

ECOLOGY

Photosymbiosis and the Evolution of Modern Coral Reefs

George D. Stanley Jr.

Symbiosis is the most relevant and enduring biological theme in the history of our planet. Photosymbiosis—whereby photosynthetic microorganisms (symbionts) live inside an animal (host), deriving benefits, sometimes mutual—is found today among calcifying foraminifers and giant clams but is best exemplified in corals, the master builders of reefs. Photosymbiosis fosters diversity and novel adaptations. Recent studies on global change, coral degradation, and the future of coral reefs highlight the relevance of photosymbiosis to reef evolution (1–3).

Living corals called scleractinians, along with algae and other calcifying organisms on reefs, extract CaCO_3 from seawater, secreting it in massive skeletons collectively known as reefs. Reefs initiate voluminous carbonate deposition, affect ocean chemistry, and even mediate climate. Behind rapid reef growth are photosynthetic algae, especially the dinoflagellate genus *Symbiodinium* or zooxanthellae.

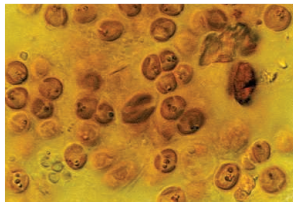
These symbionts enhance calcification rates orders of magnitude faster than in most nonzooxanthellate species, allowing their hosts to dominate choice places on the reef. Living safely encysted within coral tissue, zooxanthellae use the host's CO_2 and nitrogenous wastes. Zooxanthellae photosynthesize carbon and transport it intracellularly to the coral, supplementing 90% of the coral's nutrition, thus resolving the paradox of why so much life flourishes on nutrient-deficient reefs (4). The obligate relationship restricts corals to shallow-water tropics where they modify their shapes to maximize sunlight. Protecting corals from damaging ultraviolet radiation, their symbionts even manufacture “sunscreen.”

A majority of living corals are zooxanthellate and build reefs. Deciphering fossil zooxanthellate corals is problematic because symbionts aren't preserved. Symbiosis is inferred from colony size and shapes indicating light adaptation, corallite size and integration, and skeletal characteristics. Such indirect assessments relegate zooxanthellate presence to a working hypothesis. Carbon and oxygen isotopes fractionated within modern and Mesozoic coral skeletons provide quantitative methods

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Reef building. Colorful life teems on a Pacific coral reef where diverse ecosystems flourish in otherwise nutrient-deficient waters. This reef and others like it owe their existence to symbiosis between algae and corals.



Mutual benefits. Artist's view of a living reef coral cut to reveal a polyp and massive white skeleton. Soft polyps cover the entire surface of the colony and contain a profusion of microscopic symbiotic algae (zooxanthellae). (Upper left) A photomicrograph of zooxanthellae cells. They live encysted in the coral's tissues, enhancing metabolism and calcification.

The algae in coral reefs do not leave behind fossils, so deciphering their coevolution with corals is difficult. Isotope measurements can help reveal these ancient relationships.

for detecting zooxanthellae, thus serving as a proxy for photosymbiosis (5).

End-Permian mass extinctions decimated reefs and Paleozoic corals. Scleractinians appeared in the Middle Triassic some 8 to 10 million years later, evolving from anemone-like ancestors (6). Small and non-reef-building, these early corals were surprisingly diverse and integrated. Succeeding middle and early Late Triassic species remained non-reef-building. Vigorous Late Triassic (Carnian-Norian) biotic turnover and adaptive radiation culminated in the evolution of coral-framework reefs (7). The hypothesis that the coevolution of coral-zooxanthellate symbiosis occurred at this time is supported by skeletal stable isotopes and organic matrix analyses (5, 8). Both techniques yielded positive signals for Carnian-Norian photosymbiosis. The Triassic-Jurassic dinoflagellate-cyst family *Suessiacea* is closely related to zooxanthellae. Triassic occurrence and increasing diversity of these dinoflagellates coincide in space and time with those of reef-building scleractinians, suggesting their coevolution (9). End-Triassic mass extinctions witnessed sudden reef collapse and an 8- to 10-million-year reef eclipse. Coral species suffered 98% losses followed by Jurassic coral reorganization (7), a trend reflected also among *Suessiacea*.

Middle and Late Jurassic reefs reveal two major radiations and coral expansions. Zooxanthellate-like seasonal growth bands and indirect criteria categorize most corals as photosymbiotic, but inexplicably, symbiosis in Triassic and Jurassic corals does not appear as efficient as in modern counterparts (7, 10). Zooxanthellate and nonzooxanthellate corals existed during Cretaceous time, but reefs gradually became dominated by coral-mimicking rudistid bivalves. Zooxanthellate corals maintained diversity but rarely built reefs. Before the Cretaceous/Tertiary mass extinction, rudistids and shallow reefs died out as many ecosystems collapsed in stepwise fashion. Across the extinction boundary, greater numbers of zooxanthellates versus nonzooxanthellates perished (11). A 17-million-year early Tertiary reef eclipse, followed by recovery and several Paleogene biotic turnovers, led to modern reef ecosystems of the Neogene (12).

Throughout Phanerozoic history, reefs frequently collapsed during mass extinctions, with eclipses lasting 8 to 20 million years (13). Collapses and recoveries were postulated to correlate with symbiont loss and symbiosis renewal, respectively (11, 12, 14). Global warming-cooling cycles, sea-level change, acid rain, eutrophication, and sunlight reduction—all of which have been proposed to accompany Mesozoic reef extinctions—appear inimical to zooxanthellae-coral symbiosis. High nutrient levels interpreted for some Paleozoic reefs don't fit this model (15), but post-Paleozoic nutrient-limited reef settings may do so.

Evidence of ancient reef collapse validates concerns about susceptibility of present-day reefs to climate change, bleaching, coral diseases, and nutrification—all of which involve zooxanthellae. Perceptions of coral reef fragility seem paradoxical given the resilience of Tertiary corals and rapid reef recoveries, especially after staggering Neogene upheavals, climate swings, and sea-level changes (12, 13). Answers to this enigma may lie in discoveries that living zooxanthellae belong not in one species but rather combinations of diverse clades with different symbionts adapted dynamically to changing light and temperature regimes (2, 16). Coral bleaching, traditionally thought detrimental, may actually be adaptive (17). Expulsion of less desirable symbionts in favor of more tolerant ones after environmental change would explain reef resiliency, allowing necessary adaptations to survive extinction (18). Brooding corals transmit zooxanthellae directly to offspring, whereas broadcasting spawners acquire symbionts from seawater, the latter promoting greater partner recombinations. Symbiont evolution among corals with geographic range expansions, driven by climatic fluctuations, could explain their



Reef death. Bleached Caribbean elkhorn reef coral, *Acropora palmata*, turns ghostly white when photosymbiotic algae are lost. Whether this “white death” is the beginning of the end for reefs is currently debated, underscoring the relevance of photosymbiosis for modern reef evolution.

adaptability and success (19). Coral-zooxanthellae symbiosis initially may have coevolved loosely, dissolving when advantages decreased, like the rare facultative (apozooxanthellate) corals today. If early corals lacked modern symbiont adaptations, this could account for their limited Mesozoic success (7, 10). Considering symbiosis dynamics, perhaps algae and not corals are the masters of the reef. Future insights into the coevolution of photosymbiosis in both ecologic and geologic time should arise from a synthesis and integration of ideas from paleobiology, life histories, and genetics.

PLANT SCIENCE

Auxin Transport, but in Which Direction?

Tobias Sieberer and Ottoline Leyser

Many aspects of plant growth depend on transport of the hormone auxin across tissues, directed by specific transporter proteins.

The plant hormone auxin has remarkably diverse roles in the regulation of growth and development. Auxin, synthesized in shoot apices, is moved along specific transport routes through the plant by unique polar transport machinery (1). Polar auxin flow is primarily dependent on polar efflux from cells, with the resultant directed transport providing a constant stream of information. Auxin flow can be influenced by both exogenous and endogenous stimuli, triggering redistribution of auxin and specific growth and developmental responses. This intercellular communication system is conceptually similar to the animal nervous system, and its transmission rate of 1 cm/hour is fast enough for systemic signaling in a sessile organism.

Over the past decade, several classes of

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integral membrane proteins have been implicated in auxin flow. Mutations in these protein families perturb auxin distribution, causing diverse phenotypes, but their interrelationships and the biochemical basis for their action have remained obscure. On page 914 of this issue, Petrásek *et al.* (2) provide long-awaited evidence that PIN-FORMED (PIN) proteins act directly in transporting auxin out of cells, substantially independently of the PGP family of auxin pumps. Moreover, on page 883, Wiśniewska *et al.* report that polar PIN localization in cells is a primary determinant of the direction of auxin efflux (3). And, coming in from the opposite direction, a third report by Dharmasiri *et al.* in this week's *Science Express* (4) identifies a candidate regulator for the localization of AUX1, a protein that mediates cellular influx of auxin.

The PIN-FORMED family was so named because mutations in one family member,