branches. New autozooecia arise at the growing edge of the mesotheca by septal formation on the mesotheca.

In Hexagonellidae, autozooecia have relatively long, narrow, recumbent portions and are hemispherical in cross section. They may be partly contiguous, with partial keel and sinus development, or isolated by extrazooidal vesicular tissue. Autozooecia are more commonly contiguous with adjacent autozooecia in longitudinal ranges and may be teardrop- or club-shaped in outline at their contact with the mesotheca. The ranges are not separated by compound range walls in the endozone or exozone.

In the Cystodictyonidae, autozooecia range from partly isolated and almost entirely contiguous to completely isolated by vesicular tissue. Compound range walls, which arise on the mesotheca, separate ranges of autozooids. Autozooecia generally have a narrow proximal end and a club- to teardrop-shaped outline at their contact with the mesotheca (see Fig. 205,*1f*; 207,*1e*). Many genera display right- and left-handed autozooecia, and branches have a plane of bilateral symmetry perpendicular to the mesotheca. Some forms have a pronounced compound vertical plate (librium) in the plane of symmetry.

The Goniocladiidae have cylindrical to laterally compressed branches with a "vertical" mesotheca extending from the center of a reverse side, where it protrudes, forming a ridge or carina, to the center of an obverse side of a branch. Primary branches may have secondary and tertiary branches (generally perpendicular to the plane of the mesotheca), which are paired and laterally or distolaterally directed or alternating and distolaterally directed. Secondary and tertiary branches may fuse to produce reticulate, fenestrate, or pinnate growth forms. New autozooecia arise by septal formation on the mesotheca, at the growing tip of the branch. At the mesotheca, they are partially isolated by vesicular tissue, are hemispherical in cross section, and may have keels and sinuses developed. They curve distally and laterally to open on the rounded to sloping flanks of the obverse surface, in indistinct ranges.

Autozooecia originating on a basal layer or mesotheca in radial or linear series commonly alternate in adjacent ranges so that a basically rhombic packing pattern is achieved. This arrangement is commonly retained into the exozone to produce a rhombic or subrhombic surficial arrangement of autozooecia in large to small areas of a colony.

Little information is available for some genera of Cystoporata and much work is needed on details of autozooecial budding.

Ancestrula and astrogeny.—Virtually no details of the ancestrula, its shape and development, or the early astogenetic development of cystoporate colonies are known. Evidently most encrusting cystoporate zoaria have narrow, subcircular primary zones of astogenetic change (Boardman & Cheetham, 1969, p. 208), and the colony consists mostly of the primary zone of astogenetic repetition

(Boardman, Cheetham & Cook, 1970, p. 302). Subsequent zones of astogenetic change would be represented, for example, by development of branches in a plane other than the plane of the mesotheca in bifoliate fistuliporines. It is likely that the cystoporates had a funnel-shaped early stage (see Fig. 168,*1d*), like the lichenoporids. The early funnel-shaped stage is covered by later parts of the zoarium. The study by Perry and Hattin (1958) provides almost the only quantitative information to date on changes in the size and spacing of autozooecia along ontogenetic gradients in a portion of a large colony.

CLASSIFICATION

Genera here included in the order Cystoporata have commonly been placed in three orders; Tubuliporata (formerly Cyclostomata), Trepostomata, and Cryptostomata. The first edition of this *Treatise* (Bassler, 1953) and *Fundamentals of Paleontology* (Sarycheva, 1960) generally reflect the classifications used in the first half of this century. Bassler (1953), included the Ceramoporidae, genera now included in the Anolotichiidae, Fistuliporidae (including the Botrylloporidae), Hexagonellidae, and Goniocladiidae in the suborder Ceramoporoidea and order Cyclostomata (now Tubuliporata). The Constellariidae were included in the order Trepostomata. The Sulcoreteporidae (=Cystodictyonidae), Rhinoporidae, and Actinotrypidae were included in the order Cryptostomata. Bassler further included most of the more obviously fistuliporine bifoliates (that is, those with extensive vesicular tissue) in the Cyclostomata (now Tubuliporata) and the less obviously fistuliporine bifoliates (that is, those with fewer vesicles and more stereom) in the Cryptostomata. The classification in Sarycheva (1960) is similar but the Hexagonellidae and Goniocladiidae were included in the Cryptostomata, which thereby contained nearly all bifoliate fistuliporines.

Astrova (1964) established the order Cystoporata to include the Ceramoporidae and Dianulitidae in the suborder Ceramoporoidea and the Constellariidae and Fistuliporidae in the suborder Fistuliporoidea of the order Cystoporata. Utgaard (1968a, p. 1035) suggested that the order Cystoporata should include the Ceramoporidae, Anolotichiidae, Fistuliporidae, Hexagonellidae, and possibly the Lichenoporidae. The latter family of post-Paleozoic tubuliporates shows some features, probably produced by convergence, in common with the Cystoporata but most likely are not living cystoporates. Further increase in the content of the order Cystoporata was suggested (Utgaard, 1973, p. 319) and the Cystoporata was expanded to include the Ceramoporidae in the suborder Ceramoporoidea and the Constellariidae, Anolotichiidae, Fistuliporidae, Hexagonellidae, Goniocladiidae, Botrylloporidae, Actinotrypidae, and some genera in the Sulcoreteporidae (=Cystodictyonidae) and Rhinoporidae in the suborder Fistuliporoidea. Morozova (1970) proposed the suborder Hexagonelloidea to include the bifoliate cystoporates in the Hexagonellidae, Goniocladiidae, Sulcoreteporidae (=Cystodictyonidae), and Etherellidae.

PRESENT CLASSIFICATION

In this *Treatise,* the order Cystoporata Astrova, 1964 is considered to contain two suborders, Ceramoporina Bassler, 1913 and Fistuliporina Astrova, 1964. The Ceramoporina contains only the family Ceramoporidae Ulrich, 1882. The Fistuliporina contains eleven families: Anolotichiidae Utgaard, 1968a; Xenotrypidae Utgaard, new family; Constellariidae Ulrich, 1896; Fistuliporidae Ulrich, 1882; Rhinoporidae Miller, 1889; Botrylloporidae Miller, 1889; Actinotrypidae Simpson, 1897; Hexagonellidae Crockford, 1947; Cystodictyonidae Ulrich, 1884; Etherellidae Crockford, 1957, and Goniocladiidae Waagen & Pichl, 1885.

The Cystoporata is a rather heterogenous order. It includes a variety of growth forms and wall microstructures. In many important respects it resembles other orders, notably the Trepostomata and Cryptostomata of the class Stenolaemata. The major, unifying characters of the Cystoporata are the tubular autozooecia and the lunarium in most, but not all genera and families. No single character separates cystoporates from all other Bryozoa and thus, the classification used here is polythetic. Cystoporates differ from other Paleozoic stenolaemates in generally having a lunarium and generally possessing either communication pores, extrazooidal vesicular tissue, or stereom. Autozooecia may be long and tubular with diaphragms, resembling those in most trepostomates, or relatively short and tubular without diaphragms, resembling some cryptostomates.

The suborder Ceramoporina with one family contains forms having most or all of the following features: well-laminated walls, exilazooecia, communication pores, and lunaria. They do not have extrazooidal vesicular tissue or stereom and most do not have acanthostyles.

The suborder Fistuliporina with eleven families contains forms having extrazooidal vesicular tissue or stereom. Most have lunaria, and in most zoarial growth forms the autozooecia are partially to completely isolated at the budding surface by vesicular tissue. They lack communication pores and exilazooecia. Some, such as the Goniocladiidae, are monothetic; many others are polythetic.

Arrangement of families of Fistuliporina in the systematic descriptions is in order of first stratigraphic occurrence and, except for the Etherellidae, does not represent presumed phylogenetic relationships.

STRATIGRAPHIC DISTRIBUTION

This summary of stratigraphic distribution should be used with caution. It is based upon ranges of genera that are given with the systematic descriptions. Some reported occurrences were difficult to evaluate, and ranges used in this discussion are based only on specimens available to me and on available illustrations in which I had reasonable confidence. Cystoporates show good biostratigraphic potential but need further study to increase their usefulness.

Cambrian.—Cambrian fossils reported to be Cystoporata are either unrecognizable or belong to other taxa. No undoubted Cambrian cystoporates are known.

Ordovician.—The Ordovician was the time of origin and flourishing of four families of Cystoporata; the Ceramoporidae, Xenotrypidae, Constellariidae, and Anolotichiidae. Species in all families, but particularly the Ceramoporidae and Constellariidae, are potentially useful in stratigraphic studies of Ordovician rocks.

The oldest known cystoporates, the Lower Ordovician genera *Lamtshinopora* and *Profistulipora,* are members of the family Anolotichiidae and the suborder Fistuliporina. Both are known only from the Soviet Union. A questioned occurrence of *Xenotrypa* has been reported from the Lower Ordovician of the Baltic region.

Middle Ordovician rocks have yielded six described genera of Ceramoporidae, three genera of Anolotichiidae, two genera of Constellariidae, and one Xenotrypidae.

The Ceramoporidae continued to flourish during the Late Ordovician, with seven known genera. Two genera of Anolotichiidae and one constellariid have species reported from Upper Ordovician rocks.

Silurian.—The Silurian apparently was a time of transition for the Cystoporata. The Ceramoporidae were on the decline, with only three known genera. No undoubted

Anolotichiidae has been reported from Silurian rocks and the last genus of the Xenotrypidae and of the Constellariidae are known. The small family Rhinoporidae is known only from the Lower and Middle Silurian. In addition, six genera of the family Fistuliporidae occur in rocks of Silurian age, with two genera reported in the Lower Silurian and four genera in the Middle and Upper Silurian.

Devonian.—The Devonian yields the youngest representative of the Ceramoporidae and of the Anolotichiidae. The greatest generic diversity in the Fistuliporidae, 13 genera in the Middle Devonian, and the occurrence of the sole representative of the Botrylloporidae in the Middle Devonian, are also recorded. The origin and expansion of bifoliate Hexagonellidae and Cystodictyonidae took place during the Devonian, with five hexagonellid genera and seven or eight genera of the Cystodictyonidae being represented in the Middle Devonian. It was the time of greatest diversity for the Cystodictyonidae. The greatest number of cystoporate genera (26 or 27) have been reported from Middle Devonian rocks.

Mississippian.—Rocks of Mississippian age have yielded at least four or five genera of the Fistuliporidae, the earliest representative of the Actinotrypidae, five genera of Hexagonellidae, three genera of Cystodictyonidae and four, possibly six, genera of Goniocladiidae, the oldest representative of the latter family. During the Mississippian, dominance changed from encrusting, massive, and ramose colonies to erect bifoliate, trifoliate, and multifoliate forms.

Pennsylvanian.—The Pennsylvanian has yielded only a few Fistuliporidae: one or two genera. The Hexagonellidae, with three genera, and the Cystodictyonidae, with one genus, declined. The Goniocladiidae have at least three, possibly five, genera from Pennsylvanian rocks.

Permian.—Three new genera of Fistuliporidae increased the total to five genera known from Permian rocks. Two new genera of Actinotrypidae and three new genera of Hexagonellidae evidence a slight revival of those families during Permian time. One Cystodictyonidae is known from the Lower Permian and the two genera in the poorly known family Etherellidae may be cystodictyonids. The Goniocladiidae reached their greatest diversity with six genera known from the Permian. No undoubted post-Paleozoic cystoporates are known.

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