ZOOID AND COLONY GROWTH IN ENCRUSTING CHEILOSTOME BRYOZOANS

by SCOTT LIDGARD

ABSTRACT. An initial comparison of growth patterns of encrusting cheilostome bryozoans reveals that the ways by which zooids and colonies grow are often important determinants of the comparative success of different species and colony forms among different habitats. These patterns appear to have changed in a major evolutionary trend, increasing morphological and taxonomic diversity, and causing the appearance of more versatile and more highly integrated modes of growth through time. The growth of colonies in encrusting cheilostomes can be regarded in terms of different processes and geometries of zooid budding. I present here a model of growth based on bud expansion, partitioning, and position. The model permits reconstruction and comparison of different modes of growth in both living and fossil colonies.

SOLITARY and colonial animals grow in very different ways. In most solitary animals, individuals are physically separate and genetically different. In contrast, the units (zooids, polyps, etc.) of a colonial animal, whose structure and development are most comparable to solitary individuals, are all physically connected and have the same genotype. Bryozoan colonies can grow into many different forms by altering the direction and rate of zooid origination and growth, with some colonies even changing form during different stages of growth. Colonies of species with different patterns of zooid development often have the same overall form. It therefore seems reasonable to assume that bryozoan evolution involves changes in developmental patterns of both zooids and colonies. Little is known, however, of the extent to which these factors are interdependent.

Differences in the ways in which zooids and colonies grow are important not only in understanding the evolution of form, but also in understanding the ecology of species in different habitats. Moreover, these differences can be related to evolutionary changes in the distribution and abundance of taxa through time. Most bryozoans and other colonial animals are sessile, so movement to escape competition, predation, or injury is accomplished only by growth or, in successive generations, by arval dispersal. Consequently, the way a colony grows can profoundly affect how successfully it occupies space and competes for resources, or the likelihood of its surviving predation or injury Jackson and Buss 1975; Buss 1979, 1980, 1981; Jackson 1979*a*, *b*, 1981, 1983; Jackson and Palumbi 1979; Jackson and Winston 1981). The appearance of new modes of growth in the fossil record apparently resulted in several major evolutionary trends in encrusting colony form, altering patterns of species richness and local abundance, and also apparently shifting the balance of competition among encrusting species by introducing new mechanisms for competitive overgrowth (Lidgard and Jackson 1982; Lidgard 1983; see also Jackson 1981 and references therein). The ecological structure of living faunas of encrusting cheilostomes is in many ways a culmination of successive evolutionary changes: a progressive trend towards increasingly varied and more versatile modes of growth.

Attempts to generalize about modes of colony growth have been characterized by a tendency to extrapolate from detailed studies of one or a few species. However, the cumulative diversity of modes of growth revealed by previous studies (e.g. Lutaud 1961, 1983; Schneider 1963; Banta 1968, 1969, 1970, 1971, 1972; Gordon 1971*a*, *b*; Hakansson 1973; Silen 1982; and others) has demonstrated the need for a more synthetic approach (Cheetham and Cook 1983).

Zooids within colonies form sequentially, preserving a morphological record of growth in both the zooid skeleton and that of the colony as a whole. This second record relates to an additional level of development not present in solitary animals, reflecting a pattern of overall growth of the colony as

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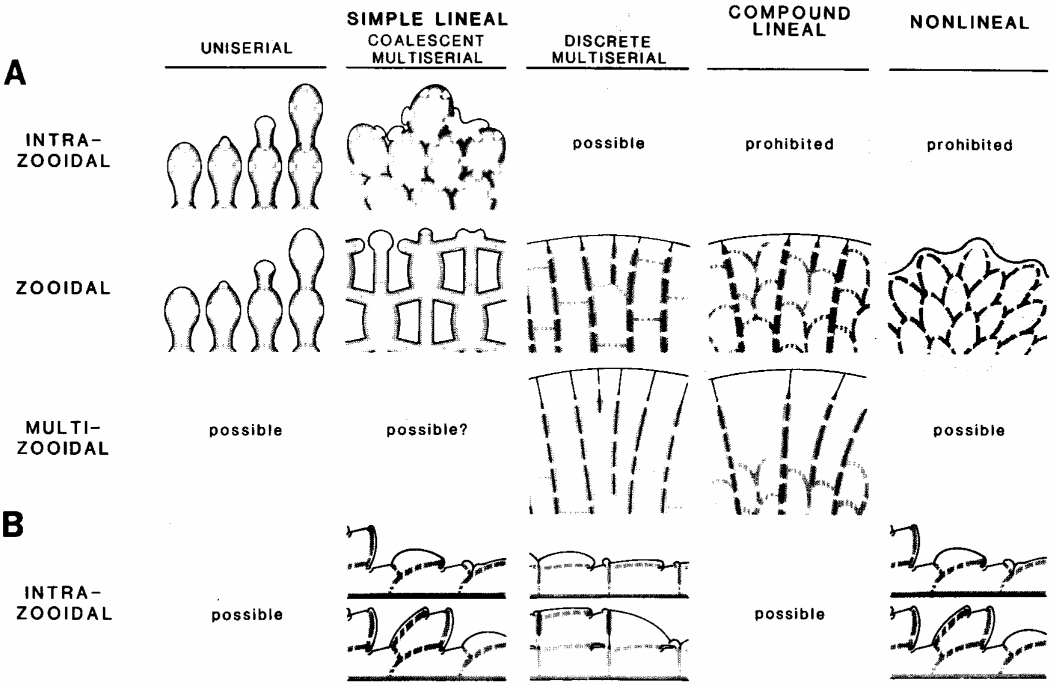
well as the ontogeny of individual zooids. Within a given colony a nearly complete sequence of zooid ontogeny can be reconstructed by comparing zooids at different stages of development. While growth of colonies is obviously linked to the formation of new zooids it may not be rigidly dependent on all aspects of zooid ontogeny. Colony development may actually exert some degree of control over zooid development, for example by determining the geometric arrangement of zooids or the rate at which successive ontogenetic stages are reached. This relationship between zooid and colony development has remained remarkably flexible throughout the history of cheilostomes.

In this paper I present a model of growth for encrusting cheilostomes (text-fig. 1). The model is primarily descriptive rather than predictive, being a means of reducing the inherent variability and morphological complexity of growth to relatively few elemental structures and processes. The model is a simple matrix of possible combinations of budding processes and geometries (Lidgard, in press). The different combinations do not represent individual species, but rather morphogenetic states that may occur singly or in combination within a single species or a single colony. For example, a given species may initially encrust a substrate by single-layered sheet-like growth, then develop a mound-like form by multilayered growth. Recognizing which combinations are shared by different taxa and which ones may be prohibited by structural, functional, or developmental constraints can only be accomplished empirically by determining boundary conditions from budding morphologies in a wide range of species, and not from *a priori* consideration of the patterns themselves (Boardman and



TEXT-FIG. 1. Growth model for encrusting cheilostome bryozoans based on patterns of zooid budding. Matrix rows represent budding processes; columns represent budding geometries. Combinations of process and geometry are morphogenetic states that may occur singly or in combination within a given species or colony. Known combinations are shown as idealized horizontal sections (in plan view) of zooids at the growing edges of colonies for (A) single layered growth; and as longitudinal sections for (B) multilayered growth. Exterior walls are shown with bounding cuticle (lines) and skeleton (stippled); interior walls with skeleton only.

Cheetham 1969). I first develop a framework for defining and comparing different budding processes and geometries, and extend this framework to include newly recognized modes of encrusting growth. I then consider how these modes of growth may be related morphologically, and finally how their evolution may be related to ecological patterns of occurrence and interaction of species, and to phylogenetic development within the major clades of cheilostome bryozoans through time.

MATERIALS AND METHODS

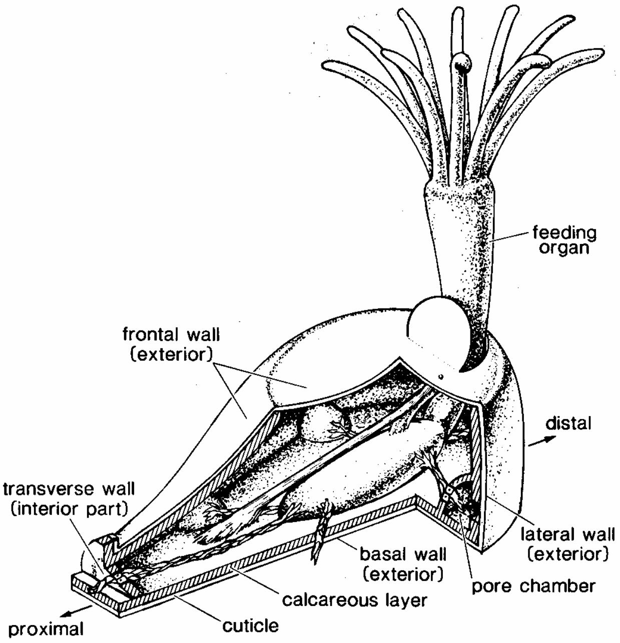
Budding patterns vary among cheilostome species, so any comprehensive study of growth must include a comparative survey of zooid and colony morphology. Many aspects of the model presented here resulted from a survey of more than three hundred fossil and Recent species in the collections of the United States National Museum of Natural History and in my own collections from the Atlantic Coastal Plain of North America. A preliminary model of budding patterns was derived from observations of whole-colony morphology, geometric arrangement of zooids, and the relative positions of zooid body walls and their apparent sequence of formation. Species were chosen to maximize the sample range of colony morphologies and higher taxa, and in some cases to duplicate previously described budding processes and geometries (Cheetham and Cook 1983, and references therein). Based on this survey a representative subset of species was selected for more intensive study using thin section and SEM techniques.

The advantages of epoxy resin embedding and thin sectioning to determine relationships of calcified and 'soft' tissue morphology *in situ* have been demonstrated in several recent studies of cheilostome growth (Banta 1968, 1969, 1970, 1971, 1972; Cook and Chimonides 1981*a*; Cheetham and Cook 1983; and others). In particular the developmental sequence of membranous, cuticular, and calcified zooid body walls can be inferred from sections cut through zooids and zooid buds at growing edges, or through zones of frontal budding from the surface of a colony. These, in turn, may be used to infer developmental sequences in analogous skeletal structures in fossil material. Thin sections of living colonies were prepared by embedding in epoxy resin (Reichhold epotuf 37-128 with hardener 37-614) under vacuum following the method of Nye *et al.* (1972). Sections were then cut, polished, attached to microscope slides, and stained with crystal violet to increase contrast of tissues. While this procedure allows detailed comparison of 'hard' and 'soft' tissue growth it has the disadvantage of being confined to a two-dimensional plane. Complex spatial relationships of three-dimensional morphologies may be obscured by section orientation. In addition, some aspects of body wall morphology, such as the extent of cuticular layers in calcified walls, require magnification beyond the normal range of light microscopy (Sandberg 1983).

In order to circumvent these problems I developed a technique for preparation of three-dimensional internal sections of colony skeletal fragments suitable for scanning electron microscopy. Specimens were treated with sodium hypochlorite, rinsed, air-dried, and placed in small glass vials partially filled with filtered canada balsam. The vials were heated to lower the viscosity of the balsam prior to embedding under vacuum. Parts of the specimens and the balsam were then removed by grinding on a medium grit carborundum wheel, followed by flat surface sanding on fine grit carborundum paper. The glass vials reduced crazing and edge fracture in the brittle embedding medium. The prepared surfaces were then given a final high polish using an 1800 grit tin oxide slurry on a polishing wheel. The exposed edges of skeleton were etched for 20 seconds in 0·5% formic acid to reveal fine skeletal structure and enhance the relief of non-calcified cuticle in the body walls. The balsam embedding medium was then removed by heating and transfer of each specimen through several xylene baths. Trial and error with various drying techniques revealed that a final acetone bath prior to critical point drying (Denton DCP-1) of the specimens significantly reduced meniscus formation and structural distortion at skeletal grain boundaries. Specimens were then coated with gold-palladium and photographed in the SEM (Cambridge S4 Stereoscan). Unless otherwise noted, figured specimens are SEM photographs prepared by the above method. Specimens with USNM catalogue numbers are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

THE ELEMENTS OF ZOOID BUDDING

Consider the bryozoan colony as a system of interconnected zooids joined to one another by their walls. In addition to body walls and enclosed body cavities the zooids include feeding organs and other organ systems essential to the functioning of the colony (text-fig. 2). Polymorphic zooids such as avicularia and kenozooids generally lack feeding organs and therefore depend on connections with feeding zooids for nutrients. Conversely, feeding zooids may depend on polymorphs for other colony



TEXT-FIG. 2. Idealized anascan cheilostome zooid showing conventions of zooid orientation and body wall morphology related to budding. Exterior walls include cuticular or membranous external layer, inner cellular layer(s), and generally an intermediate skeletal layer, whereas interior walls generally include only skeletal and cellular layer(s) (inner cellular layers not shown). Figure modified from Cheetham and Cook (1983).

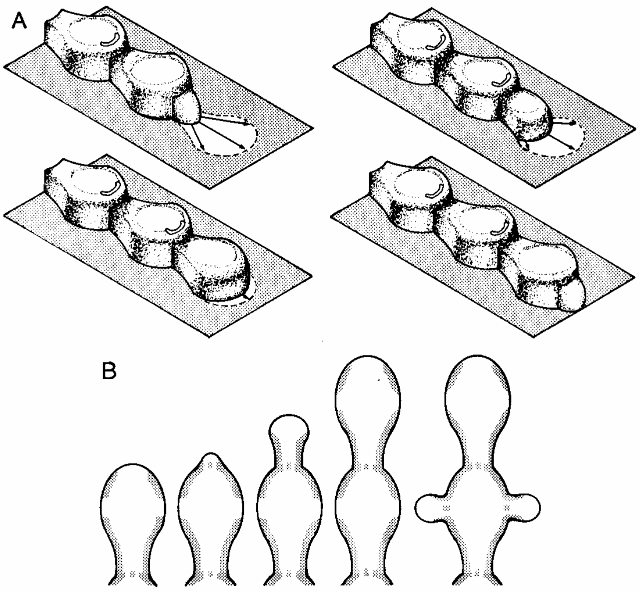
functions such as defence or structural support. Colonies gain new living space by asexually budding new zooids from pre-existing ones. A crucial element of this process is the formation of body walls that delimit zooids.

Cheilostomes have two distinct types of body walls (Silen 1944, 1982; Banta 1969; Cheetham and Cook 1983). *Exterior walls* extend the body of the zooid and the colony during growth. They are the boundary walls that actually or potentially separate the interior coelomic space and tissues of a colony from the environment. As they grow these walls include an outermost cuticular layer and inner cellular layers. In all but the simplest and morphologically primitive groups the principal exterior walls also include an intermediate calcified skeletal layer. *Interior walls* grow into body cavities of zooids or of multizooidal parts of the colony. Their growth partially or completely divides existing space. They are generally calcified and may or may not include a cuticular layer. However, no part of an interior wall is in contact with the external environment and therefore a cuticle in an interior wall cannot be an exterior cuticle.

Budding geometries. Buds originate from specific parts of parental zooids and also from specific parts of the colony as a whole. Consequently the geometric pattern of budding is unavoidably linked to potential budding sites on individual zooids as well as the spatial arrangement of surrounding zooids (Gordon and Hastings 1979). Budding sites on autozooids can be distinguished relative to the principal growth direction of the zooid (text-fig. 2). Buds originate from body walls situated laterally, frontally, or transversely to the proximal-distal growth axis of the parental zooid. Proximal budding is rare, apparently limited to repair of damaged zooids (Banta 1969) and early post-metamorphosis growth in a few species. Budding from the basal wall, which occurs in some erect and rooted cheilostomes, is precluded in most encrusting species by their close attachment to the substrate. Budding sites are further dependent on the placement of uncalcified windows in skeletal walls, and on structures such as areolae that are commonly associated with frontal budding (Pl. 26, fig. 5; see also below).

Budding sites relate more generally to colony geometry. An encrusting colony form reflects the arrangement of groups of zooids that depend on the substrate for support. The positions of new zooids are constrained by the arrangement of existing ones. *Single-layered growth* enables a colony to expand and occupy an area on a two-dimensional substrate, while *multilayered growth* permits expansion in the third dimension above the substrate in the area already occupied (text-fig. 1). Single-layered budding therefore generally occurs at the edge of a colony on or directly above the substrate. Buds form at the ends of runner-like strings of zooids or at the margins of sheet-like colonies where many zooids are connected laterally. Mound-like colonies are formed by multilayered frontal budding or by single-layered budding with repeated episodes of self-overgrowth.

Zooids in a cheilostome colony are typically arranged in *lineal series* (text-fig. 3A), reflecting the parent–daughter budding relationship of successive zooids (i.e. not sexual reproduction). It is important to note here the distinction between a lineal relationship, based on the immediate ancestry of individual zooids, and a linear one, which specifies only a spatial arrangement (e.g. linear rows of zooids) without regard to budding relationships. Within a lineal series the outermost cuticle and at least some parts of skeletal and cellular layers originate as multizooidal layers that are continuous from one zooid to the next (Cheetham and Cook 1983). Some of these layers are also continuous within a series from basal through lateral and frontal walls. As the body wall of a single-layered colony expands, a transverse interior wall begins to develop by infolding of the inner cellular layers of adjacent exterior walls. When the transverse wall is complete and the bud attains the form of a complete zooid the multizooidal layers of the body wall can be considered part of the new zooid. This developmental sequence is then repeated, successively adding new zooids to the distal end of the series.



TEXT-FIG. 3. A, idealized sequence of distal bud formation in an anascan cheilostome; successive zooids are arranged in a single lineal series (modified from Cheetham and Lorenz 1976). B, uniserial budding geometry shown as horizontal sections through zooids at the growing edge of a colony; budding sequence corresponds to A, while figure at far right illustrates the formation of lateral buds; interior and exterior body walls depicted as in text-fig. 1.

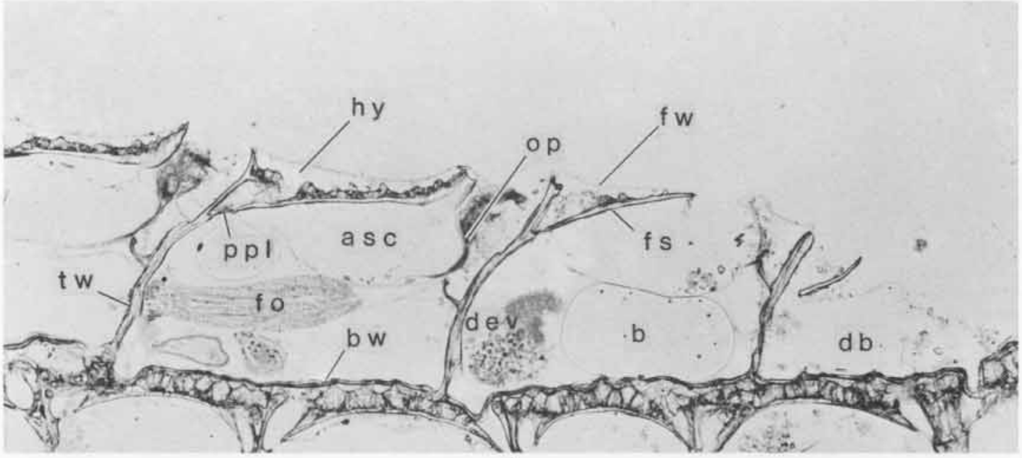
Budding processes. Budding involves two structural processes: expansion of the body cavity and enclosing walls beyond the existing limits of the parental zooid(s), and partitioning of this expanded region into one or more buds separate from the parental zooid(s). Each bud can be regarded as an early stage in zooid ontogeny, i.e. it will ordinarily develop into a functional zooid. It is therefore important to distinguish the space that will, in the normal course of development, become a new zooid (a bud) from the space that will remain part of a parental zooid.

Expansion begins as an outswelling by growth of cuticular and cellular layers of the parental zooid's exterior wall (Pl. 26, fig. 1; Lutaud 1961, 1983; Banta 1969; Tavener-Smith and Williams 1972), or of the multizooidal exterior wall of a budding zone adjacent to more than one parental zooid (Hakansson 1973). In calcified exterior walls, skeletal deposition generally begins in a zone of cell division proximal to the advancing edge of the bud. Expansion continues as the bud assumes the external morphology of a complete zooid.

An interior wall that partitions a bud from its parent may begin to develop before, during, or after bud expansion. Growth is initiated from the inner cellular layers of an exterior wall or, subsequently, from an existing interior wall. The new wall eventually grows into contact with the existing body walls, completely partitioning the original body cavity except for one or several uncalcified openings left during growth. These openings will become filled by communication organs composed of skeletal pore plates and 'special cells' (Banta 1969; Gordon 1975; Bobin 1977) that connect the funicular systems and body cavities of adjacent zooids. Communication organs are here termed *intraserial* when developed within a lineal series during distal or lateral budding (text-figs. 3, 4), or at the distal bifurcation of series (Pl. 26, fig. 2; text-fig. 5). They are formed as part of the normal growth of interior walls (Pl. 26, fig. 4). Adjacent series may also develop new communications laterally through *interserial* (between lineal series) communication organs (Pl. 26, fig. 3; see Silen 1944; Banta 1975; Banta and Wass 1979). The growing edges of adjacent series advance in unison, leaving matching uncalcified windows in their respective lateral walls. In these windows the double cuticle layer is dissolved, breaching the walls (Banta 1969). Simultaneously a small interior wall consisting primarily of a pore plate and cellular layers extends from the breached exterior wall into the more proximal of the two zooids. The completed wall will become part of a communication organ linking the adjacent zooids. While these two types of communication organs differ in their mode of formation, their function in completed zooids appears to be the same.

EXPLANATION OF PLATE 26

Figs. 1–5. *Metrarabdotos unguiculatum cookae* (Cheetham), Ghana, west Africa, Recent. 1, USNM 243229 (Cheetham and Cook 1983); 2–5, USNM 376699. 1, sequence of zooid development is apparent in succession of newly budded zooids at growing edge of a colony. Longitudinal thin section through a single lineal series illustrates concurrent development of body walls and other organ systems. Growing edge is encrusting another portion of the same colony. Calcified basal wall (bw), transverse walls (tw), and membranous frontal wall (fw) enclose zooid body cavities. Distal bud (db) at far right has no frontal shield, ascus, or feeding organ. Progressive development of these structures is shown in successively more proximal zooids. Areolae, which include communication organs with skeletal pore plates (ppl) that develop in the frontal shield, permit communication between the hypostegal coelom (hy) and principal body cavity (Banta 1972, 1973). Body walls, ascus (asc), operculum (op), and feeding organ (fo) are fully developed in zooid at left. Bubble (b) is an artifact of the embedding process, × 70. 2, frontal skeletal surface of colony growing edge; budding geometry is discrete multiserial; budding process is zooidal (note quincuncial arrangement of zooids and bifurcation of lineal series at centre), × 35. 3, side view of fig. 2 reveals internal skeletal morphology of lineal series, inter- and intraserial pore plates, and transverse walls that separate zooids within lineal series, × 35. 4, detail of interior transverse wall (tw) showing intraserial pore plates (ppl) and lack of cuticle, × 200. 5, detail of skeletal morphology of areola (ar) and pore plates (ppl) in frontal shield, × 275.



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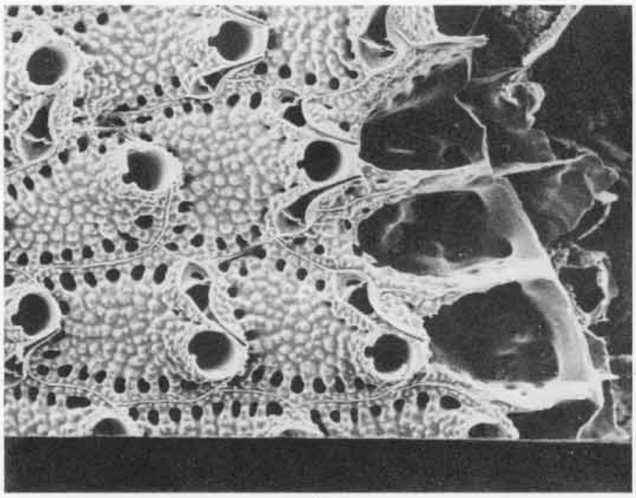

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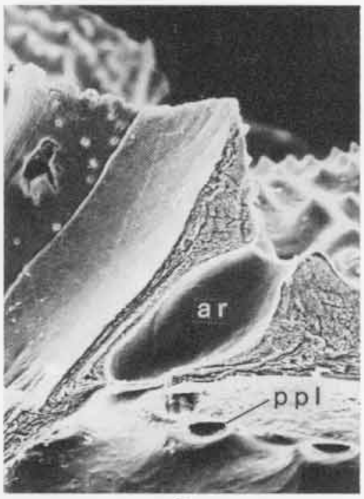

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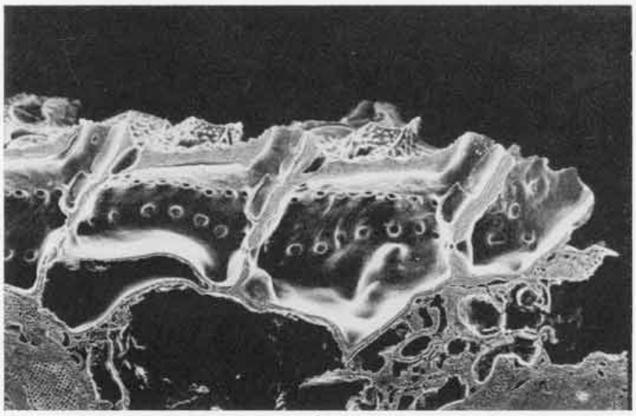

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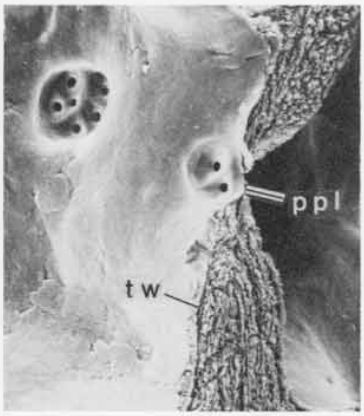

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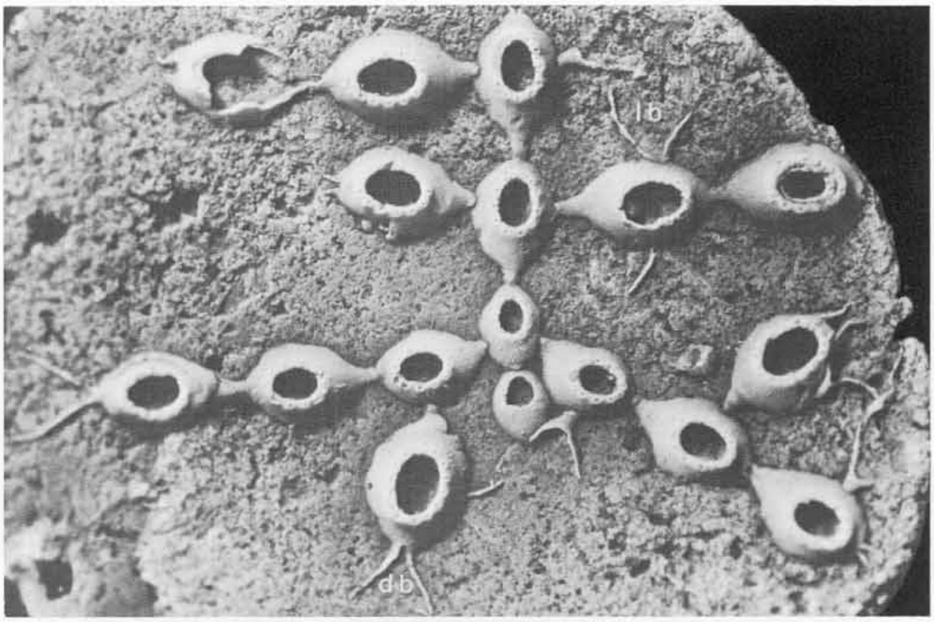


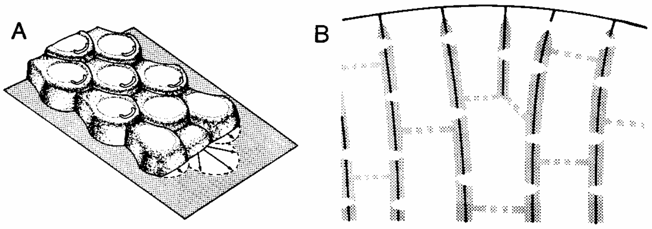
TEXT-FIG. 4. *Allantopora irregularis* (Gabb and Horn), USNM 242558, Noxontown Millpond, Delaware, Palaeocene. (Cheetham and Cook 1983), uniserial budding geometry showing both distally (db) and laterally (lb) budded zooids. Budding process is zooidal. Light photograph; specimen stained, coated with ammonium chloride, × 28.

The model presented here resolves morphology only to the coarsest level of body wall development. This implicitly assumes that post-larval developmental processes at other levels (i.e. cellular mechanisms of skeletal secretion, organogenesis, and others) are related to body wall development in a predictable way. While available evidence suggests that this is indeed the case (Tavener-Smith and Williams 1972; Sandberg 1983; Lutaud 1983, and references therein), development of feeding organs and most other intra- and extra-zooidal parts will not be considered here. Nor will I explicitly consider the budding of polymorphic zooids other than to note that the concepts of budding process and geometry presented here for the development of feeding zooids should apply to polymorphs as well.

SINGLE-LAYERED BUDDING

Geometries

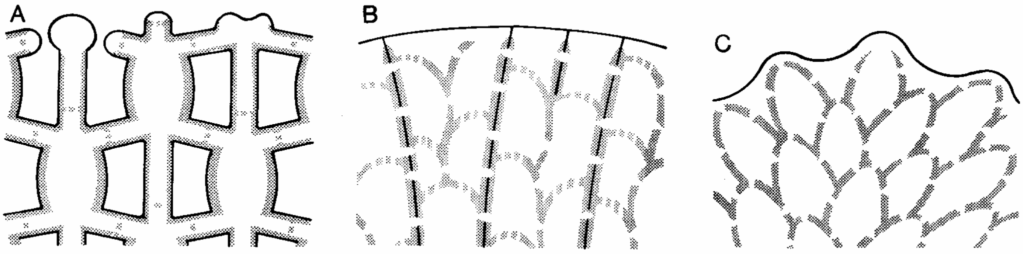
Simple lineal geometries. Colonies in which lineal series remain more or less separated from one another, forming a runner-like colony morphology, are termed *uniserial* (text-figs. 3, 4). In uniserial species such as *Pyripora catenularia* (Fleming), contacts between series are irregular, and interserial communication organs are rarely if ever developed (Banta 1975; but see also Gordon and Hastings 1979). Budding is not limited to the distal end of a series. New series may be initiated from laterally placed budding sites by the same developmental sequence as distal budding. The interior wall that partitions a parental zooid from a laterally positioned bud is formed without dissolution of exterior cuticle. Therefore the communication organs at this junction between series are intraserial rather than interserial (Silen 1944). However, only a fraction of lateral budding sites ever give rise to new lineal series. Lateral budding enables a uniserial colony to form new zooids in any region of the original series, even after the growing edge has advanced past the point of lateral bud formation. This ability can be recognized in fossil species by the presence of partially developed calcified walls in older regions of the colony (text-fig. 4) and is present even in the earliest uniserial colonies (Pohowsky 1973).



TEXT-FIG. 5. Discrete multiserial budding. A, idealized anascan colony showing distal bud formation in three adjacent lineal series (modified from Cheetham and Lorenz 1976). B, horizontal section through zooids at the growing edge of a colony; interior and exterior body walls depicted as in text-fig. 1; intra- and interserial communication organs shown as openings in body walls; note the bifurcation of lineal series at centre.

In *discrete multiserial* colonies, frequent or continuous contact of adjacent lineal series results in a sheet-like colony form (Pl. 26, fig. 2; text-fig. 5). Lineal series abut one another along a double wall of two exterior walls whose outermost cuticular layers face one another directly. In sheet-like colonies of *Membranipora*, *Cryptosula*, *Schizoporella*, and many other genera, distal budding occurs simultaneously in a number of lineal series. However, buds in adjacent series are rarely at the same developmental stage. This is due at least in part to the quincuncial arrangement of zooids typical of many multiserial colonies, wherein each zooid borders two distolateral and two proximolateral neighbours. Lateral budding is constrained by the adjacent series blocking potential budding sites, except where lineal series diverge sufficiently to allow intercalation of a new series. Laterally adjacent lineal series do, however, develop intraserial communication organs, the formation of which involves processes that have been compared to budding (Silen 1944; Banta 1969).

As a multiserial colony expands, new lineal series must be intercalated at the widening colony margin. The apparent bifurcation of lineal series is a normal aspect of simple lineal budding (Pl. 26, fig. 2; text-fig. 5B). A longitudinal division appears at the advancing distal margin of a lineal series, usually in a medial position (Lutaud 1983). A portion of the membranous exterior wall becomes stationary at this division as the rest of the wall expands distally. Subsequent growth past the resulting indentation yields two 'buds' that will eventually become mature zooids. Since the advancing exterior body wall remains continuous with the centred stationary portion, the lateral wall separating the two new zooids is a double wall complete with intercalary cuticle. The process is comparable to distal and lateral bud formation in uniserial colonies, while here the lateral bud is moved to a distolateral location. As in the case of uniserial budding, the communication organs of the partitioning interior transverse wall are intraserial (Pl. 26, fig. 4). Growth of the new buds may laterally displace adjacent lineal series due simply to the width of the additional new series. A quincuncial arrangement of zooids is generally maintained as the new zooids will typically grow to different lengths. In some species the width of the parental zooid may increase to accommodate series bifurcation.



TEXT-FIG. 6. A, coalescent multiserial budding; new zooids are formed at the growing edge by fusion of proximally and laterally adjacent buds. B, compound lineal budding; each lineal series is composed of two or more adjacent rows of zooids partitioned by both interior and exterior lateral walls. C, nonlineal budding; zooids are partitioned by interior vertical walls within a laterally confluent budding zone. All are horizontal sections of zooids at growing edges of colonies; interior and exterior body walls depicted as in text-fig. 1.

Coalescent multiserial budding results from the fusion of adjacent buds to form a single zooid (Pl. 27, fig. 1; text-fig. 6A). This geometry is well developed in species of *Beania* in which zooids are connected by tubular extensions of the exterior body walls. The buds develop from two or more parental zooids, expand and contact one another, then dissolve the cuticular body walls at their point of contact to produce a single confluent bud (Silen 1944; Cheetham and Cook 1983). Thus lineal series are constantly anastomosing. The resulting bud will either begin a new series or produce subsequent anastomosis. It is assumed that bud fusion occurs only when buds contact before calcification (Banta 1975).

Compound lineal geometry. This multiserial geometry superficially resembles simple lineal budding (Pl. 27, fig. 2; text-fig. 6B). It is commonly developed in *Parasmittina* and is the same as the 'multizooidal budding' described by Silen (1982) in *P. trispinosa* (Johnston). As the body wall expands distally it forms a bud, two or more zooids in width and bounded by exterior walls as in an ordinary lineal series. Interior walls then develop to partition the coelomic space and form a compound lineal series of two or more rows of zooids. Interior walls thus separate zooids laterally as well as transversely within the series.

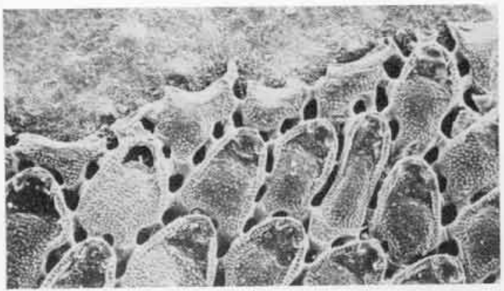
EXPLANATION OF PLATE 27

Fig. 1. *Beania simplex* (Heller), USNM 376700, Amalfi, Italy, Recent; frontal surface of colony with cuticle intact showing fusion of buds at colony margin; budding geometry is coalescent multiserial; budding process is zooidal, × 45.

Fig. 2. *Parasmittina nitida* (Verrill), USNM 376701, U.S. Fishing Comm. Sta. 5522, Vineyard Sound, Massachusetts, Recent; frontal skeletal surface of colony growing edge; budding geometry is compound lineal; budding process is multizooidal; light photograph of stained specimen coated with ammonium chloride, × 19.

Figs. 3, 4. *Cupuladria biporosa* (Canu and Bassler), USNM 376702, Nassau, Bahamas, Recent. 3, distal view of colony growing edge showing zooids at different stages of development; at left, basal wall (bw) is partially formed between laterally adjacent zooids; at right, bud with incomplete transverse wall (tw) prior to completion of pore plate, × 60. 4, frontal skeletal surface showing basal wall of bud at left in fig. 3; zooids are partitioned by interior vertical walls in a laterally confluent budding zone surrounded by membranous external cuticle (not shown); budding geometry is nonlineal; budding process is zooidal, × 70.

Figs. 5, 6. *Schizoporella floridana* (Osburn), USNM 376703, Pescaderabaai, Curacao, Recent. 5, frontal skeletal surface showing zooids in different lineal series at different stages of development, together with greatly elongated distal bud (cf. Pl. 26, figs. 2, 3); budding geometry is discrete multiserial; budding process is multizooidal, × 60. 6, side view of fig. 5, showing internal skeletal morphology of developing zooids, × 60.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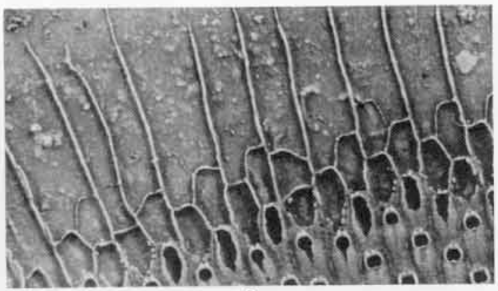
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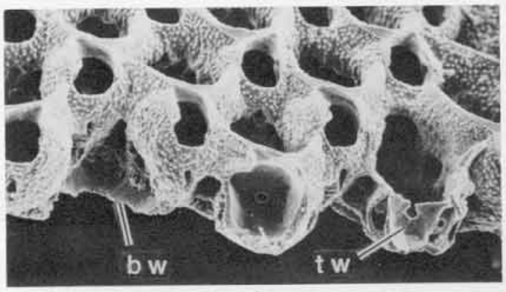

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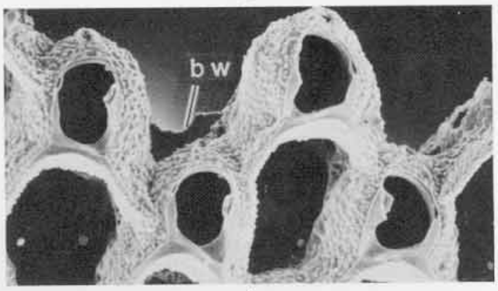

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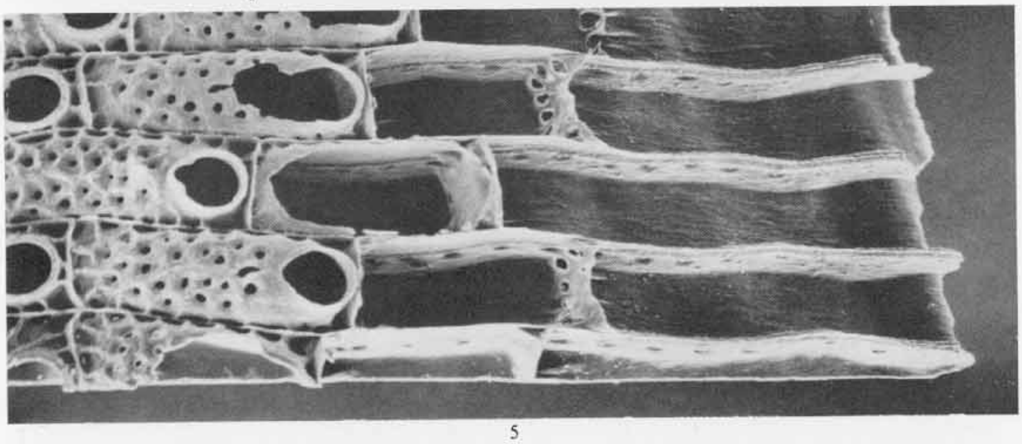
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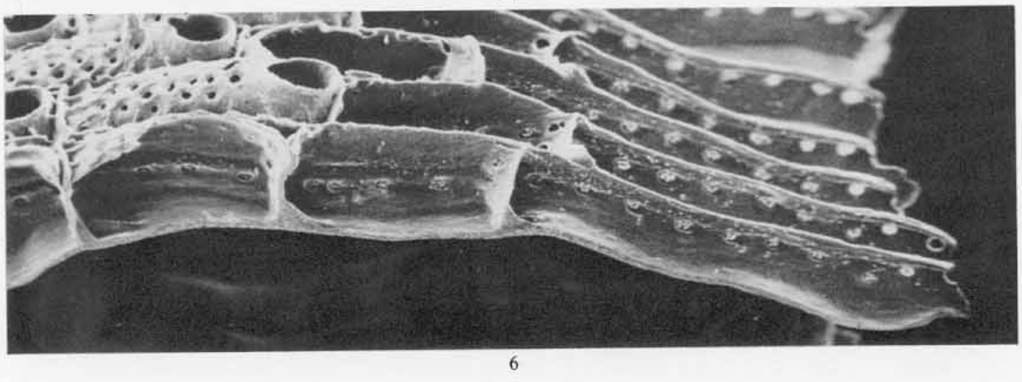
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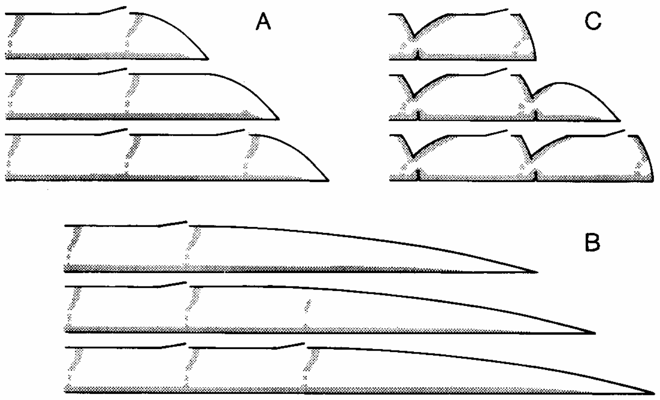
LIDGARD, *Beania*, *Parasmittina*, *Cupuladria*, *Schizoporella*

Within a compound lineal series, zooids are positioned in quincunx and apparently communicate entirely through intraserial communication organs in lateral and transverse interior walls. Laterally adjacent zooids in different compound lineal series communicate through interserial communication organs formed in the same way as those in simple lineal colonies. Because of observed similarities in the structure and geometry of the growing edge the process of bifurcation of lineal series can be inferred to be the same as that in simple lineal budding.

Nonlineal geometry. Confluent budding zones also exist in cheilostomes where lineal series are absent (Pl. 27, figs. 3, 4; text-fig. 6c). In the encrusting early stages of *Cupuladria*, new zooids arise in a budding zone that is laterally confluent around the entire colony margin (Hakansson 1973). Lineal relationships are obscure or non-existent, as new zooids within this zone are partitioned exclusively by interior vertical walls. During budding the exterior wall at the colony margin expands distally (and later basally, if the end of the substrate is reached). Buds arise on the colony margin not as separate units but rather as localized extensions of the confluent budding zone. During zooid formation a small area of uncalcified body wall begins to expand at the growing edge of the colony. Skeletal material is then deposited at the base of pre-existing zooid walls. Formation of the basal skeletal walls is continuous with deposition of interior lateral walls and, eventually, a transverse distal wall. The vertical walls are completed with the formation of communication organs (comparable in their mode of formation to intraserial communication organs; see below) between zooids. As the colony expands radially, new buds arise in the spaces between newly completed zooids, producing a quincuncial arrangement.

The usual transition from an encrusting to a free-living state in *Cupuladria* and similar forms is accomplished by expansion of the colony margin beyond the limits of the substrate. This transition is accompanied by basal expansion of the body wall and coelomic space to form extrazooidal structures that commonly complete the enclosure of the original substrate (Hakansson 1973, pl. 1).



TEXT-FIG. 7. Budding processes in single-layered growth. A, zooidal budding; zooids are partitioned by growth of interior wall proximal to the growing edge in a more or less continuous process. B, multizooidal budding; zooids formed as in zooidal budding, but buds are greater than two zooids in length. C, intrazooidal budding; zooids formed directly at the growing edge of the colony by a discontinuous process of bud expansion from pore chamber of parental zooid; note that pore chamber is completed prior to expansion of successive zooid bud. All are longitudinal sections of anascan zooids in lineal series showing different sequences of zooid formation at the growing edges of colonies; interior and exterior body walls depicted as in text-fig. 1.

Nonlineal budding is also regularly present in a number of free-living and loosely attached genera, some of which develop basal rootlets. In many species of *Selenaria*, *Conescharellina*, *Stichopora*, *Euthyrisella*, and others, zooids are partitioned by interior vertical walls in a laterally confluent budding zone enclosed by a membranous exterior cuticle (Cook and Chimonides 1981*a*, *b*; Hakansson pers. comm.). While colony form in these species differs significantly (and in many cases may not involve an extensive encrusting phase), the nonlineal budding process appears to be little different from that described for *Cupuladria*.

All vertical walls in *Cupuladria* and other species with nonlineal budding are interior walls, and hence communication organs do not breach exterior cuticle. However, use of the term intraserial to describe these communication organs is misleading since lineal relationships between zoöids are obscure. Banta (1969) showed that the communication organs developed in exterior walls form a peripheral ring of cuticle (annulus) where the intermediate cuticle has been breached. Communication organs formed in interior walls lack this structure. The terms annular and nonannular were proposed to distinguish between these differences in morphology and development. I have not adopted these terms here because they lack the utility of intraserial and interserial in defining position and lineal relationship as well as developmental process in the majority of cheilostome species.

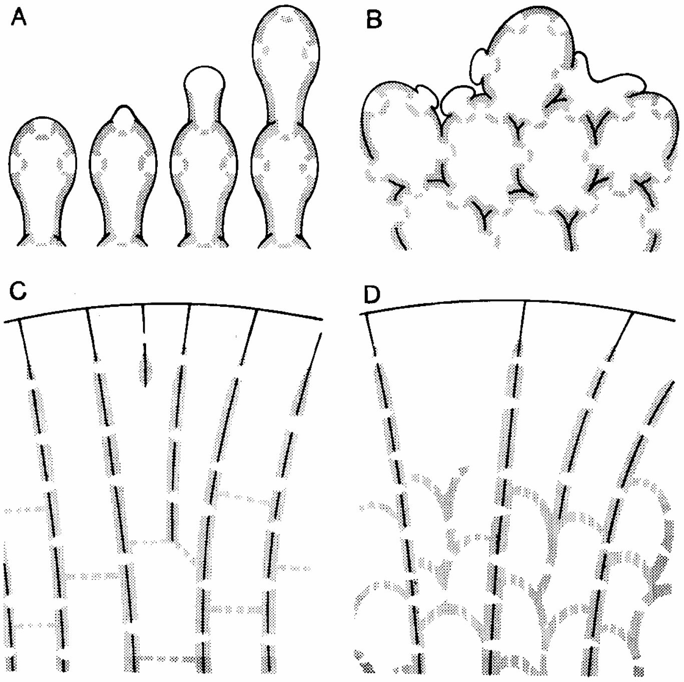
Processes

Zooidal budding. The relative timing of bud expansion and partitioning may also differ in single-layered growth. In genera such as *Aplousina*, *Cryptosula*, *Watersipora*, and *Smittoidea* the expanding bud generally extends beyond the distal margin of the parental zooid before or during the completion of its partitioning transverse wall (Pl. 26, figs. 1–3; text-fig. 7A). The transverse wall is shared by the newly formed zooid and the expanding bud that will form the next zooid. This process can be termed *zooidal*. Bud expansion appears to be a relatively continuous process, although the rate of growth may vary considerably with the condition of the colony or certain environmental factors. However, large changes in growth rate or even cessation of growth appear to be random with respect to the developmental stage of any given zooid (cf. Lutaud 1983). Zooidal budding is the dominant budding process among living cheilostomes. All of the budding geometries described in the previous section occur in species with zooidal budding.

Multizooidal budding. Buds that expand to two or more zooidal lengths before transverse walls begin to partition them are here termed *multizooidal* (Pl. 27, figs. 5, 6; text-fig. 7B) and are equivalent to giant buds described by Lutaud (1961, 1983; see also Cheetham and Cook 1983). Multizooidal and zooidal budding are end members of a continuum involving virtually the same continuous developmental process, but with striking differences in the timing of zooid ontogeny. Although some species such as *Membranipora membranacea* (Linnaeus), *Stylopoma spongites* (Pallas), and *Schizoporella floridana* (Osburn) commonly exhibit both budding processes, most species never develop multizooidal buds. Therefore, the potential for multizooidal budding can be regarded as a morphologically useful if somewhat arbitrary division.

Multizooidal budding is most commonly present in species having a simple lineal discrete multiserial budding geometry (text-fig. 8C). Most of these species also bud zooidally in some parts of the colony or during different stages of colony growth. Increased bud length in *M. membranacea* and other species is positively correlated with growth rate and colony size, and in some cases its expression may be dependent on environmental factors (Lutaud 1961, 1983; see also Edmundson and Ingram 1939; Menon 1972; Menon and Nair 1974; Mawatari 1975; Winston and Jackson, in press). Multizooidal budding is also present in some species of *Parasmittina* with compound lineal geometries (text-fig. 8D; Silen 1982). Multizooidal budding in uniserial and nonlineal geometries, though seemingly possible, is not known. Coalescence of multizooidal buds is rare or absent in most species with multiserial geometries, but may possibly occur when lineal series at the growing edges of a colony are constricted by an obstacle on the substrate (in most cases, lineal series simply terminate without coalescence). Multizooidally budding species that consistently employ a coalescent budding geometry (as in *Beania*) are not known.

Intrazooidal budding. In the majority of encrusting cheilostomes the partitioning body wall is completed during or after the expansion of a bud beyond the boundary wall of a parental zooid. However, as is apparent in colonies of *Microporella*, *Fenestrulina*, or *Cribrilina*, this is not always the case. *Intrazooidal* buds develop from a region within a parental zooid that will subsequently become part of a new zooid (Pl. 28, figs. 1, 2; text-fig. 7c). Before bud expansion begins this region is partitioned from the principal body cavity of the zooid by an interior wall containing intraserial



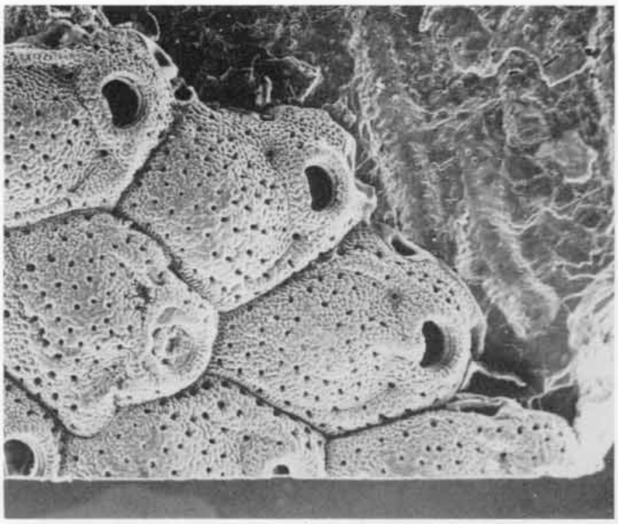
TEXT-FIG. 8. A, intrazooidal budding process with uniserial geometry; note pore chamber formation prior to bud expansion. B, intrazooidal budding process with multiserial geometry; both discrete multiserial and coalescent multiserial geometries (involving bud fusion) are often present in the same colony. C, multizooidal budding process with discrete multiserial geometry; buds are two or more zooids in length; new zooids are partitioned proximal to the growing edge. D, multizooidal budding process with compound lineal geometry; lineal series are composed of two or more rows of zooids partitioned by both interior and exterior lateral walls. All are horizontal sections of zooids at growing edges of colonies; interior and exterior body walls depicted as in text-fig. 1.

EXPLANATION OF PLATE 28

Figs. 1–4. *Monoporella nodulifera* (Hincks), USNM 376704, Albatross Sta. 2843, Unalaska, Alaska, Recent. 1, frontal skeletal surface showing predominance of fully developed zooids at the growing edge; budding geometry is discrete multiserial (although zooid at top centre may have formed by bud fusion and would therefore reflect coalescent multiserial geometry); budding process is intrazooidal, × 40. 2, side view of fig. 1, showing internal skeletal morphology including pore chambers (pch), × 40. 3, detail of distal bud showing calcified basal wall (bw) and remnants of cuticle insertion (cut) marking the distal extent of the parental zooid prior to bud expansion. Before a bud begins to expand the pore chamber (pch) is separated from the external environment by calcified external wall and an uncalcified window with a membranous exterior cuticle, × 125. 4, detail of pore chamber (pch) showing interior transverse wall (tw) with intraserial pore plates (ppl) and absence of exterior cuticle, × 230.

Fig. 5. *Pyriporopsis*(?) *texana* (Thomas and Larwood), USNM 242556 (Cheetham and Cook 1983), Fort Worth, Texas; Fort Worth Formation, Albian, Cretaceous. Frontal skeletal surface of colony showing uncalcified openings of distal and lateral pore chambers (pch); budding geometry is uniserial; budding process is intrazooidal; light photograph of stained specimen coated with ammonium chloride, × 45.

Fig. 6. *Wilbertopora mutabilis* (Cheetham), USNM 186568 (Boardman and Cheetham 1973); frontal skeletal surface of colony showing zooids in uniserial geometry succeeded by others in coalescent multiserial geometry; budding process is intrazooidal; light photograph of stained specimen coated with ammonium chloride, × 35.



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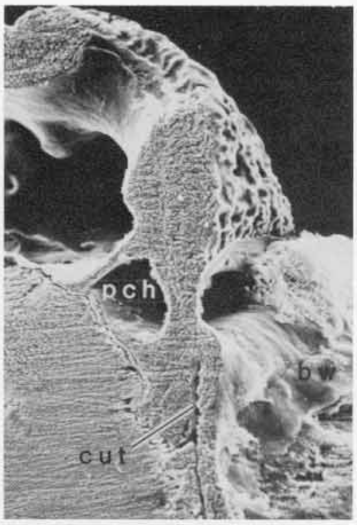

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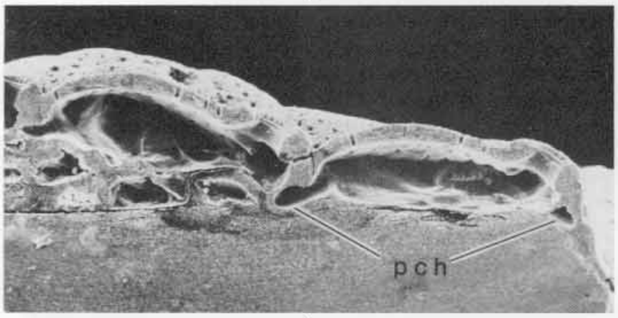

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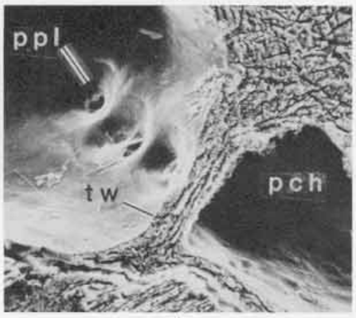

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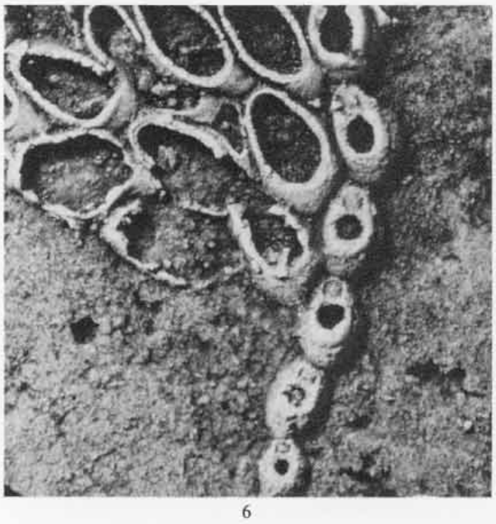

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LIDGARD, *Monoporella, Pyriporopsis, Wilbertopora* communication organs. The partitioned region is a pore chamber, and the part of the exterior body wall adjacent to it contains an uncalcified window, which forms a potential budding site (Banta 1975; Gordon and Hastings 1979).

Budding begins with the expansion by growth of the uncalcified exterior wall adjacent to the pore chamber. Expansion beyond the limits of the parental zooid transforms the pore chamber into what can then be regarded as part of the bud. The pore chamber will eventually form the proximal end of the completed zooid, confluent with its body cavity and partitioned from the parent by the pore chamber's interior proximal wall.

Unlike zooidal and multizooidal budding the growth process in intrazooidal budding is typically discontinuous. Completion of a mature zooid marks a pause in development before the expansion of a new bud. Expansion and formation of pore chambers at the distal and lateral margins of the new zooid are apparently a relatively rapid series of events. Thus complete zooids frequently appear at the colony margin; zooids at intermediate stages of development are rare.

Several previous authors have variously regarded pore chambers as heterozooids or aborted zooid buds (Silen 1944; Banta 1969; Gordon 1971*b*). In the context of the model presented here I consider pore chambers part of the parental zooid until expansion of the body wall beyond that zooid transforms them into part of a bud (see Banta 1975; Gordon and Hastings 1979). This transformation is similar in kind but reversed in polarity to that by which a multizooidal body wall becomes part of an individual zooid (Cheetham and Cook 1983). It is difficult to regard pore chambers as fully formed heterozooids (Gordon 1971*b*), since the chamber will often be confluent with the body cavity of the new zooid and body walls are continuous through the proximal part of that zooid. Silen (1944) regarded lateral pore chambers in multiserial colonies as aborted buds that were prohibited from forming zooids by the presence of adjacent lineal series. This view is not consistent with the observation that, in uniserial colonies, most lateral pore chambers never develop into zooids, yet presumably have the potential and space to do so.

Finally, pore chambers can be compared with the ascophoran hypostegal coeloms that are associated with frontal budding. Both structures are essentially coelomic chambers partitioned from the perigastric coelom by interior walls containing communication organs. Most workers have considered the hypostegal coelom to be an integral part of the zooid rather than an aborted bud, especially in species that do not form frontal buds. Even in those species that do bud frontally the space occupied by the hypostegal coelom and the calcified frontal shield are considered part of the parental zooid until the frontal wall begins to expand. After expansion begins these parts belong to the body cavity and basal wall of the frontally budded daughter zooid, a transformation equivalent to that in distal or lateral intrazooidal budding.

Uniserial colonies with intrazooidal budding often have virtually the same geometric arrangements as colonies with zooidal budding (text-fig. 8A), as can be seen by comparing *Pyriporopsis* and *Allantopora* (Pl. 28, fig. 5; text-fig. 4). Lineal series are separate and interserial communication organs rare or absent. New series are budded distally or laterally from pore chambers with intraserial communication organs.

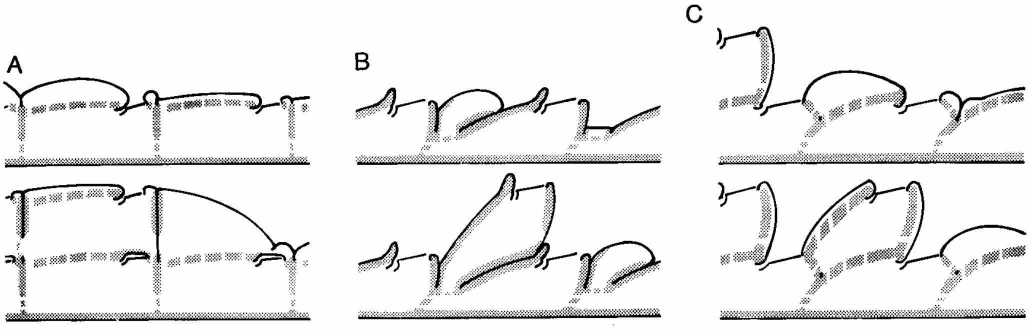
Coalescent budding is commonly present in multiserial colonies of most species with intrazooidal budding, even among the earliest species with multiserial geometries that appeared in the early Cretaceous (Pl. 28, fig. 6; text-fig. 8B). Zooids formed by intraserial budding develop directly at the growing edge of a colony in such a way that the timing of budding events in adjacent zooids rarely coincides. Gordon's (1971*a*, *b*) studies of budding in *F. malusii* (Audouin) suggest that bud fusion may occur at any time prior to calcification, forming complete zooids wherever space permits, regardless of lineal series relationships. Multiserial colonies may also exhibit discrete lineal budding; within a given colony, both geometries may be present and occur repeatedly (Pl. 28, fig. 1).

MULTILAYERED BUDDING

Geometries

Mound-like colonies in cheilostomes result from one of two kinds of growth. Most such colonies grow by multiserial frontal budding of successive layers of zooids. The underlying layers are partially or completely cut off from the environment, but physiologic connections may be maintained with the new outer layers. Many-layered colonies may also be formed without frontal budding by new encrusting layers partially or completely overgrowing pre-existing layers; the frontal surfaces of underlying zooids are completely sealed and vertical connections are absent. Self-overgrowth evidently depends on single-layered budding processes, sometimes modified in ways that I will consider in the next section.

Simple lineal geometries. Uniserial frontal budding, though possible, is apparently absent in encrusting species. However, erect uniserial groups such as the Scrupariidae may bud frontally (Harmer 1957). In colonies with *discrete multiserial* frontal budding, buds generally arise from upward growth of the frontal membranous cuticular wall that covers the hypostegal coelom (that part of the body cavity above the calcified frontal shield) (Pl. 29, figs. 1, 2; text-fig. 9A). The expanding hypostega forms the bud that is destined to become the new zooid (Banta 1972). In *S. floridana* (Osburn) the bud expands over the cuticular operculum and fuses with a distal portion of the hypostegal coelom, becoming confluent between the points of cuticle insertion on the distal, proximal, and lateral walls of the underlying zooid (Pl. 29, fig. 3). The operculum is covered by a segment of exterior wall that overlies a superopercular space. As the bud enlarges, calcified exterior walls grow upward from the lateral (exterior) and transverse (interior) walls of the parental zooid (Pl. 29, fig. 4). Interserial communication organs develop as in single-layered growth between adjacent frontally budded zooids. The upper surface of the expanding bud will eventually form the frontal wall of the new zooid. This zooid communicates with its parent through areolae that originally linked perigastric and hypostegal coeloms. These areolae (frontal pores provided with communication organs) appear to be necessary for the possession of a hypostegal coelom in ascophorans (Banta 1973). The hypostegal coelom, frontal shield, and areolae of the parental zooid are thus transformed into parts of the new zooid. Consequently, multiserial frontal budding should be regarded as an intrazooidal process.



TEXT-FIG. 9. Budding geometries in multilayered growth. A, discrete multiserial budding in *Schizoporella floridana* (Osburn); frontal buds arise from upward expansion of hypostegal coelom in simple lineal series (modified from Banta 1972). B, discrete multiserial budding in *Celleporella hyalina* (Linnaeus); frontal buds arise from upward expansion of frontally directed pore chambers, literally overgrowing the parental zooid. C, coalescent and nonlineal frontal budding. Frontal buds formed by expansion of hypostegal coeloms in adjacent parental zooids. Buds contact and fuse to form a single daughter zooid. Note remnants of original bounding cuticle dissolved in fusion process. In some species, extensive bud fusion produces a laterally confluent budding zone in which new zooids are partitioned by interior vertical walls and lineal relationships are lost. All are longitudinal sections through parental and frontally budded zooids; interior and exterior walls depicted as in text-fig. 1.

A new colony surface is produced with each generation of frontally budded zooids. With access to the environment reduced or totally lacking, covered zooids can no longer be fully functional. Feeding organs soon begin to degenerate but some tissues remain viable long after the overlying layer is complete. Zooids in successive layers are connected through communication organs that provide pathways for nutrient regression during periods of environmental stress (Cummings 1975). Successive generations form closely packed columns of zooids, each column a vertical lineal series contacting along double exterior walls. New vertical lineal series begin with the formation of an interior vertical wall bisecting a developing bud to form two smaller zooids (Pl. 29, fig. 3; Banta 1972). Each zooid will subsequently give rise to a separate vertical lineal series, budding new zooids in the normal manner. This aspect of frontal budding in *Schizoporella* is in some ways analogous to ordinary row bifurcation in single-layered multiserial growth.

Zooids in successive vertical generations frequently lose the polarity of the quincuncial arrangement in the original layer and appear to be oriented at random. However, quincuncial order may be re-established by formation of a new encrusting layer on the colony surface. Frontally budded zooids may subsequently bud 'laterally', eventually forming an encrusting layer of zooids that may cover some or all of the colony surface. The interaction of self-overgrowth and frontal budding often makes the history of a colony's development seem extremely complex.

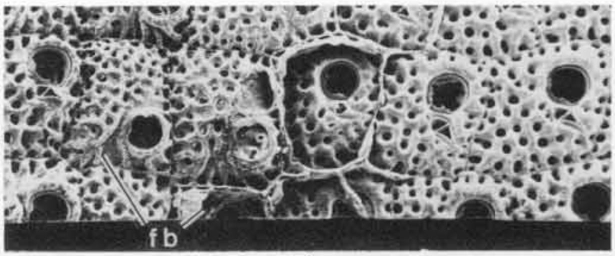
Celleporella hyalina (Linnaeus) grows by discrete multiserial frontal budding even though lacking a hypostegal coelom. Frontal buds develop from frontally directed pore chambers located near the proximolateral margins of the zooids (Pl. 29, figs. 5–7; text-fig. 9B). The upper body wall of the pore chamber is an uncalcified membranous cuticle. As the membranous wall of the pore chamber grows upwards the bud expands distally and overgrows the calcified frontal wall of the parental zooid. A calcified skeletal layer is deposited in the exterior walls of the bud as it advances over the parent and matures to become a recumbent zooid. Interserial communication organs may develop between laterally adjacent frontally budded zooids by a process inferred to be the same as in single-layered growth. Bud fusion is not necessarily precluded, but in areas where developing zooids were clearly visible, coalescent budding was not observed.

The frontal buds in *Celleporella* are intrazooidal because they are partitioned from the parental zooid by the pre-existing interior wall that floors the pore chamber (Pl. 29, fig. 7; Gordon and Hastings 1979). The pore chambers communicate with the perigastric cavity of the parental zooid

EXPLANATION OF PLATE 29

Figs. 1–4. *Schizoporella floridana*(?) (Osburn), USNM 376705, Cedar Keys, Florida, Recent. 1, frontal skeletal surface showing frontally budded zooids (fb) arising from individual parental zooids in the underlying layer of the colony, × 40. 2, side view of fig. 1, showing internal skeletal morphology and lineal relationship between zooids in successive layers (note continuity of vertical walls between layers); budding geometry is discrete multiserial; budding process is intrazooidal, × 40. 3, detail of frontal bud showing partially developed vertical walls conforming to frontal outline of parental zooid; at bottom, vertical wall (vw) of another bud bisects the frontal surface of the underlying zooid, presumably forming two daughter buds and initiating a new vertical lineal series, × 75. 4, detail of exterior vertical wall of frontally budded zooids and interior transverse wall of parental zooids (note the lack of cuticle in the lower portion followed by the inception of exterior cuticle (cut) in the upper portion); cuticle originally inserted only at the frontal wall boundary between adjacent zooids in the underlying layer, then grew upward during bud expansion, × 440.

Figs. 5–7. *Celleporella hyalina* (Linnaeus), USNM 376706, Whiting River, Maine, Recent. 5, frontal skeletal surface showing frontally budded zooids, calcified walls of frontal bud (fb) at an early stage of development, and uncalcified windows of frontally directed pore chambers (pch; chambers themselves are not visible), × 160. 6, side view of fig. 5 showing internal skeletal morphology of parental and overlying frontally budded daughter zooid and skeletal pores connecting adjacent zooids at both levels within the colony; budding geometry is discrete multiserial; budding process is intrazooidal, × 160. 7, detail of frontally directed pore chamber (pch) showing interior wall with pore plate and inception of cuticle (cut) in exterior walls of frontally budded zooid, × 375.



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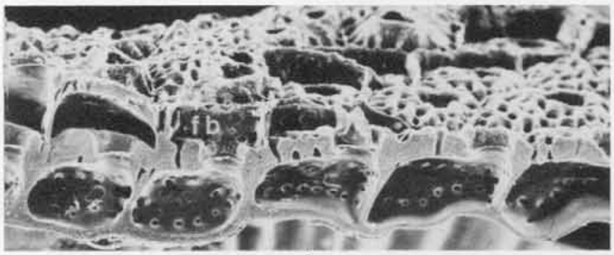

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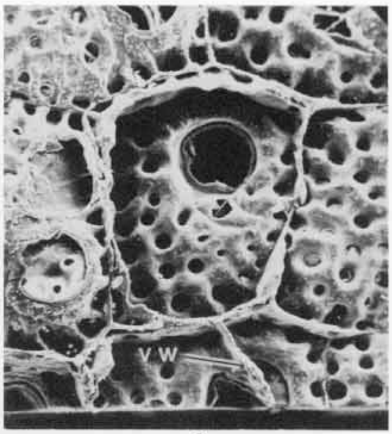

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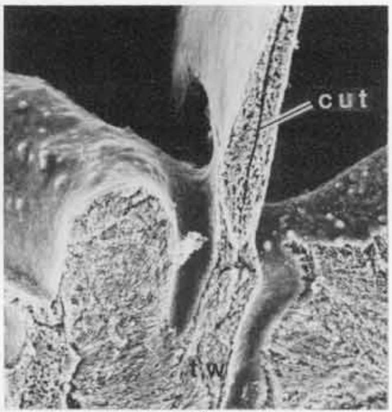

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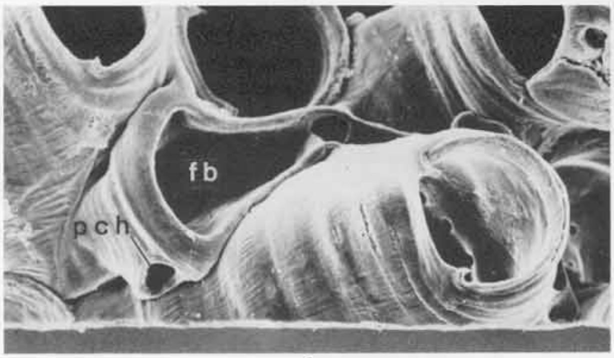

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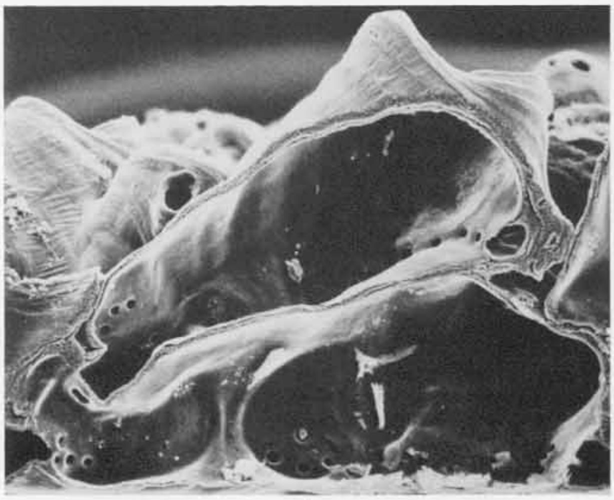

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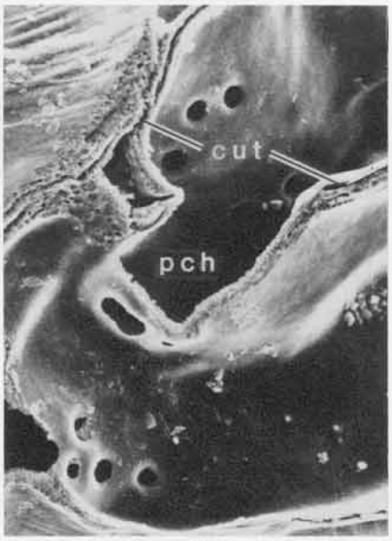

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LIDGARD, *Schizoporella*, *Celleporella* through communication organs developed in their interior walls. The sequence of wall formation can be observed directly behind the growing edge of the colony; the floor of the chamber is completed prior to the completion of the zooid.

Coalescent and nonlineal geometries. These multiserial geometries occur together in many ascophoran cheilostomes. Frontal buds in *Stylopoma spongites* (Pallas) and other similar species originate from the hypostegal coeloms of two or more adjacent parental zooids, generally at the same vertical level in the colony. The frontal walls of the parental zooids swell upward, contact one another, then fuse by dissolution of the intermediate cuticles (Pl. 30, figs. 1, 2; text-fig. 9c). The now coalesced bud continues to develop above its parents, forming vertical exterior skeletal walls as it grows. Areolae that originally connected perigastric and hypostegal coeloms now provide vertical connections to the developing zooid. As in simple lineal frontal budding the areolae, frontal shield, and hypostegal coelom become parts of the bud at the onset of body wall expansion. The transition from coalescent to nonlineal budding may occur rapidly and is often difficult to distinguish, as was found for several species of *Celleporaria* and *Stylopoma*. Bud fusion is often quite extensive, producing still larger laterally confluent budding zones that extend over the area of a number of zooids and only later become partitioned into individual zooids. New zooids formed in these zones can no longer be attributed to the coalescence of two or three lineal buds. The resulting pattern is therefore nonlineal, in which zooids are partitioned by interior vertical walls (Pl. 30, fig. 6).

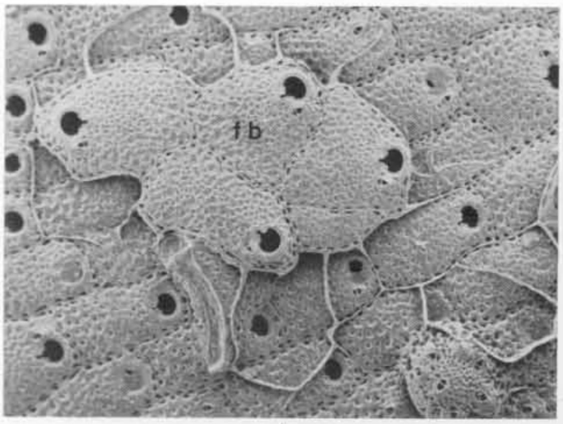
Colonies that grow in this way have highly irregular frontal surfaces with functional zooids at two or more vertical levels (Pl. 30, figs. 3, 4). This irregularity is due in part to the discontinuous nature of intrazooidal frontal budding. The process of bud fusion permits new zooids to develop wherever space permits, even directly above the operculum of a zooid at some lower level (Pl. 30, fig. 7). Transitions from coalescent to nonlineal budding also confound the interpretation of vertical wall formation; cuticle insertions are visible around the margins of some zooids, whereas in others they are not (Pl. 30, figs. 4, 5). The latter are presumably formed completely by interior walls in confluent budding zones. This complex developmental pattern totally obscures vertical lineal relationships and creates the jumbled and seemingly random orientations of zooids in frontally budded layers.

Based on a preliminary survey of several hundred encrusting species, coalescent and nonlineal geometries appear to be the dominant mode of frontal budding in cheilostomes. The development of

EXPLANATION OF PLATE 30

Figs. 1, 2. *Stylopoma spongites* (Pallas), USNM 376707, Rio Bueno, Jamaica, Recent. 1, frontal skeletal surface with frontally budded zooids (fb) (note lack of conformity between quincuncially arranged zooids in underlying layer and frontally budded zooids formed by bud fusion); budding geometry is coalescent multiserial; budding process is intrazooidal, ×25. 2, calcified vertical walls (vw) of partially developed frontally budded zooids frequently traverse the frontal surfaces of several underlying parental zooids; calcified basal walls partially separate the body cavities of developing frontal buds from the cavities of underlying zooids by covering frontal pores, orifices (or), and ovicells (ov), ×60.

Figs. 3–7. *Celleporaria magnifica* (Osburn), USNM 376708, North Carolina, Recent. 3, frontal skeletal surface with typically irregular arrangement of functional zooids and frontal buds at several vertical levels; frontal bud (fb) at right centre showing internal pore openings that connect both vertically and laterally to adjacent zooids; budding geometry is predominantly nonlineal; budding process is intrazooidal, ×40. 4, side view of fig. 3, showing internal skeletal morphology (note striking lack of conformity between basal (bw) and vertical (vw) body walls of frontal bud at left and frontal and vertical walls of underlying zooids), ×40. 5, detail of cuticle insertion (cut) in colony frontal surface; the transition between coalescent and nonlineal budding geometry is inferred to represent an increase in the lateral extent of fusion among frontal buds of contiguous zooids; as the zone of bud fusion extends beyond the boundaries of identifiable parental zooids, lineal relationships are no longer recognizable, ×500. 6, interior vertical wall of a bud prior to completion of pore plate (ppl), ×230. 7, portion of calcified basal wall covering the orifice (or) of an underlying zooid, ×170.



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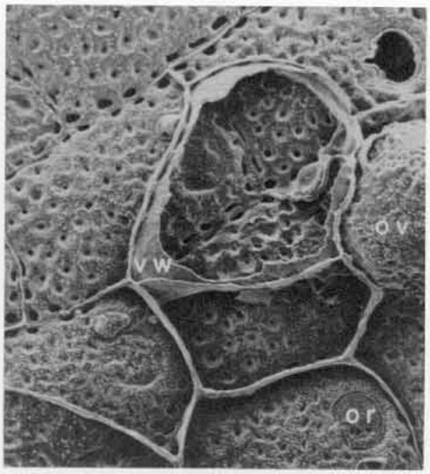

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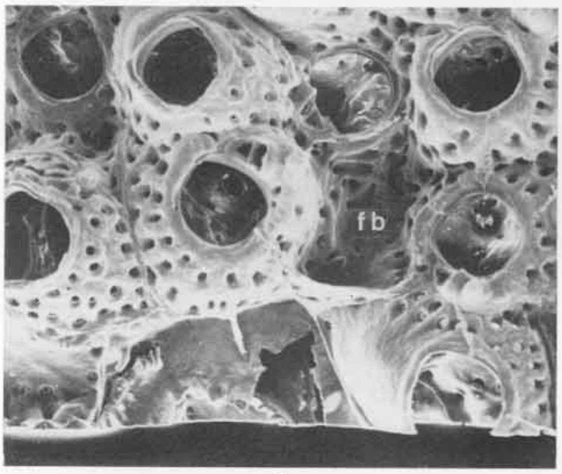

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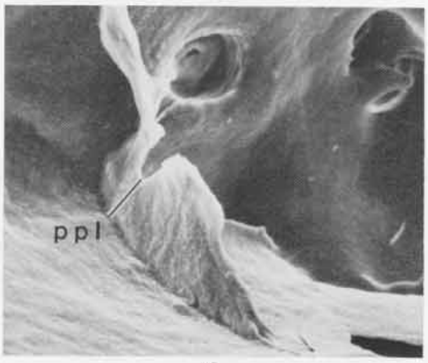

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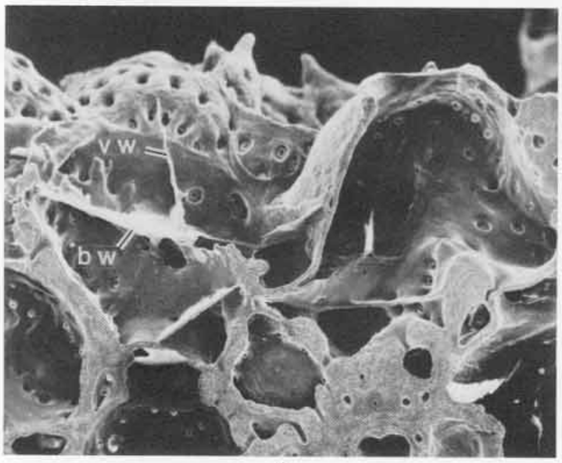

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LIDGARD, *Stylopoma*, *Celleporaria*

a confluent budding zone in species with frontal budding is analogous in many respects to the formation of extrazooidal parts in *Metrarabdotos* (Boardman and Cheetham 1973). A second analogy may be drawn with nonlineal single-layered growth in the Cupuladriidae (Hakansson 1973) and Euthyrisellidae (Cook and Chimonides 1981*a*). Some species with nonlineal frontal budding show little or no evidence of a transition from a coalescent geometry. This is particularly true for a number of conescharelliniform and orbituliporiform species that develop rootlets and never grow beyond a few zooids in size (Cook and Chimonides 1981*a*, *b*). In species such as *Sphaeropora fossa* (Haswell), zooids formed by frontal budding beyond the ancestrular stage are partitioned almost entirely by interior walls.

Processes

It was shown above that the frontal budding process in encrusting cheilostomes is intrazooidal (text-fig. 1B). Frontal budding by zooidal or multizooidal processes may not be viable. Should the entire frontal surface be expanding in a manner analogous to that in single-layered growth, new zooids would be partitioned 'proximally' to the expanding frontal surface and would therefore be completely separated from the external environment prior to their completion. This apparent prohibition of zooidal and multizooidal frontal budding should, however, be treated with caution until complex architectures of frontal budding in erect groups such as scrupariids have been more fully investigated.

The capacity for frontal budding has been considered previously to depend on the presence of areolae and a hypostegal coelom covering the frontal shield (Banta 1973). While this is generally the case, frontal buds can also develop from structures not associated with the hypostegal coelom, as in *Celleporella hyalina* (Linnaeus) which lacks both areolae and hypostega. The ability to bud frontally from frontally directed lateral pore chambers is apparently an independent evolutionary accomplishment. An indication that comparable structures have evolved in other groups is found in the Catenicellidae (Banta and Wass 1979). While they do not bud frontally, some species in this group develop an extrazooidal skeleton from laterally situated coelomic chambers provided with communication organs. In any event, frontal budding does appear to be restricted to ascophorans with partitioned coeloms connected through intrazooidal communication organs. In the great majority of cases, frontal buds arise from a hypostega separated from the main body cavity by a calcified frontal shield.

Hypostegal coeloms in anascans are not fully partitioned in that they lack communication organs and are confluent with the perigastric cavity through opesia or opesiules. The lack of hypostegal coeloms with communication organs appears to represent a constraint to the development of frontal buds. Anascans have, however, circumvented frontal budding to produce multiple layered colonies. Different groups have evolved modifications of single-layered budding processes and geometries that enable colonies to overgrow their own frontal surfaces.

EXPLANATION OF PLATE 31

Fig. 1. *Steginoporella* sp. nov. Jackson, 1979*a*, USNM 376709, Rio Bueno, Jamaica, Recent; zooids regenerated from injured region on right grow above the level of injured zooecia, subsequently re-establish discrete multiserial geometry, and encrust the original colony surface; light photograph of stained specimen coated with ammonium chloride, × 12.

Figs. 2–5. *Antropora tincta* (Hastings), USNM 376710, Hancock Sta. 396-t114, Western Pacific, Recent. 2, frontal skeletal surface of colony, × 60. 3, side view of fig. 2 showing internal skeletal morphology; zooid on right with pores connecting to two daughter zooids (centre) at different levels in the colony, × 60. 4, detail of interior transverse wall without cuticle (note pores (p) connecting parental zooid with under- and overlying daughter zooids), × 140. 5, upper skeletal surface of colony showing early development of a self-encrusting layer of zooids, × 28.

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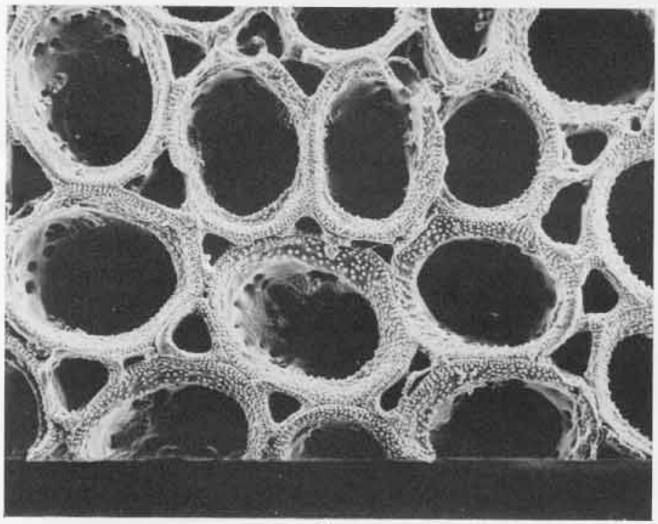

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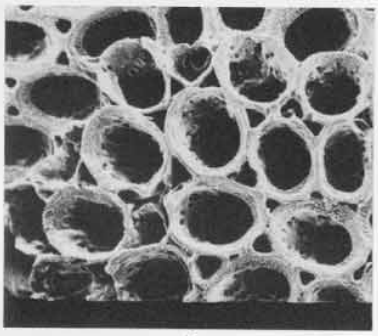

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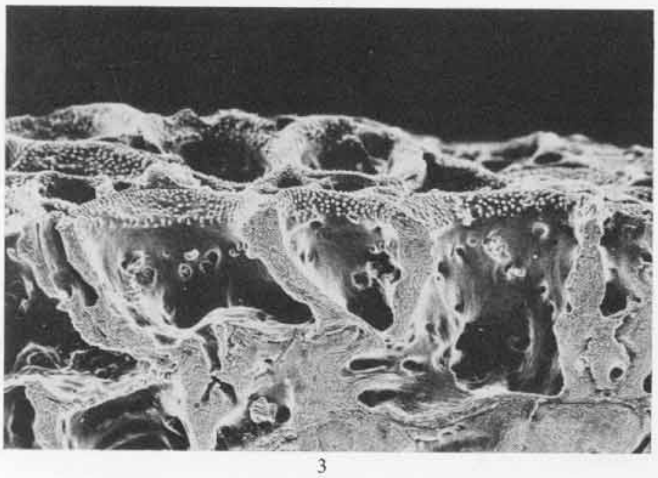

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LIDGARD, *Steginoporella*, *Antropora*

Self-encrusting growth. New encrusting layers in ascophoran cheilostomes may develop from frontally budded zooids or, in many anascans, from an original encrusting layer in which two regions of the growing edge have become juxtaposed, enabling one to overgrow another. Reparative budding introduces another variation to self-overgrowth, occurring frequently in species such as *Membranipora arborescens* (Canu and Bassler). Budding is initiated from the communication organs of zooids surrounding an empty zooecium (in some cases the result of injury or predation). If more than one bud develops, fusion will occur to produce a single confluent bud. The bud's exterior walls lie against the inner surfaces of the zooecium and will eventually be extended above the zooecium (Pl. 31, fig. 1). A new encrusting layer develops by subsequent single-layered growth, generally re-establishing a quincuncial pattern. This process differs significantly from polypide regeneration because it involves development of new exterior walls. Separate zooid margins (sometimes including gymnocyst or cryptocyst) of the original and resurrected zooids can be easily distinguished. In some cases, zooid regeneration occurs over broad areas, and re-growth produces a subsequent overgrowing layer. Self-overgrowth by reparative budding frequently occurs among anascans that lack hypostegal coeloms connected to the perigastric cavity by areolae. Although intrazooidally budding species also undergo reparative budding, I have found no evidence of self-overgrowth by this process.

Antropora tincta (Hastings) initiates new encrusting layers in a very different way. Two daughter zooids, one atop another, are budded from the same parent but at apparently different times (Pl. 31, figs. 2, 3). The developmental sequence can be inferred from the positions and lineal relationships of parent and daughter zooids. *Antropora* produces successive generations of distal zooids by multiserial zooidal budding. During or after this process some zooids continue to grow vertically, extending their vertical walls above the frontal surfaces of distally adjacent zooids (Cook, in press). This subsequent expansion is possible without budding because of the simple membranous frontal wall of the completed zooid. Expansion of a second distal bud begins, growing over the frontal surface of the first daughter zooid (Pl. 31, fig. 4). This upper zooid also apparently develops by zooidal budding. It will eventually cover the underlying zooid with an exterior basal wall and may potentially give rise to a new encrusting layer.

The temporal sequence of these events can only be inferred indirectly. Small patches of self-encrusting zooids are widely distributed over the colony surface, often at some distance from the distal growing edge of the underlying layer (Pl. 31, fig. 5). These patches may begin to develop at the growing edge, then cease to grow as the edge advances. Alternatively, the new encrusting layers may develop from parental zooids that resume their vertical growth some time after the growing edge has moved on. The second scenario appears more likely, given that the size of the encrusting patches varies greatly, even when at similar distances from the growing edge. Local variability in zooid height (sometimes as great as three-fold within a colony) is also consistent with this hypothesis, since zooids at the growing edge are uniformly short. The potential for extensive (and possibly delayed) vertical growth gives *Antropora* an unusual flexibility in the formation of new encrusting layers. As demonstrated by Buss (1981), this flexibility can provide an important advantage in overgrowth abilities relative to competition for space. While the pattern of self-overgrowth in *Antropora* differs from that in other species, the budding processes involved are inferred to be virtually the same. Extensive vertical growth of an individual zooid does not represent a budding event; it is merely a continuation of that zooid's ontogeny.

EVOLUTIONARY TRENDS IN ZOOID AND COLONY GROWTH

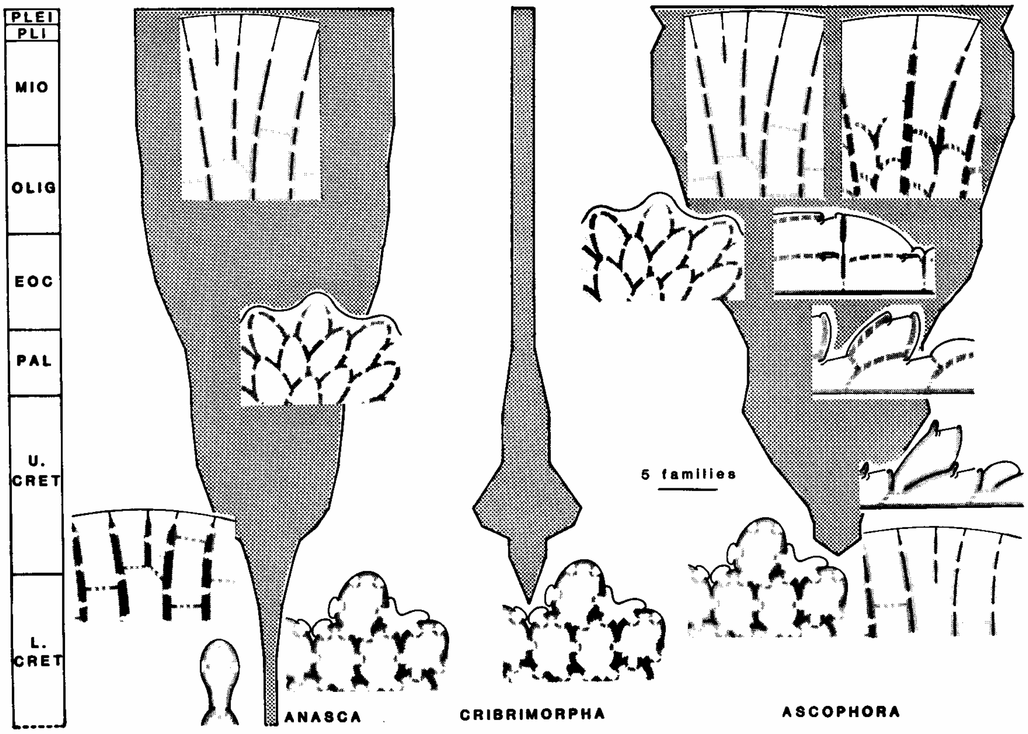
The degree to which the morphology and functions of zooids differ from that of solitary animals because of their membership in a colony expresses the degree of control that the colony has over member zooids. In cheilostome bryozoans, which as a group are exclusively colonial, these differences in colony integration represent the degree to which zooid structure and function are subordinated to colony structure and function (Boardman and Cheetham 1973; Cheetham and Cook 1983). At lower levels of integration, zooids and zooid buds retain a high degree of autonomy. At higher levels, zooid autonomy decreases and budding is influenced by more than one zooid, sometimes incorporating large sections of the colony. Thus the extensive development of interzooidal communication organs, coextensive budding zones, and partitioning interior walls indicate higher levels, while more restricted communication systems and widely developed exterior bounding walls indicate lower levels (Cook and Chimonides 1981*a*). In defining categories of budding process and geometry, I have provided a set of morphological standards for constructing a series of different levels of integration based on how colonies grow. This series is eventually testable against the occurrence of different developmental sequences in colonies preserved in the fossil record. If zooid autonomy was higher in primitive cheilostomes than in more advanced ones, as the fossil record strongly suggests, more integrated budding patterns should represent more derived rather than primitive morphological conditions.

The level of integration in individual lineages of cheilostomes, however, often seems not to have evolved in a simple stepwise progression to more highly integrated types (Boardman and Cheetham 1973). Several factors relate to this. There appears to be a broad range of integration within each major group of cheilostomes. Budding process and geometry may vary within species and even within a single colony; for example, in *Membranipora* budding is at first zooidal and later multizooidal when colonies have attained sufficient size. These mutual occurrences clearly establish that some types of budding can be transitional to others. Equally significant is the fact that a number of potential combinations of budding processes and geometries predicted by the model are not transitional. These combinations have not been found in nature. They are either undiscovered, have not yet evolved, or are in some way constrained from doing so. Geometric and developmental constraints can often be made conspicuous by determining boundary conditions of morphologies related to growth from existing colony structure. Certain other morphologies may be further restricted by conflicting functional requirements of parent and daughter zooids. Relationships between the presence or absence of certain morphological features and the ability to grow in a particular way can be established empirically by comparative study. More rigorous testing of these relationships may, however, depend on biomechanical or detailed phylogenetic analyses, often within more limited taxonomic groups (Cheetham and Thomsen 1981; Lauder 1981; Cheetham and Hayek 1983).

Perhaps most importantly the same budding processes and geometries have arisen independently many times in taxonomically distinct groups and often in different temporal sequences (text-fig. 10). These appearances strongly suggest parallel or convergent trends combined with an overall mosaic pattern of evolution in the several major stocks within the order. Until more fossil evidence is available the inferred evolutionary progression from less integrated to more integrated modes of growth can only be interpreted as a broad evolutionary pattern that cuts across phylogenetic boundaries. The most striking result is that this pattern is remarkably consistent with progressive evolutionary trends in zooid structure from simple anascan to complex anascan and cribrimorph to ascophoran (Harmer 1902); in the successive appearance of increasingly more integrated and morphologically complex structural types in the genera of the early–late Cretaceous; and in the marked diversification of taxa and of colony morphologies during the two major radiations of cheilostomes during the late Cretaceous and the Eocene (Cheetham 1971; Boardman and Cheetham 1973; Cheetham and Cook 1983, and references therein).

In this section I focus on three major evolutionary trends in encrusting growth that appear to have greatly altered the diversity of cheilostome taxa and colony forms through time: from intrazooidal to zooidal and multizooidal budding; from uniserial to multiserial budding; and from single- to multilayered growth by frontal budding. This pattern of increasing colony integration, particularly in the ways colonies grow, appears to be a dominant theme in cheilostome evolution, and indeed in the evolution of many other colonial animals (Coates and Jackson, in press). It is important to note, however, that less integrated morphologies have persisted throughout the history of the group, though they now constitute a much smaller proportion of overall cheilostome diversity.

Intrazooidal, zooidal, and multizooidal budding. The intrazooidal budding process in single-layered colonies typically corresponds to a relatively low level of colony integration, all zooids being formed principally by exterior body walls. Each zooid has morphogenetic control over certain structures



TEXT-FIG. 10. Diversity of families within the three suborders of cheilostomes from the early Cretaceous to the Recent. Similar budding processes and geometries have evolved repeatedly, even in distantly related taxa and in different temporal sequences. In many cases, initial diversification of groups with new modes of growth (shown as in text-fig. 1) correspond with periods of major increases in familial diversity, as in the late Cretaceous and Eocene. Note especially transitions from uniserial to multiserial budding in early Cretaceous anascans, appearance of zooidal budding in anascans and ascophorans in the late Cretaceous, and diversification of frontal budding in ascophorans in the Palaeocene and Eocene. Diversity data modified from Cheetham (1971) and Hakansson and Thomsen (1979), with timescale adjusted according to Berggren (1972) and Obradowich and Cobban (1975).

(i.e. pore chambers) even though those structures can eventually become part of another zooid. Intrazooidal budding presumably represents the most primitive cheilostome budding pattern, appearing in the first known Jurassic cheilostome (Pohowsky 1973) and in similar uniserial species that continued to be abundant through the early Cretaceous.

Zooidal budding evolved in late Cretaceous multiserial genera after the initial appearance of multiserial geometries in genera with intrazooidal budding (text-fig. 10). Zooidal budding radiated rapidly through anascan and ascophoran suborders; its recurrent evolution in large numbers of taxa with disparate zooid morphologies strongly suggests widespread parallelism and convergence. Taxa with zooidal budding continued to diversify throughout the Tertiary, producing a sustained, directional evolutionary trend leading to the eventual dominance of zooidal budding in both encrusting and erect cheilostomes. A lack of fossil evidence precludes all but the most general inferences of phylogenetic relationships between intrazooidal and zooidal budding. That intrazooidal budding arose and diversified in Cretaceous species long before the appearance of species with zooidal budding has been clearly established (Larwood *et al.* 1967; Banta 1975; Cheetham 1975). What remains uncertain is which of several morphogenetic transitions (i.e. intrazooidal multiserial to zooidal multiserial) occurred and whether this transition took place in simple sequence or may have happened repeatedly. One indication of repeated occurrences is present in Recent species of *Electra* where distal budding is zooidal and lateral budding intrazooidal (Silen 1944). Neither is it clear whether such transitions are reversible, as may have been the case if *Fenestrulina* (with intrazooidal budding) descended from the Microporellidae and Schizoporellidae (the latter with zooidal budding). While some degree of morphogenetic polarity is implied by increasing levels of colony integration, it may not be absolute.

Direct evidence of multizooidal budding is present in colonies of *Parasmittina* from the Pliocene of the Atlantic Coastal Plain (Lidgard, unpubl.). However, an earlier origin is likely based on the occurrence of similar skeletal morphologies related to budding in species extending back to the late Cretaceous. Many of these earlier forms are congeneric with later multizooidally budding species, and have comparable skeletal architectures and geometrical arrangements of zooids. The fragile nature of multizooidal growing edges, together with the emphasis of previous studies on zooid morphology which typically excluded morphology related to growth, may have prevented the recognition of multizooidal budding in geologically older faunas. Multizooidal budding has also apparently evolved independently in a number of distantly related anascan and ascophoran groups (text-fig. 10).

Zooidal and especially multizooidal budding represent important advances in integration in that they decouple colony growth from individual zooid ontogeny. In species with intrazooidal budding, colony growth is directly dependent on zooid growth. Exterior transverse walls delimit completed zooids at the colony growing edge prior to the onset of development of each successive zooid (Pl. 28, figs. 1, 2). In species with zooidal and multizooidal budding, colony and zooid growth proceed concurrently, but the size of the growing area of the colony and the rate of growth are no longer coincident with finite zooidal size and ontogenetic stage (Pl. 27, figs. 3, 4). In some species, interior transverse walls may not begin to develop until multizooidal buds have extended the colony growing edge several zooid lengths beyond the last completed zooid. The transition from sequential to concurrent development at zooid and colony levels can also be viewed as a key evolutionary advance, increasing both the potential rate of colony growth over the substrate and the morphogenetic flexibility of the growing edge (see below). Decoupling of colony and zooidal development also implies that pre-emption of space on the substrate by colony growth does not determine what size zooids developed there eventually must be. While this decoupling of developmental processes has increased in the course of evolution across many cheilostome lineages, it can never completely individuate the colony as the unit of growth. Colonies are still ultimately dependent on zooid development and the repertoire of zooid function to initiate and maintain colony growth.

Uniserial and multiserial budding. The early Cretaceous transition from vine-like uniserial to sheet-like multiserial colonies represents an increase in integration of growth regulation among adjacent lineal series (Banta 1975; Cheetham and Cook 1983). From the earliest cheilostomes in the Jurassic through much of the early Cretaceous, all known genera retained a morphologically simple anascan zooid structure and a uniserial budding geometry (Thomas and Larwood 1956, 1960; Pohowsky 1973; Cheetham 1975; Dzik 1975; Larwood 1975). Coincident with the evolution of multiserial forms, growth of adjacent lineal series within colonies became more or less coordinated and interzooidal communications developed between zooids in laterally adjacent series. The formation of matched uncalcified windows with pore plates or pore chambers must have depended on a level of coordination in the development of adjacent lineal series not present in uniserial budding (Banta 1975). When uniserially budded zooids come into contact they generally do so at an angle, rather than in parallel rows. Buds in physically separate lineal series more frequently abut mature zooids than other buds at the same stage of development. As is apparent in *Pyriporopsis* (Pl. 28, fig. 5), normal zooid development in one of the series commonly stops; interserial communications are rarely if ever developed.

Uniserial and multiserial geometries coexist in several closely related early Cretaceous species, all of which budded new zooids intrazooidally. While multiserial colonies of *Wilbertopora* are commonly arranged in discrete lineal series, zones of coalescent budding are also invariably present (Pl. 28, fig. 6). Coalescent budding presumably arose during the early Cretaceous with the regularization of the multiserial budding pattern in *Wilbertopora* or *Wilbertopora*-like species (Banta 1975). Coalescence depends on the close proximity of buds prior to calcification, an unlikely event in uniserial *Pyriporopsis*. The two forms overlap broadly in skeletal characteristics (Banta 1975; Cheetham 1975). In fact, early growth stages in some colonies of *Wilbertopora* are uniserial; these are succeeded by generations of zooids arranged in more typical multiserial geometries. The morphogenetic and phylogenetic transition between uniserial and multiserial forms probably initially occurred in the early Cretaceous, between *Pyriporopsis* and a *Wilbertopora*-like descendant (Cheetham 1975; Cheetham and Cook 1983).

Although uniserial colonies persisted in cheilostomes throughout the Tertiary to the present, there is little evidence that they ever constituted a major proportion of cheilostomes following the early evolution of multiserial forms. Only a few uniserial genera are known in either the cribrimorphs or the ascophorans. Uniserial and multiserial cribrimorphs are known to coexist in the late Cretaceous (Larwood 1962), but the transition from a uniserial ancestral stock to a number of multiserial descendant groups, as apparently occurred in anascans, cannot be inferred from available fossil evidence. Among the ascophorans, uniserial budding is rare and probably secondarily derived. The earliest well-documented occurrence of uniserial geometry is in the gymnocystidean species *Hippothoa flagellum* (Manzoni) from the Miocene of Europe (Morris 1980). Uniserial budding in ascophorans with cryptocystidean or umbonuloid frontal walls is extremely rare or absent.

Taxa with multiserial zooidal budding had become well established by the end of the late Cretaceous, appearing successively through parallel or convergent evolution in many anascan and ascophoran families (text-fig. 10). Zooidally budding species with coalescent and compound lineal geometries did not appear until the middle Eocene and lower Pliocene, respectively (Canu and Bassler 1923; Larwood *et al.* 1967; Lagaaij 1968). Coalescent lineal budding occurs rarely in a great many species but is only extensively developed in species of *Beania*, whose fossil record is sporadic, but extends back at least to the Eocene. *Beania* possesses a relatively unspecialized morphology whose relationship to other zooidally budded groups is obscure (but see Silen 1944). The remaining geometries form a morphologically related series based on increasing levels of colony integration. Uniserial forms lack the interserial communication organs that are regularly developed in multiserial genera. These forms are morphogenetically (but not necessarily phylogenetically) related to successively more integrated forms with discrete multiserial budding (as in *Membranipora*) and compound lineal budding (as in *Parasmittina*). Colony control increases in the latter groups as space is pre-empted by a major region of the colony rather than zooid by zooid, and is then transformed into several zooids. Interior walls similarly play a greater role in partitioning new zooids.

Multilayered growth. The development of frontal budding represents a third major evolutionary trend in cheilostome growth, following earlier transitions from the predominance of uniserial to multiserial geometries, and from intrazooidal to zooidal and multizooidal budding processes. As with these earlier transitions, frontal budding involves an increase in overall colony integration, here relative to single-layered modes of growth. Frontal budding involves the loss of full functional capability in underlying zooids, increasing colony dependence and lessening these zooids' autonomous function. Frontally budding colonies also develop an additional zone of astogenetic change, formed subsequently to the initial zone of change surrounding the first zooid (ancestrula) and extending to the following zone of repetition (Boardman and Cheetham 1973). Astogeny is the sequential development of asexual generations of zooids, beginning with the ancestrula formed at larval metamorphosis.

Discrete lineal multiserial colonies apparently first occur in late Cretaceous *Celleporella* that develops frontal buds from laterally placed pore chambers (Voigt, pers. comm.). *Celleporella* probably evolved after the initial radiation of cheilostome taxa with single-layered multiserial growth. Diversification of ascophoran species with discrete lineal frontal buds developed from hypostegal coeloms most probably began in Eocene species of *Schizoporella* (Canu and Bassler 1920). Both variations of this geometry are present in living ascophorans, although neither appear to be widespread taxonomically.

The first evidence of coalescent and nonlineal frontal budding in encrusting colonies probably occurs in Palaeocene species such as *Bathosella aspera* (Canu and Bassler), although available specimens do not permit certain determination. These geometries did not become widespread until the middle Eocene when they evolved convergently in several rooted, loosely attached genera such as *Batapora*, and in a number of mound-like genera such as *Celleporaria* that generally encrusted hard substrates (Canu and Bassler 1920; Cheetham 1966; Cook and Lagaaij 1976; see also Cook and Chimonides 1981*b*). Coalescent and nonlineal geometries continued to appear among different encrusting taxa throughout the later Tertiary and are most probably the dominant modes of frontal budding in cheilostomes. While the evolution of these budding geometries in encrusting taxa was apparently delayed until the Tertiary, the possibility of an earlier origin cannot be ruled out. Zooid morphology indicative of nonlineal frontal budding occurs in abundant erect species of '*Kleidionella*' and *Beisselina* from the Maastrichtian of Europe (Voigt 1959).

Nonlineal frontal budding decouples colony growth from the ontogeny of single zooids in a manner analogous to nonlineal and other geometries and budding processes in single-layered growth. Zooids are partitioned by interior walls in a confluent budding zone that often covers large areas of a colony's surface. In loosely attached rooted species such as *Sphaeropora fossa* (Haswell), nonlineal lateral and frontal budding begin with the first generation of zooids developed from the ancestrula and constitute nearly all subsequent colony growth. The development of frontal budding appears similarly fixed in many mound-like encrusting species such as *C. magnifica* (Osburn) that almost invariably develop frontal buds within the first few generations of zooids. However, in many species, for example *Schizoporella floridana* (Osburn), lineal frontal budding occurs irregularly and possibly as a response to limitation of substrate. Frontal budding of zooidal polymorphs such as avicularia may occur irregularly or in an almost invariant pattern. This range of variability in the development of frontal buds suggests an enormous flexibility in colony control of development, much of which may be responsive to environmental cues.

Finally, multiple layered colonies formed by extensive self-overgrowth have a fossil record extending back at least to the late Cretaceous in genera such as *Conopeum* (Kues 1983). While not necessarily involving frontal budding, this mode of multiple layered growth appears to have been regularly developed by many different groups throughout the Tertiary. As stated above, self-overgrowth depends primarily on single-layered budding processes and geometries.

DISCUSSION

Ecological consequences of encrusting growth patterns. To the extent that different budding processes and geometries do not simply express inherent developmental or structural constraints or random variation, they must reflect pressures imposed by the environment. Growth patterns which evolved convergently in lineages with phylogenetically independent sets of constraints should be especially closely linked to similar ecological traits (Jackson 1979*a*). This appears to be the case in a great many fossil and Recent encrusting species. Different combinations of budding process and geometry (text-fig. 1) correlate strongly with ecological success in different habitats, regardless of the taxonomic affinities of the species involved.

A general correlation between ecological variables and colony form has been demonstrated repeatedly (Stach 1936; Cheetham 1963, 1971; Lagaaij and Gautier 1965; Schopf 1969; Rider and Cowen 1977; and others). This relationship becomes even more striking when different modes of zooid and colony development are compared to ecological parameters, such as the stability and longevity of different substrates. For example, the majority of species with single-layered nonlineal budding geometries (some also exhibit nonlineal frontal budding) live on sand or mud bottoms rather than on hard substrates (cf. Lagaaij 1963; Cook and Lagaaij 1976; Cook 1981; Cook and Chimonides

1981*a*, *b*, 1983; Cheetham and Cook 1983; and others). Although the functional reasons are not understood, this empirical correlation suggests that nonlineal budding may not be so much the result of shared phyletic origins as the convergent development of beneficial ways of growing in similar habitats. Nonlineal geometries have evolved repeatedly in morphologically distinctive anascan and ascophoran groups with a wide range of zooidal structural complexity, apparently first occurring in the free-living Palaeocene Cupuladriidae (Gorodiski and Balavoine 1961; Cook and Chimonides 1983), and later in the free-living Eocene lunulitid *Trochopora* (Hakansson, pers. comm.). A number of conescharelliniform and orbituliporiform genera, all with nonlineal budding, also appeared in the Eocene (Cheetham 1966; Cook and Lagaaij 1976; Cook and Chimonides 1981*b*). Their small colonies develop cuticular rootlets from uncalcified regions of the body wall; the rootlets presumably anchor colonies to sand grains in the absence of hard substrates. Whereas *Cupuladria* and *Trochopora* are anascans, these rooted genera are all ascophorans. Nonlineal budding occurs again in loosely encrusting sheet-like and erect branching Euthyrisellidae, which lack a fossil record (Cook and Chimonides 1981*a*). The complex zooidal structure of this group clearly differentiates it from other ascophoran taxa with nonlineal geometries.

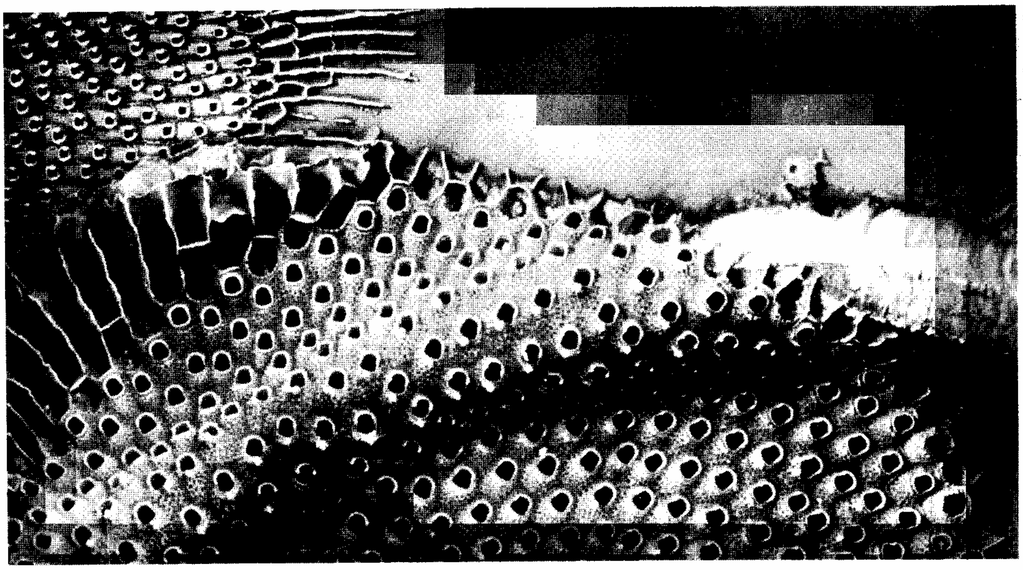
Single-layered sheet-like colonies with zooidal and commonly multizooidal budding similarly dominate cheilostome faunas on macroalgal substrates in temperate and many tropical environments (Mawatari 1975; Bernstein and Jung 1979; Jackson 1981; and others). Bryozoans often encrust all available surfaces on these ephemeral substrates; competition for space may be intense. The rapid rate of growth afforded by multizooidal budding may reflect part of a life history suited to the predictable disappearance of the substrate (Seed and O'Connor 1981; Yoshioka 1982).

Moreover, the dominant encrusting species on more stable and long-lasting substrates such as temperate-zone pilings and panels, temperate-zone cobbles and boulders, and the undersurfaces of foliaceous reef corals are frequently those with multizooidal budding, frontal budding, or both (Osman 1977; Sutherland and Karlson 1977; Sutherland 1978; Jackson 1979*b*, 1981, 1984; Kay and Keough 1981; Jackson and Winston 1982; and many others). The rapid growth and resulting increased colony size afforded by multizooidal budding have been shown to significantly increase colony survivorship in a variety of habitats (Sutherland and Karlson 1977; Sutherland 1978; Jackson 1981, 1984; Jackson and Winston 1981; and others), and also to increase long-term fecundity in many species (Hayward 1973; Hayward and Ryland 1975; Yoshioka 1982; Jackson and Wertheimer, in press; Winston and Jackson, 1984). In addition, colonies with zooidal and multizooidal budding are frequently capable of growing upward away from the substrate, overtopping a competitor and quickly overgrowing it (text-fig. 11; Jackson 1979*a*; Lidgard and Jackson 1982). Species with intrazooidal budding typically lack these overgrowth capabilities.

Frontal budding better enables a colony to overgrow potentially detrimental organisms settled on the colony surface. Vertical sections through frontally budded colonies commonly reveal secondarily encrusting organisms such as barnacles and serpulids embedded in the skeletal matrix, evidence that settlement on the colony surface is a common phenomenon. Similarly, outer layers of zooids killed by severe environmental fluctuations or predation can be regenerated from protected underlying zooids in a manner not possible in colonies that grow only as single-layered forms (Cummings 1975). Frontal budding also increases the vertical stature of the colony, better enabling it to withstand the advances of competitors and providing a vertical platform from which to overgrow their frontal surfaces (Jackson and Buss 1975; Buss 1981). Based on these observations, colonies with multizooidal and frontal budding can be expected to be relatively larger and more abundant than those with other modes of encrusting growth where competition is frequent and in stable environments where colony longevity may be at a premium. Again, these patterns of ecological dominance cut across phylogenetic boundaries.

It is not coincidental that these patterns are consistent with the evolutionary trend toward increased colony integration, both in the fossil record as new modes of growth evolve, and in modern faunas where many different modes of growth are present in species with a broad range of life history strategies (Jackson 1979*a*, 1981, 1984; Lidgard and Jackson 1982; Lidgard 1983; Winston and Jackson, 1984). In this sense, integration may be coupled with the role of the colony as the unit of selection in the environment (Schopf 1973). As cheilostomes evolved more diverse colony forms and more integrated modes of growth, the potential versatility of these new groups increased as well. Species with higher states of integration and more versatile modes of growth often retain the ability to revert to lower states as the situation demands. For example, species such as *Schizoporella floridana* (Osburn) that are capable of frontal budding may revert to exclusively single-layered growth, maximizing their allocation of resources to rapid growth across a substrate. Alternatively, mound-like frontally-budding colonies may subsequently develop zooids budded by a single-layered growth process in the act of overgrowing a competitor or an organism settled on the colony surface. Newly evolved growth patterns may have better enabled colonies to exploit new situations or face existing ecological problems, leading to the displacement of groups with less versatile modes of growth by others with higher potential versatility (Vermeij 1973*a*, *b*). Species with uniserial budding generally fare poorly in competitive overgrowth (Jackson 1979*a*) and decrease in relative abundance from the late Cretaceous onward. Diversification of multiserial taxa with zooidal and later multizooidal budding processes coincides with an increase in within-habitat abundance and with a high frequency of overgrowth success versus intrazooidally budding forms. A similar pattern apparently exists for groups with frontal budding. A vast amount of descriptive data from living and fossil cheilostome faunas tends to support these trends, but little of it provides rigorous quantitative evidence for relationships between colony integration, developmental patterns, and ecological patterns of distribution and abundance. These relationships are none the less apparent and their ecological and evolutionary consequences quite obviously important; they will be more fully explored elsewhere (Lidgard, in prep.; Lidgard and Jackson, in prep.).

Finally, we must recognize that morphological, ecological and evolutionary patterns in encrusting species are not wholly independent of those in erect taxa. While I have not attempted here to examine



TEXT-FIG. 11. *Cryptosula pallasiana* (Moll) overgrowing *Parasmittina nitida* (Verrill), USNM 376698, 376701, U.S. Fishing Comm. Sta. 5522, Vineyard Sound, Massachusetts, Recent. In the area of contact between the two species the normally zooidal budding process of *Cryptosula* has become multizooidal. The leading edge of the colony has grown upward away from the substrate, overtopping the competing colony. This appears to be a common occurrence in competitive overgrowth involving species capable of multizooidal budding. Light photograph of stained specimen coated with ammonium chloride, × 12.

budding patterns in erect cheilostomes, the eventual comparison of encrusting and erect modes of growth seems inevitable. A significant number of Recent cheilostome faunas are dominated by erect species (Lagaaij and Gautier 1965; Ryland 1974; Dyrynda and Ryland 1982), yet few have been examined in the same detail as have encrusting faunas (Jackson 1981). While encrusting colonies may respond to one suite of environmental factors, erect colonies may be subjected to a largely different suite. Encrusting colonies must contend with substrate-associated factors such as sedimentation, competitive overgrowth, or the development of feeding currents in a boundary layer flow (Cook 1977; Buss 1979; Jackson 1979*b*; Lidgard 1981; and others). On the other hand, most of an erect colony is removed from processes acting on or directly above the substrate. Erect colonies are affected by the need for branch spacing, by the risk of breakage in flow, and possibly by differential predation by fish and invertebrates (Jackson 1979*a*, 1981, 1984; Vance 1979; Bernstein and Jung 1979; Russ 1980; Cheetham and Thomsen 1981; Cheetham and Hayek 1983). Whether these implied ecological differences are reflected in differences in budding processes and geometries should provide an interesting measure of the range of variability in growth patterns that may have evolved in different selective regimes.

Some phylogenetic considerations. Bryozoans demonstrate such an enormous degree of developmental flexibility that interpreting the origins of variable developmental patterns in different taxonomic groups poses something of a dilemma. Attempts to generalize about modes of growth and to base classifications on limited suites of characters have produced a history of instability in cheilostome taxonomy (Cheetham and Cook 1983). Perceived phylogenetic relationships, especially those thought to exist among higher taxa, have been altered repeatedly to conform to the prevailing taxonomy (and preferred taxonomic characters) of the times. By giving greater weight to certain characters in a taxonomic hierarchy we may inadvertently produce apparent changes in other characters that we regard as convergent rather than non-convergent. Some of the recurrent appearances of the same budding processes and geometries in combination with different states of other characters could, in fact, reflect a natural phyletic progression rather than a complex mosaic evolution or convergence from different phyletic origins.

How then should we interpret evolutionary trends in different characters, especially those related to growth? At one level this may mean deciding which potential taxonomic characters are more variable within and between species and how much of this variability is genetically controlled. Certainly we can reasonably infer that budding processes and geometries are to some degree under genetic control. Yet species-specific characters can be tightly controlled genetically, be almost invariable intraspecifically, and yet still form a convergent or mosaic evolutionary pattern at generic and higher levels. To the extent that convergent or mosaic evolution has occurred, and I believe this has often been the case, a polythetic approach to phylogenetic relationships is likely to be most fruitful (Cheetham and Cook 1983).

At least some combinations of budding process and geometry are undoubtedly polyphyletic (text-fig. 10). It is almost inconceivable, for example, that uniserial ascophorans descended directly from uniserial anascans or cribrimorphs. Substantial differences in the overall morphology and in the respective fossil records of these groups indicate independent evolutionary origins. However, it is often unclear how much different modes of growth are constrained by phylogeny or, conversely, what constraints growth patterns place on other morphological characters. If growth patterns and other morphological characters were perfectly correlated, this would presumably reflect a hierarchical series of constraints on morphology and permit phylogenetic reconstructions based on growth patterns alone. This is decidedly not the case for the majority of cheilostome species. Individual species often possess innate flexibility in their developmental systems, so much so that the morphogenetic potential for different ways of growing is retained but rarely if ever expressed. The potential for single-layered coalescent budding, for example, is frequently present in zooidally budding multiserial colonies, but is only rarely developed, as when lineal series are constricted by an obstacle on the substrate. In some species, different budding geometries can be evoked simply by altering food sources, temperature, or water currents (Marcus 1926; Menon 1972; Winston 1976).

Differences also exist among species in the details of development and structure of homologous body walls. When different combinations of budding process and geometry occur together in a single colony, this occurrence cannot of itself demonstrate a phylogenetic pathway leading from one to another. Except in cases where there is clear historical evidence (e.g. in the *Pyriporopsis–Wilbertopora* sequence in the mid-Mesozoic), only comparative studies enable us to reasonably infer which pattern is the primitive and which the derived.

The model presented here provides a framework for comparison that should alleviate many of these difficulties. It may be that more derived modes of zooid and colony growth represent higher levels in a progressive series of states of integration in which the potential for development of some or all less integrated modes of growth is retained (e.g. coalescence in many multiserial groups). Regardless of whether these states are truly atavistic, the phylogeny of budding patterns must be interpreted with care and with these different expressions of colony integration firmly in mind.

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