

# Palaeozoic reefs: a microcosm of the geobiological system

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The Palaeozoic occupies a central place in the development of the global geobiological system. Palaeozoic reef systems were repeatedly produced globally in regions with 'high' diversity and productivity. Palaeozoic reef types are as follows: 1) archaeocyathid-calcimicrobe reefs; 2) stromatoporoid-tabulate-calcimicrobe reefs; 3) calcareous algal reefs; 4) calcisponge-bryozoan reefs; and 5) microbial reefs. Palaeozoic reefal features can be elucidated from both biological and geobiological viewpoints.

Biological points. 1) developmental: the basic body plans of most, if not all, reef-forming animal phyla had already been established in the Cambrian; 2) phylogenetic: the main reef-forming animals changed over time, and their rise and fall approximately reflect phylogenetic successions (e.g., Porifera to Cnidaria). Different groups within the same phyla (e.g., Archaeocyatha, 'stromatoporoids', and 'Calcareia') flourished individually in turn; 3) physiological: calcification ability, which was commonly acquired in the earliest Cambrian, contributed largely to the maintenance of life positions and the enlargement of body size in reef-building animals. Skeletons originated as aragonite and calcite; 4) ecological: reef-building animals were filter-feeders or suspension-feeders (partly carnivores). As recorded in skeletons, bioerosional activity was very weak in the Palaeozoic. Symbiosis with autotrophs has not yet been fully resolved. Given that certain regimes persisted, multilayered, ecological successions developed in varied reef systems; 5) structural: reef-building animals belong to taxa that include colonial forms; and 6) morphological: ongoing three-dimensional growth in some taxa produced larger reefs.

Geobiological points. 1) greenhouse/icehouse periods: reefs developed intensively in greenhouse periods, whereas provincialism developed following the marked differentiation of climatic zones in an icehouse period. The development of framework-builders produced hard substrates, which led to the creation of more three-dimensional habitats; 2) oligotrophic/eutrophic period: particularly in eutrophic periods, it was common for reef-builders with simple morphological organisations to construct reefs from their own 'mechanical' aggregations; 3) extinction/background period: microbial reefs repeatedly became conspicuous during extinction periods. A marked difference took place in calcimicrobial composition during the Late Devonian mass extinction; 4) calcite sea/aragonite sea period: in a calcite sea, stromatoporoids and tabulate corals flourished enough to form reefs, whereas in an aragonite sea, calcareous algae and calcisponges flourished similarly; and 5) carbonate poorly saturated/highly saturated period: in the Early to Middle Palaeozoic, high saturation enabled several kinds of calcimicrobes to flourish, occasionally culminating in the formation of reefs, alone or together with skeletal metazoans.

The Palaeozoic was an interval of evolutionary experimentation for the basic body plans of reef-forming groups. Long-term, secular changes in environments can be considered to be circular fluctuations that originated from material cycles within or between earth subsystems. Viewed in perspective, Palaeozoic reefs were characterised not only by a history of 'progressive internal development' of reef-constructors, but also by complicated interactions related to the advent of new regimes, the subsequent opportunistic development of preexisting reef builders, and the exploitation of niches within reef-building organisms. Reef ecosystems are products of complex interactions among varied geobiological agents (i.e., a microcosm of the geobiological system). Additionally, the present is not necessarily the key to the past (especially for the Palaeozoic). Palaeozoic reef ecosystems may be used to decipher the evolution of their geobiological constituents and interrelationships that are not yet fully understood.