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An Outline History of Tropical Organic Reefs¹

BY NORMAN D. NEWELL²

ABSTRACT

Organic reefs, especially shallow-water coral reefs of warm seas, are built by stable communities of organisms in a narrow adaptive zone of low stress. They have an extraordinarily good fossil record that may be applied to broad problems of evolution of the tropical marine biota and ancillary questions about past climates and changing distributions of land and sea over more than one-half billion years of earth history. This essay is an attempt at a synopsis through the eyes of a paleobiologist of some of the exciting episodes in the history of the world's oceans and their organisms. The reef community is well suited for a leading role in this history.

THE REEF ECOSYSTEM

Living tropical coral-algal reefs and rain forests epitomize segregated, highly independent communities and distinctive ecosystems. Intricately organized and immensely diverse, they evoke an image of exceptional fertility and exuberant biomass. This aspect results, however, not so much from high productivity as from relative environmental uniformity, freedom

¹ I am indebted to John W. Wells, Cornell University, for sharing with me some of his great knowledge of scleractinian systematics. Several of my colleagues at the American Museum of Natural History, as well as Robert S. Dietz, Atlantic Oceanographic and Meteorological Laboratories, Miami, and Ernst Mayr, Harvard University, have critically read and discussed with me many of the ideas here set forth. But, of course, they are not accountable for my shortcomings.

² Chairman and Curator, Department of Invertebrate Paleontology, the American Museum of Natural History.

from seasonal interruptions, and other sources of stress in life processes.

The environments of both ecosystems are so dominated by the inhabitants that, in a very real sense, they constitute habitats created and maintained by the organisms themselves. Here, the physical factors of environment are so buffered that the most evident selection relates to interspecific accommodations in space, nutrition and shelter, and ever increasing narrowness of adaptation.

In general, their microhabitats are created by the physical arrangements of the associated organisms and by their physiology and behavior (fig. 1). The correlated increase in taxonomic diversity through geologic time has resulted in proliferation of new adaptive opportunities and niches. Environmental resources of these communities are shared among the inhabitants with varying degrees of coadaptation and with little sign of reaching any ultimate limit in subdivision short of failure of some essential external condition of the environment, as has frequently occurred in the history of reefs.

The reef ecosystem with its plankton and many benthonic plants and plantlike animals shares many similarities with rain forests of the tropics. Both are phototropic and they have adopted the same method for controlling and filtering sunlight through a stratified canopy. Like man-built cities, the reefs are densely populated and commonly surrounded by contrasting, more sparsely inhabited areas. The specific diversity of a modern tropical coral reef probably exceeds by one order of magnitude the diversity of the most nearly comparable other marine community, the littoral and neritic rocky bottom biota. Judged from the fossil record, a similar disparity in diversity between the two probably has obtained since the middle Paleozoic.

To press a metaphor further, reef communities are outstandingly adapted to cope with problems of a city, such as crowding, ventilation, nutrition, and waste disposal. And, of all marine communities, reef organisms alone have the capability of building their rocky substrate laterally and upward in opposition to the processes of attrition. They create and maintain favorable substrate, food, and shelter by a kind of community homeostasis. Their organisms are superlatively coadapted.

Because of insufficient observations and experimentation, much about living coral reefs remains poorly understood. Even today, after much work, there is uncertainty about the energy avenues and ultimate sources and amounts of inorganic nutrients needed by teeming coral atolls which characteristically are surrounded by comparatively sterile wastes of shallow tropical waters. The external contributions of plankton to the reef community are still to be measured (Yonge, 1963, p. 254).

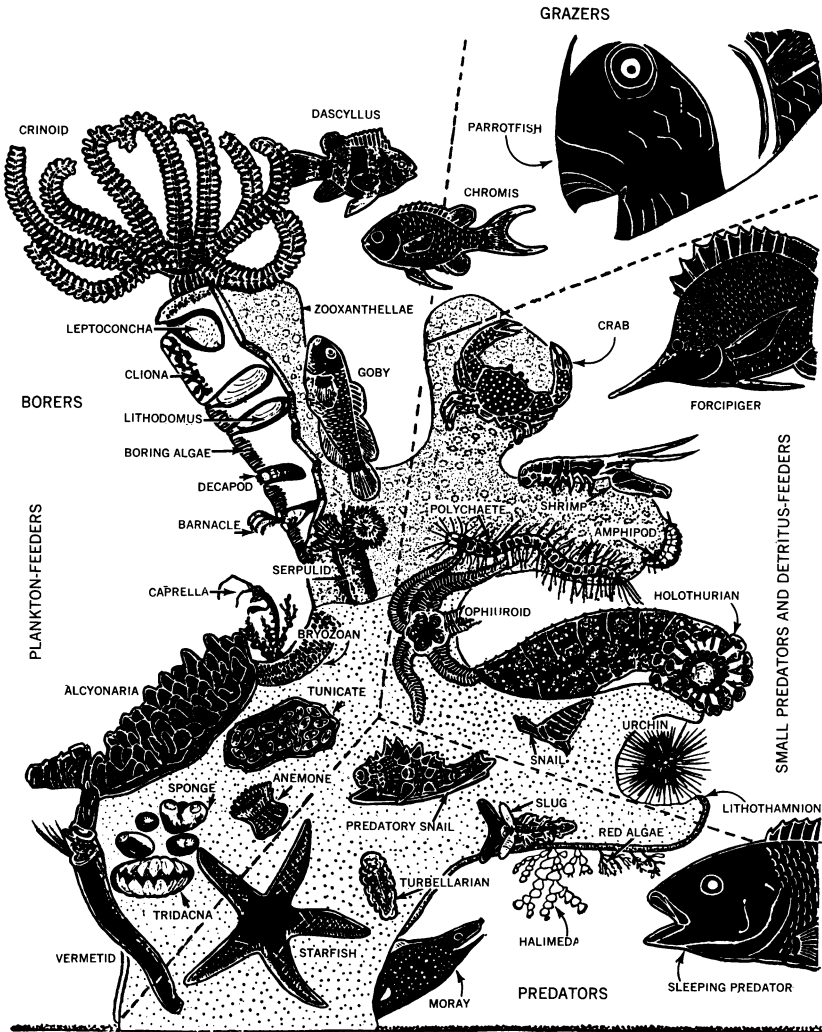


FIG. 1. Some of the varied constituents of the coral reef community. Stippled area with rosettes, living corals and zooxanthellae. Stippled area without rosettes, dead corals and perforating blue-green algae (data from Gerlach, 1960).

As with the tropical rain forest, most of the nutrition of a reef community probably is stored in living protoplasm of the standing crop. Income and losses are small and therefore difficult to assess. One external increment of nutrients is the guano of roving sea birds that roost on sand cays and rocky

islets of coral reefs. Another is the dissolved salts in the runoff from neighboring land masses and their terrestrial vegetation.

The distribution of coral reefs with respect to islands is of interest in this connection. The most flourishing reefs commonly lie near, but not too near, the most extensive lands. On the other hand, wholly submerged shallow banks farthest away from lands ordinarily are only sparsely or not at all colonized by living reefs. Some of the so-called drowned atolls of the Pacific apparently have been abandoned by the reef community. Although a number of these lie well within the euphotic zone and are in proximity to actively growing atoll reefs, they tend to be poor in reef builders.

Mogami Bank and a dozen or so drowned atolls west of Namonuito, in the eastern Caroline Islands (Shepard, 1970), and Alexa Bank (Fairbridge and Stewart, 1960) northwest of Fiji, are examples of such shallow, atoll-shaped banks without active coral reefs. All are alike in being devoid of supra-tidal lands and nitrogen-fixing land vegetation. It is, of course, possible that their reefs have been killed by biological causes, for example, by an irruption of a predator such as *Acanthaster planci*, or a nonselective parasite. But they may also be starved for nutrients. In any case, the shallower examples can hardly have been drowned by rapid submergence.

The most conspicuous, but not necessarily the most important, organisms of the reef community are animals, not plants, and the most evident animals, the corals, are microphagous carnivores. This fact is noteworthy when the reef community is compared with most terrestrial communities in which the visible herbivores vastly outnumber the carnivores. Undoubtedly, the zooxanthellae and the benthic algae are primary producers but the exact role of phytoplankton in the economy of coral reefs remains uncertain.

The food web of the reef ecosystem has been assessed in an admirable preliminary study by Hiatt and Strasburg (1960). But this survey was directed primarily to the fishes. These investigators recognized five successive trophic levels ranging from the algal primary producers to small and large herbivores, algal and detritus feeders, omnivores, and successive grades of carnivores. Their interpretation of the food web, with fourteen major feeding categories is a useful qualitative analysis of the industry of some of the reef organisms.

THE CONTRIBUTION OF GEOLOGY

The reef community, with its multitude of species and microhabitats, clearly is remarkably efficient in exploitation of space and conservation of energy. Intuitively, one might suppose that a well-integrated reef biocoenose must be the product of a very long evolutionary history of accom-

modation and niche subdivision. The fossil record abundantly confirms such an estimate.

The ecosystem of organic reefs is certainly the oldest for which there is a preserved record. Remains of reef assemblages scattered through geologic time provide evidence of increasing diversity since the early Paleozoic, very long before modern reef organisms appeared on the scene. These records tell much about oscillations in physical environments through geologic time, on a local and worldwide scale.

Throughout reef history, the leading role, in fact a dual role, has been played by the algae. They have been the primary producers and certainly were always important limestone reef builders. First the blue-green filamentous forms appeared; later they were joined by green and red algae and at some unrecorded date by those remarkable symbionts, the zooxanthellae, essential partners in any hermatypic union. Phytoplankton are conspicuously lacking from fossil reef deposits.

After the organization of the oldest animal reefs in the early Paleozoic, the stony coelenterates and calcareous sponges commonly were more conspicuous than the algae, but the corals, possibly deriving benefits by diffusion from the zooxanthellae, nonetheless are obligate carnivores high in the food web of the ecosystem (Yonge, 1963).

Massive contributions to the reef limestones also have been supplied by diverse encrusting and interstitial bryozoans, foraminifera, brachiopods, echinoderms, and molluscs, all of which, by the accumulation of their skeletons, have added greatly to the bulk of calcareous deposits in and around the reefs.

Hundreds of pages have been written about classification of reefs based mainly on their physical form and inner rock fabric (Stoddart, 1969). However, much of the resulting terminology, based on mature living reefs, has little meaning in the over-all understanding of their genesis. In the total life history of an individual reef it is certain that a reef community is prerequisite to the reef structure, and an upward growing reef may originate in sheltered waters many meters below the surface of the sea. So, the ecology of a reef must change with reef growth. These changes are reflected in chronological and ecological successions of genera and species.

Geologists have been preoccupied with the problem of distinguishing and analyzing long-past reef environments in the records of ancient marine sedimentary rocks. In spite of repeated and meticulous descriptions of living reefs based on surface observations and borings into reef limestones, a persistent misconception remains that organic reefs are mainly composed of a wave-resistant framework of rigidly cemented *in situ* skeletons of corals and algae (Achauer, 1969; Dunham, 1970).

Many reefs living today are structural complexes more than nine-tenths of which are composed of detrital sand bound together by cemented and anchored organisms and quickly converted without exposure to air, I believe, to friable limestone by biochemical and physical processes. In fossil reefs contemporaneous lithification is indicated by the abundance of reef talus of angular fragments composed of cemented grains, and by fossil epibiota of hard bottoms unlike the burrowing faunas of sand banks. Thus, the distinction is paleoecological rather than lithologic and an organic reef is best considered a complex of many kinds of rocks and sediments generated by a reef community of organisms. It is not limited to the rigid frame of *in situ* skeletons.

Not all reef organisms add significantly to the reef structure. Many are neutral inhabitants, or even reef destroyers. Characteristically, many polychaetes, most of the arthropods, and nearly all the fishes of the reefs are without any fossil record because their skeletal remains are systematically destroyed by scavengers that abound in this strongly oxidizing environment. Consequently, the history of coral reef crabs and fishes and some other groups must be inferred from the evidence provided by other preserved groups and the circumstantial evidence of inferred relationships. For the most part, the arthropods and fishes probably have always stood in relation to the reefs much as do the birds of the tropical forest, lords and tenants with but subordinate roles in the history and destiny of the whole community of which they form a small part.

Throughout geologic history, many sessile reef-dwelling invertebrates and plants have been characterized by (a) the ability to grow upward rapidly under stress of crowded conditions so that they maintain an artificial surface in agitated waters above the floor of accumulating sediments, and (b) by their high rates of calcium metabolism. These functions certainly have been aided by symbiotic zooxanthellae (Yonge, 1963), and the essential presence of the zooxanthellae may be inferred when these conditions are demonstrable in the fossil record.

One characteristic aspect of reef building has been the production of bottom prominences of open-textured and cavernous limestone with great potentialities for production of varied microhabitats. This open-textured substrate is multitiered and stratified in the ecologic and geologic sense. It shelters and supports an astonishing variety of cryptic borers and cave dwellers representing nearly every animal phylum, and many kinds of algae, most of which exist very well at quite low levels of illumination.

The work of making taxonomic and ecologic inventory of coral reefs has only been started, and many of the most obvious questions of environmental dynamics of living and fossil reefs still are matters for speculation.

Consequently, we can take only the broadest view of trends in community succession. Certainly, the communities responsible for living reefs as we now find them, represent the latest stage in an evolutionary history. They are of comparatively late origin, from a geological point of view.

In summary, through their life activities organic reef communities have created the most complex and one of the oldest habitats in the sea. But the history of these communities is not simply a quiet and gradual proliferation of lineages passively living together within this habitat. Rather, their history involves dramatic and disconnected episodes, repeated radiations, stagnation, replacement of dominant groups by ecologically similar but unrelated groups, selective extinction, and even worldwide obliteration of entire communities, leaving ecological vacuums for millions of years. Present distributions are rarely reliable indications of past distributions. Surely, these events faithfully reflect significant environmental vicissitudes on a vast scale, especially climatic and diastrophic changes among which sea-floor spreading and continental drift are assuming ever more emphasis among students of earth history.

The following remarks summarize some highlights of this story. Details must await further geological and paleontological research.

EARLY FOSSIL REEFS

When, where, and how did the earliest reef communities arise? These questions, of course, cannot be answered directly, but geology and paleontology provide many clues.

Limestone accumulations of algal stromatolites flanked by fragmental reef debris are known over the world in Precambrian rocks two billion years or more old, (see, for example, Knight, 1968). By analogy with modern stromatolites (Ginsburg, 1967), it may be supposed that those ancient deposits were built by filamentous blue-green algae. But there are no traces of associated animals in the Precambrian reefs. Indeed, it is quite probable that animals were not yet in existence when the earliest reefs were formed (Cloud, 1968).

We may surmise that natural selection was already working on a basic problem of benthic marine organisms, that is, most effective utilization of substrates in areas that supplied other requisites for habitation. Individual algal colonies of some Precambrian reefs grew upward several feet by entrapping calcium carbonate grains or by precipitation of calcium carbonate to form hemispherical masses and trunklike columns of limestone that rose above the sediment floor.

Organic mounds, "bioherms," of Cambrian age show little advance-

ment. Some were built by stromatolites. In others, stromatolites were joined by stony spongelike organisms, the extinct archaeocyathids (Okulitch, 1955) assembled in low thickets or meadows. Doubtless, unfilled spaces within and between the animal colonies provided shelter for trilobites and naked invertebrates without aptitude for preservation. By the close of the Middle Cambrian, the archaeocyathids had vanished and widespread limestone seas of the Upper Cambrian and Lower Ordovician (Canadian) were left for an extended time without comparable animal reef builders. Only small bioherms or reef mounds of algal stromatolites date from this time.

In mid-Ordovician (Chazyan) time a complex algae-invertebrate reef community appeared in North America (Pitcher, 1964, 1971) and the adaptive zone vacated by the archaeocyathids came to be occupied by coralline red algae (*Solenopora*), stony bryozoans, stromatoporoid sponges, and tabulate and rugose corals (Hill, 1956). These constructed the oldest known "coral reef" community, progenitor of an algal-coral association which evolved and proliferated through a long chronological succession spanning 130 million years, until unidentified environmental changes wiped out the reef community near the close of the Devonian Period (Frasnian-Famennian interval) in a worldwide episode (McLaren, 1970; Jamieson, 1971). This was followed by a well-defined interval (beginning in the Famennian and continuing into the earliest Lower Carboniferous) of impoverishment of the reef community throughout the world marking, no doubt, an environmental event that eliminated the middle Paleozoic reef community.

Many of the middle Paleozoic reefs grew in shallow agitated waters, as indicated by sedimentary and paleontologic contexts (Lowenstam, 1957; Playford and Lowry, 1966), encouraging speculation that some of the reef builders of those times enjoyed symbiotic union with zooxanthellae.

The late Paleozoic (Mississippian, Pennsylvanian, and Permian periods) was characterized by scattered shelf-edge organic sand banks and reef complexes stabilized and consolidated by stromatolites, cemented and anchored brachiopods, bryozoans, sphinctozoan (chambered calcareous) sponges, red and green algae (solenoporoids, dasycladaceans, and codiaceans) with local contributions of great quantities of scree and debris from echinoderms, brachiopods, foraminifera, and molluscs of a highly organized community that bore little resemblance to mid-Paleozoic reef builders. Through middle and late Paleozoic times reef commensals, such as brachiopods and crinoids, became increasingly varied in taxonomic diversity and, in limited parts of the geologic column (e.g., Cooper, 1946; Grant, 1971), attaining hundreds or even thousands of species.

During the Permian Period, a pantropical seaway, Tethys, extended nearly around the globe (fig. 4). Because of the extraordinary diversity of invertebrate faunas in Tethyan Permian deposits it may be supposed that this seaway was a low latitude circumtropical belt distinguished from temperate to cold waters of higher latitudes (Newell et al., 1953), a conclusion subscribed to by Stehli (1957).

The tropical marine Permian faunas of the Americas represent the extreme eastern outpost of the marine tropics of the time. The preserved Permian to Miocene deposits of Tethys now are mainly limited to the great orogenic belt that extends from the Mediterranean region on the west, across the Middle East, south Asia, and Indonesia, to Japan in the east.

In any case, when the scleractinian corals first appeared in Middle Triassic rocks of western Tethys in south Europe and the Mediterranean region, they were moving into an important ecological zone that had been unoccupied or only sparsely inhabited by coelenterates since the catastrophic decline of the tabulate corals and stromatoporoid sponges in the middle Paleozoic. The superficially similar rugose corals of the Paleozoic in most cases favored quiet, frequently turbid, waters. Generally, they were not primary reef builders although they formed thickets in some cases.

The first scleractinian corals, progenitors of the modern reef community, appear in Middle Triassic rocks (Anisian-Muschelkalk) of Germany, the southern Alps, Corsica and Sicily, where they are represented by scattered reef patches containing six distinct families. Gradually, these six families evolved in well-documented stratigraphic sequences over the world into a score or more of still living families and a dozen extinct families (fig. 2) that span Mesozoic and Cenozoic history (Wells, 1956).

By Late Triassic time the scleractinians played an important, but still subordinate, role in reef building. Especially in the southern Alps there are magnificent displays of Late Triassic reefs in which sphinctozoan sponges, bryozoa, and algae played leading roles. Although Triassic coral colonies generally are quite small as compared with living hermatypic corals, some alpine examples of the genus *Thecosmilia* exceed one meter across (A. G. Fischer, personal commun.).

The known latitudinal range of Upper Triassic reefs is different from that of modern reefs, from latitude 60° N. to 10° S. (fig. 3), suggesting that geographic conditions may have been unlike those of today (fig. 3).

Southern Europe and lands marginal to the Mediterranean contain the best records of Jurassic and Cretaceous coral reefs. In this region of western Tethys the reef community underwent continued diversification from mid-Jurassic time until the close of the Cretaceous (fig. 2). Besides

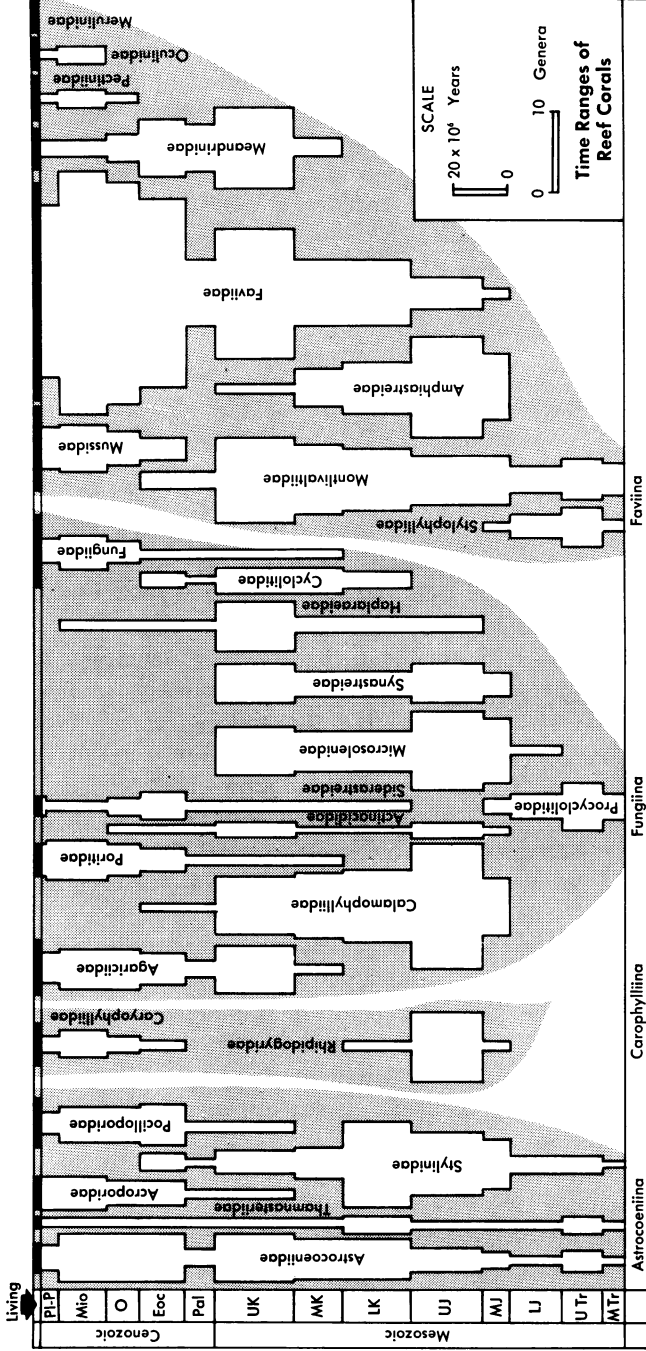


Fig. 2. Fluctuations in diversity of reef (hermatypic) corals through geologic time. Note marked retrenchment in the Paleocene (data from Wells, 1956).

being one of the richest known coral assemblages of all time (in generic diversity), the community consisted of lithothamnian algae (Wray, 1971), organisms very like stromatoporoids (LeCompte, 1956), sphinctozoans (Rigby, 1971), and a very diverse assemblage of molluscs, echinoderms, and other commensals.

Little or no reef development is known anywhere in earliest Cretaceous rocks, reflecting, no doubt, one of many epochs of unfavorable world conditions. But a worldwide epoch of reef building began a little later

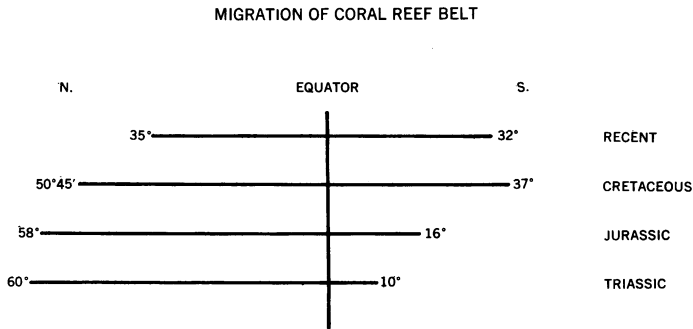


FIG. 3. Latitudinal range and displacement of coral reefs through time, possibly an effect of northward drift of fossiliferous deposits (data from Wells, 1956).

(Urgonian episode of the Barremian and Aptian), near the present tropical belt. Many new families of corals and other members of the reef community appeared in western Tethys and tropical America. Although these regions clearly lay within a circumtropical zone, regional differences are evident and the influence of the deep Atlantic, as a barrier to migration, was well established.

A previously obscure group of marine bivalve molluscs, the rudists (Coogan, Dechaseaux, and Perkins, 1969), underwent a remarkable evolutionary radiation during the Cretaceous Period and at times challenged the dominance of the corals among reef animals. The rudists successfully competed with, and even largely supplanted, the corals along the sheltered inner margins of fringing and barrier reefs, but the corals generally maintained dominance along the seaward margins of the reefs (B. F. Perkins, personal commun.). Many of the rudists developed tightly packed aggregates of cylindrical or conical cemented shells that grew upright in many cases simulating solitary corals. The rudist-coral reefs are limited to low latitudes and this distribution suggests that the northern limit of the tropical zone of Cretaceous times lay not far from the present

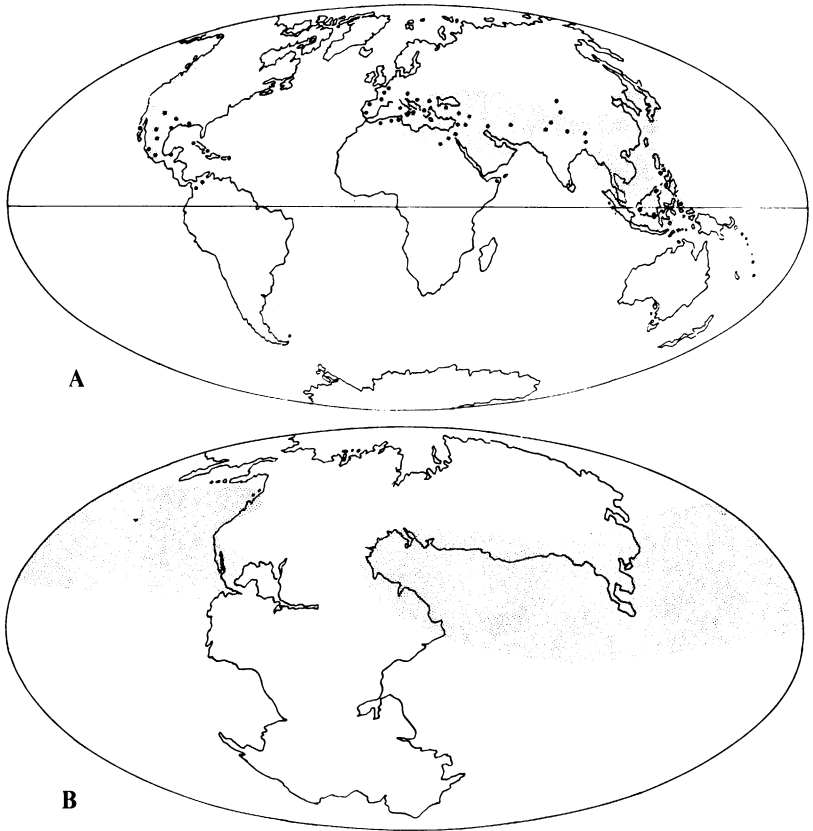


FIG. 4. A. Present distribution of fossil tropical faunas of Permian (stippled) and Cretaceous (circles) ages in the Tethyan orogenic belt. The former is based on distributional area of neoschwagerine fusulinids and richthofeniid brachiopods; the latter indicates most important localities of the rudist-scleractinian reefs (data from Dacqué, 1915; Joleaud, 1939; Stehli, 1957; and B. F. Perkins, personal commun.). B. Permian paleogeography showing an interpretation of Tethyan seaway (based in part on Wilson, 1963).

tropics (fig. 4). At the very close of the Cretaceous Period the rudists became extinct over the world, leaving no descendants, and this extinction was concurrent with disappearance of the dinosaurs and ammonites and with a sharp decline in diversity of reef corals and many other great groups of animals (fig. 5) of the time (Newell, 1966).

CORAL REEFS AND CONTINENTAL DRIFT

In the past few years converging lines of evidence from studies of paleomagnetism, stratigraphy, and paleontology have supplied increasingly compelling evidence that the southern continents and India were joined together in late Paleozoic times in a single great continent, Gondwana, and at least for part of this time (during the Carboniferous and Permian periods), this continent supported ice sheets presumably near the geographic south pole (fig. 4). The deep Atlantic Basin did not then exist and North America and Eurasia were joined by more or less continuous land. The complete lack of evidence of Triassic ice caps is an enigma which also involves the remarkably cosmopolitan distributions of terrestrial and marine biotas that display hardly any evidence of climatic zonation. Gondwana was ice-free by Triassic time, and for long thereafter the whole earth apparently was relatively ice-free.

The precise time, or times, of separation of the several continents is still under debate (Funnell and Smith, 1968) but the proto-Atlantic Basin as a broad oceanic barrier to faunal migrations is clearly discernible in the distribution of Atlantic marine strata of Cretaceous age and in the endemic character of many Caribbean fossils of this age (Hallam, 1967).

Evidence from paleontology generally is not in conflict with these interpretations. Permian and Mesozoic reefs and other tropical elements are mainly (but not wholly) limited to the orogenic regions that form a belt at low latitudes across southern Eurasia and America, roughly parallel with, but generally somewhat to the north of, the present tropics (fig. 4).

Before the Cenozoic, the southern continents generally lay at higher latitudes than their present locations and it is not surprising, therefore, that fossil hermatypic corals are lacking in the nuclear land masses of South America, Africa, Australia, India, and Antarctica. Shifting of the continents in response to sea-floor spreading clearly has involved a northward component. Africa and India moved across the ancient ocean floor (Tethys) against the southern flanks of Eurasia, crumpling, and displacing tropical deposits of mid-Cenozoic Tethys. Probably, it is because of this global tectonism that the marine tropical record of Permian to Miocene times occupies an east-west belt not much broader than, but well to the north of, the present tropics (figs. 3 and 4).

EARLY CENOZOIC (PALEOGENE) REEFS

Worldwide collapse and reordering of very many animal communities at the close of the Cretaceous Period plainly is written in the fossil record (Newell, 1966, 1967). The immediate causes of this biological revolution

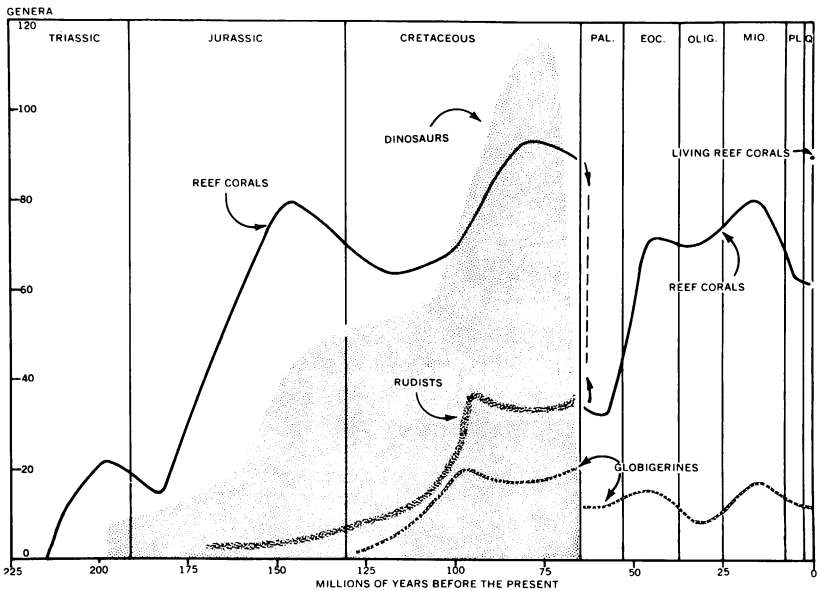


FIG. 5. Mesozoic-Cenozoic fluctuations in generic diversity of some important fossil groups as evidence of a post-Cretaceous faunal revolution. Shaded area represents dinosaurs. Late Cretaceous diversity peaks correspond closely with the time of maximum spread of epicontinental seas and maritime climates. Discrepancy between Pleistocene and Recent corals indicates insufficient collecting and provides some evidence bearing on reliability of evidence (data from Newell, 1966, and Treatise on Invertebrate Paleontology, R. C. Moore, ed.).

are uncertain but they probably stem from ecological dislocations that originated in sweeping geographical and climatic changes at the end of the Mesozoic. Some of these have been long known and substantially documented (Hallam, 1963).

The terrestrial vertebrates were greatly decreased as a result of the elimination of the dinosaurs, which were still dominant land animals until near the end of the last stage of the Cretaceous (fig. 5). Extinctions depleted many elements of the marine fauna. The rudists, diverse and abundant until near the close of the Maastrichtian Stage, became extinct in a remarkably short time, from a geological viewpoint. These various changes were concurrent (but may have proceeded at different rates) in the last part of the Cretaceous Period (Newell, 1966, 1967). Altogether, nearly one-third of the families of Upper Cretaceous animals failed to survive this episode of extinction. Although some of these groups started to

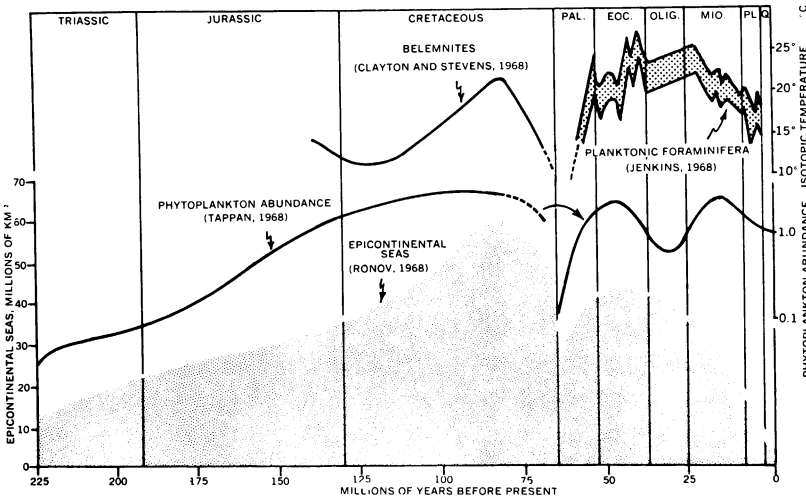


FIG. 6. Parallel trends in isotopic paleotemperatures (New Zealand), phytoplankton abundance (diversity), and areas (shaded portion) of epicontinental seas.

decline 10 or 15 million years before their extinction, others were diverse, cosmopolitan, and numerically abundant shortly before their disappearance. The Paleocene opened with an impoverished fauna composed of slightly modified survivors from much more diverse Cretaceous faunas.

The reef community participated in, and for at least 10 million years, did not recover from, this episode of world extinctions. Coral reefs are unknown in Paleocene rocks over most of the world. The hermatypic coral genera were survivors from the Cretaceous Period and not a single genus is known to have originated in the Paleocene.

Sweeping changes in planktonic foraminifera and a notable decline of phytoplankton at the end of the Cretaceous also underscore the universality of the factors responsible for this biological revolution (figs. 5, 6).

One probable cause of the biological crisis near the Cretaceous-Paleocene boundary may have been the onset of seasonal oscillations in temperature and rainfall to which the Cretaceous organisms were not adapted (Axelrod and Bailey, 1968). This was a time of drainage of epicontinental seas from the continents, caused, presumably, by ocean basin subsidence, a trend that continued through the Cenozoic (fig. 5).

A new radiation of hermatypic corals populated the tropical seas of the Eocene with genera unknown in older rocks and many of these have survived until today. But for unknown reasons Eocene reefs generally are sparse and poorly developed. Planktonic foraminifera likewise experienced

early Cenozoic radiations, one in the Paleocene, another in the Eocene (Cifelli, 1969), followed by sharp reduction of diversity in late Eocene and Oligocene times correlated with climatic oscillations (fig. 5).

Oligocene reduction also is evident in the hermatypic corals, molluscs, and phytoplankton over much of the world. This trend, together with supporting evidence of paleotemperature estimates from oxygen isotopes, has suggested an episode of cooling (figs. 6, 7), or at least greater seasonal range of temperatures at intermediate latitudes during the Oligocene (Fleming, 1967; Devereaux, 1968; Edwards, 1968; Gill, 1968; Hornibrook, 1968; Jenkins, 1968; Tappan, 1968; Addicott, 1969). However, the hermatypic corals and coralline algae locally built extensive fringing and patch reefs in the Gulf of Mexico, the Caribbean area, southern Europe, and southeast Asia (Wells, 1956). The Caribbean fauna of latest Oligocene age shows heightened isolation from Europe, probably an effect of the spreading of the Atlantic Basin.

GEOLOGIC BASIS OF CENOZOIC CLIMATIC TRENDS

The volcanic foundations of many Pacific coral atolls are known to be of Cretaceous and early Cenozoic age having subsided many hundreds and even thousands of meters since they lay exposed at seal level (Menard, 1964). The vast volumes of oceanic rocks involved in lateral transport probably are sufficient to account for subsidence over great areas of the ocean basins and withdrawal of marine waters from the continents during the past 60 or 70 million years. Such withdrawal is plainly recorded by coastal belts of marine rocks of Cenozoic age that girdle many of the continents.

Ronov (1968) has estimated from the present, and inferred, from original distributions of marine strata on the continents, that the land areas have progressively increased by about 65 per cent since the great inundation of the Cretaceous Period. At the Cretaceous maximum transgression the coverage of the earth by marine waters must have been around 90 per cent (fig. 6). The remarkable recession of the seas since the Cretaceous, and especially since the early Miocene (Tanner, 1968), has affected the later history of coral reefs in particular, and all life in general, by altering the areal extent of habitats and by influencing world climates. Stratigraphic geology provides many records of the former, and analysis of the fossil record supplies documentation of the latter.

Bottom waters of the present oceans are heavy because they are cold. In each ocean bottom water, cooled and aerated at the surface around Antarctica, spreads out meridionally and zonally along the bottom accord-

ing to bottom topography. Very little oceanic bottom water is of Arctic origin (Defant, 1961). This gravity circulation of ocean waters from Antarctica into the ocean basins of the world provides ventilation and lowers the mean temperatures of the oceans and overlying atmosphere (Kremp, 1964).

Emiliani (1966) has shown that oxygen isotope ratios of deep-sea benthonic foraminifera indicate a decline of around 12° C. since late Cretaceous time some 75 million years ago (fig. 7). From this we may deduce that contributions of very cold water from Antarctica are of fairly recent

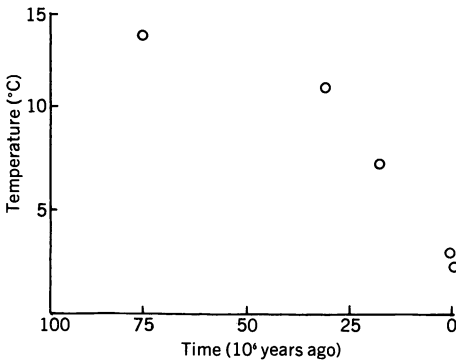


FIG. 7. Secular cooling of deep ocean waters, as indicated by oxygen isotope analyses of benthonic foraminifera (data from Emiliani, 1966).

date, geologically. Oxygen isotope determinations of fossil invertebrate skeletons, and faunal and floral analyses from many parts of the world (fig. 6) provide compelling indications of increasingly sharp climatic zonation and seasonality through the Cenozoic. More direct evidence bearing on the history of the Antarctic ice cap is coming to light in field work now in progress.

Tertiary floras from the Antarctic Peninsula indicate temperate climates through the Lower Miocene (Adie, 1964). Extensive glacial pavement and tillite below lava in the Jones Mountains of western Antarctica are dated by potassium-argon as also probably Miocene, presumably Late Miocene (Rutford, Craddock, and Bastien, 1968; Denton, Armstrong, and Stuiver, 1970).

Isotopic paleotemperatures and paleontologic data over the world converge to indicate a climatic amelioration during the early Miocene, followed by cooling in later Miocene concurrently with the establishment of the Antarctic ice sheet and complex glacial oscillations of Quaternary times (Dorf, 1957; Dawson, 1968; Tappan, 1968; Addicott, 1969; Bandy, Butler and Wright, 1969; Denton and Armstrong, 1969). Margolis and Kennett (1970) reported ice-rafted sands as old as Eocene and Oligocene