Ontogeny in Animal Colonies: A Persistent Trend in the Bryozoan Fossil Record

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The principal modes of zooid and colony growth in encrusting cheilostome bryozoans have undergone a major evolutionary transition during the last 100 million years. Comparisons of species within successive North American fossil faunas reveal a persistent trend in which one mode of growth is gradually supplanted by another. Ecological evidence from living faunas and the polyphyletic nature of this trend suggest that the transition has adaptive significance.

THE IDEA THAT DEVELOPMENTAL mechanisms play an important role in determining rates and patterns of evolution is now relatively widespread (*1*). Yet few examples in the fossil record show how changes in the ways organisms grow could have affected large-scale evolutionary trends in morphology or diversity (*2*). The fossil record is a record of adult morphology. Embryos and larval forms are seldom fossilized, and in only a few groups of organisms can an accurate record of growth be deduced from an individual's skeleton (*3*). Cheilostome bryozoans are a diverse, geologically abundant group of marine invertebrates whose colonial organization preserves a record of ontogeny in both the zooid skeleton and that of the colony as a whole (*4*). To resolve better the evolutionary roles played by substantially different growth patterns, I analyzed changes through time in the principal modes of growth of encrusting cheilostomes (*5*). I present evidence indicating that an ancestral mode of growth has been gradually displaced by a more highly integrated mode in a major evolutionary trend extending through the last 100 million years.

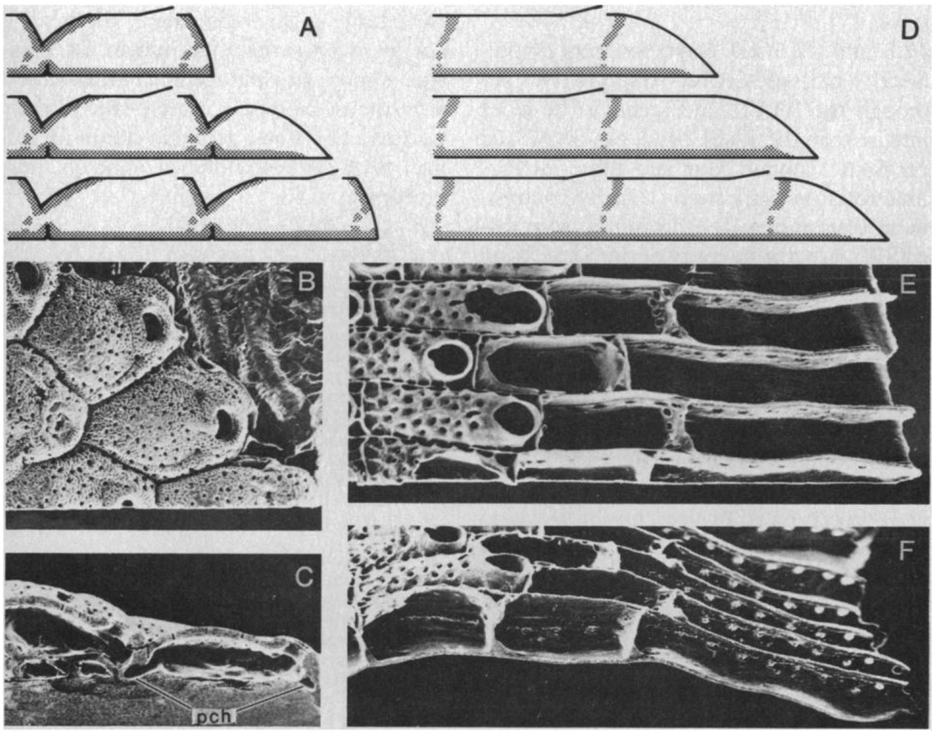

Fig. 1. Longitudinal sections illustrating formation of zooids at the growing margins of encrusting colonies. In (A) intrazooidal budding is idealized to show the discontinuous process of formation of a single zooid. Buds form through expansion by outward growth of an uncalcified portion of a zooid body wall. Expansion of the body cavity and outer wall begins from pre-existing chambers formed within one or more antecedent zooids. These pore chambers are subsequently transformed by budding into parts of a single developing zooid. Completion of each zooid is generally marked by an apparent pause in growth prior to the initiation of the next bud. Exterior zooid body walls are shown with outer bounding cuticle (lines) and calcified skeleton (stippling). Interior walls are shown with skeleton and no cuticle (inner tissue layers and other organ systems are not shown). In (B) intrazooidal budding is illustrated in a top view of *Monoporella nodulifera* with numerous complete zooids bearing pore chambers present directly at the colony margin. Uncalcified tissue of this Recent colony was removed in order to reveal zooid wall structure as it appears in fossils (USNM 376704) magnification, × 25. (C) In a side view of (B) note that the pore chamber (pch) is completed before expansion of the next zooid bud. In (D) zooidal budding is shown to be a relatively continuous process. Body walls are portrayed as in (A). Transverse walls grow into the body cavities of expanding buds, partitioning older regions into now-discrete zooids proximal to the growing margin of the colony. These walls lack pore chambers and their growth does not involve transformation of parts connate to one zooid into parts of another. (E) An extremely prominent form of zooidal budding is developed in *Schizoporella floridana*. In this extreme form, growth of interior transverse walls lags far behind the advancing colony margin such that a number of successively older zooids coexist in a series of different ontogenetic stages. Morphologically complete zooids are absent from the colony margin (USNM 376703). Magnification, × 35). (F) A side view of (E) shows calcified interior walls that partition zooids within lineal series. In a living colony, uncalcified cuticular and tissue layers enclose the body cavity and calcified skeleton. Figure modified from (*5*).

The distinction between intrazooidal and zooidal budding is a fundamental division in the ways cheilostomes grow (*5, 6*). These asexual budding processes, together with the geometric arrangement of zooids, determine the overall pattern of growth at margins of encrusting colonies. Intrazooidal budding is a typically episodic process marked by a pause in outward growth before initiation of each new bud from an antecedent zooid (Fig. 1, A–C). In contrast, zooidal budding involves more or less continuous expansion of buds (Fig. 1, D–F). At some stage of development, buds exceed the length of single zooids. Growth of successive zooids is therefore not strictly dependent on antecedent zooids having reached a particular stage in their development. In this sense, zooidal budding partly decouples the outward growth of the colony as a whole from the finite ontogeny of individual zooids. To the extent that zooid autonomy is reduced during growth, zooidal budding represents an increase in the level of integration of the colony relative to its intrazooidal counterpart (*5, 7, 8*). Since colony growth emerges as a less discontinuous process no longer strictly dependent on individual zooid ontogeny, it may become more rapid in the more highly integrated forms (*9*).

Proportions of encrusting species with intrazooidal versus zooidal budding were determined for 66 fossil and 18 living cheilostome faunas from North America (*10*). These data are not based on extrapolations to regional or worldwide levels of species diversity but rather on a large sample of within-fauna diversity patterns characteristic of much of the known cheilostome fossil record. Analyses were confined to the Gulf of Mexico, Caribbean, and Atlantic Coastal

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Plain to ensure a relatively continuous and representative record occurring primarily in tropical to temperate, shallow shelf environments where bryozoans are most abundant and most diverse (*11*). The faunas themselves make up well-documented, well-preserved local assemblages having recognizable geographic and stratigraphic boundaries, thus minimizing potential biases of transport and mixing. Because species proportions are tabulated within temporally and areally restricted assemblages, they are directly comparable regardless of geologic age (*12*).

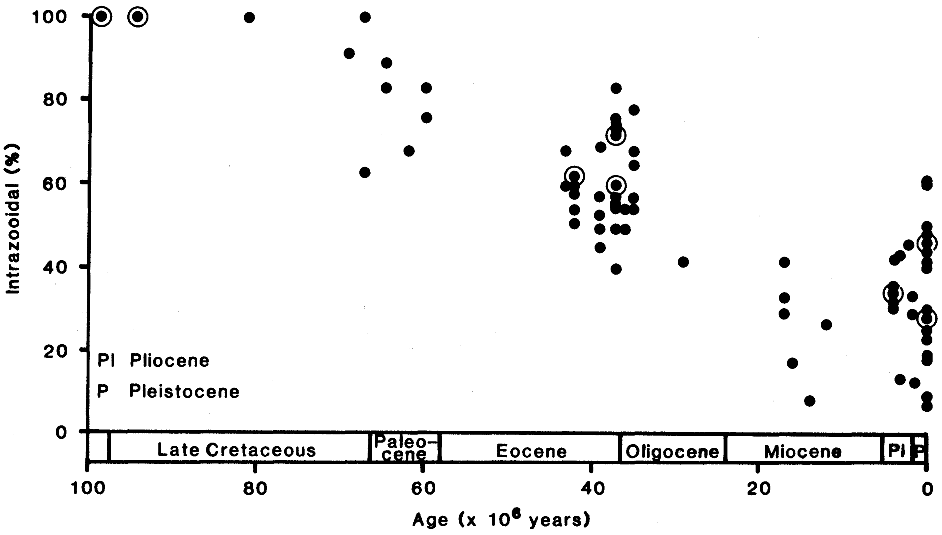

Fig. 2. Proportion through time of species with intrazooidal budding within North America faunas of encrusting cheilostome bryozoans (*10*). Proportion of species with zooidal budding is the inverse. Open circles represent overlap of more than one fauna. These proportions show no statistically significant correlation with diversity levels within individual faunas, whether they are considered as fossil only ($r = -0.07, P > 0.1$), living only ($r = 0.22, P > 0.1$), or a combination of both ($r = -0.12, P > 0.1$; all proportions arcsine transformed).

The results summarized in Fig. 2 indicate that encrusting cheilostomes have undergone a sustained, directional evolutionary trend from the dominance of intrazooidal budding during the Cretaceous and early Tertiary through the eventual dominance of zooidal budding in the later Tertiary and Recent (*13*). Although the proportion of intrazooidally budding species within faunas decreases considerably from the Late Cretaceous onward, aggregate worldwide diversity of cheilostomes increases. Few data are available to estimate the magnitude of this increase at species level. Generic diversity, however, is known to have arisen from five or fewer genera during the Early Cretaceous to several hundred that are now extant (*8*). Hence, although groups with intrazooidal budding persisted through this interval, those with zooidal budding proliferated and possibly survived at higher rates and became increasingly dominant in the structure of successive faunal assemblages.

The most striking aspect of this trend is the broad phylogenetic distribution of different modes of growth (*5, 8*). Intrazooidal budding represents the most primitive cheilostome budding process, appearing in the earliest known Jurassic species and in subsequent lineages throughout the Early Cretaceous. Zooidal budding apparently first evolved in the Late Cretaceous, then recurred differentially in independent lineages well into the Tertiary, sometimes co-occurring with intrazooidal budding even within the same genus. This trend did not result simply from bauplan constraints, nor is it an artifact of directional changes in environmental factors or of sampling biases alone. First, these budding processes are not strongly correlated with most morphological traits, particularly traits of the zooidal frontal surface upon which most phylogenetic inferences are based (*8*). Second, consistent temporal changes are not apparent in climate, depth, substrate, or depositional regime, and several faunas often span a range of these environmental factors even within a particular geologic age. Finally, intermittent or chance perturbations such as mass extinctions show little indication of uniformly affecting groups with one mode of growth more than groups with another mode (*14*). The recurrent development of zooidal budding in morphologically, phyletically, and temporally distinct lineages thus strongly suggests parallel or convergent patterns in the several major evolutionary stocks within the order (*5*).

Differences in budding processes are important determinants of ecological success in many environments; the measure of this success gives further indication that zooidal budding represents a major adaptive innovation. Among nearly all well-studied living faunas of encrusting cheilostomes on hard substrates, the dominant species in terms of both relative abundance (percentage of cover) and competitive overgrowth success are those with zooidal rather than intrazooidal budding (*15*). Since larval production and colony survivorship are positive functions of colony size, the role of budding processes in enhanced rates of growth that increase size or in overgrowth interactions that limit or reduce size must also be related to individual fitness (*15, 16*). These patterns of ecological dominance are developed among fossil as well as living faunas and among phylogenetically different groups of species (*5, 9, 17*). Thus it seems evident that species with different budding processes may be characterized by substantially different potentials for evolutionary change. Whether these potentials are realized in differential rates of speciation and extinction will depend on separating these alternatives, a difficult task. The results presented here document a striking evolutionary trend from the predominance of one mode of growth to another. Perhaps most intriguing is the fact that this trend should involve such a sustained increase in such an apparently adaptive trait as zooidal budding.

REFERENCES AND NOTES

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2. A. H. Cheetham, L. C. Hayek, and E. Thomsen, [*Paleobiology* 7, 68 (1981)] and D. Jablonski and R. A. Lutz [*Biol. Rev.* **58**, 21 (1983)] provide recent examples.
3. Some mollusks, for example, preserve the shape of the larval shell and an incremental record of successive shapes by accretionary growth of the shell. Growth patterns of fossil organisms are more commonly reconstructed by analogy with related living forms or, where skeletal remains are sufficiently abundant, from an aggregate series of juveniles and adults.
4. Following larval metamorphosis a nearly complete sequence of zooid ontogeny can be reconstructed within a colony by comparing genetically identical zooids at different stages of development. Although fossilization generally preserves only skeletal body walls, available evidence indicates that histologic and organogenic processes parallel that of skeleton formation [R. Tavener-Smith and A. Williams, *Phil. Trans. R. Soc. London Ser. B* **264**, 97 (1972); G. Lutaud, in *Treatise on Invertebrate Paleontology*, part G (revised), *Bryozoa*, R. A. Robison, Ed. (Geological Society of America, Boulder, CO, and University of Kansas, Lawrence, 1983), pp. 208–237; P. A. Sandberg, *ibid.*, pp. 238–303].
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6. ——, in *Bryozoa: Ordovician to Recent*, C. Nielsen and G. P. Larwood, Eds. (Olsen & Olsen, Fredensborg, Denmark, in press).
7. R. S. Boardman and A. H. Cheetham, in *Animal Colonies*, R. S. Boardman, A. H. Cheetham, and W. A. Oliver, Eds. (Dowden, Hutchinson, & Ross, Stroudsburg, PA, 1973), pp. 121–220.
8. A. H. Cheetham and P. L. Cook, in *Treatise on Invertebrate Paleontology*, part G (revised), *Bryozoa*, R. A. Robison, Ed. (Geological Society of America,

Boulder, CO, and University of Kansas, Lawrence, 1983), pp. 138–207.

9. Few studies document comparative growth rates for species with different modes of growth that co-occur in the same habitat. Where such data do exist, the species having the highest growth rates and attaining the largest colony sites are generally those with zooidal budding [for example, J. E. Winston and J. B. C. Jackson, *J. Exp. Mar. Biol. Ecol.* **76**, 1 (1984)].
10. Budding processes were determined for representative colonies in several hundred species with encrusting growth habits (*5, 6*). Frequencies of species having zooidal versus intrazooidal budding were tabulated for nearly all well-documented fossil faunas and selected Recent faunas from North America. Mean number of species per fauna is 21 (standard deviation, 13.9). A lower limit of ten species was imposed to minimize small sample biases, especially those associated with the patterns of occurrence of rare species [M. A. Buzas *et al.*, *Paleobiology* **8**, 143 (1982)]. Several Cretaceous faunas are exceptions in that only a few species are present; these faunas are nonetheless representative because they occur repeatedly in numerous Gulf Coast localities [A. H. Cheetham, in *Bryozoa 1974, Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, S. Pouyet, Ed. (Université Claude Bernard, Lyon, 1975), pp. 547–564. Most faunas included in the analysis (virtually all type and referred specimens) were examined directly in collections of the U.S. National Museum of Natural History, Washington, DC, and my own collections from the Atlantic Coastal Plain. Principal references include: R. C. Osburn, *Bull. Bur. Fish.* **30**, 205 (1912); *N.Y. Acad. Sci.* **16**, 321 (1940); F. Canu and R. S. Bassler, *Bull. U.S. Natl. Mus.* **106**, 1 (1920); *ibid.* **125**, 1 (1923); *ibid.* **165**, 1 (1933); *U.S. Geol. Surv. Prof. Pap. 137* (1926), p. 32; F. J. S. Maturo, *J. Elisha Mitchell Soc.* **73**, 11 (1958); A. H. Cheeham, *Geol. Soc. Am. Mem.* **91**, 1 (1963); J. B. Rucker, *Bull. Mar. Sci.* **14**, 603 (1964); N. G. Shaw, *J. Paleontol.* **41**, 1393 (1967); J. E. Winston, *Bull. Am. Mus. Nat. Hist.* **173**, 99 (1982).
11. T. J. M. Schopf, *Proc. Am. Phil. Soc.* **113**, 464 (1969); in *Animal Colonies*, R. S. Boardman, A. H. Cheetham, W. A. Oliver, Eds. (Dowden, Hutchinson, & Ross, Stroudsburg, PA, 1973), pp. 247–303. Cold- and deep-water faunas are poorly represented in the cheilostome fossil record compared to faunas considered to have lived in warmer and shallower depositional environments.
12. Although the diversity of some fossil faunas may be reduced in comparison to their Recent counterparts as a result of taphonomy, there is no indication that species with zooidal or intrazooidal budding are preserved differentially. See also the discussion of within-fauna diversity comparisons by R. K. Bambach [*Paleobiology* **3**, 152 (1977)].
13. The increase in the relative frequency of zooidal budding through time would have been still more dramatic if erect taxa were included. Preliminary evidence indicates that intrazooidal budding is relatively rare among both living and fossil erect species (*5*). Although greatly outnumbered by encrusting taxa, erect taxa evolved repeatedly from the Late Cretaceous through the Cenozoic to become the most abundant bryozoans in many marine habitats.
14. More rigorous evaluation of the role of chance perturbations may be precluded by the resolution of available data and by the choice of model parameters that can affect the outcome of such an evaluation [P. H. Harvey *et al.*, *Annu. Rev. Ecol. Syst.* **14**, 189 (1983); J. F. Quinn and A. E. Dunham, *Am. Nat.* **122**, 602 (1983)].
15. J. B. C. Jackson, *Univ. Tenn. Stud. Geol. 5* (1981), pp. 22–36; *J. Anim. Ecol.* **75**, 37 (1984). Since bryozoans are clonal organisms capable of both fission and fusion of colonies, abundance is considered here as percentage of cover rather than the number of colonies.
16. P. J. Hayward and J. S. Ryland, *Pubbl. Staz. Zool. Napoli.* **39** (suppl.), 226 (1975); J. B. C. Jackson and S. P. Wertheimer, in *Bryozoa: Ordovician to Recent*, C. Nielsen and G. P. Larwood, Eds. (Olsen & Olsen, Fredensborg, Denmark, in press).
17. At least a partial test of an adaptive hypothesis is provided by the extent to which the distribution of developmental traits can be predicted across taxa on ecological criteria [T. H. Clutton-Brock and P. H. Harvey, *Proc. R. Soc. London Ser. B.* **205**, 547 (1979)]. The method is equally applicable to fossil species since the skeletal remains of colonies preserve patterns of distribution, abundance, colony size, and competitive overgrowth interactions; preliminary results are consistent with ecological patterns observed in the Recent [S. Lidgard and J. B. C. Jackson, *Geol. Soc. Am. Abstr. Progr.* **14**, 547 (1982); S. Lidgard, *ibid.* **15**, 627 (1983); unpublished data].

18. I thank especially A. H. Cheetham and J. B. C. Jackson for discussion of the work. They and R. S. Boardman, P. L. Cook, R. E. Plotnick, S. M. Stanley, and R. K. Wayne provided helpful criticism. D. A. Dean, J. Sanner, and L. W. Ward assisted in laboratory and fieldwork, and M. J. Keough and J. W. Winston kindly made available unpublished faunal data. Supported by grants from the Geological Society of America and by a Smithsonian Institution Predoctoral Fellowship.

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Concurrent Overproduction of Synapses in Diverse Regions of the Primate Cerebral Cortex

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Synapses develop concurrently and at identical rates in different layers of the visual, somatosensory, motor, and prefrontal areas of the primate cerebral cortex. This isochronic course of synaptogenesis in anatomically and functionally diverse regions indicates that the entire cerebral cortex develops as a whole and that the establishment of cell-to-cell communication in this structure may be orchestrated by a single genetic or humoral signal. This is in contrast to the traditional view of hierarchical development of the cortical regions and provides new insight into the maturation of cortical functions.

THE CEREBRAL CORTEX IS DIVIDED into numerous cytoarchitectonic areas that are specialized structural and functional units (*1*). Cortical differentiation is most fully expressed in the human brain and underlies the subdivision of the cortex into sensory, motor, and associative systems. Although this cortical diversity is of major conceptual and biomedical importance, the mechanisms of its development are unknown (*2, 3*). Studies based on histological and histochemical parameters such as the density and distribution of myelin (*4*), levels of various enzymes (*5*), and metabolic activity (*6*) tend to support a hierarchical model of cortical development in which primary sensory and motor areas mature before adjacent secondary areas, and the association regions differentiate last. Although this model has had a major influence on physiological and psychological studies (*7*), a number of recent findings are not entirely consistent with it. For example, neurons in the primary visual cortex begin and complete their genesis later than neurons in the adjacent secondary visual areas (*8*), and the columnar organization of connections in the prefrontal association cortex (*9*) emerges prior to that of ocular dominance columns in the primary visual cortex (*10*).

We examined the pre- and postnatal course of synaptogenesis in five areas of the monkey cerebral cortex that mediate, respectively, visual, somatosensory, motor, associative, and limbic functions. On the basis of the available literature (*3–6*), we expected that synaptogenesis would proceed in clearly segregated waves in different cortical regions, with the sensory areas achieving maturation earlier than association areas. We also predicted that synaptogenesis would exhibit laminar specificity, and perhaps follow the inside to outside pattern of cortical neurogenesis (*11*) or the sequence of ingrowth of various afferents. Contrary to these expectations, however, our results revealed a simultaneous synaptogenesis in all areas and layers examined.

Rhesus monkeys (*Macaca mulatta*) of various pre- and postnatal ages were perfused with mixed aldehydes (*12*), and 1 by 2 by 3 mm blocks were dissected from the visual, somatosensory, motor, and prefrontal cortices, and the dentate gyrus of the hippocampus, and processed for electron microscopic analysis (Fig. 1). More than 500,000 synapses were identified from 22 monkeys in a total of 25,000 electron micrographs. Twenty percent of these synapses were selected randomly for further classification on the basis of their termination (on spines, dendritic shafts, or somas) or their morphology (symmetrical or asymmetrical) in each layer (*13*). The data are expressed as density of synapses per unit area of neuropil to provide a measure that is unaffected by age-related changes in the extracellular space, by the growth of neuronal perikarya, or by the addition of glial cells, myelin sheaths, or blood vessels.

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