

# Global CO<sub>2</sub> and evolution among the Scleractinia

by

Robert W. BUDDEMEIER <sup>(1)</sup> and Daphne G. FAUTIN <sup>(2)</sup>

<sup>(1)</sup> *Kansas Geological Survey, Lawrence, KS USA 66047;*

<sup>(2)</sup> *Department of Systematics and Ecology,  
University of Kansas, Lawrence, KS USA 66045.*

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## ABSTRACT

Radioimmunoassay indicates that sea anemones (Orders Actiniaria and Corallimorpharia of anthozoan Subclass Hexacorallia) evolved from hard corals (hexacoral Order Scleractinia). We estimate that actinians diverged from corals in the Cretaceous (ca. 75 Ma BP) and corallimorpharians in the Eocene (ca. 55 Ma BP). During these periods, atmospheric CO<sub>2</sub> level was higher and carbonate compensation depth was shallower than now. Calcification rates of some modern reef organisms are sensitive to saturation state; we suggest that evolution of non-skeletogenic scleractinians may be linked to reduced mineral saturation in surface oceans. This temporal pattern is analogous to modern spatial distributions of calcifying and symbiotic hexacorals.

## INTRODUCTION

In a recent review, SMITH and BUDDEMEIER (1992) pointed out evidence suggesting that growth and calcification rates of coralline algae and reef-forming corals are responsive to the degree of calcium carbonate supersaturation of the water. This is consistent with the fact that modern coral-algal reefs are found only in highly supersaturated conditions. All reef-forming (= hermatypic) corals – members of cnidarian Subclass Hexacorallia, Order

Scleractinia – possess intracellular symbiotic algae known as zooxanthellae. Surprisingly, there is little direct experimental evidence on the relationships among saturation state, calcification rates, and algal symbiosis.

Ocean and atmospheric chemistry have fluctuated substantially over the history of the scleractinian lineage, with periods of probable increased levels of atmospheric and oceanic CO<sub>2</sub>. CO<sub>2</sub> added to the ocean waters tends to lower carbonate saturation state by reducing pH and the concentration of carbonate ion. Paleogeochemistry is not sufficiently precise to determine in detail the saturation state of ancient surface waters, but the possibilities of relationships among saturation state, calcification, and skeletalization have implications for both evolutionary and paleogeochemical studies. This paper explores the possible relationship of saturation state and global CO<sub>2</sub> to divergence of skeletal sea anemones (*sensu lato* – members of hexacoral Orders Actiniaria and Corallimorpharia) from the scleractinian lineage.

## EVOLUTIONARY RELATIONSHIPS

HAND (1966) concluded on the basis of morphology that sea anemones are descended from scleractinian corals. This idea has not displaced the long-standing dogma that sea anemones are ancestral to corals (e.g. HYMAN, 1940), perhaps because of a conviction that soft-bodied animals gave rise to those that form skeletons. However true that may be, it is certainly not the case that contemporary skeletal taxa must be ancestral to related contemporary skeletogenic taxa. Radioimmunoassay (RIA) investigations of relationships among scleractinians and sea anemones of orders Actiniaria and Corallimorpharia support Hand's thesis that naked polyps arose from those with skeletons (FAUTIN and LOWENSTEIN, 1993). Figure 1 summarizes the hypothesized phylogeny of certain anthozoans: five species from what are considered to be four lineages of scleractinians, and nine species from three classes of non-skeleton-bearing anthozoans: three species of corallimorpharians, five of actinians, and a cerianthid, which serves as the outgroup. The time scale of the diagram was calibrated at the divergence of *Goniopora* and *Porites*, in the early Eocene (POTTS and GARTHWAITE, 1990). This implies critical branching events in the mid-Cretaceous and the late Eocene.

## ENVIRONMENT AND EVOLUTION

Skeletonless descendants of the scleractinian lineage arose at least twice. What environmental pressures may have resulted in the evolution and survival of the new branches? We infer from the literature on the ancient carbon cycle that both periods of evolutionary divergence coincided with increased atmospheric CO<sub>2</sub> levels and other conditions consistent with decreased oceanic carbonate mineral saturation state.

Figure 2a shows the estimated variation in the Pacific Ocean carbonate compensation depth (CCD) since the late Mesozoic [Cretaceous data from THIERSTEIN (1979), Tertiary data from BERGER (1977)]. A shallow CCD indicates less saturated ocean water, a lower rate of carbonate production at the surface, or both. Figure 2b shows the mid-Cretaceous pattern of Pacific basin vulcanism (ARTHUR *et al.* 1985), indicating probable elevated levels of volcanic CO<sub>2</sub> released into both atmosphere and ocean around the time of

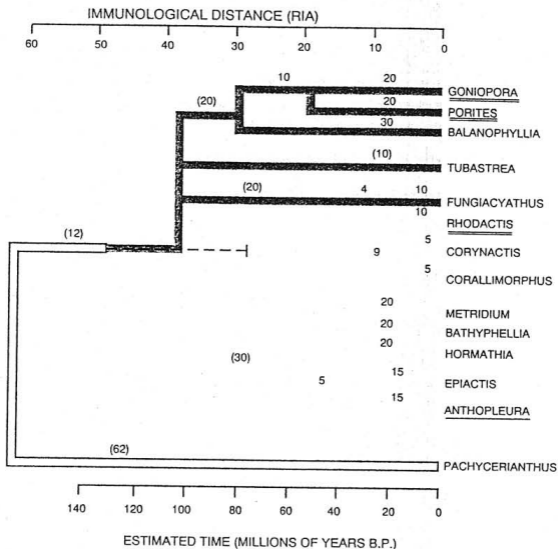


Figure 1 – Phylogeny of certain anthozoans deduced from RIA; a cerianthid serves as the out-group. The figure shows the incidence of skeletalization and algal symbioses. The time scale is calibrated at the divergence of *Goniopora* and *Porites* (POTTS and GARTHWAITE, 1990).

the first evolutionary divergence. Figure 2c shows selected patterns for CO<sub>2</sub>-related parameters in the past 100 million years, based on a geochemical model by LASAGA *et al.* (1985). Although indicative rather than conclusive, these lines of evidence support the idea that some evolving organisms severed their dependence on deposition of calcium carbonate during periods when surface ocean water may have been less supersaturated with respect to CaCO<sub>3</sub> than it is at present or was during most of the Cenozoic. Such conditions would not necessarily interfere with some of the advantages of a symbiotic lifestyle, but could impose a significant energy penalty on the process of skeletogenesis. If this mechanism has operated in the past, we might expect to find present-day patterns of organism distribution and dominance that similarly reflect saturation state distributions.

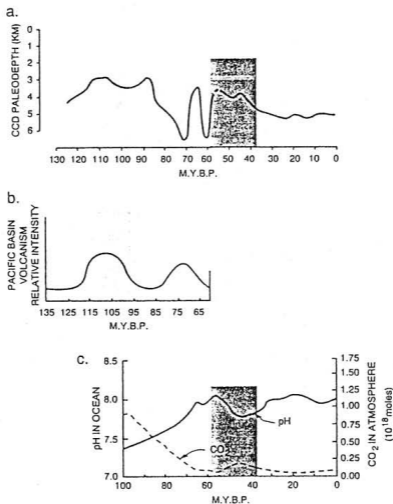


Figure 2 – (a) Estimated variation in Pacific Ocean carbonate compensation depth (CCD) since the late Mesozoic [Cretaceous data from THIERSTEIN (1979), Tertiary data from BERGER (1977)]. (b) Mid-Cretaceous pattern of Pacific basin volcanism (ARTHUR *et al.*, 1985), indicating probable elevated levels of volcanic CO<sub>2</sub> release. (c) Selected patterns of relevant parameters in the Eocene, based on a geochemical model by LASAGA *et al.* (1985).

## BIOGEOGRAPHY OF CALCIFICATION AND SYMBIOSIS IN MODERN HEXACORALS

Azooxanthellate species of contemporary actinians, corallimorpharians, and scleractinians have virtually coincident latitudinal distributions, and extend from the littoral zone to several thousand meters (anemones live much deeper because of the solubility of calcium carbonate at depth). They typically occupy similar or identical habitats, with slight alterations in the physico-chemical environment shifting ecological dominance from one group of hexacorals to another (FAUTIN, 1989). However, as discussed in more detail by BUDDEMEIER and FAUTIN (1994), zooxanthellate corals are limited to tropical and sub-tropical waters (VERON, 1986); all high-latitude scleractinians are azooxanthellate. This is not because of the requirements of zooxanthellae for either high temperatures or seasonally consistent irradiance, since zooxanthellate actinians extend into high latitude – even subpolar – seas.

Where reef-forming corals dominate the benthic environment, the concentrations of calcium and carbonate in surface water correspond to at least 2-3 times supersaturation with respect to aragonite, the mineral of coral skeletons (LYAKHIN, 1968). At lower saturation states, their skeletal and/or azooxan-

thellate relatives replace them as representatives of the hexacoral lineages. Algal symbiosis is apparently necessary for the rapid calcification rates exhibited by reef-forming corals (e.g. BARNES and CHALKER, 1990).

## SUMMARY

We regard corals and sea anemones as members of a single evolutionary lineage, and many belong to a single ecological guild. Scleractinians are striking in life and leave persistent and readily identifiable fossils, so have garnered more scientific attention than their soft and ephemeral siblings. However, we believe that their evolutionary relationships and paleodistributions may contain important information on the history of the oceanic carbon cycle. Sea anemones are essentially skeletonless corals; we speculate that lack of a skeleton permits them greater habitat diversity than their skeletalized forebears by making them less sensitive to the carbonate chemistry of sea water.

When we consider those members of the lineage symbiotic with zooxanthellae, skeletogenic taxa dominate in areas of high aragonite supersaturation (although non-skeletogenic species are present as well). The opposite is true in less supersaturated high latitude waters, where scleractinians are greatly reduced in diversity, do not form massive skeletons, and are typically solitary or form small colonies. This distribution appears to support our inferences based on paleogeochemical evidence that past changes in the carbonate saturation state may have been a driving force in the evolution of skeletal descendants of Scleractinia.

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