Comparative Ecology of Bryozoan Radiations: Origin of Novelties in Cyclostomes and Cheilostomes

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Cyclostome and cheilostome bryozoans diversified at different times and consequently in different ecological contexts. Cyclostomes began their rebound from a Permo-Triassic bottleneck in the early Jurassic, prior to increases in bioturbation, durophagous predation, and other ecological changes of the Mesozoic Marine Revolution. Cheilostomes did not appear until the latest Jurassic and rapid diversification began only in the mid-Cretaceous, when the Mesozoic Revolution was well under way. We compare the radiations of these two groups to test for similarities in the within-group patterns of origin of biologically significant novelties, and for between-group differences that might be due to ecological context or group attributes. As seen for other invertebrate taxa, within-group novelties were not concentrated in onshore settings, in contrast to origination patterns at the ordinal level. Differences in environment of first occurrence and rapidity of novelty acquisition were not obviously related to the Mesozoic Revolution, or to the distinction between zooid- and colony-level characters. The contrast in novelty acquisition rates may partly reflect group-specific constraints. In cyclostomes, novelties appeared rather evenly over 100 Ma, whereas in cheilostomes many of the novelties appeared in the Late Albian-Early Cenomanian during a period of rapid diversification. Despite a slow start (Late Jurassic–mid Cretaceous), the cheilostome radiation entered an explosive phase that may characterize successful establishment of groups founded late in the Phanerozoic.

INTRODUCTION

Evolutionary radiations have received increasing attention in recent years, particularly the explosive diversification of metazoans in the early Paleozoic. However, comparative studies of diversifications have rarely been attempted, despite the potential for such analyses to reveal general principles, and for differences in tempo and mode to yield insights on group-specific, time-specific, or habitat-specific factors (Valentine, 1973; Erwin et al., 1987; Jablonski and Bottjer, 1990b). Here we present an ecological comparison of the radiation of two of the major groups of post-Paleozoic marine invertebrates, the cyclostome and

cheilostome bryozoans. This comparison is interesting for several reasons: both orders are colonial, and include species with similar morphologies, life histories, ecological roles and habitat distributions (McKinney and Jackson, 1989); and preliminary cladistic analyses (Carle and Ruppert, 1983; Anstey, 1990; Cuffey and Blake, 1991) indicate a close phylogenetic relationship of these two bryozoan orders (although not as sister-groups), thereby holding constant a number of potential confounding factors.

Cyclostomes and cheilostomes are both sessile suspension-feeding groups that generally encrust or extend from solid substrata in environments ranging from the intertidal to abyssal depths. The two groups have been shown to interact competitively for substratum space through overgrowth in the Recent (McKinney, 1992) and in the fossil record (McKinney, 1995), further increasing the likelihood that both groups were subject to similar challenges. However, their post-Paleozoic radiations occurred in strikingly different ecological contexts. The cyclostomes were rebounding from the end-Permian mass extinction into a relatively impoverished world, whereas the cheilostomes diversified into a far richer setting, in the midst of the profound changes collectively termed the Mesozoic Marine Revolution (Vermeij, 1977, 1987, 1994; Harper and Skelton, 1993; Roy, 1994). We examine here the timing and environmental context of the first appearances of major evolutionary novelties, many of them convergent, to test for differences between the groups that might derive from the contrasting ecological contexts of the two radiations.

CYCLOSTOMES AND CHEILOSTOMES

Phylogenetic relationships among the orders and classes of bryozoans have been a contentious matter and remain rather speculative (Dzik, 1975; Carle and Ruppert, 1983; Cheetham and Cook, 1983; Boardman, 1984; Anstey, 1990; Taylor and Larwood, 1990; Cuffey and Blake, 1991; Nielsen, 1995). Nonetheless, the consensus of most systematic work is that cyclostomes and cheilostomes are not sister taxa, and that the cheilstomes are, instead, most closely related to the poorly mineralized ctenostomes. Diagnostic features of these taxa are discussed and figured in detail by Robison (1983), Reed (1991), and Nielsen (1995).

Cyclostomes are probably a paraphyletic group sharing

various skeletal characters with other stenolaemate orders (Cystoporata, Cryptostomata, Trepostomata, Fenestrata) that did not survive beyond the Triassic. Presumed apomorphic characters of living cyclostomes that are lacking in gymnolaemates (ctenostomes plus cheilostomes) include polyembryony and a membranous sac (peritoneum) with annular musculature (Nielsen and Pedersen, 1979; Reed, 1991). The muscles of the membranous sac function together with the longitudinal ectodermal muscles to evert the feeding polypide (Taylor, 1981).

Gymnolaemates also possess a suite of characters that are apparently lacking in cyclostomes and other bryozoans, including parietal muscles that traverse the body cavity and function in polypide eversion, a comparatively "normal" pattern of embryology, and an organ system for metabolic transport (funiculus) that is differentiated into multiple vessels within and among zooids (Bobin, 1977; Cheetham and Cook, 1983; Reed, 1991). Opercula and similar structures equipped with paired occlusor muscles for closing the zooidal orifice are present in most cheilostomes and in a few ctenostomes (Cheetham and Cook, 1983; Taylor, 1990). Non-brooded larvae characterize some genera of ctenostomes and anascan cheilostomes. Genera of cheilostomes with such cyphonautes larvae are similar in skeletal morphology to the earliest cheilostomes appearing in the fossil record (Taylor, 1988). An acellular pleated collar around the everted polypide is present in most ctenostomes and a few cheilostomes, including a morphologically primitive anascan, but is not known to occur in any other bryozoans (Banta et al., 1995).

The unmineralized ctenostomes first appeared in the Ordovician as borings (Pohowsky, 1978; Mayoral et al., 1994), and encrusting forms very similar to, but antedating, the earliest recorded cheilostomes are preserved as bioimmurations in the Middle and Upper Jurassic (Taylor, 1990). Based on these and other lines of evidence, ctenostomes are generally considered ancestral to cheilostomes (see Banta, 1975; Taylor, 1990; Banta et al., 1995), and preliminary cladistic studies indicate that cheilostomes are monophyletic (Carle and Ruppert, 1983; Anstey, 1990; Cuffey and Blake, 1991; Banta et al., 1995; but for an opposing view see Jebram, 1991). Therefore, despite the clear need for further phylogenetic analyses of bryozoan inter-relationships, cyclostomes and cheilostomes can be reasonably seen as distinct though closely related groups with separate origins and phylogenetic histories for the purposes of our comparisons.

From the Early Ordovician to the Early Cretaceous, bryozoan diversity was overwhelmingly dominated by stenolaemates, the class that includes the cyclostomes. However, cyclostomes were only a minor component of Paleozoic bryozoan faunas. The stenolaemates suffered massive losses at the end of the Paleozoic, including about 85% of the 27 families known from the Late Permian and, thus, conformed to the global pattern of this largest of mass extinctions, which removed 78–86% of marine genera and an estimated 90–95% of marine species (Erwin, 1993; Jablonski, 1995). Cyclostomes survived this profound bottleneck, were rare in the Triassic and Early Jurassic, but began to radiate in the late Early Jurassic (Taylor and Larwood, 1990). By the Bathonian, the group's global diversity stood at approximately 9 families and 32 genera (Fig. 1; see also Sepkoski, 1990). Whereas Triassic cyclostomes all had
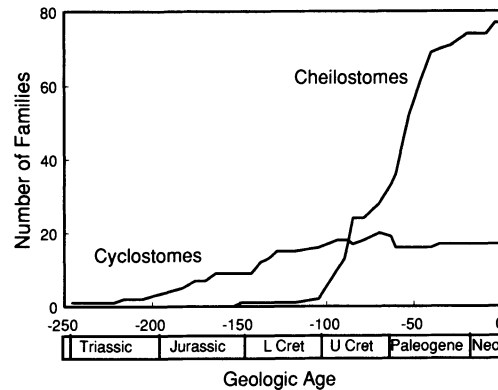

FIGURE 1—Family-level diversity of cyclostome and cheilostome bryozoans from the beginning of the Triassic through the Pleistocene. Diversity totals are based on Taylor (1993), and are plotted at the midpoint of stages, using boundaries as designated by Harland et al. (1990).

simple encrusting colonies, a variety of more complex and erect colony-forms appeared in the Jurassic.

Cheilostome bryozoans first appeared in the late Jurassic, with the oldest known species, *Pyriporopsis pohowskyi* Taylor (1994a), from the Oxfordian/Kimmeridgian of Yemen. Although this species occurs in the Madbi Formation, which is interpreted as a relatively deep-water deposit (Haitham and Nani, 1990), the colonies encrust a shallow-water gastropod thought to be allochthonous and probably from slump deposits (N. J. Morris, pers. comm. to DJ and PDT). The shallow-water origin of the cheilostomes is supported by all other Late Jurassic and earliest Cretaceous occurrences (Jablonski and Bottjer, 1990a; Radley, 1991). *P. pohowskyi* and other early cheilostomes were anascans with simple zooid morphologies and runner-like or sheet-like encrusting colonies.

After a latest Jurassic–early Cretaceous interval of low global and within-habitat diversity (see: Taylor, 1988; Jablonski and Bottjer, 1990a,b; Lidgard et al., 1993), the cheilostomes began a burst of diversification in the mid-Cretaceous, roughly 50 Ma after their initial appearance, and had overtaken the cyclostomes in overall diversity by the Late Cretaceous (Fig. 1). Cheilostomes are now the dominant bryozoan order in marine ecosystems by virtually any measure, from global taxonomic diversity to local community composition to colony-level competitive interactions (McKinney and Jackson, 1989; McKinney, 1992, 1993, 1995; Lidgard et al., 1993). The change in dominance was achieved, however, without any major drop in cyclostome diversity, on either global or assemblage level (Lidgard et al., 1993). Rather than exhibiting the reciprocal relationship in their standing diversities that might have been expected from their relative competitive abilities (McKinney 1992, 1995), the cyclostomes experienced only a slight decline in diversity while the cheilostomes diversified from the mid-Cretaceous onwards. The cheilostome diversification occurred in the face of an interaction-rich, diverse Cretaceous biota that included not only cyclostomes but such superior competitors as sponges, cnidarians, and ascidians (e.g., McKinney and Jackson 1989).

The question, then, is how the two radiations were influenced by their contrasting ecological and evolutionary contexts, i.e., whether novelties originated at a different

rate or in a different environmental pattern during the cheilostome radiation compared to the post-Paleozoic radiation of the cyclostomes. A simple set of predictions might draw on a general model of incumbency and its macroevolutionary consequences (e.g., Valentine, 1980; Van Valen, 1985; Hallam, 1987, 1990; Rosenzweig and McCord, 1991; see also Sepkoski, 1996). This model inherently assumes an evolutionary role for biotic interactions. In terms of temporal patterns, one prediction might be that the cyclostomes radiated into a comparatively empty setting in which many previous ecological guilds had become depauperate. Therefore, the rate of novelty acquisition should have been rapid early on. This pattern is seen, for example, among early Cenozoic mammals after the demise of dinosaurs and other groups apparently created ecological opportunities. The cheilostomes radiated into a more densely occupied world, and so should have diversified more slowly and novelties should have appeared over longer periods of time.

Environmental predictions may follow as corollaries. Earlier work on post-Paleozoic invertebrates suggests that ordinal origination tends to be concentrated in onshore settings, but that the origin of lower-level novelties depends on group-specific bathymetric diversity gradients. Given that this contrast appears to hold from the start of the Mesozoic for crinoids, tellinacean bivalves, and a smaller group of cheilostome novelties (Jablonski and Bottjer, 1990a, 1991), the broader set of bryozoan novelties analysed here may be expected to originate more or less randomly among environments. For example, these novelties may simply follow a bathymetric diversity gradient such as that seen today (Schopf, 1969; McKinney and Jackson, 1989; Lidgard, 1990), thereby arising preferentially in higher diversity inner- to mid-shelf settings.

METHODS

We compiled the oldest known occurrences of 12 striking and biologically significant novelties for the cyclostomes and 12 for the cheilostomes (Table 1). We chose innovations that clearly affected the basic functional, structural, or ecological working of colonies or their constituent zooids, expanding on a list presented by Voigt (1985). Some of these novelties represent apparent evolutionary convergences between the two groups, while others represent innovations unique to one group or the other. Some novelties represent reorganization of the entire colony, while others represent the origin of specialized zooid morphologies within the colony. A number of these innovations, even those presently used to define higher taxa, may have arisen more than once within a single bryozoan order. In the absence of resolved phylogenies at the appropriate levels, we have used the oldest recorded appearance of each feature; we cannot yet distinguish these multiple origins or track the environmental history of each novelty as a monophyletic trajectory. Data are drawn from the literature and the collections of Ehrhard Voigt (Hamburg, Germany) and The Natural History Museum (London, U.K.).

The first occurrences of these evolutionary novelties were placed into the onshore-offshore environmental categories discussed by Bottjer and Jablonski (1988), using sedimentary and stratigraphic criteria as outlined in that

TABLE 1—Morphological innovations that are unique to cyclostomes or cheilostomes, or apparently derived convergently in the two groups. Geologic stages of first occurrences are given in the Appendix.

	Convergent novelties	
	Cyclostomes	Cheilostomes
1. Larval brood chambers	Gonozooids	Ovicells
2. Frontal budding	+	+
3. Calcified opercula	+	+
4. Mandibulate polymorphs	Eleozooids	Avicularia
5. Erect bilaminate colonies	+	+
6. Erect cylindrical colonies	+	+
7. Fenestrate colonies	+	+
8. Articulated colonies	+	+

Unique cyclostome novelties
1. Nanozooids
2. Fascicles
3. Fungiform colonies
4. Lateral branching

Unique cheilostome novelties
1. Articulated spines
2. Cribrimorph grade frontal shields
3. Ascophoran grade frontal shields
4. "Free-living" lunuliform colonies

paper. These lithologic data are cited in the Appendix along with the relevant taxonomic and geographic information. We recognize that the appearance of an individual novelty in a particular category of the onshore-offshore gradient might be subject to the biases of incomplete sampling (bryozoans have not been as thoroughly studied in the Mesozoic as most other commonly fossilized phyla, and appear to be strongly "Eurocentric" in distribution). The overlap of the two groups in assemblages from the latest Jurassic onward provides a measure of control for this potential bias, as does our examination of a number of different novelties for both cyclostomes and cheilostomes.

NOVELTIES

Convergent Novelties

Larval Brood Chambers (Fig. 2A,D)

Most Recent bryozoans brood their young, and in living cyclostomes and cheilostomes brooding generally occurs in calcified protective structures (Strom, 1977; Reed, 1991). Cyclostomes have a unique embryology (polyembryony) in which the developing embryo cleaves into secondary embryos and may undergo further cleavages into tertiary embryos. Many genetically identical embryos thus typically fill an enlarged modified zooid (gonozooid) and complete their development to the larval stage. Cheilostomes exhibit a more "normal" embryology and have a variety of brooding patterns. However, most taxa brood only one or a few embryos in cap-like brood chambers (ovicells) located between distally adjacent zooids and topologically outside the main body cavity of the colony. A few genera do brood embryos in enlarged, modified zooids (e.g. *Adeonellopsis*), but these were unquestionably derived independently from the gonozooids of cyclostomes. The first appearance of ovicells may signal the origin of brooding in cheilostomes and the acquistion of nonplanktotrophic development.
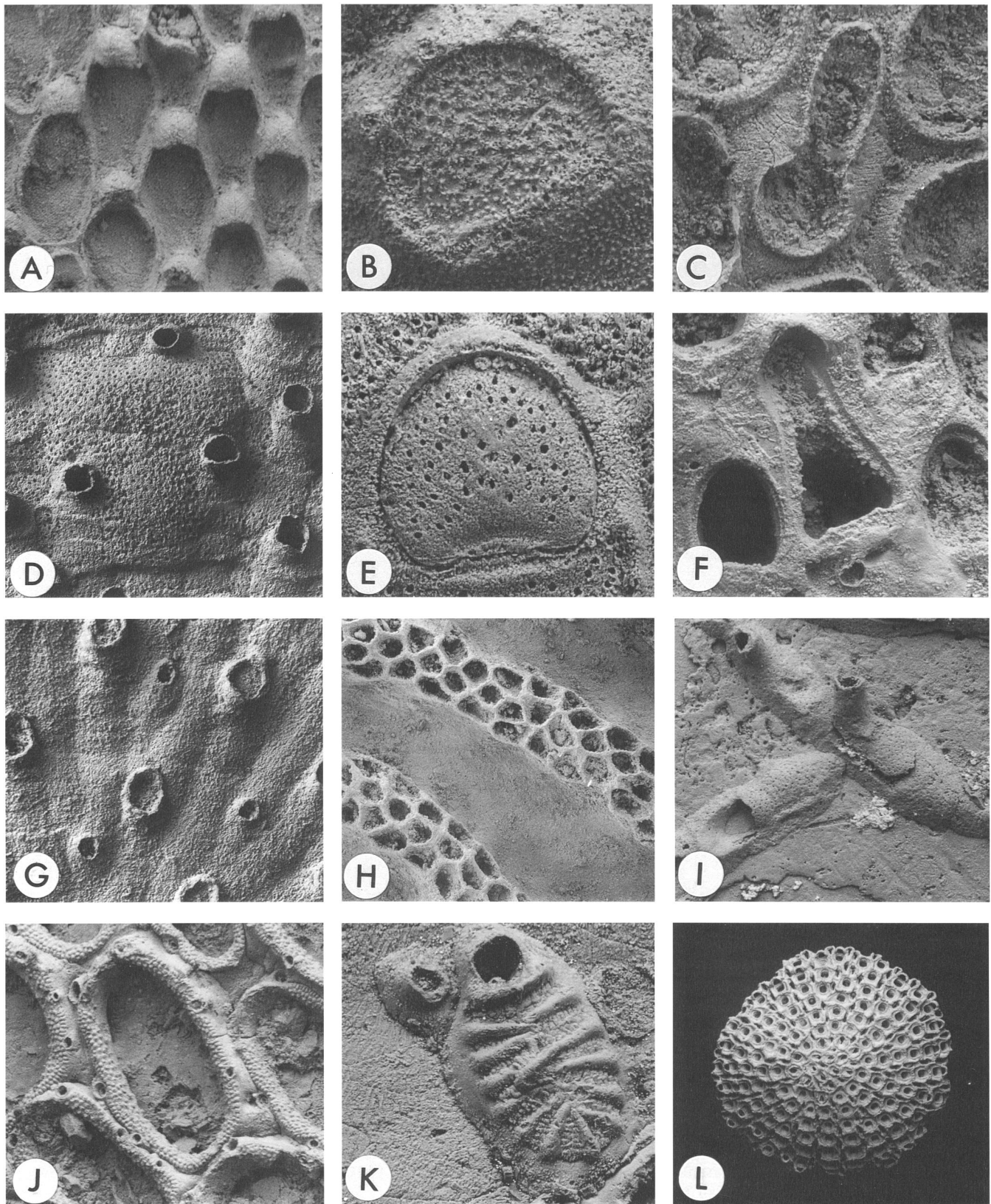
FIGURE 2—Some evolutionary novelties in cyclostome and cheilostome bryozoans. The examples shown have been selected for their clarity from the wider range of novelties analyzed in this paper; only H, J, and K represent the earliest occurrences of the novelties. Figures A–F show convergent novelties in cheilostomes (A–C) and cyclostomes (D–F); figures G–L show novelties unique to cyclostomes (G–I) or to cheilostomes (J–L). (A) Brood chambers (hood-shaped ovicells) in the cheilostome "*Wilbertopora*" sp. (BMNH BZ3294 (1); Cretaceous, Albian, Fort Worth Formation, Denison, Texas; × 50). (B) Calcified operculum in the cheilostome *Macropora grandis* (Hutton) (BMNH D36630;

That is, development via non-feeding larvae that spend little time in the plankton (Taylor, 1988; see: Santagata and Banta, 1996, for an alternative view).

The first appearance of gonozooids in cyclostomes perhaps also signals the acquisition of nonplanktotrophic development (Taylor and Larwood, 1990), although here the evidence is more equivocal for two reasons. First, the most primitive form of brooding may be in peristomial gonozooids (Harmelin, 1974) which would normally be broken-off and lost in fossils. Second, no Recent cyclostomes are known to have non-brooded, planktotorphic larvae. Hence, there is no modern analogue against which to judge fossil cyclostomes inferred to lack brooding (e.g., Taylor, 1979a).

Frontal Budding

Frontal budding of feeding zooids is best explained in reference to the topology of encrusting colonies, although it also occurs in many erect and free-living forms. Zooid buds are formed from the upper "frontal" surface of the colony, perpendicular to the substratum surface, rather than laterally along that surface. In encrusting forms, frontal budding confers advantages in resisting overgrowth by other sessile organisms and in regeneration of damaged zooids (Lidgard, 1985, 1986; McKinney and Jackson 1989). Frontal budding in cheilostomes generally occurs through the outward expansion of a partitioned region of the body cavity (Banta, 1973; Lidgard, 1985). Frontal budding may produce normal feeding zooids or a variety of zooid polymorphs. With several notable exceptions (i.e., bud fusion and secondary calcification of the colony surface), most frontal budding events produce only a single zooid. We consider only frontal budding of feeding zooids here. Over cheilostome history, an increasing number of taxa exhibit frontal budding (Lidgard and Jackson, 1989).

Among cyclostomes, budding of zooids onto the frontal surface of the colony occurs in a variety of taxa but has not been as thoroughly investigated as frontal budding in cheilostomes. Cyclostome frontal budding usually involves "intrazooecial fission" (Hillmer et al., 1975), a process in which the apertural area of the body cavity of a parent zooid is partitioned into several chambers by new skeletal walls—thereby producing multiple zooids at once, in constrast to cheilostomes. In melicerititid cyclostomes (Taylor, 1994b), and some related groups (Taylor and Weedon, 1996), there are typically seven such chambers—a central

chamber continuous with that of the parent zooid, surrounded by six smaller chambers. Through upward growth, the central chamber becomes a "pseudoancestrula" with a new aperture, and the six smaller chambers develop into radially-orientated zooids that initiate overgrowth of the old colony surface. Cyclostome frontal budding, although not as labile morphologically, presumably has the same functional role as in cheilostomes. In the Appendix we list two alternatives for the earliest example of cyclostome frontal budding: one is an older, less precise equivalent to cheilostome frontal budding, and one a younger, closer analog; results are unchanged in either instance.

Calcified Opercula (Fig. 2B, E)

In cheilostomes, the operculum is a fold of the outer wall of the primary zooid orifice. It is closed by paired occlusor muscles and blocks the zooid orifice when the lophophore is retracted into the main body cavity. The operculum, often considered to be an apomorphy of the crown-group Cheilostomata and lacking in very few species, serves a protective function and is often heavily sclerotized. Calcification of the operculum, which presumably provides the most robust protection, appears to have evolved repeatedly and occurs in a small minority of taxa scattered across a wide range of cheilostome families; e.g., Electra crustulenta (Electridae), Inversaria spp. (Onychocellidae), Castanopora lambi (Pelmatoporidae), Macropora spp. (Macroporidae).

Cretaceous-Paleocene "melicerititid" cyclostomes (Family Eleidae) evolved similar opercula which presumably shared a protective function, although the mechanism allowing their opening and closing is as yet unclear (Taylor, 1994b). There is no indication that melicerititids or any other extinct cyclostomes possessed uncalcified opercula as a precursory stage to the calcified condition.

Mandibulate Polymorphs (Fig. 2C, F)

In certain clades of both cyclostomes and cheilostomes, the opercula of some polymorophic zooids have become enlarged and transformed to produce mobile structures termed mandibles or, if particularly elongate, setae. In cheilostomes, these mandible-bearing polymorphs are termed avicularia; most are incapable of feeding, and the majority are smaller than the feeding zooids in the same colony, sometimes being borne on the surface of a feeding

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Miocene, Canterbury, New Zealand; × 130). (C) Mandibulate polymorph (avicularium) in the cheilostome "Wilbertopora" sp. (BMNH BZ3294 (1); Cretaceous, Albian, Fort Worth Formation, Denison, Texas; × 140). (D) Brood chamber (gonozooid) in the cyclostome Hyporosopora portlandica (Gregory) (BMNH D53642; Jurassic, Portlandian, Portland Stone, Tisbury, Wiltshire, England; × 70). (E) Calcified operculum in the cyclostome Reptomultelea goldfussi Taylor (Voigt Collection, Universität Hamburg, no. 10426; Cretaceous, Cenomanian, Mülheim, Westfalia, Germany; × 175). (F) Mandibulate polymorph (eleozooid) in the cyclostome Meliceritites sp. (Voigt Collection, Universität Hamburg, no. 10406; Cretaceous, Campanian, Kalshamn, Sweden; × 105). (G) Nanozooids in the cyclostome Diplosolen sp. (BMNH D45005; Cretaceous, Campanian, Upper Chalk, Norwich, England; × 80). (H) Fascicles in the cyclostome Theonoa bowerbanki Haime (BZ3293; Jurassic, Aalenian, Lower Inferior Oolite, Cleeve Hill, Gloucestershire, England; × 17). (I) Lateral branching in the cyclostome Voigtopora sp. (Voigt Collection, Universität Hamburg, no. 10501; Cretaceous, Maastrichtian, Navesink Formation, Poricy Brook, New Jersey; × 27). (J) Spines (represented by basal articulation sockets) in the cheilostome Spinicharixa pitti Taylor (Université Claude Bernard, Lyon, no. EM30401b; Cretaceous, Aptian, Utrillas, Spain; × 95). (K) Cribrimorph-grade frontal shield in the cheilostome Ctenopora pecten Lang (BMNH BZ3295; Cretaceous, Cenomanian, Chalk Marl, Cambridge, England; × 82). (L) Free-living, lunulitiform colony of the cheilostome Lunulites tenax Brydone (BMNH D39167; Cretaceous, Campanian, Upper Chalk, East Harnham, Wiltshire, England; × 5).

zooid (adventitious avicularia). The functional significance of avicularia is widely assumed to be defensive, although a number of other possibilities have also been suggested (Winston, 1984, 1986). Circumstantial evidence for a defensive role comes from reports of probable zooid predators such as amphipods and errant polychaetes being trapped and held by avicularia, often for more than 24 hours (Kaufmann, 1971; Winston, 1984). Among the cyclostomes, structural and presumed functional analogs of avicularia occur only in meliceritidids (= Family Eleidae) and are known as eleozoids. Unlike cheilostome avicularia, however, many meliceritidids have eleozooids which are larger than the normal feeding zooids in the colony, while others possess opercula of reduced size (Taylor, 1985).

Erect Bilaminate Colonies

One divergence from the primitive encrusting habit of both groups is the evolution of rigidly erect colonies formed by back-to-back sheets of zooids with apertures facing outward in opposite directions. Erect growth diminishes the constraints of substratum size, the risks of competitive overgrowth, and depletion of food in the slow-moving boundary layer; it may also confer advantages in increasing colony biomass and success in reproductive output and dispersal (Cheetham, 1971, 1986; Jackson, 1979; McKinney and Jackson, 1989). Bilaminate colonies can possess narrow, strap-like branches ("adeoniform" colonies), or broad, foliaceous fronds or sheets ("eschariform" colonies). We treat these growth forms together because the two forms intergrade in living taxa, and sometimes co-occur in the same species and even within a single colony (Schopf, 1969; McKinney, 1989). However, there are functional differences between the growth forms in the feeding currents they create—bilaminate branches lack specific regions (maculae) for venting excurrents, whereas bilaminate sheets are invariably maculate (McKinney, 1986a,b).

Erect Cylindrical Colonies

Rigidly erect branching colonies with cylindrical cross-sections (vinculariiform growth form), in which zooid apertures face outward in several opposing directions from the central axis, differ in their basic architecture from bilaminate colonies. For example, zooids are not usually budded from a central lamina, but instead may originate anywhere within a zone (endozone in cyclostomes) centered on the branch axis. However, the ecological advantages that accrue from an erect growth habit (above) are the same.

Fenestrate Colonies

Erect colonies that form a net of cross-linked branches with zooids opening only on one side were extremely diverse and abundant in Paleozoic seas, as typified by the stenolaemate order Fenestrata. This growth form, often termed "reteporiform," evolved independently in both cyclostomes and cheilostomes during the post-Paleozoic (e.g., Bigey, 1981; Taylor, 1987).

Fenestrate colony form is a variety of the unilaminate erect growth category whose repeated evolutionary success has been documented by McKinney (1986a,b). Whereas fenestrate colonies are distinctive and have a good fossil record, non-fenestrate unilaminate taxa can be confused with encrusting colonies detached from their substrata, and many Recent examples have weakly-mineralized colonies and lack a fossil record. Unilaminates are characterized by an efficient one-way flow of feeding currents, generally from the frontal side through to the reverse side of the colony. The cross-linked branches of fenestrate colonies probably diminish the risk of colony breakage due to current induced drag experienced by unilaminate colonies, all of which are characterized by narrow branch diameters.

Articulated Colonies

In some erect colonies, feeding zooids are distributed along rigidly calcified internodes that are articulated with other internodes at uncalcified nodes, and are often anchored to particulate or other substrata via organic rootlets (e.g., Silén, 1980). The flexibility of such articulated ("cellariiform") colonies reduces effective drag and permits colonies with small branch cross sections to exist in environments of strong ambient flow. This growth form evidently permits the colonization of turbulent waters as well as unconsolidated sediment substrates (Voigt, 1985; McKinney and Jackson, 1989). Articulated colonies have originated repeatedly in cheilostomes (e.g., Szczechura, 1992; Viskova, 1991) and at least once in cyclostomes (Silén, 1977a).

Post-mortem disarticulation means that the identification of articulated colonies can be problematical in fossil material. Although fossil colonies are occasionally found with internodes in close juxtaposition, articulated colonies are normally inferred from the following features: branches of uniform length; lack of branch bifurcation; tapered branch proximal ends and corresponding sockets at branch distal ends; and, in cheilostomes, kenozooids, which can be inferred to have borne rootlets (e.g., *Dioptropora*, Voigt, 1979).

Unique Cyclostome Novelties

Nanozooids (Fig. 2G)

Nanozooids are small zooids with a single long and thin tentacle without cilia. Their function is not clearly understood, but it is thought that the sweeping motion of the tentacle plays an antifouling or cleaning role (Silén and Harmelin, 1974; Viskova, 1989).

Among Recent cyclostomes primary nanozooids characterize the tubuliporine genus *Diplosolen,* but inferred primary nanozooids have also been recorded from some Cretaceous cancellate genera by Brood (1972). Secondary nanozooids, formed within the chambers of feeding zooids after degeneration of the polypide, occur in Recent species of the tubuliporine *Plagioecia* (Silén and Harmelin, 1974) and the rectangulate *Disporella* (Moyano, 1982), as well as some Palaeozoic Fenestrata (Bancroft, 1986). The wide taxonomic distribution of nanozooids suggests multiple origins.

Fascicles (Fig. 2H)

In some species of cyclostomes, the apertures of feeding zooids are grouped together to form fascicles. Apertures within a fascicle are separated only by narrow interior walls. Fascicles tend either to form radial ridges of biserial or oligoserial apertures, or subcircular raised clusters of apertures (e.g., Balson and Taylor, 1982; Walter, 1986). Fascicles probably form foci of inhalent feeding currents (Taylor, 1979b), but may have additional functional roles.

Fungiform Colonies

Fungiform colonies have a narrow stalk supporting an expanded head on which the feeding zooids are located, either evenly distributed or aggregated into fascicles. Sometimes multiple heads are developed on a single stalk, or colonies can comprise stacks of subcolonies each with a stalk and a head. The functional morphology of fungiform colonies is not well understood, although Scholz and Hillmer (1995, p. 136) interpreted this colony-form as " . . . an escape from the substrate surface to [a] more elevated level." Fungiform colonies have clearly evolved several times within the cyclostomes (Voigt, 1974).

Lateral Branching (Fig. 2I)

Uniserial and narrowly multiserial encrusting cyclostomes generally increase their branch numbers through bifurcation of the distal tip of a growing branch. An alternative pattern of branch multiplication is lateral branching in which new branches originate adventitiously from the sides of established branches proximally of their growth tips. The mechanism of lateral branching is poorly understood, but it seems likely that skeletal resorption is involved (Harmelin, 1976). Lateral branching has the advantage of allowing colonies to infill patches of unoccupied substratum space between older branches in the interior of the colony.

The earliest post-Paleozoic occurrence of lateral branching is in Hauterivian colonies of *Voigtopora* sp., and several other Cretaceous encrusting cyclostomes are known to have developed lateral branches (Illies, 1976, 1982; Pitt and Taylor, 1990). Whereas lateral branching is an infrequent supplement to bifurcation in most species, some branching encrusters from the Upper Cretaceous grew entirely by lateral branching. Lateral branching also occurs in Paleozoic cyclostomes, notably a group interpreted to be the closest known relatives of the post-Paleozoic cyclostomes (Taylor and Wilson, 1996). However, the trait appears to have been subsequently lost before reappearing in the Early Cretaceous.

Unique Cheilostome Novelties

Articulated Spines (Fig. 2J)

The spines that are often present on the frontal surface of anascan zooids are known to serve a defensive function. Cook (1985) noted that the presence of well-developed spines in *Electra* deterred the movement of nudibranch predators, and that one nudibranch had been "speared" while traversing the bryozoan. Harvell (1984, 1986) demonstrated experimentally that the presence of a predatory nudibranch induced the formation of spines in *Membranipora*.

The earliest spines in the cheilostome fossil record were apparently articulated basally (Taylor, 1986) and are often interpreted as specialized polymorphs ("spinozooids," see: Silén, 1977b).

Cribrimorph Grade Frontal Shields (Fig. 2K)

Some cheilostomes produce an arched frontal wall formed of marginal spines that fuse above the flexible frontal membrane of the zooids, creating a calcified shield with an array of small, discontinous gaps. The sieve-like cribrimorph frontal shield protects the frontal membrane of the zooid while permitting the passage of water necessary for tentacle eversion (Ryland, 1970; Taylor, 1981; McKinney and Jackson, 1989). This skeletal morphology constitutes an evolutionary grade (Gordon, 1984), which may have arisen polyphyletically through the loss of mobility of articulated spines (Moyano, 1991; Gordon, 1994), followed by their overarching and fusion.

About four genera in which the marginal spines are elongate and arched but not fused, thus appearing to be an evolutionary precursor to the true cribrimorphs, occur along with some of the earliest cribrimorphs in the lower Chalk Marl of England (Lang, 1921; Larwood, 1985); these intermediate "myagromorphs" persisted at least until the Late Campanian.

Ascophoran Grade Frontal Shields

Another evolutionary response to the problem of a vulnerable zooidal frontal surface is seen in the fully calcified frontal shields of ascophorans, the suborder that includes over half of the living species of cheilostomes (Gordon, 1993). These frontal shields are formed by a variety of different developmental pathways, including skeletal growth over an anascan-like flexible frontal membrane, and differentiation of a membranous sac (ascus) that functions as part of the hydrostatic mechanism for eversion of the feeding organ (Ryland, 1970; Cheetham and Cook, 1983; Gordon, 1984). The ascophoran condition in fossil material is recognized by "a pore in the frontal wall (the ascopore) or by a tubular prolongation of the apertural rim (the spiramen) or by a proximal apertural sinus or slit" (Voigt, 1985: 334), which allows the entry of seawater beneath the calcified shield to compensate volumetrically for lophophore eversion.

As with cribrimorphs, ascophorans are an evolutionary and functional grade of skeletal organization treated as a natural group by some earlier authors, but which are almost certainly polyphyletic (Banta and Wass, 1979:31; Taylor, 1981:244; Cheetham and Cook, 1983:196; Gordon, 1984; Voigt and Gordon, 1995). At least some ascophorans were likely derived from cribrimorphs (Gordon and Voigt, 1996).

"Free-living" Lunulitiform Colonies (Fig. 2L)

Cup-shaped or discoidal (lunulitiform) colonies that are attached to tiny substrata (e.g., sand grains) have originated repeatedly in the cheilostomes (Cook and Chimonides, 1983, 1994). Feeding zooids are located only on the
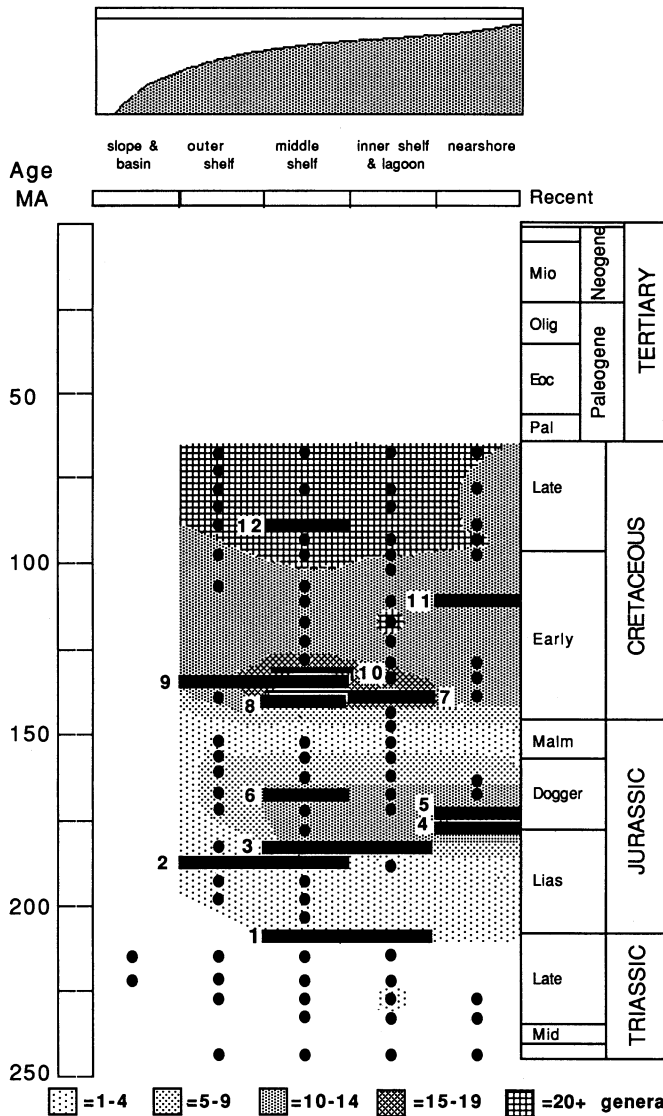
FIGURE 3—Environmental history of within-habitat diversity and first occurrences for cyclostome novelties. Numbers correspond to first occurrences as listed in the Appendix; points outside of shaded contours represent occurrences of taphonomic controls sensu Bottjer and Jablonski (1988), in this case trepostome bryozoans. Onshore-offshore categories follow those outlined by Bottjer and Jablonski (1988).
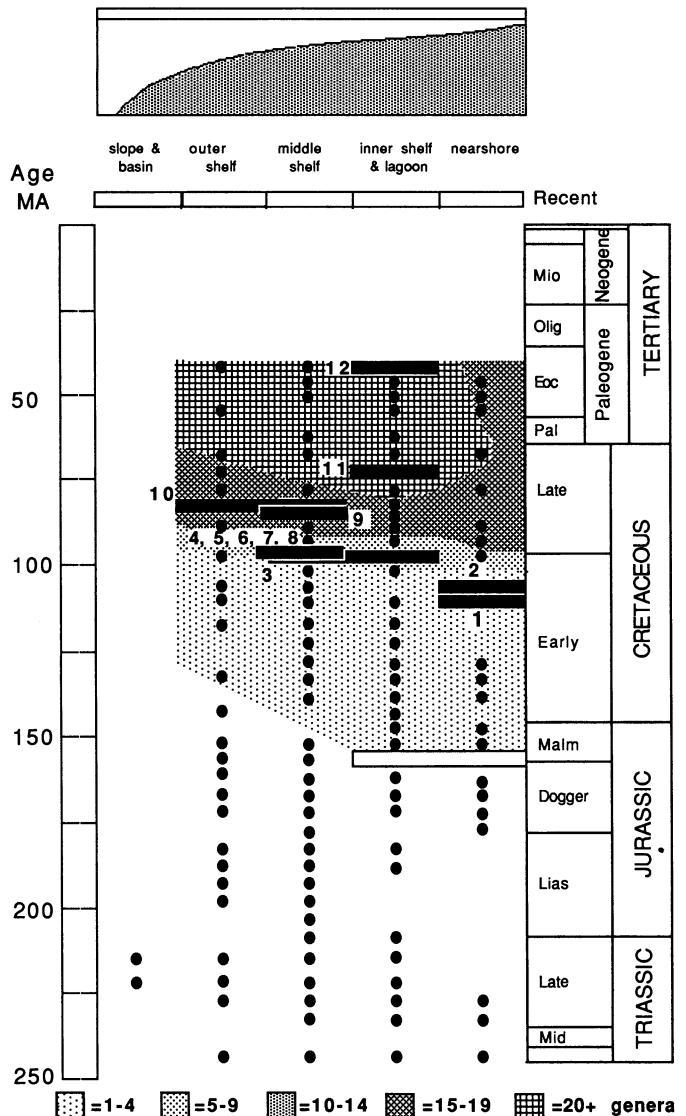
FIGURE 4—Environmental history of within-habitat diversity and first occurrences for cheilostome novelties. Numbers correspond to first occurrences as listed in the Appendix; open box = time and probable environment of oldest known members of the order. Points outside of shaded contours represent occurrences of taphonomic controls sensu Bottjer and Jablonski (1988), in this case cyclostome and trepostome bryozoans. Onshore-offshore categories follow those outlined by Bottjer and Jablonski (1988).

upper, convex surface of the colony; the underside of the colony is generally concave and may accumulate thick calcification that totally envelops the small substratum. This unusual morphology allows colonies to exploit habitats of mobile, unconsolidated sediment that effectively exclude many other colony forms (McKinney and Jackson, 1989). Lunulitiform species belonging to *Selenaria* are mobile and supported at or near the sediment-water interface by active, hair-like setae of polymorphic zooids termed vibraculae.

The earliest examples of this remarkable colony form are placed in the family Lunulitidae, a family possibly derived polyphyletically from several stocks of the highly paraphyletic family Onychocellidae (which may itself be polyphyletic) (Voigt, 1981; Cook and Chimonides, 1983, 1986; Cook and Voigt, 1986). The mid-Cretaceous genera

Reptolunulites and *Pavolunulites* have been interpreted as functional intermediates between onychocellids and lunulitids (Cook and Voigt, 1986; Voigt, 1991:508), but it is not clear whether they are true phyletic intermediates or separate evolutionary experiments towards discoidal colony organization.

COMPARATIVE ORIGINS OF NOVELTIES

The temporal and environmental patterns of origination for cyclostome and cheilostome novelties are shown in Figures 3–6. Both groups are at very low per-locality diversities for a considerable portion of their post-Paleozoic histories (Figs. 3, 4). Cyclostomes are so sparse prior to the
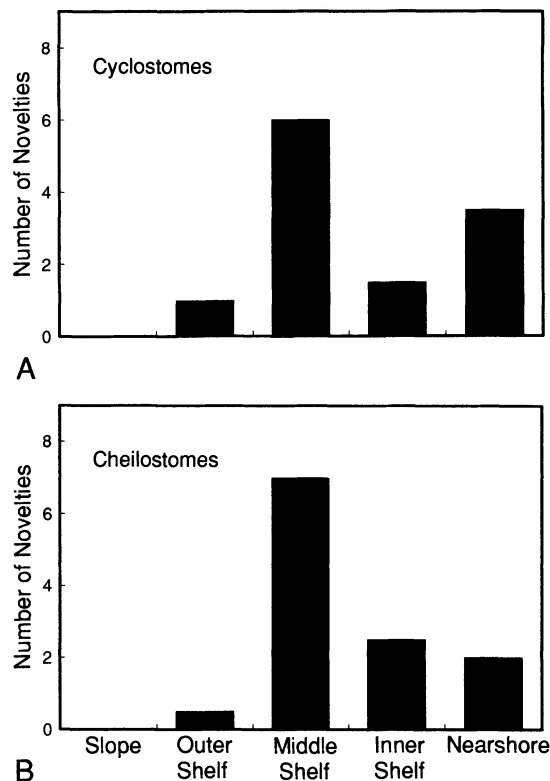
FIGURE 5—Distribution of cyclostome and cheilostome novelties among onshore-offshore categories (see: Figs. 3–4). Categories range from nearshore (A) to offshore (E); novelties for which temporal or environmental resolution was insufficient to place first occurence within a single occurrence are scored as fractions. Proportions of onshore versus offshore origins do not differ significantly (p > 0.50, Kolmogorov-Smirnov test).

mid-Jurassic that we can say little of the environmental distribution or early Mesozoic behavior of the survivors of the end-Permian mass extinction. The cheilostomes originate in onshore habitats as documented by Jablonski and Bottjer (1991), spread across the shelf at low within-habitat diversities, and then diversify rapidly in the mid-Cretaceous, a within-habitat pattern mirrored by their global diversity history (Fig. 1). The apparent Late Jurassic drop in cyclostome within-habitat diversity is probably not an extinction event; as Taylor and Larwood (1990:213) point out, the abundance of Lazarus taxa across this interval strongly suggests collection or preservation artifacts rather than a significant global pattern.

Environmentally, the patterns of origination for novelties within the two orders are statistically indistinguishable (Fig. 5). For both cyclostomes and cheilostomes, novelties are rather evenly distributed between onshore and offshore environments, and their appearances correspond well with contemporaneous maxima in within-habitat diversities (none of the cheilostome novelties and only two of the cyclostome novelities first appear outside the maximum diversity values for their time interval). These patterns contrast with that seen for the origin of post-Paleozoic marine orders (including the cheilostomes themselves) but are consistent with those for lower-level novelties in other groups; thus, they conform to the prediction made above.

Smith (1994) suggested that sampling artifacts alone could explain the onshore bias in ordinal originations (Jablonski and Bottjer, 1990a,b, 1991; Sepkoski, 1991, and references therein; also Fortey and Owens, 1990; Briggs and Clarkson, 1990; Miller, 1990; Crimes and Droser, 1992; Droser et al., 1993). In this view, the proportion of onshore originations should drop over the past 125 million yrs in concert with increased sampling of deeper-water deposits. However, Smith's analysis groups the poorly preserved taxa that Jablonski and Bottjer (1990a, 1991) used as controls for sampling bias with the well (i.e., frequently) preserved taxa. When the two preservation classes are separated, three of the five well-preserved orders appearing in the past 125 million yrs, but only one of the seven poorly preserved orders, begin onshore. The numbers are small but trend in the same direction as the larger dataset analysed by Jablonski and Bottjer (1991), where onshore originations were significantly more frequent (p < 0.025) for the well-preserved orders than for the poor-preservation sampling controls. Smith's (1994) second test found no significant difference between the proportion of echinoid orders appearing onshore 125–250 million yr ago and that of genera of the order Calycina (=Salenioida) "for the same period". However, Calycina only appeared in the mid Jurassic, ca 175 million yr ago. The order began onshore and took at least 10 million yr to occupy the entire shelf, so it is an inappropriate basis for comparison. For an array of echinoderm genera that fully spans the interval in question (i.e., the crinoids documented in Jablonski and Bottjer, 1990b, 1991), 42% of genera that do not found new orders originate onshore, in contrast to 77% for ordinal originations. Simlarly, of the bryozoan novelties that arise within this 125–250 Ma interval, three appear onshore, and four offshore, again unlike the ordinal pattern. These contrasts are limited by inevitable subdivision of a small dataset, but again coincide with those seen for the full post-Paleozoic interval (Jablonski and Bottjer, 1991, where the distributions are significantly different at p < 0.001). The preferential onshore origination of post-Paleozoic orders thus appears to be robust to sampling and is not a simple extrapolation of species-level patterns.

In contrast, the two orders differ in the rapidity of the appearances of novelties (Fig. 6). In the cyclostomes, the first appearances of novelties are rather evenly spread over 100 Ma, whereas in the cheilostomes six of the novelties appear in a pulse coinciding with the Late Albian-Early Cenomanian period of rapid diversification; when the shapes of the distributions are compared using the Kolmogorov-Smirnov test, they differ at p < 0.10 using 25 Ma intervals, p < 0.05 using 10 Ma intervals. The more rapid appearance of novelties in cheilostomes is opposite to the prediction made at the start of the paper.

The end-Permian extinction and Mesozoic Marine Revolution both involved major ecological reorganizations in the oceans. The first occurred through an enormous reduction in global biodiversity, with an evolutionary rebound that established the dominance of the Modern Fauna (sensu Sepkoski, 1984, 1992). The second occurred by evolutionary turnover during a time of ongoing diversification, and was virtually unchecked by the end-Cretaceous mass extinction (e.g., Vermeij, 1987; Jablonski, 1989). Although numbers are low, the patterns of novelty acquisition in
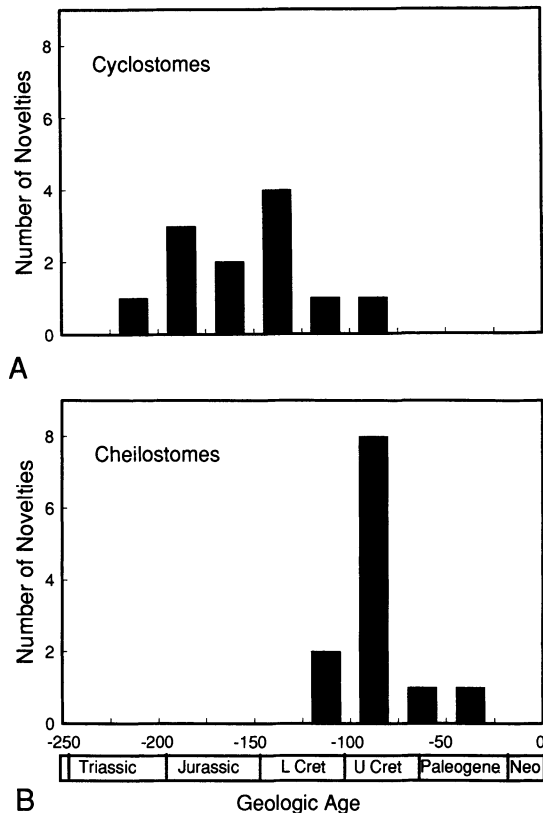
FIGURE 6—Distribution of cyclostome and cheilostome novelties through post-Paleozoic time (see: Figs. 3–4).

bryozoans appear to be remarkably unresponsive to these fundamental differences in ecological context.

Cyclostomes exhibit a slow, steady production of novelties and taxonomic diversification, even though they radiated into what might be considered a relatively empty marine realm, following the demise or extreme reduction of other bryozoan groups (Taylor and Larwood, 1988) and many other epifaunal encrusters. Cheilostomes radiated amidst the ecological reorganization of the Mesozoic Marine Revolution, in which the cyclostomes and other potential competitors were long-established and abundant. Yet they exhibit an explosive increase in morphological and taxonomic diversity during the Late Cretaceous and early Tertiary (although not at the expense of cyclostome diversity, see: Lidgard et al., 1993; Fig. 1). Neither group shows environmental patterns of novelty origination consistent with the onshore bias seen in the first occurrences of post-Paleozoic orders but, as noted above, those patterns map closely onto contemporaneous within-habitat diversity trends.

These patterns are consistent with the view that the generation of low-level novelties (i.e., those accorded taxonomic rank below the ordinal levels) are effectively driven by speciation rates. Hence, patterns depend on group-specific diversity dynamics rather than the larger biotic or environmental context. Novelties within orders of crinoids and echinoids, and within the tellinoidean bivalves, exhibit similar diversity-dependence (Jablonski and Bottjer, 1990a,b, 1991). Morphological disparity, a more richly quantified but somewhat indirect measure of novelty pro-

duction (among other processes), also appears to accumulate within Paleozoic clades at a pace unrelated to time of subclade origin. It is more closely related to species-level diversification than to the branching events that established the major groups in the early Paleozoic (Foote, 1995, 1996; Wagner, 1995; Anstey and Pachut, 1995).

The failure of cyclostomes to radiate explosively after the end-Permian extinction may indicate that this setting was not as free of biotic interaction as sometimes assumed. In terms of potential competitors, uncalcified ctenostome bryozoans date back to the Ordovician as borings (Pohowsky, 1978; Mayoral et al., 1994) and non-boring species are preserved by bioimmuration in mid-Triassic (Todd and Hagdorn, 1993) and younger encrusting communities (Taylor, 1990; Todd, 1994); the last trepostome bryozoans were sparse but environmentally widespread during the Triassic as well. Many of the other occupants of marine hard substrata are known (Taylor and Michalik, 1991) or can be inferred on phylogenetic grounds to have been present from the Triassic, including serpulid worms, cemented brachiopods and bivalves, encrusting foraminifers, scleractinians and other cnidarians, sponges, ascidians, and some groups of coralline algae (Steneck, 1983; Benton, 1993). Today encrusting bryozoans, belonging to both the cyclostomes and cheilostomes, commonly lose competitive encounters for space with many of these other encrusting groups (Jackson and Hughes, 1985; McKinney and Jackson, 1989).

The diversity and intensity of predation during the time of cyclostome radiation are more difficult to infer. Fossil evidence for the activities of known predators in the Recent—euteleost fishes, camarodont echinoids, starfish, nudibranch gastropods, nematodes and pycnogonids—can be difficult to assess. This is because post-mortem boring and grazing of skeletons is common, and because some predators, such as nematodes and nudibranchs, often attack uncalcified parts of zooids. The oldest well-documented predatory drillholes in bryozoans are Late Cretaceous in age and could have been produced by tiny gastropods (Taylor, 1982; see also Kabat, 1990). Some of these potential predators probably originated too late in the Mesozoic to have played a role in damping the cyclostome radiation. We do not doubt that the Mesozoic Revolution brought a major increase in the intensity, diversity, and ferocity of both competitors and predators. However, we suspect that the unimpressive cyclostome rebound may be attributable, in part, to the large-scale ecological pattern invoked by Erwin et al. (1987) to explain the failure of the post-Paleozoic radiations to generate new phyla or classes. Despite the huge end-Permian loss in taxonomic diversity, the basic adaptive zones of the marine benthos remained occupied, albeit less densely than in the Late Paleozoic; this point is driven home by the pervasive environmental distribution of the trepostome bryozoans that serve as the taphonomic control points in the Triassic portion of Figure 2. Overgrowth and predation studies of Triassic to mid Jurassic cyclostomes, prior to the advent of cheilostomes, would help to evaluate this hypothesis. However, the absence of a major diversity decline in the cyclostomes despite the massive radiation of the competitively superior cheilostomes further testifies to the difficulty of translating ecological interactions into macroevolutionary pat-

terns (e.g., Miller and Sepkoski, 1988; Lidgard et al., 1993; Sepkoski, 1996).

Given this pre-emption argument for the sluggish cyclostome pattern, the explosive mid-Cretaceous cheilostome radiation becomes even more striking, coming as it does in an even more crowded and presumably less favorable setting; encrusting cheilostomes consistently overgrow cyclostomes but they in turn typically lose competitive interactions with all of the groups listed above (McKinney, 1992, 1993, 1995; Lidgard et al., 1993). Taylor (1988) has suggested that cheilostome diversification was triggered by a shift to low-dispersal, brooded larvae, as signalled by the acquisition of calcified ovicells. By analogy with marine gastropods (see: Jablonski, 1986, for review), the low dispersal ability of such larvae may impart low rates of gene flow and, thus, greatly accelerated speciation rates. This hypothesis, although plausible both by virtue of the timing of the onset of rapid diversification and what little is known of genetic structure in bryozoan populations, is weakened by the fact that the acquisition of gonozooids in cyclostomes during the late Triassic evidently failed to impart accelerated speciation rates comparable to those of cheilostomes in the mid Cretaceous.

Direct analysis of species-level turnover in Mesozoic bryozoan clades with contrasting larval strategies is needed to test this hypothesis further, underscoring the need for more detailed phylogenetic studies. Comparative data on bryozoan turnover rates are sparse, but an analysis of Neogene species in the Mediterranean region shows cheilostomes to have significantly shorter durations overall than cyclostomes ($p < 0.05$, Kolmogorov-Smirnov tests on both the total species pool and extinct species only; P.D. Taylor, unpublished data).

This positive relation between environmental variation in the production of within-clade novelties and speciation rates is consistent with Jablonski and Bottjer's (1983) hypothesis—still neither falsified nor strongly corroborated—that rare, ordinal novelties are more likely to originate in small isolates drawn from panmictic (and thus high-dispersal) populations than in genetically subdivided populations. Their proposed mechanism would decouple high-level novelties from simple speciation rates, but places no restrictions on within-clade novelties arising in the context of more conventional speciation events and, thus, positively related to speciation rates.

A speciation-driven process, if verified, would be an intriguing mechanism for the establishment of a post-Paleozoic clade. Several authors have shown that the more frequent situation is for high-turnover taxa to be replaced over geologic time by low-turnover taxa. This differential in evolutionary dynamics may have driven the successive replacement of each of Sepkoski's Evolutionary Faunas (Sepkoski, 1984, 1987, 1992; Valentine, 1990a,b). The bryozoans appear to be a counter-example. The cyclostomes, members of the Paleozoic Fauna, evidently radiated slowly and the cheilostome members of the Modern Fauna rose to greater diversity levels via rapid speciation.

These data emphasize how poorly understood are the mechanisms that permit the establishment or radiation of major clades under different macroecological conditions. Comparative analysis of clade dynamics for taxa becoming established under conditions of contrasting global diversity levels, using taxa where data are sufficient to quantify speciation and extinction rates in greater detail than presently available for bryozoans, would be a useful approach to this problem. A comparative analysis of morphospace occupation, as performed for Paleozoic clades by Foote (1995, 1996, and references therein), would also be a valuable complement to our apomorphy-based approach.

CONCLUSION

Comparisons among evolutionary radiations have been few in number. An analysis of the post-Paleozoic bryozoans yielded some surprises. Unlike the the early Paleozoic pattern, evolutionary novelties did not arise in an early Mesozoic burst followed by more gradual production in a more densely occupied ocean. Rapidity of novelty acquisition does differ significantly between the two groups, but in a way opposite to our initial prediction. Instead, the pattern conforms to the contrasting patterns of genus- and family-level taxonomic diversification of the respective orders. Environmentally, neither group shows the onshore origination bias exhibited by the first appearance of post-Paleozoic orders, but like other within-group novelties, shows group-specific environmental patterns. These results are consistent with the view that the taxonomic hierarchy records important aspects of the evolutionary process. Taxa usually ranked as orders, classes, and phyla exhibit an evolutionary dynamic that contrasts temporally and environmentally to patterns shown at lower levels within those major groups. Our data show first that species-level dynamics can shape many aspects of group histories including when and where novelties are acquired, and second that those dynamics are not the entire story.

ACKNOWLEDGMENTS

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APPENDIX

Time and environment of first occurrences of morphological novelties in cyclostome and cheilostome bryozoans, sequenced from oldest to youngest for each order. Numerical ages denote 5-Ma increments used in Figures 3 and 4.

I. Cyclostome Novelties

1. Gonozooids
205–210 Ma, Inner/Middle Shelf
Taxon: *Reptomultisparsa hybensis* (Prantl)
Age and Strata: Rhaetian, Hybe Beds, Hybe, West Carpathians, Slovakia.
References: Michalik (1980); Taylor and Michalik (1991).

2. Erect cylindrical colonies
185–190 Ma, Middle/Outer Shelf
Taxon: *"Entalophora"* base
Age and Strata: Late Pliensbachian (Domerian, presumably Margaritatus Zone); encrusting hiatus concretions in Almatheentonen, Am Osterfeld brick pit near Goslar, NW Germany.
References: Voigt (1968); Illies (1971).
Taxon: *Spiropora liassica* Tate (also *Mesenteripora inconstans* (Walford), which, along with *M. wrighti* Haime *sensu* Walter and Powell, may be a junior synonym, although systematic revision is needed)
Age and Strata: Latest Pliensbachian and earliest Toarcian, Marlstone Rock Bed, near Banbury area, Northamptonshire, England.
References: Whitehead et al. (1952); Walter and Powell (1973); Howarth (1980).

3. Frontal budding
180–185 Ma, Inner/Middle Shelf
Taxon: *Radicipora radiciiformis* (Goldfuss)
Age and Strata: Late Early Toarcian (Falcifer Zone), "calcaires à entroques mineralisés", NE Exit of the St-Paul-le-Jeune tunnel, near Les Avelas, Banne, Ardèche, France.
References: Elmi (1967); Walter (1970); Elmi et al. (1989).
Note: This record comprises regularly multilayered colonies built up of overgrowths formed by frontal budding *sensu lato*. This species forms dendroid erect colonies composed of stacked, *Berenicea*-like subcolonies; judging from Walter's (1970) figures and Oxfordian material in The Natural History Museum, London, the zooids at the centers of the subcolonies remain in a free-walled condition and are able to grow upwards to initiate a new layer of subcolonies. A closer analogue of cheilostome frontal budding occurs when overgrowth results from intrazooecial fission (see above; Hillmer et al., 1975); this is sporadically present in Jurassic encrusting cyclostomes but its earliest occurrence is very uncertain. One early example is *Reptomultisparsa walfordiana* Canu & Bassler from the Lower Bathonian (Progracilis Zone), Sharp's Hill Beds, Snowshill Hill Quarry, Gloucestershire (e.g. BMNH D58036); this species was originally described as from the Bajocian of Shipton Gorge, Dorset, but in fact the type material is almost certainly of the Bathonian age given here; probably inner shelf (Channon, 1950:249; Torrens, 1968; Sellwood and McKerrow, 1974).

4. Fascicles
175–180 Ma, Nearshore
Taxon: *Theonoa diplopora* (Branco), *T. bowerbanki* Haime, *T.* sp., and *"Kololophos terquemi"* (Haime) *sensu* Gregory
Age and Strata: Late Aalenian, basal Murchisonae Zone, Lower Inferior Oolite, Cheltenham area, Gloucestershire, England.
Reference: Mudge (1978).

5. Erect bilaminate colonies

170–175 Ma, Nearshore (both (a) and (b) occur in the same unit)
(a) Narrow, strap-like branches ("adeoniform")
Taxon: *Multisparsa* cf. *M. calloviensis* (d'Orbigny)
Age and Strata: Late Aalenian, Murchisonae Zone, Lower Inferior Oolite, Cheltenham area, Gloucestershire, England. Found commonly in the Polyzoa Bed at the base of the Lower Freestone. In modern terms, the Polyzoa Bed corresponds to the massive fossiliferous oolites at the top of the Cleeve Hill Oolite Member of the Inferior Oolite.
Reference: Mudge (1978).
(b) Broad, foliaceous fronds ("eschariform")
Taxon: *Multisparsa davidsoni* (Haime), *M.* aff. *M. davidsoni* (Haime), *M.* cf. *M. eudesiana* (Milne Edwards), *M.* sp.
Age and Strata: Same as preceding.

6. Fungiform colonies
165–170 Ma, Middle Shelf
Taxon: *Apsendesia cristata* Lamouroux *sensu* Walter, 1967.
Age and Strata: Late Bajocian (Parkinsoni Zone), Burton Limestone, Upper Inferior Oolite, Shipton Gorge, Dorset, England.
References: Richardson (1929); Wilson et al. (1958); Walter (1967, 1970); Parsons (1975).

7. Fenestrate colonies
140–145 Ma, Nearshore and Inner Shelf
Taxon: *Chartecytis compressa* Canu and Bassler
Age and Strata: Late Berriasian, Boissieri Zone, Vions Formation, Musièges (Haute-Savoie), France.
References: Steinhauser and Charollais (1971); Clavel et al. (1986); Walter (1997).
Note: This species, along with the fenestrate form *Retenoa campicheana* (d'Orbigny), also occurs in the Early Valanginian Marnes d'Arzier, Calcaire Roux, and related units; and in the Late Valanginian, Marnes à bryozoaires and Calcaire à Alectryonia; these are inner and middle shelf deposits (Haefeli et al. 1965; Cotillon and Walter 1965; Guillaume 1966–67; Walter 1972, 1986). *Filisparsa reticulata* d'Orbigny is probably a separate derivation of fenestrate colony organization, and first occurs in the basal Cenomanian of Mülheim-Broich, Germany (E. Voigt, in litt.).

8. Articulated colonies
135–140 Ma, Middle Shelf
Taxon: *Crisia? nozeroyensis* Voigt and Walter, *Filicrisia? neocomiensis* Voigt and Walter.
Age and Strata: Late Valanginian, Marnes jaunes à Bryozoaires, Morteau (Doubs), France; Marnes grises à Bryozoaires, Nozeroy (Jura), France; Ste Croix (trinodosum Zone) and Auberson (callidiscus Zone) (Vaud), Switzerland. Also Early Hauterivian, radiatus Zone, Marnes à serpules, Montlebon (Doubs), and Calcaire à spatangues, Ancerville (Meuse) France.
References: Haefeli et al. (1965); Guillaume (1966–7); Anonymous (1968); Walter (1972); Voigt and Walter (1991); Walter (1994).

9. Lateral branching
130–135 Ma, Middle/Outer Shelf
Taxon: *Voigtopora* sp. (BMNH D52797).
Age and Strata: Late Hauterivian, Lower Tealby Clay, Nettleton, Lincolnshire, England.
References: Rawson (1971); Kent (1980); Gaunt et al. (1992)

10. Calcified opercula
130–135 Ma, Middle Shelf
Taxon: *Meliceritites semiclausa sensu* Walter et al. 1975 (*non* Michelin).
Age and Strata: Early Barremian, Marnes de Fontaine-Graillière, Fontaine-Graillière, SE France.
References: Walter et al. 1975.

11. Eleozooids
110–115 Ma, Nearshore?
Taxon: *Meliceritites dendroidea* (Keeping)
Age and Strata: Late Aptian (nutfieldensis Zone) Bargate Stone, Guildford, Surrey, England.
References: Dines and Edmunds (1929); Kirkaldy (1933); Casey (1961); Middlemiss (1962, 1975).
Note: This species is also common in the Aptian Faringdon Sponge

Gravel (Pitt and Taylor, 1990), but the Faringdon "population" lacks eleozooids; the eleozooids from the Bargate Stone "population" have apertures about 1.5 × larger than autozooid apertures but of essentially the same shape.

12. Nanozooids
85–90 Ma, Middle Shelf
Taxon: *Diplosolen sp.*
Age and Strata: Late Turonian, Soester Grünsand, Mülheim, Germany.
References: Lommerzheim (1976); Jansen and Drozdzewski (1986); E. Voigt (in litt. to PDT, 1 March 1992).
Note: Next oldest is Coniacian *Diplosolen,* in Voigt (1981:457), Fécamp and Vaucotte, Normandy, France.

II. Cheilostome Novelties

1. Articulated spines
110–115 Ma, Nearshore
Taxon: *Spinicharixa pitti* Taylor.
Age and Strata: Late Aptian, probably Formacion Lignitos de Escucha, Utrillas, Prov. Teruel, Spain.
References: Aguilar et al. (1971); Pardo Tirapu and Villena Morales (1979); Taylor (1986).

2. Frontal budding
105–110 Ma, Nearshore
Taxon: cf. *Charixa?* sp. (BMNH D59364).
Age and strata: Early Albian, upper Glen Rose Fm, Bed 10 of Bergan (1990), Barker Branch, Somervell County, Texas, USA.
References: Bergan (1990).

3. Ovicells
95–100 Ma, Inner/Middle Shelf
Taxon: *Marginaria* sp. of Taylor (1988)
Age and Stata: Late Albian, *inflatum* Zone, A Beds, Red Chalk (Hunstanton Red Chalk Formation), Norfolk, England.
References: Larwood (1961); Rawson et al. (1978); Gallois (1994); Owen (1995).
Taxon: *Wilbertopora mutabilis* Cheetham
Age and Strata: Late Albian, *Adkinsites bravoensis* Zone (approximate equivalent of *inflatum* Zone), Kiamichi Formation, Washita Group, Texas.
References: Cheetham (1954, 1975); Scott et al. (1978); Taylor (1986).

4. Erect cylindrical colonies
95–100 Ma, Middle Shelf
Taxon: n. gen., n. sp. of Taylor (1986: p. 199 [BMNH D38164]).
Age and Strata: Late Albian, *inflatum* Zone, Cowstones, Dorset, England.
References: Tresise (1960); Ager and Smith (1965); Taylor (1986); Garrison et al. (1987).
Note: This specimen was misinterpreted by Larwood (1975) as a membranimorph cheilostome encrusting a heteroporid cyclostome, but is actually just a cheilostome resembling *Chiplonkarina* (Taylor and Badve, 1995).

5. Avicularia
95–100 Ma, Middle Shelf
Taxon: *Wilbertopora mutabilis* Cheetham *sensu lato.*
Age and Strata: Early Albian, Fort Worth Formation, Fort Worth, Tarrant County, Texas, USA.
References: Scott et al. (1978).
Note: Not *Wilbertopora mutabilis* s.s., which lacks avicularia; the "avicularium" in Cheetham (1975: pl. 3, fig. 3) from the older Kiamichi Formation of Texas is probably a dwarf autozooid or a kenozooid.

6. Cribrimorph grade frontal shield
95–100 Ma, Middle Shelf
Taxon: *Andriopora* sp., and several other species (genus indet.)
Age and Strata: Basal Cenomanian, *carcitanense* Subzone of *mantelli* Zone, Untercenoman Rötkalke, Mülheim-Broich, Germany.
References: Hancock et al. (1972); Wiedmann and Scheider (1979); Voigt (1981).
Taxon: *Otopora auricula* Lang, *Ctenopora pecten* Lang, *Andriopora mockleri* Lang.

Age and Strata: Early Cenomanian, 5, 10, 15, and 20 ft above the base of the Chalk Marl, Cambridge, England.
References: Lang (1921); Kennedy and Garrison (1975); Carter and Hart (1977).
Note: Lang (1921) listed several other supposed cribrimorph species from the Chalk Marl at Cambridge: *Anaptopora disjuncta, A. cantabrigiensis* (= *A. disjuncta,* according to Larwood 1985: 173), *A. mockleri, Anotopora inaurita.* However, these are not true cribrimorphs: the spines do not fuse over the midline of the zooid and, thus, these are myagromorphs, considered evolutionary intermediates between the more primitive membranimorphs and cribrimorphs (Larwood 1985).

7. Erect bilaminate colony
95–100 Ma, Middle Shelf?
a) Narrow, strap-like branches (=adeoniform)
Taxon: *Onychocella sp.*
Age and Strata: Basal Cenomanian, carcitanense Subzone of *mantelli* Zone, Untercenoman Rötkalke, Mülheim-Broich, Germany.
References: Hancock et al. (1972); Wiedmann and Scheider (1979); Voigt (1981); E. Voigt pers. comms to DJ and PDT.
Note: Next oldest are: *Onychocella cenomana* (d'Orbigny), from the mid-Cenomanian, Grès et Sable du Maine à *Scaphites aequalis,* Le Mans, Sarthe, France, from an unknown level in the Cenomanian at Isle Madame, Charente Maritime, France, and the Late Cenomanian Sables du Perche at the Carrière du Moulin-Ars, St Calais, France (Voigt, 1972, 1981); and *Biflustra carantina* d'Orbnigny, which occurs with the preceding species at Le Mans and Isle Madame (Voigt, 1981). These occurrences appear to be mainly inner shelf (Juignet et al., 1978; Juignet and Louail, 1987; Néraudeau and Moreau, 1989).
b) Broad, foliaceous fronds (eschariform)
Taxon: *?Foratella* sp. (BMNH BZ 3250–3255).
Age and Strata: Early Cenomanian, Wilmington Sands, Devon, England.
References: Kennedy (1970); Smith et al. (1988).
Note: This undescribed eschariform species is ovicellate, has avicularia larger than the autozooids, and conspicuous muscle impressions on the basal walls of the zooids (cf. Medd, 1964). Generic assignment is difficult but the combination of the bifoliate colony-form and the large avicularia suggest a possible affinity with *Foratella,* a little-used genus erected by Canu (1900) as a subgenus of *Membranipora* whose Upper Cretaceous type species is *Membranipora forata* d'Orbigny. The undescribed Wilmington Sands species in particular resembles *Biflustra heteropora* d'Orbigny which was regarded as a junior synonym of *M. forata* by Canu.

8. Articulated colony
95–100 Ma, Middle Shelf
Taxon: *Cellarinidra sp.*
Age and Strata: Basal Cenomanian, *carcitanense* Subzone of *mantelli* Zone, Untercenoman Rötkalke, Mülheim-Broich, Germany.
References: Hancock et al. (1972); Wiedmann and Schneider (1979); Voigt (1981); E. Voigt in litt. to DJ (2 July 1986 and 9 December 1987).
Note: Next oldest is *Cellarinidra clavata* (d'Orbigny) from the mid-Cenomanian, Grès et Sable du Maine à *Schaphites aequalis,* Le Mans, Sarthe, France (Voigt, 1972, 1981, 1985).

9. Free-living lunulitiform colonies
85–90 Ma, Middle Shelf
Taxon: *Lunulites* sp. (possibly *Pavolunulites* sp.).
Age and Strata: Late Turonian or early Coniacian, Plänerkalk, Halle, Westfalia, Germany.
References: Voigt (1962, 1979, in litt. to Jablonski 9 Dec 1987); Ernst and Schmid (1979); Ernst et al. (1983, 1984); Wood et al. (1984).

10. Ascophoran grade frontal shields
85–90 Ma, Middle/Outer Shelf
Taxon: *Platyglena* (?) *culveriana* (Brydone), *P.* (?) *altonensis* (Brydone).
Age and Stata: Upper Turonian, *Holaster planus* Zone, Hampshire, England.
References: Brydone (1930); Voigt (1972, 1991); Mortimore (1986);

Mortimore and Pomerol (1987); Pomerol et al. (1987); Jablonski and Bottjer (1990a).

Note: This is the oldest known ascophoran frontal shield of any kind. Platyglenids have a lepralioid (= cryptocystidean) frontal shield morphology (Gordon and Voigt, 1996). *Porina cenomana* Lecointre, previously regarded as the oldest ascophoran, is a cyclostome (Voigt, 1991).

11. Calcified operculum
70–75 Ma, Inner Shelf
Taxon: *Inversaria flabellula* (von Hagenow)
Age and Strata: Late Campanian, mucronata Zone, Stafversvad and Hemmingslycke, Sweden.
References: Voigt and Williams (1973); Georgala and Brood (1974).
Note: The next oldest examples, each undoubtedly derived independently, are the Early Maastrichtian cribrimorph *Castanopora lambi* Turner, 1975, from outer shelf deposits, Navesink Formation, Big Brook, Monmouth County, New Jersey, USA (Turner, 1975), and the Early Maastrichtian anascan (?Macroporidae) *Monoporella exculpta* (Marsson) from outer shelf deposits, White Chalk, Basbeck, Hemmoor, Germany (Voigt 1989: pl. 19, fig. 3).

12. Fenestrate colony
35–40 Ma, Inner shelf
Taxon: *Sertella beaniana* (King) *sensu* Labracherie.
Age and Strata: Middle Eocene, La Citadelle/Blayais, Aquitaine Basin
References: Labracherie and Prud'Homme (1967); Labracherie(1970, 1971); Mouline and Mouissé (1977).

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