

THE ECOLOGICAL EVOLUTION OF REEFS

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KEY WORDS: reef, ecology, evolution, predation, photosymbiosis

ABSTRACT

Many groups of extinct and extant organisms have aggregated to form reefs for over 3.5 billion yr (Ga). Most of these communities, however, grew under ecological and environmental controls profoundly different from those that govern modern coral reefs. Not only has the global distribution of reefs varied considerably through geological time—determined largely by sea level, and latitudinal temperature/saturation gradients—but more importantly the trophic demands of reef-building organisms have changed, as has the degree of biological disturbance faced by sessile biota in shallow marine environments.

Reefs differentiated into open surface and cryptic communities as soon as open frameworks developed in the Proterozoic, some 1.9 million yr ago (mya) and diverse and complex ecosystems were established by the early Cambrian (~520 mya). Calcified heterotrophs were conspicuous in reefs during the Paleozoic and early Mesozoic, but considerable rigidity was imparted to these often otherwise fragile communities both by indirect microbial processes that induced the formation of carbonate and by rapid early cementation. While photosymbiosis was probably acquired by scleractinian corals early in their history (~210 mya), this does not appear to have immediately conferred a superior reef-building ability. Large, modular corals and coralline algae showed notable powers of regeneration after partial mortality but poor ability to compete with macroalgae for limited substrate in the absence of intense herbivory; they did not rise to prominence in reef communities until the early to mid-Cenozoic. This may be related to the appearance at this time of major predator groups such as echinoids, limpets, and particularly fish that are capable of rapid algal denudation and excavation. The existence of this reciprocal relationship is corroborated by the observation that branching corals, which appear to flourish because and not in spite of breakage,

show a particularly dramatic increase in diversity coincident with the increase in predation pressure from the late Mesozoic onwards.

INTRODUCTION

Although estimates suggest that modern coral reefs occupy only 0.2% of Earth's ocean area (47), their influence is global and multifaceted. As substantial topographic structures, coral reefs protect coastlines from erosion and help create sheltered harbors. Reefs and their associated carbonate sediments are also important as storehouses of organic carbon and as regulators of atmospheric CO₂, which in turn may influence climate and sea-level fluctuations (61). Being highly porous structures, ancient subsurface reefs provide extensive reservoirs for oil and gas. From a biological standpoint, however, the greatest significance of reefs lies in the fact that they generate and maintain a substantial proportion of tropical marine biodiversity.

It is widely assumed that the complex and varied photosymbiotic association of scleractinian corals with dinoflagellate algae provides both driving energy and physical structure for the whole coral reef community. Photosymbiosis confers a variety of advantages to reef-building organisms, including rapid rates of growth and calcification, and the potential for host selection of optimal symbionts in the highly dynamic tropical marine environment (2, 11–13, 77). In addition, a substantial and increasing body of research continues to underline the importance of predation, in particular herbivory, in maintaining the coral reef ecosystem (see summaries in 32, 37). Yet the fossil record of reef-building shows that both the acquisition of photosymbiosis and the appearance of modern predator, herbivore, and bioeroding groups are relatively recent geological occurrences: Many ancient reefs clearly grew under profoundly different ecological controls than those that govern the functioning of modern coral reefs. Moreover, the global distribution of reefs has varied considerably through geological time, determined largely by sea-level, geochemical, and climatic fluctuations. Present day sea level is relatively low compared to that in much of the geological record such that the area of shallow water tropical seas is small, resulting not only in a reduced volume of shallow-water carbonates being formed, but also in an absence of analogs for the very extensive shallow seas (known as epeiric or epicontinental seas) that were common when sea levels were high. The extensive carbonate platform reefs and atolls of today are also the product of an unusually prolonged period of stable sea level, which, together with relict topography, have exerted a strong influence over modern reef form and style of sedimentation. Present-day climate is also relatively cool, with well-developed polar ice caps. During significant periods of geological

time, ice caps were not present, and at times such as the mid-Cretaceous, northern hemisphere mean annual surface temperatures may have been 15 to 25° warmer than today (4, 62). In addition, 60% of modern carbonate production is accounted for by calcareous plankton that produce pelagic ooze deposited on the deep ocean floor, but before the evolution of such plankton during the mid-Mesozoic, shallow marine carbonate deposits represented up to 90% of global production (27). Consequently, for much of geological time, marine carbonate distribution, and possibly carbonate saturation levels, were very different from those found in modern seas.

It is clear then that the origins of the ecosystems that dominate Earth today cannot be fully understood without a historical perspective. Reefs are highly susceptible to environmental change, and a substantial proportion of modern coral reefs are currently under threat (5). In the past few years, we have learned how reefs respond to global change and catastrophe on a human timescale, but the origins of many characters we seek to explain are in the past. Only study of the geological record can reveal the dynamics of long-term evolutionary change.

This review details some of the recent advances in the reconstruction of ancient reef ecologies and explores the relationship between evolutionary innovation and environmental opportunity. The last few years have seen some radical developments of our understanding of how modern reef communities and reef corals function, but ancient reefs have too often been studied solely as geological phenomena with little regard to biological interactions. Yet, being the result of in situ growth, reefs frequently preserve exquisite details of past ecological interactions lost from most other fossil communities. Such ecological interactions are of profound importance and interest, as they are the ultimate determinants of reef growth. The theme developed here is to explore the evolution of reefs as biological phenomena: Reefs concern the biological occupation of space, but the demands on sessile reef organisms to achieve this have changed over the course of geological time.

What Is a Reef?

If only the characteristics of modern coral reefs are taken as diagnostic, then very few fossil examples would qualify as reefs. This is due to two interrelated reasons: Modern coral reefs appear to possess unique ecological features and environmental requirements, but these characteristics are notoriously difficult to detect in the geological record.

Attempts to understand ancient ecologies by direct reference to modern communities is hampered by several obstacles. First, processes of physical and biological destruction, the incomplete nature of the fossil record, and diagenesis all obscure the original reef community structure and form. As a result,

detection of a wave-resistant framework, determination of the depth at which a reef community grew, and reconstruction of original topographic relief can all be problematic in ancient examples. Second, the impossibility of dating and correlating geological strata at the fine temporal and spatial scale appropriate to modern ecological analysis makes the direct transfer of information and techniques inappropriate. This problem is compounded by the general coarsening of temporal resolution with increased time back from the present. Third, there are clearly no modern analogs for many ancient ecologies, not only because many of the constituent organisms are extinct, but also because the environmental conditions under which they grew have changed radically. A full appreciation of ancient reef ecology clearly both calls for a nonuniformitarian approach and also necessitates the formulation of universally applicable criteria for the recognition of reefs.

Reefs are here considered to form as the direct or indirect result of organic activity, developing due to the aggregation of sessile epibenthic marine organisms, with the resultant higher rate of in-situ carbonate production than in surrounding sediments.

The Diversity of Modern Reefs

Some understanding of the processes common to all reef formation can be gained through an appreciation of the diversity of communities that form reefs in modern seas. In addition to corals, microbes, algae, and many invertebrates aggregate to form reefs in modern seas, in an apparently wide range of environmental settings. But as reef formation is contingent upon the successful occupation of space by sessile organisms, it is not surprising that all modern reef-building communities develop under specific environmental conditions that allow such growth. Possession of a sessile nature makes organisms vulnerable to disturbance—both to physical destruction and biological attack by predation—which is probably the major control on both the distribution and the morphology, of epibenthic organisms (19). The distribution of modern reefs shows that their development is dictated by avoidance of competition and predation, or by specialized adaptation to physical or biological attack.

Modern coral reefs are specialized communities that develop in tropical and subtropical environments characterized by warm temperatures, aragonite supersaturation (that is where concentrations of calcium and carbonate exceed the thermodynamic mineral solubility product), and high light intensities, where stable, elevated substrates are available for colonization, and typically where nutrient levels are low. Except for some reefs built by cyanobacteria and calcified algae, many modern reefs are constructed by organisms that possess little inherent stability under agitated conditions and, being nonphotosynthetic, are

not dependent upon light. Consequently, they often develop in low-energy settings, either in relatively deep waters or in marginal, shallow water environments. These include sabellariid and serpulid polychaetes, vermetid gastropods, bryozoans, and cyanobacterial communities (60a, 78a). Deep-water habitats, such as the area supporting bryozoan-sponge reef growth off the shelf of south-eastern Australia, receive minimal or no light but offer abundant nutrients (7). These environments are relatively benign in that predation pressure and turbulence are often low. Shallow water noncoral reefs are usually constructed by organisms able to grow under conditions (such as nonmarine salinity) that exclude normal marine competitors or predators. Such reefs often grow in embayments protected from wave destruction.

What Is a Reef Community?

Current ecological thought considers that biological communities are not fixed entities with precise boundaries, but are chance associations of species with similar ecological requirements. This notion is supported by several models that adequately predict community composition only on the basis of immigration and extinction, spatial distribution of environments, and the size of the species pool (23, 39). Communities constantly change through local extinction and recruitment of component species, and new communities, developed in previously unoccupied habitats, are composed of species from the available population that have geographic access to the new area (16). It has been well documented that formerly co-occurring species are now found in associations entirely different from those they occupied in previous times, e.g. in Indo-Pacific reefs, corals responded to changing shelf area and water depth as sea level fluctuated during the Pleistocene by changing community membership (68). Associations within local reef communities have clearly changed as new species have evolved while order taxa persist. Clearly, community traits are not heritable: Natural selection cannot operate upon communities, only upon their constituent species.

Such observations undermine the notion of strong cohesion with communities and support the view that communities are chance associations. While it is now commonly accepted that many marine communities are not discrete entities, this has not yet been universally accepted for reefs (43, 63). The sheer abundance of specialized interactions and symbioses as well as diversity of ecological niches seem to indicate long-lived coexistence between organisms. However, it is now apparent (49a) that such seemingly specific interactions are, in fact, frequently modified as species membership of a reef community changes so that, like the constituent species, the way in which organisms interact is not fixed. This suggests an enormous ecological redundancy of species in reefs, that is, many species can occupy a broadly similar niche.

PHYSICOCHEMICAL CONTROLS ON THE DISTRIBUTION OF REEFS

Much debate has concerned the relative importance of biologically and chemically controlled factors in predicting suitable sites for carbonate production and, in particular, reef growth (cf 53a, 62). It is now clear that elevated ambient seawater supersaturation with respect to calcium carbonate broadly corresponds to sites of carbonate sediment generation, and this is related to a number of factors, most importantly surface seawater temperature (12, 14, 15, 47, 62). Most notable is that the broad documented patterns of change in accumulation rate with latitude are very similar to those defined by saturation values, and those calculated from laboratory growth of carbonate minerals are also in very close agreement (62). These data support the contention that the latitudinal variation of seawater composition is therefore indistinguishable from biological factors related to the ecological demands of carbonate-producing biota in controlling the broad global distribution, rates, and composition of shallow water carbonate accumulation (62).

Rates of shallow-water carbonate deposition are strongly dependent upon the latitudinal temperature/saturation gradient, with carbonate deposition greatest between 15° and 20°, and decreasing both polewards and toward equatorial regions. The latitudinal distribution of carbonate deposits thus records ancient climatic gradients in the temperature and saturation state of seawater. For example, the latitudinal extent of Cretaceous limestone deposition occurred some 10° more poleward than at present, suggesting that the temperature between the equator and 38°N was some 5°C warmer than at present (62). However, higher atmospheric pCO₂ most likely existed during the Cretaceous (4), which may have controlled the dominant mineralogy of carbonate-secreting marine organisms, favoring those with calcitic rather than aragonitic skeletons (36). This might explain the dominance of rudist bivalves with outer calcitic layers, rather than wholly aragonitic corals at this time.

THE COMPLEXITY OF ANCIENT REEF ECOSYSTEMS

In principle, any sessile organism with a sufficiently stable habit capable of producing carbonate production has the ability to form a reef, and indeed, the geological record shows that many microbial communities, algae, and skeletal metazoans (most now extinct) have formed reefs since the early Archean, some 3.5 Ga. An understanding of reef evolution—such as the response of biota to environmental change, and the way in which reefs control sedimentation across shelf margins—is wholly dependent upon accurate description of ancient reef

ecology. Study of a wide variety of Paleozoic reefs is now revealing hitherto unexpected levels of ecological complexity. Moreover, although some Paleozoic reefs achieved rates of accretion similar to modern coral reefs (e.g. 3–4 mm yr⁻¹ for the Permian Capitan reef; 30), the trophic structure and relative contributions of inorganic and organic carbonate were profoundly different. In particular, Paleozoic reefs appear to have grown in the absence of the photosymbiosis, and in some examples, much of the preservable biodiversity was housed within cryptic communities. Reef construction by relatively fragile organisms was made possible by the absence of biological destruction and by rapid inorganic lithification. Such detailed ecological analyses confound the long-held belief (29, 86) that photosymbiosis and large, skeletal metazoans are vital prerequisites for successful reef building. I illustrate these new-found complexities with two examples: the oldest metazoan reefs and reefs from the Upper Permian.

The Oldest Metazoan Reefs (~570–543 mya)

The oldest known reefs were constructed by microbialites—calcareous organosedimentary deposits formed by the interaction of benthic microbial communities and detrital or chemical sediments. From their first appearance 3.5 Ga and for the next 2.5 Gyr, these microbialites were expressed solely as stromatolites, which may be a reflection of their cyanobacterial origin. Prior to 2.3 Ga, oceans and the atmosphere were essentially anoxic, and atmospheric oxygen levels probably continued to be very low during the Paleoproterozoic (2–1.65 Ga). Reefs were differentiated into distinct open surface and cryptic communities as soon as crypts formed in the Proterozoic 1.9 Ga (38).

Coincident with the decline of stromatolites at the end of the Proterozoic was a rise in abundance and diversity of thrombolites and calcified cyanobacteria, and the appearance of metazoans. The early evolution of animals probably proceeded as a single, protracted evolutionary radiation lasting some 55 myr (34) before culminating in the Cambrian explosion, which records widespread skeletonization and the expansion of behavioral repertoires, although there is evidence to support the presence of a terminal Proterozoic extinction event (49). The first metazoan reefs are known from the latest Neoproterozoic, and are particularly diverse in the widespread carbonates of the Nama Group of southern Namibia. Indeed, some of the earliest skeletal metazoans known were sessile, gregarious, and probably heterotrophic organisms capable of forming limited topographic relief. These include weakly skeletonized cup- or goblet-like solitary, sessile organisms, such as the globally distributed *Cloudina* (possibly a cnidarian or worm tube; 33), as well as seven other as yet undescribed forms (AH Knoll, personal communication). The stratigraphic range of these sessile organisms overlaps with the most diverse Ediacaran soft-bodied fossil

assemblages (34). Probable borings have also been recorded from this time (3), and a detritivorous fauna associated with reef cavities had developed by the earliest Cambrian (102).

Although stromatolites remained common in intertidal-supratidal environments, the first biotically diverse metazoan-algal reefs formed subtidally at the base of the Tommotian (530 Ma; 9) on the Siberian Platform. These reef communities comprised the highly gregarious calcified sponges known as archaeocyaths, which lived in cyanobacterial-thrombolitic communities, became globally distributed, and persisted until the virtual demise of the archaeocyaths at the end of the Toyonian, some 520 mya (9).

Contrary to earlier reports (77a), the earliest metazoan reefs at the base of the Tommotian, as exposed on the Aldan River, Siberia, were already ecologically complex (75). While possessing low diversity, they had erect framework elements of branching archaeocyaths, with a cryptic biota of archaeocyaths and calcified cyanobacteria. These reefs were associated with skeletal debris of a diverse associated fauna; microburrowing deposit-feeders continued to proliferate within the sheltered areas of the framework.

By the middle Tommotian, archaeocyath-cyanobacterial reefs became more diverse and ecologically complex (52) due to the appearance of other sessile, calcified organisms inferred to have been suspension- or filter-feeders. These organisms included radiocyaths, a variety of simple cup-shaped forms known as “coralomorphs,” globally rare but locally abundant large skeletal tabulate corals and other cnidarians (53, 78), and stromatoporoid sponges (69). Possible calcarean sponges appeared in the early mid-Tommotian (52); probable sponge borings have been noted within coralomorph skeletons from the Canadian Rocky Mountains (70), and silt-sized microspar grains resembling “chips” from clionid-type sponges have been identified within Lower Cambrian reef cavities (50).

These reefs were taxonomically diverse and ecologically complex, and they were differentiated into distinct open surface and cryptic communities: This differentiation may have been promoted by intense competition for limited hard substrates. Indeed, crypts housed a substantial proportion of overall reef biodiversity: solitary archaeocyath sponges, calcified cyanobacteria, and a microburrowing (?)metazoan were the most ubiquitous and abundant elements; coralomorphs, spiculate sponges, and various skeletal problematica were also common (102). The rigidity of Lower Cambrian reefs was enhanced substantially by the growth of syngedimentary cements—but this may also have contributed to the limited longevity of the cryptic community by rapid occlusion of the reef framework. These elements produced one of the most diverse and ecologically complex reef ecosystems known from the Paleozoic (Figure 1).

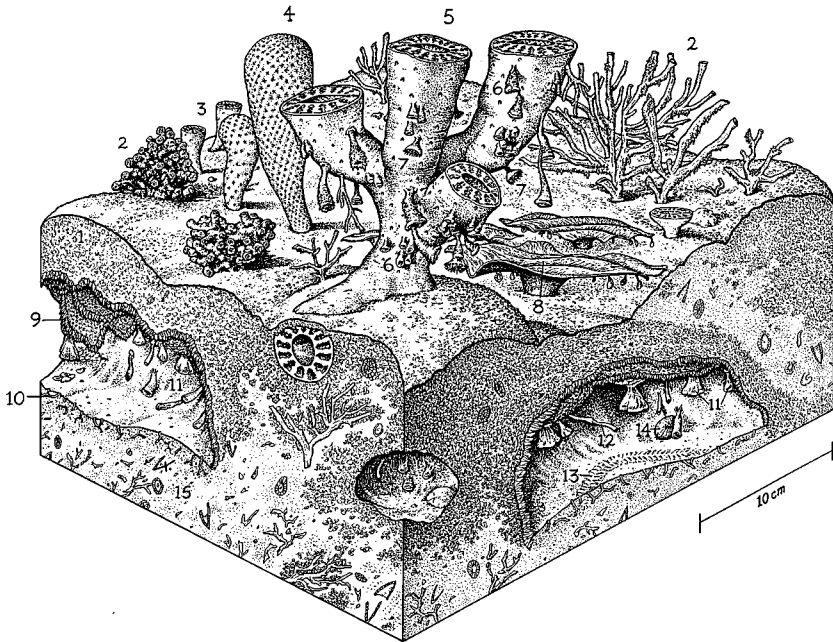


Figure 1 Reconstruction of a Lower Cambrian reef community (from 97). 1. *Renalcis* (calci-fied cyanobacterium); 2. branching archaeocyath sponges; 3. solitary cup-shaped archaeocyath sponges; 4. cancellorid (?sponge); 5. radiocyath (?sponge); 6. small, solitary archaeocyath sponges; 7. cryptic 'coralomorphs'; 8. *Okulitchicyathus* (archaeocyath sponge); 9. early fibrous cement forming within crypts; 10. microburrows (traces of a deposit-feeder) within geopetal sediment; 11. cryptic archaeocyaths and coralomorphs; 12. cryptic cribricyaths (problematic, attached skeletal tubes); 13. trilobite trackway; 14. cement botryoid; 15. sediment with skeletal debris.

Upper Permian Reefs (~260 Ma)

Upper Permian reefs are characterized by frondose bryozoan (e.g. *Gonipora*, *Polypora*) sponges and calcified sponges, as well as by the problematicum *Tubiphytes* and various algae including *Archaeolithoporella*. Volumetrically, late Permian reefs are dominated by bioclastic sediments and early cements, but they were capable of forming well-developed rimmed margins with zonation from fore-reef talus to reef slope, crest, reef flat, and back-reef lagoon. In many examples, including the Zeichstein reef of northern England, and the Capitan Reef of west Texas and New Mexico, the stabilization of sediments and aggregating communities of frondose bryozoans was aided by rapid cementation and/or encrusting microbialite formation that created a wave-resistant reef rock along the shelf edge and slope (89, 98, 99).

The Capitan reef forms one of the finest examples of an ancient rimmed carbonate shelf, marking a prominent topographic boundary between deep-water basinal deposits and shallow shelf sediments. Established ecological reconstructions have emphasized the role of various baffling branching or solitary organisms (sphinctozoan calcified sponges, bryozoans, and *Tubiphytes*) and massive putative algae (*Collenella*, *Parachaetetes*, and *Solenopora*) in the construction of the Capitan reef, together with the binding and encrusting contribution of *Archaeolithoporella* and extensive early marine cementation (29). However, the reef was, in fact, strongly differentiated into distinct open surface and cryptic communities. Unlike modern phototrophic coralgall reefs, most of the preservable epibenthos was housed within the cryptos, and zonation developed only in the shallow parts of the reef. Most sphinctozoan sponges did not grow upright to form a baffling framework but rather were pendent cryptobionts as were nodular bryozoans and rare solitary rugose corals and crinoids (98, 99). Indeed, many members of the cryptos appear to have been obligate cryptobionts. Much of the Middle Capitan reef framework was constructed by a scaffolding of large frondose bryozoans (Figure 2a). Bathymetrically shallow areas of both the Middle and Upper Capitan reef, however, were characterized by abundant platy sponges. In parts of the Upper Capitan, some forms reached up to 2 m in diameter and formed the ceilings of huge cavities that supported an extensive cryptos (Figure 2b).

In the absence of destructive forces (both biotic and physical) prevalent on modern reefs, the relatively fragile Capitan reef remained intact after death of the constructing organisms. Rigidity was imparted to this community by a post-mortem encrustation of *Tubiphytes* and *Archaeolithoporella*, together with microbialite. The resultant cavernous framework was partially infilled with sediment and preserved by symsedimentary intergrowth of aragonitic botryoid cements and *Archaeolithoporella* (Figure 2). Extensive cement precipitation was favored by factors including deep anoxia, which generated upwelling waters with elevated alkalinity (35). So although the accumulation rate of the Capitan may be comparable to that of modern coral reefs, both the trophic structure and relative contributions of inorganic and organic carbonate were profoundly different (99).

THE IMPORTANCE OF MICROBIAL COMMUNITIES

Although the recognition of microbialites in the geological record is problematic and controversial (for example, see 58), presumed microbialites are common as primary framebuilders and secondary encrusters within many Phanerozoic reefs; indeed, it is probable that they are more important than currently

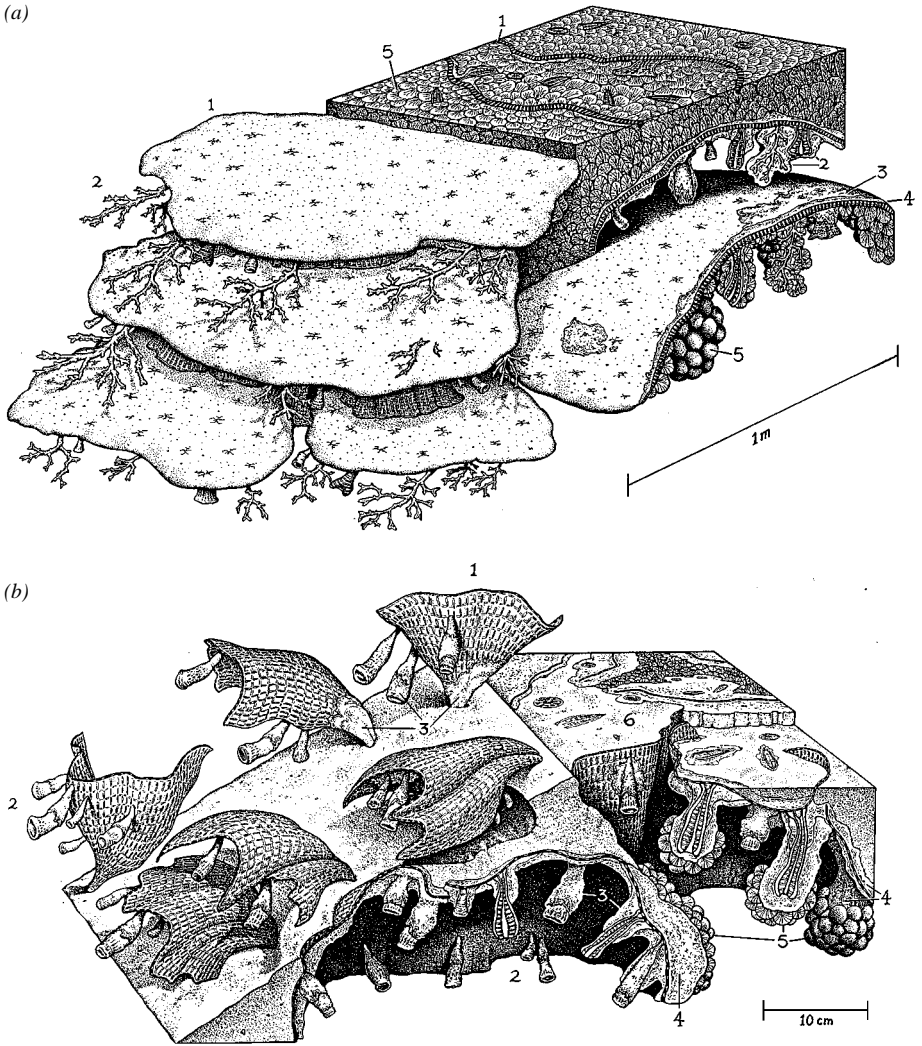


Figure 2 Reconstruction of an Upper Permian reef: the Capitan Reef, Texas and New Mexico (260 Ma) (from 97). (a) Platy sponge community. 1. *Gigantospongia discoforma* (platy sponge); 2: solitary and branching sphinctozoan sponges; 3: *Archaeolithoporella* (encrusting ?algae); 4: microbial micrite; 5: cement botryoids. (b) Frondose bryozoan-sponge community. 1. Frondose bryozoans (*Polypora* sp.; *Goniopora* sp.) 2: solitary sphinctozoan sponges; 3: *Archaeolithoporella* (encrusting ?algae); 4: microbial micrite; 5: cement botryoids; 6: sediment (grainstone-packstone).

recognized (71, 93, 99). Likewise, they were probably widespread in the Proterozoic but are difficult to identify unequivocally (48).

Most living cyanobacteria and other microbes are unable to produce directly a calcareous skeleton (64), so lithification within microbial communities is due either to the indirect post-mortem inorganic cementation processes (induced by decay or indirect metabolic processes) prevalent in hypersaline or brackish waters (with cements precipitated either on or within microbial sheaths), or to direct carbonate particle entrapment. For example, modern stromatolites appear to form only where two environmental criteria are satisfied (72):

1. High sedimentation rates (e.g. Exuma Cays, Bahamas) or low nutrient levels (e.g. Shark Bay) exclude the growth of potential macroalgal algae competitors for substrate space, and
2. Oceanographic conditions create a water chemistry favorable for carbonate precipitation, such as high levels of supersaturation of carbonate, rapid degassing (loss of CO₂) rates, or local elevations of sea water temperature.

The geological distribution of microbialites may therefore be controlled by physicochemical factors including the saturation state of seawater driven by changes in pCO₂ or Ca/Mg ratios, and global temperature distribution (48, 93). The decline in abundance of reefal microbialite after the Jurassic may be the result of low saturation states of sea water due to increased sequestration of carbonate by the newly evolved calcareous plankton (31, 93). However, although the relative importance of microbialites within modern coral reefs is not clear, the increasing numbers of examples recognized also suggest some role (e.g. 73, 74). Two examples are given below of how recognition of microbial fabrics has radically altered our understanding of ancient reef formation.

Upper Devonian Reefs (~360 Ma)

The Devonian, in particular the mid-late Devonian (Givetian-Frasnian), is considered to represent possibly the largest global expansion of reefs in the Phanerozoic (21). During this interval, the climate was equable and sea level high. Extensive reef tracts, in size exceeding those of the present day, are known from Canada and central Asia, and large reefs are also found throughout Europe, western North Africa, South China, southeast Asia, and most famously from the Canning Basin, Western Australia.

As so many Devonian reef tracts are subsurface and/or dolomitized, exact reef geometry, ecology, and zonation details are poorly known for many examples. However, mid-late Devonian reefs are generally assumed to have been built by large, heavily calcified metazoans—stromatoporoid sponges and tabulate corals—together with calcified cyanobacteria, and to a far lesser extent rugose

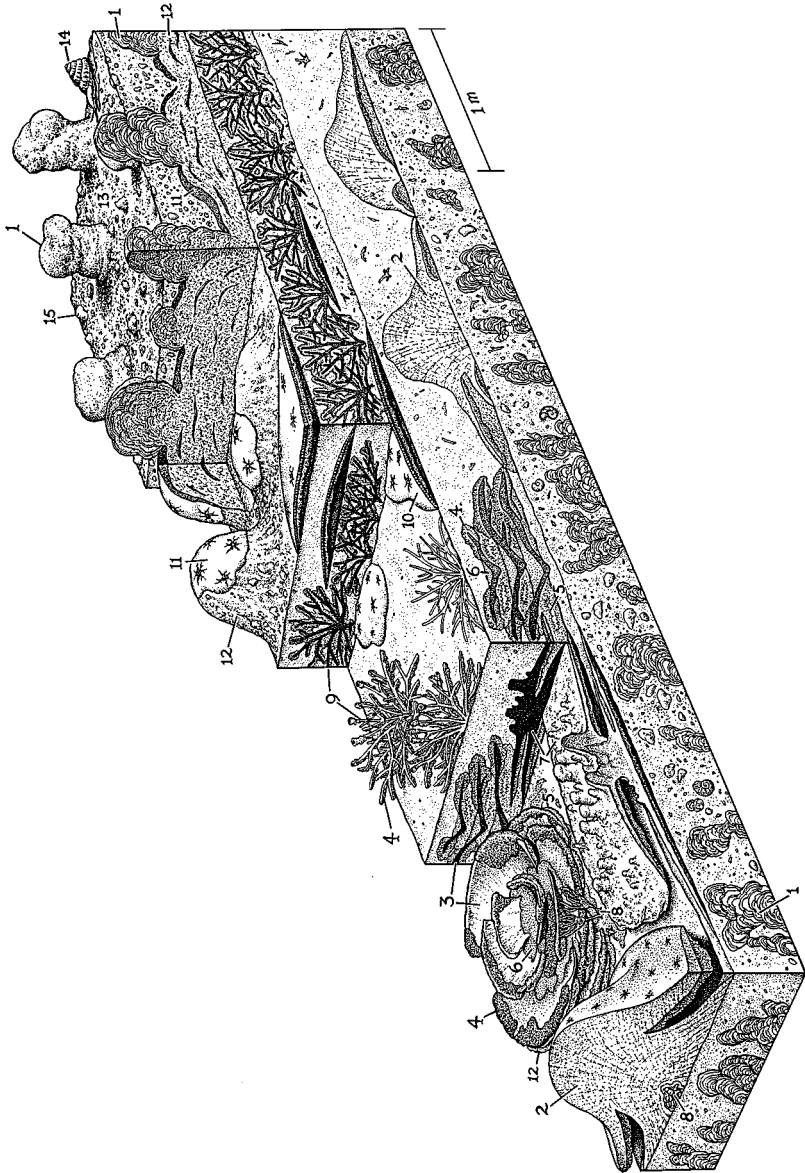
corals. Receptaculitids and lithistid sponges are common in foreslope or deeper water reef communities or in low energy shallow settings. The faunal diversity of shallow water reefs is high, with metazoan reef-builders showing a tremendous variety of unusual morphologies (Figure 3) and growth rates as high as some modern scleractinian corals. Brachiopods were common, sometimes nestling within crypts, but especially attached to the undersurface of laminar/tabular stromatoporoids or tabulate (often alveolitid) corals (22, 85). Some were cementers (e.g. *Davidsonia* and *Rugodavidsonia*); others such as atrypids attached by means of spines (97).

Microbialite, as free-standing mounds, heads and columns, or encrusting components (Figure 3), were volumetrically important components of many Frasnian reefs (18, 60, 88, 97), as were the calcified cyanobacteria *Renalcis* and *Rothpletzella* [*Sphaerocodium*] (60, 93). Many stromatoporoids and other calcified metazoans grew attached to these lithified substrates, only rarely intergrowing themselves to form a reef framework (97). Early marine cements were also volumetrically important in many Frasnian reefs, in part reflecting the abundance of substantial and intact framework cavities formed beneath large skeletal metazoans; up to 50% cement by volume is recorded from the Golden Spike Reef, Canada, and syndimentary radial cements account for 20–50% by volume for the reefs of the Canning Basin (41, 45). The importance of early cementation both within cavities and of microbial communities in the Canning Basin is manifest by the numerous, huge reef-talus blocks (up to 100 m) incorporated into fore-reef strata and basin debris flows, and the extensive development of neptunian dykes and other fractures subparallel to the reef front. The presence of spur-and-groove structures (67) is testament to the growth to sea level and wave-resistant capacity of these reefs.

Waulsortian Mud Mounds

The Carboniferous was a time of great climatic and sea-level fluctuations with polar glacial events and depressed global temperatures (82). Continents were fused into one landmass that straddled the equator, thus restricting circulation and excluding the possibility of any equatorial currents (21). Deep-water mud mounds, known as Waulsortian mounds, form a group of reefs that flourished during the Early Carboniferous, although Waulsortian-like reefs are known from the Late Carboniferous of Ellesmere and Axel Heiberg Islands of the Canadian Arctic (26).

Waulsortian mounds are distinctive reefs characterized by a core facies containing many generations of micrite (lime mud), complex micrite-supported cavity systems infilled by marine cements (including the enigmatic stromatactis), and fenestrate bryozoans, that are generally considered to lack any framework. These mounds are proposed to have originated in deep waters below



wave base (up to 280 m) (on the basis of the evidence of regional sedimentology and general absence of photic organisms), but they could grow into fairly shallow waters in higher energy regimes (81). Waulsortian mounds bear steep depositional slopes and were commonly surrounded by flanking beds rich in disarticulated crinoids.

Although bryozoans and crinoids were probably capable of baffling and trapping locally fine-grained mud (especially from slightly turbid water) due to unidirectional cilia-generated currents (57), they were not ubiquitous components of Waulsortian reefs and were often equally common in level bottom sediments. Moreover, it is clear that sediment-baffling alone could not create slopes up to 50° and reefs up to 100 m high; such steep slopes suggest that unrecognized reef framework must have been present. Sediments surrounding deep-water mounds are typically thinner and contain significantly higher quantities of fine-grained siliclastic sediment than those of the mound itself; mounds in shallow settings show a massive, muddy appearance at variance with the coarser-grained

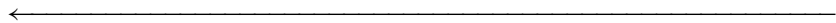


Figure 3 Reconstruction of an Upper Devonian back-reef community: Canning Basin, western Australia (360 Ma) (from 97). Back-reef sediments show distinctive shallowing-upwards cycles, which are interpreted to reflect the lateral zonation of four communities:

1. The onset of carbonate sedimentation, probably induced by deepening, is marked by the colonization of large stromatoporoids on stabilized coarse clastic sediment. These include domal (*Actinostroma* sp.), and inferred whorl-forming foliaceous (?*Actinostroma* sp.), and platy-columnar growth forms. Many appear to have initiated upon crinoids, and their considerable elevation above the substrate is reflected by the accumulation of the same geopetal infill within their tiered growth. These stromatoporoids were heavily encrusted by *Renalcis* and microbialite, particularly on sheltered undersurfaces.
2. The next zone characterized by thickets of the branching stromatoporoid (*Stachyodes* sp.), and thin, laminar stromatoporoids that arched over the sediment. These show either encrusting collars of *Renalcis*, or cryptic *Renalcis* attached to sheltered undersurfaces.
3. This was followed by the extensive growth of large mounds of microbialite, which were encrusted by the stromatoporoid (?*Clathrocoilona spissa*).
4. Columnar heads of stromatolites develop as the sediments became more shallow, energetic and dominated by very coarse sands, together with patches of large oncolites (coated grains with irregular and overlapping laminae, which were probably also microbially-mediated) and large gastropods.

1: stromatolites; 2: domal stromatoporoid (*Actinostroma*); 3: inferred whorl-forming foliaceous stromatoporoids (?*Actinostroma* sp.); 4: calcified cyanobacterium (*Renalcis*); 5: fibrous cement; 6: geopetal sediment infill; 7: platy stromatoporoid; 8: crinoids; 9: branching stromatoporoid (*Stachyodes* sp.); 10: laminar stromatoporoid; 11: Encrusting stromatoporoid (?*Clathrocoilona spissa*); 12: microbialite; 13: coarse clastic sediment; 14: gastropods; 15: oncolites.

surrounding sediments, indicative of mobile, winnowed sediments and high or turbulent water energies (65). Such observations indicate that the carbonate mud within the mounds was generated in situ under a stabilizing biological control.

There is now agreement that diverse and complex microbial processes, involving auto- and heterotrophic communities, were important in Waulsortian reef formation, especially in the shallow water facies (e.g. 54, 65), while the contribution of skeletal organisms was variable and probably relates to depositional setting and opportunistic colonization. A classic Waulsortian mound, known as Muleshoe, in the Sacramento Mountains, New Mexico, has been revealed to be constructed by bulbous, micrite masses with thrombolitic fabrics that are lined by early marine cements (46). In the upper parts of the mound, inferred to have grown in shallow waters, there may be a pronounced high-angle orientation of digitate micrite masses and intervening in-situ bryozoan fronds that matches the regional orientation of other current indicators such as crinoid segments.

Encrusting, often cryptic stromatolites and thrombolites, and occasional *Renalcis* colonies, offer direct evidence of microbial activity (46, 65). Peloidal and clotted micrites (thought to have been primarily calcite) are also common in many Tournasian and Viséan mounds, and they are thought to have formed within surficial microbial mats or biofilms that trapped bioclasts and stabilized the accreting reef surface, allowing the development of steep depositional slopes. Encrusting and boring organisms are often associated with the microbialites (e.g. 92); such features confirm the primary origin and early lithification of the micrites.

The initiation of deep-water mud-mound growth remains a mystery, but some have suggested that reduced sedimentation rates may favor the growth of microbial communities, as mounds seem to form preferentially during transgressions and high sea-level stands (10). Cold, nutrient-rich waters may also have favored inorganic cement precipitation and the growth of microbial communities and suspension-feeding metazoans; indeed, some early Carboniferous mud-mound development coincides with areas influenced by oceanic upwelling (101). The intermound and basin strata of Muleshoe, as well as other build-ups in the Lake Valley area and in other Lower Carboniferous mound complexes in Alberta and Montana, are dominated by dysaerobic and anaerobic strata alternating with thin oxygenated horizons. This inferred ocean stratification, which suggests a tendency to ocean anoxia during the Tournasian, may also be related to the ecology or diagenesis of mound growth (46).

THE ORIGINS OF THE MODERN CORAL REEF ECOSYSTEM

This section explores the evolutionary origin of two major ecological aspects of modern coral reefs: photosymbiosis and predation.

The Appearance of Photosymbiosis: Invasion of New Habitats?

Symbiosis can be better understood as an evolutionary innovation to acquire access to novel metabolic capabilities rather than by means of the more traditionally cited notion of mutual benefit (28). Microbial symbionts often possess a capability lacking in their host, and access to a new capability can enable the host to exploit a new food resource or invade a previously inhospitable environment.

Contrary to the widely accepted belief that corals harbor only symbionts of one type, recent work on many Caribbean and Indo-Pacific corals has shown that colonies growing at different depths can contain more than one type of zooxanthella (2, 76, 77). This suggests that symbionts exist as complex communities that can track gradients in environmental radiance within a colony. Although bleaching is a poorly understood response to environmental stress, it has also been suggested that it may be an adaptive strategy that allows corals to recombine with a different algal type (13). That recombination with different algal types can occur is supported by the observation that symbiont polymorphism can explain both the depth distribution of bleaching (which predominates at intermediate depths) and within-colony patterns, as a symbiont type associated with low irradiance is preferentially eliminated from the brightest parts of its distribution, presumably due to reaching some limit of physiological tolerance (77). This is clear evidence that the patterns of symbiont distribution are highly dynamic. Although host-symbiont partnerings may be specific at any one time, if recombination with a different type is possible, then specificity may alter as environmental conditions change (13).

We are only just beginning to appreciate the complexity of many symbiotic relationships. Future development of molecular taxonomic methods will certainly revolutionize our understanding of specificity, such as the extent of intracolony and intraspecific geographic variability within different taxa and the way this might be determined by local symbiont availability. Biogeographic constraints on symbiont diversity may have profound evolutionary implications. But the apparent fragility of photosymbiotic relationship also holds the key to its success: The dynamic nature of symbiotic combinations in corals may well have allowed them to persist through hundreds of millions of years of rapid, and sometimes extreme, environmental change (12).

Were Ancient Reef Communities Photosymbiotic?

The clear correlation between photosymbiosis and the success of living scleractinian corals in reef construction has led to the widespread supposition that the ability of metazoans to build reefs is contingent upon possession of photosymbionts. Many (e.g. 24, 25, 86) have argued, therefore, that extinct groups of reef-building metazoans also possessed this metabolic capability. In addition,

the widespread loss and subsequent slow re-establishment of photosymbiotic relationships have been implicated in the long recovery time (up to 10 myr) of reef communities after mass extinction events (e.g. 29, 84). Such assumptions have not, however, been rigorously tested.

Inference of ancient photosymbiosis is highly problematic on morphological grounds alone (95). Such reasoning relies heavily upon modern analogies, but, not only are none available for several important extinct groups of reef-associated metazoans, such uniformitarian reasoning may be invalid. Collection of valid isotopic data is only possible where unaltered skeletal material is available, and such material is limited (84).

Contrary to received opinion, current evidence suggests that photosymbiotic metazoans have not always been present in reef communities. Indeed, with the probable exception of fusulinid foraminifera (Carboniferous-Permian) and alatoconchid bivalves (Permian), there are no clear data to support the presence of photosymbiotic reef-associated faunas before the Triassic (96, 97). A photosymbiotic isotopic signal has been detected in latest Triassic scleractinian corals (84): older material has not been analyzed. Based on morphological criteria, a few, nonaggregating rudists were probably photosymbiotic, but the evidence for Paleozoic tabulate corals and stromatoporoids is equivocal (20). That photosymbiosis was present in other extinct reef-building groups is, at best, unconfirmed: It is not necessary to conclude that, by virtue of their reef-building abilities, all major Phanerozoic reef-building groups possessed symbionts.

Photosymbiosis has not been a necessary prerequisite for reef-building in the past, nor did its appearance notably increase carbonate platform accumulation rates (8). Moreover, the loss of photosymbioses cannot alone account for periods in Earth's history when there was no widespread reef building, nor does its inferred presence correlate with phases of abundant reef distribution. As branching, phaceloid growth forms in Upper Triassic scleractinian corals show apparent zooxanthellate isotopic signatures (84), inferences derived from analysis of typical growth morphology in living zooxanthellate corals would appear to be a poor predictor of zooxanthellate status in ancient representatives. The need for more comparative growth rate and isotopic data within and between fossil assemblages is critical.

The evolutionary appearance and diversification of symbioses may be determined by the availability of an appropriate symbiont, together with the selection pressure to acquire the metabolic capability of that symbiont. It is highly likely that dinoflagellate symbionts—particularly the *Symbiodinium* group that is so successful at overcoming the defense systems of a host—did not evolve until the Triassic (59). Once freely available, however, such potential symbionts might infect many unrelated organisms that are in some way preadapted to acquire

photosymbiosis. Before the Triassic, groups were presumably symbiotic with either chlorophytes, rhodophytes, or cyanophytes. Such symbioses would not necessarily have conferred adaptation to clear, well-lit, and low nutrient environments characteristic of the many modern reef-associated hosts symbiotic with dinoflagellates and diatoms (95).

The Rise of Predation and Bioerosion

Although there is no evidence that routine physical processes have changed significantly over the Phanerozoic, considerable data now suggest that biologically induced disturbance has increased dramatically in shallow marine seas, especially since the Mesozoic. The Mesozoic Marine Revolution (MMR; 91) involved the origin and diversification of many groups of bioturbators, predators, and bioeroders. The differential effects of the MMR are extremely difficult to isolate, as many organisms cause disturbance in more than one way: Some predators are also bioturbators; others are capable of significant bioerosion. The MMR thus involved coincident developments that might be predicted to have had many common evolutionary consequences (87).

Grazers and carnivores throughout the Paleozoic and early Mesozoic were relatively small individuals with limited foraging ranges (91, 91a). They were incapable of excavating calcareous substrates (83). By the early Mesozoic, sessile organisms had to contend with an increasing battery of novel feeding methods as well as sediment disruption due to deep bioturbating activity (87). Biological disturbance reached new heights of intensity from the Cretaceous to early Tertiary with the appearance of deep-grazing limpets, sea urchins with camerodont lanterns (Cretaceous), and especially the highly mobile reef fishes (Eocene); with them came the ability to excavate substantially large areas of hard substrata. A concurrent radiation of endoliths began in the Triassic; deep borings are known only from the mid-Mesozoic and Cenozoic (91). The first live-borers are described from the Eocene (51), and by the Oligo-Miocene, reef bioerosion had gained a modern cast (66) (Figure 4). How did post-Paleozoic reef communities respond to these new threats?

The importance of herbivory and predation in regulating modern reef community structure suggests that profound changes must have occurred with the appearance of these new consumer groups. Tropical marine hard substrata are usually sparsely vegetated, but a richer filamentous and macroalgal flora develops when herbivores are excluded and/or nutrient input increases (6, 37, 40, 55, 83). The presence of abundant coralline algae and corals in a reef community is therefore indicative of moderate or intense, and often specialist, herbivory. In waters < 20 m deep, corals and coralline algae may cover in excess of 80% of the substratum (17). In addition, grazers also contribute notably to carbonate sediment production and redistribution (79), to algal ridge formation (1),

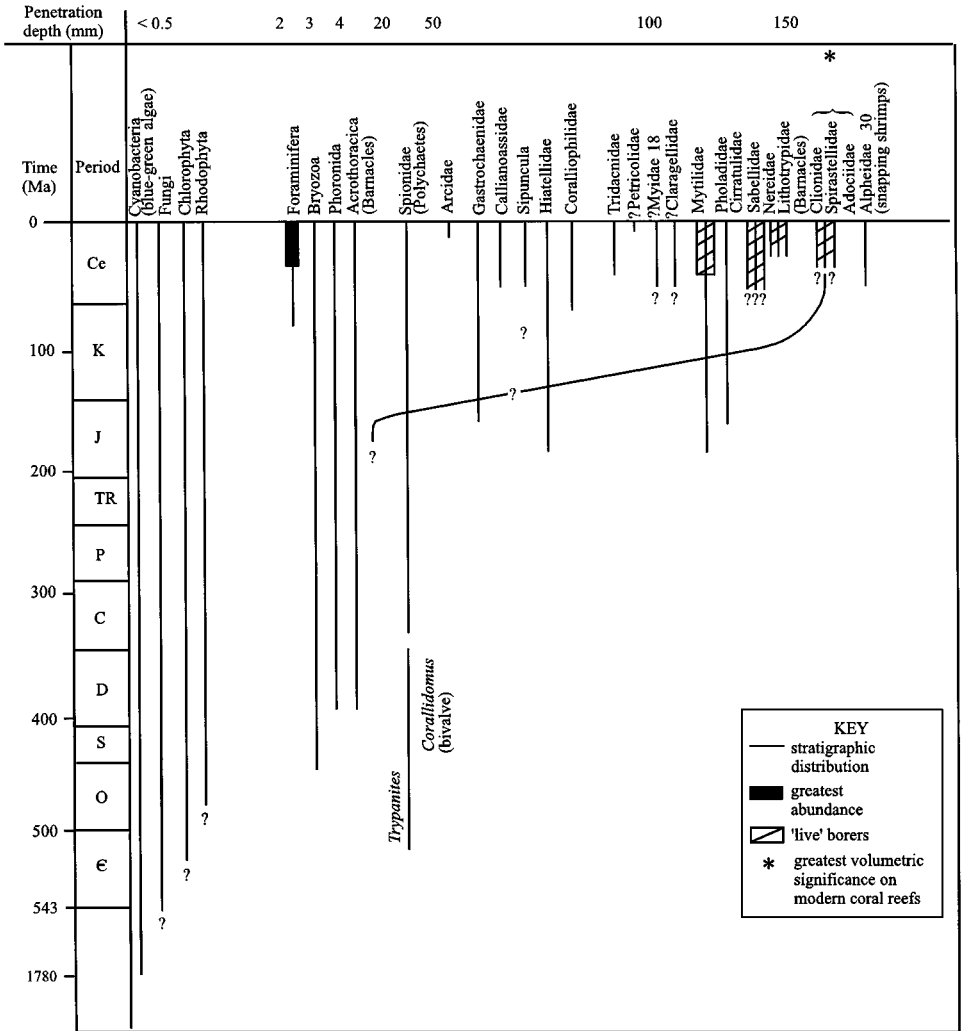


Figure 4 The rise of endolith groups arranged in order of increasing penetration depth (Data modified from 91a, from 97).

and to amelioration of the effects of competition for the maintenance of high diversity; they interact with physical controls to produce the characteristic zonation of modern coral reefs (94).

Many coral reef organisms show a vast array of supposed antipredation mechanisms, but details of their evolutionary origin and development are poorly known: The fossil record is silent on defenses concerning behavior and physiology. Sessile organisms have a relatively restricted range of antipredatory options at their disposal as they must be based upon passive constructional defences; they are also vulnerable to predators that do not rely upon prey manipulation for successful predation. Moreover, susceptibility to partial mortality and reliance upon herbivory to remove competitors or foulers usually entails loss of the prey's own tissues. This means that particular anatomies are required that allow resumption of normal growth as quickly as possible. One might predict, therefore, that the rise of excavatory herbivory would select for organisms with structural or chemical defenses and the ability to recover from partial mortality by rapid regeneration of damaged tissue.

Demonstration that habits have been acquired polyphyletically over a very short space of geological time is compelling evidence for the operation of an extrinsic selective force (80). Many of the characteristics of modern reef-building corals have antipredatory characteristics, including rapid regeneration from partial mortality (42). These traits have been present in the Scleractinia from the early origins of the group but proliferated as they subsequently proved useful for withstanding partial predation (95–97). Particularly dramatic is the spectacular rise of multiserial, branching forms in the late Cretaceous (Tithonian) coincident with the appearance of new groups of predatory excavators (Figure 5a). Such forms are easily broken as a result of both high wave activity and bioerosion, especially by boring sponges that infest the colony bases. However, branching corals are able to reanchor fragments and rapidly regenerate and grow, often fusing with other colonies, at rates up to 120 mm yr⁻¹ (90). Branching corals appear to have turned adversity into considerable advantage, and appear to flourish because, and not in spite of, breakage. Taxa such as *Acropora*, *Porites*, and *Pocillopora* appeared during the Eocene, coinciding with the radiation of reef fish and with a major expansion and reorganization of the coral reef ecosystem.

Coralline algae are able to withstand the most intense herbivore onslaught by virtue of distinct morphological structures that have been shown experimentally to serve an antipredation function, including a heavily calcified thallus that is resistant to attack, intercellular conduits (fusion cells and secondary pits) for translocating photosynthates, and armored reproductive structures (conceptacles) (83). These anatomical features were present in the oldest abundant

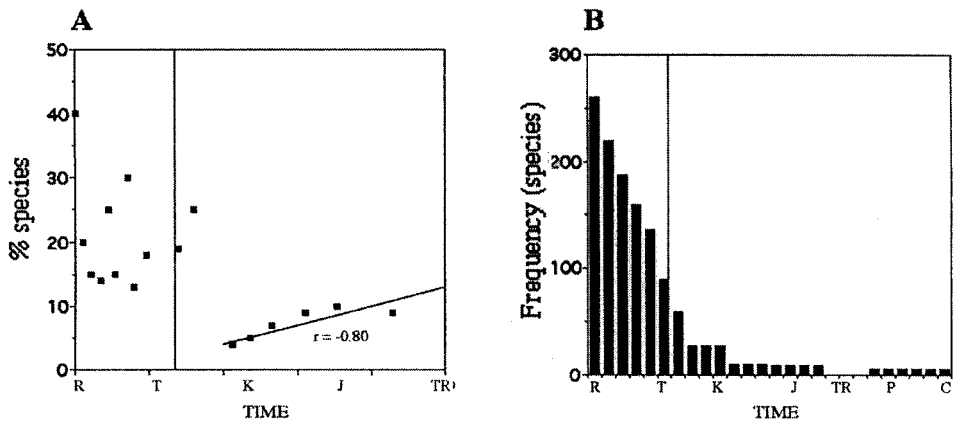


Figure 5 The rise of the modern coral reef biota. (a) Percent erect species of scleractinian corals. (replotted from 43a, data from sources in 19). (b) Species diversity of coralline algae (data from 83). C, Carboniferous; P, Permian; TR, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary; R, Recent.

coralline algae, *Archaeolithophyllum*, known from the late Carboniferous, which formed a thin, leafy ("phylloid") crust (100).

The temporal distribution of reef-associated algae through the Phanerozoic broadly follows a trend of increasing ability to withstand disturbance. Poorly defended calcified microalgae declined at the end of the Paleozoic. Many Paleozoic reef-associated algae (including algal mats) were free-lying forms that were able to cover soft-substrates, whereas most post-Paleozoic reef floras encrusted hard substrates. Solenopores (red algae with raised conceptacles and an undifferentiated thallus) sharply declined in the late Mesozoic/early Cenozoic with the onset of excavatory grazing, and this was coincident with a reciprocal rise in the abundance and diversity of coralline algae (83). Delicately branched corallines reduced in importance in the tropics after the Eocene (44), when thick crusts became more abundant (83), and the first algal ridges are known from the Eocene-Miocene—both coincident with the evolution of excavatory herbivorous fish. Escalating herbivory is also conjectured to have resulted in the progressive disappearance of fleshy macroalgae from shallow marine environments through the Mesozoic (83).

The well-developed hypothallus of corallines initially allowed rapid lateral growth required for life on an unstable substratum. The hypothallus, together with the presence of fusion cells, also allowed the corallines to encrust, acquire branching morphologies, produce conceptacles, and regenerate from deep wounds—features that probably enabled corallines to radiate as herbivory

intensified through the mid to late Mesozoic and Cenozoic. More than 100 myr elapsed between the first appearance of coralline algae and the subsequent radiation of the group (Figure 5*b*), strongly suggesting that these distinctive features of coralline algae are all exaptations (traits whose benefits are secondary or incidental to the primary function to which they are adapted). One exception might be multilayered epithallial growth, which might be an adaptation that arose in response to intense grazing by particular species of limpets in the Pleistocene (44).

The late Paleozoic decline of immobile epifauna also coincides with the rise of major bulldozing taxa, which had passed through the end-Permian extinction unscathed (87). Although the hypothesis that the loss of unattached epifauna was caused by increased bioturbation remains untested, the fact that the modern deep seas appear to suffer the same degree of bioturbation as early Paleozoic shelves, and indeed harbor an immobile soft-substrate fauna of shallow marine Paleozoic caste, is supportive of it. Stalked crinoids, articulate brachiopods, hexactinellid sponges, and free-living immobile bryozoans are all concentrated, often in considerable abundance, in the deep sea. It has long been suggested (55*a*, 79*a*) that archaic Cambrian and Paleozoic faunas migrated to deep-sea environments from shallow shelves. But alternatively, the migration from near shore to deeper waters might equally reflect competitive displacement.

Of these surveyed trends in bryozoan morphology, encrusting morphologies, forms with continuous budding of new modules (zooidal and frontal), rapid growth, and good powers of regeneration have all markedly increased since the Mesozoic, especially from the late Cretaceous-Eocene. In contrast, the incidence of erect growth in relatively small and fragile bryozoans plummeted in the Mesozoic (see summaries in 56). These trends also coincide with the rise of biological disturbance.

DISCUSSION

This review has highlighted some recent advances in our understanding of the ecological evolution of reefs and has considered this evolution as a history of the changing way in which reef organisms have successfully occupied space. To understand the record of reef-building, it is clear that we must consider not only the influence of extrinsic factors in the control of *in situ* carbonate production, but also how the biological environment has changed. Such integrative studies are in their infancy, but data are now becoming available that are enabling researchers to document evolutionary processes at a level capable of generating testable hypotheses.

ACKNOWLEDGMENTS

The continued support of the Royal Society is most appreciated. The paleoecological reconstructions were drawn by John Sibbick and Figure 4 was drafted by Hilary Alberti. Earth Sciences Publication No. 5232.

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