COMPARATIVE ECOLOGY OF BRYOZOAN RADIATIONS: ORIGIN OF NOVELTIES IN CYCLOSTOMES AND CHEILOSTOMES

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The cyclostome and cheilostome bryozoan clades 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, durgophagous predation, and other ecological changes commonly termed 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 compared the radiations of these clades to test for similarities reflecting general patterns in the origin of within-clade novelties, and for differences that might be due to ecological context or clade attributes. We examined the timing and environment of first occurrence of eight morphological novelties that evolved convergently in both clades (ovicells, cylindrical arborescent colony, multilayered encrusting growth [frontal budding s.l.], bilaminate erect colony, fenestrate colony, articulated colony, calcified operculae, avicularia), as well as novelties unique to cheilostomes (cribrimorph and ascophoran grades, and lunulitiform colonies) or to cyclostomes (apertures arranged in fascicles). First occurrences were traced from the literature, BMNH collections, and unpublished data provided by Prof. Dr. E. Voigt; environments were inferred within an onshore-offshore gradient using the protocol of Jablonski and Bottjer (1990).

As seen for other invertebrate groups, within-clade novelties were not concentrated in onshore settings for either bryozoan clade, in contrast to the origination patterns at the ordinal level (including the Cheilostomata). Differences in sequence or environment of first occurrence were not obviously related to the Mesozoic Revolution, or to the distinction between zooid- and colony-level characters. Novelties showed a weak tendency to originate in similar sequence and in similar environments for both clades, but these numbers are small. Differences in sequence may partly reflect clade-specific constraints: for example, opercula are considered a prerequisite for the development of avicularia, so that cyclostomes needed to evolve that precursor before avicularia could appear, whereas opercula are primitive (though uncalcified) in cheilostomes and thus did not constitute such a constraint. If avicularia are omitted, the rank-order correlation of novelties becomes marginally significant ($p=0.05$, Spearman rank test). The most striking difference is in the temporal pattern of novelty acquisition. In cyclostomes, these are rather evenly spread over 100 Ma, whereas in cheilostomes six of the novelties appeared in the Late Albian-Early Cenomanian during a period of rapid diversification. Despite a slow start, the cheilostome radiation enters an explosive phase that may characterize successful establishment of clades founded late in the Phanerozoic.