EVOLUTION OF EARLY REEF-ECOSYSTEMS

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Calcimicrobes dominate the earliest reef-ecosystems in the Precambrian and Cambrian. The Archaeocyatha, an early Cambrian group of calcified sponges, were the first skeletal metazoans to be associated with reefs but their role in the overall buildup form was generally subsidiary. The solitary nature of many archaeocyaths explains some of their previously supposed apomorphies - thus there are few modern analogies for their ecology. However, archaeocyaths, with irregulars in particular, show the progressive acquisition of low integration modularity in several different lineages through time. This trend is interpreted to be an adaptation to the reef-building habit and continues right up to the final extinction of the group. This suggests a relative immunity to extinction presumably on account of ecological response. Supposed species may be facultatively modular, with modular ecophenotypes always dominating biohermal settings. Modular organisation confers many ecological advantages in reef-building settings, such as indeterminate growth leading to larger size, greater powers of regeneration, and an ability to encrust and gain secure attachment to substrates. This confirms the widespread adaptive significance of integration in clonal organisms. Even though high integration, skeletally simple stromatoporoid-like forms developed in irregulars, low integration, branching morphologies were by far the most successful. This is suggested to represent adaptation to the particular conditions of the early Cambrian tropics - conditions of relatively high turbulence, sedimentation rates and possibly nutrient levels. However only genera possessing porous septa show any development of modularity, suggesting that an initially well-integrated soft-tissue is a prerequisite for acquisition of the habit. Increasing integration and simplification of the skeleton can be correlated with an increase in soft-tissue flexibility. Modularity is an advanced condition in sponges and we suggest that paedomorphosis facilitates its acquisition in archaeocyaths.

The Phanerozoic history of marine carbonate sedimentation shows considerable variations in both extent and style. Changes in nutrient flux have recently gained popularity as explanations for such variation, especially in the control of benthic production and reef-formation in tropical areas. Variations in nutrient flux can to some extent explain the general global patterns seen in the ecological style and systematic composition of reefs since the appearance of the habitat in the early Cambrian. Several convergently evolved organisations of reef-building organisms can be distinguished, most of which re-occur throughout the Phanerozoic. Such organisational types appear to favour different ambient nutrient concentrations: Solitary and low-integration forms together with considerable algal development are found in areas of relatively high nutrient levels, sedimentation rate and turbidity, whereas high integration forms with photosynthetic symbioses predominate in low nutrient conditions, with low rates of sedimentation and little turbidity. Therefore, the relative abundance of such forms, together with analysis of the associated biota, sediments and early diagenetic alteration, might be used as an indicator of changing nutrient levels in carbonate regimes throughout the Phanerozoic. Such studies highlight the extrinsic environmental constraints which may have controlled sedimentation in the carbonate regime and the evolutionary diversification of associated marine biotas.