Aspects of Pacific Coral Reefs

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Introduction

Coral reefs are the only major earth features determined by the complexly integrated operation of both organic and inorganic processes. To the biologist a reef is a dynamic organic community of tropical seas dominated by corals. To the geologist it is a constructional feature of tropical seas conditioned by the marine environment. Exploitation of the tropical Pacific Ocean by man and other terrestrial organisms has been made possible by the two disparate actions: the life processes of reef-building (hermatypic) corals and the geological processes of vulcanism and diastrophism, the former being in turn deterministically conditioned on the development by the latter of substrates at least within 100 meters of the ocean surface. In the long view they are impermanent systems due to the queasiness of the crust beneath the ocean basin. The reefs appear, from what is yet known of the geologic history of the Pacific Basin, to be a late Mesozoic development dating back about 80,000,000 years.

Coral reefs and reef-defended or associated lands are scattered thinly over a vast area of the tropical Pacific within the north and south 20 degree isocrymes, an area of about 110,000,000 square kilometers. The actual area of these lands and embryo lands is but a very small fraction of this, and while most of the existing coral reefs are steadily growing, it is doubtful if the total land area determined by reefs and volcanoes has increased significantly in the last few million years when increase is balanced against decrease by diastrophic or isostatic subsidence and marine erosion. Many high islands have been maintained against these processes by defending reefs but others have subsided, and where reefs have not been well-developed, as in the Hawaiian Islands, simply wasted away.

Given a suitable substrate, the initiation and development of coral reefs are conditioned almost wholly by the temperature of the water and the maximum depth at which photosynthesis can effectively take place. At first glance this seems paradoxical, for reef corals, being animals, are not themselves photosynthetic. The development of geomorphically resistant reef structures is enabled by the presence in the tissues of hermatypic coral polyps of great numbers of photosynthetic unicellular algae, the zooxanthellae, that serve as a highly efficient waste disposal system and source of energy increasing calcification rate and making possible the growth of large, compact colonies, in contrast to the related ahermatypic or

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non-reef-building corals that lack zooxanthellae and are either solitary or loosely colonial in habit.

The Reef Coral Fauna of the Indo-Pacific Province

The Indo-Pacific coral fauna is rich in species and widely varied in genera. Practically all of the 25 extant families of scleractinian corals have hermatypic types, and many families are exclusively hermatypic, although the hermatypic adaptation is not the exclusive copyright of any group. There are some 85 genera of hermatypic corals on Indo-Pacific reefs, constituting a fauna that is remarkably uniform over the vast reach from the Red Sea to Panama. At least 1000 species have been named among these 85[1] (many of them no doubt invalid). Sixteen genera are known only from one or two specimens from single localities; 8 others have limited geographic distribution, leaving 60 genera that are widespread and relatively common. Over the Indo-Pacific the generic and species composition on a typical reef is monotonously uniform in similar marine climates. Less than 20 genera are found everywhere to the limits of this province: *Acropora, Cyphastrea, Favia, Favites, Fungia, Goniastrea, Leptastrea, Leptoseris, Montipora, Pavona, Platygyra, Plesiastrea, Pocillopora, Porites, Psammocora, Stylophora,* and *Turbinaria.* A few of these (*Pocillopora, Porites, Pavona, Plesiastrea, Montipora*) extend into the peripheral, distant subtropics. There are no genera that are not found in the central area of highest and least seasonally-varying temperatures.

In the Pacific reef tract, here taken as extending in the tropical zone from the East Indies eastward to the Pacific coast of the Americas, there are, if we exclude about 200 species as yet known only from the Red Sea-Indian Ocean, some 800 named species. Five of the most widespread genera account for at least 500 of these: *Acropora*—250, *Montipora*—100, *Porites*—50, *Turbinaria*—50, *Pocillopora*—25, *Fungia*—25. Of the remaining genera, 34 have only one species each. The number of species in an optimum reef environment, as at Palau, depends on how one discriminates "species", but it is certainly not less than 200.

Species diversity, like that of genera, diminishes by subtraction radially from the heart of the topical Indo-Pacific, from hundreds in the Marshall Islands to one or two tens in the subtropics: 53 genera and 240 species in the Marshalls, 10 genera and 20 species at Midway Island, 7 genera and 10 species in the Bay of Panama, 12 genera and 18 species in Moreton Bay, Queensland, and 3 genera and 5 species at Easter Island.

While certainly this decrease away from the central tropics reflects the winnowing effect of great distances of open ocean, it is also attributable in great part to diminishing surface temperatures. The distribution of genera on the Great Barrier Reefs system, including 450 species, exemplifies this: on a north-south line this system extends from about 10° S. Lat. to 27° S. Lat. (if one includes Moreton

[1] In these remarks three nonscleractinian stony corals important on tropical reefs are not included—the alcyonarians *Heliopora* and *Tubipora* and the hydrozoan *Millepora.*

Bay in the system), a distance of about 2500 kilometers, and from the 27° isocryme in the north to 17° in the south, with the surface water movement more northerly than southerly. The number of genera in the north is 59, declining slightly southward to the 20° isocryme (50 genera) at 20° S. Lat. and rapidly from there on: 25 genera at 24° S. Lat. and only 12 in Moreton Bay.

Here must be entered a *caveat* to the effect that the validity of any discussion of the numbers of species on Indo-Pacific reefs is seriously limited at present by two factors, 1) the species problem in corals in general, and 2) the incompleteness of reef exploration. The first has long been notoriously vexatious for no one knows the criteria of species limits among the living forms (which suggests utter confusion in fossil forms). This has been pointed up by the recent work of Goreau and his students in Jamaica on the reef corals of the Atlantic province, which is demonstrating that species are constrained not only by ecological but also by ethological parameters. Two apparently classically morphologically identical forms living side by side may be ethologically distinct, as in species of the genus *Scolymia*, a situation that suggests that the closely allied genus *Parascolymia* of the Pacific may prove to contain more than the one species now allowed. The second factor, incompleteness of exploration, is fairly obvious. In the Indo-Pacific our present knowledge of the reef coral populations is based almost wholly on the easily reached shallow water habitats. Only scattered handfuls of specimens have been recovered from depths of more than a few meters. The work of Catala in New Caledonia in depths of 30–40 meters has uncovered at least one new genus and indicated that species very uncommon in shallow water may be dominant at depth. Goreau has shown this to be strikingly so in Jamaica. There is thus a great deal to be done in the Pacific before we can talk very intelligently about the reef coral faunas, and hopefully the new techniques of submarine exploration will be more systematically used at selected sites.

Reef Coral Subprovinces?

The generic and specific uniformity of the coral fauna over the Indo-Pacific has already been pointed out, and it seems that over the world only two reef coral provinces are clearly recognizable, the Indo-Pacific and the Atlantic. Nowhere in the Indo-Pacific is there any clear indication of subprovinces, the corals of the remotest localities being only attenuated outposts of the main body. Only by very careful study can random samples from the Seychelles and the Marshalls, 13,000 kilometers apart, be distinguished. There are a few genera that are endemic to but at the same time uncommon in certain areas, and one might conceivably entertain the idea that they are indicators of subprovinces. I mention them here with misgivings:

"Subprovince"	Indicator(s)	Distribution
I	*Siderastrea*[2]	Red Sea, Persian Gulf, Zanzibar, Seychelles, Ceylon.
II	*Anomastrea*[2]	E. Coast of Africa (Zanzibar to Natal)
III	*Anomastrea (Pseudosiderastrea)*[2]	So. China Sea, E. Indies, Great Barrier Reefs
IV	*Duncanopsammia, Moseleya*	Celebes, Great Barrier Reefs
V	*Oulastrea*	E. Indies, China Sea, Formosa, Japan
VI	*Coeloseris*	E. Indies, China Sea, Formosa Ryukyus, Great Barrier Reefs
VII	*Acrhelia*	Philippines, Marianas, Marshalls, Fiji, N. Caledonia, Great Barrier Reefs, Celebes

History of the Indo-Pacific Reef Coral Fauna

I have always thought it very dangerous to derive the phylogeny and paleobiogeography of a group of organisms solely on the basis of their existing members and their distribution, without recourse to the fossil record or in its absence. Neontologists are prone to do this, but the paleontologist, perhaps lacking in imagination, is loathe to do so. In the problem of the history of the radiation of corals and coral reefs in the Indo-Pacific, there is some understanding of the present situation and a little on the fossil record.

The scleractinian corals appeared first suddenly and cryptogenetically in the Middle Triassic, pretty well throughout the world, and by the Jurassic the two ecologic castes, hermatypic and ahermatypic, were well established and reef-building by the former was henceforth a significant feature of the tropical zone which then and until the end of the Mesozoic extended considerably farther north—well beyond 50° N. Lat.—than today.

Concerning the Indo-Pacific reefs, the Recent model of the distribution of reef corals seems to set the pattern of radiation as a function of surface temperature gradients and distance, and one is immediately biased toward the notion that the center of radiation has been from regions within the 25°—28° isocrymes, and, indeed, this can be supported from several lines of evidence. Since the Miocene this climatic regime has been the area where new genera have appeared, and one in which very few genera have become extinct. The history of one family, the Fungiidae, the common mushroom corals, is as an example. This is a small, compact

[2] These genera, including one subgenus, are all members of the same family. *Siderastrea* is an ancient genus, known from as early as the Cretaceous, widespread in the Miocene of the Mediterranean region and the Atlantic, abundant today in the Atlantic but rare in the Red Sea—Indian Ocean. The other two forms are recent derivatives of *Siderastrea.*

group that is still rapidly differentiating, and one that has become adapted to shifting sand-gravel substrates, a situation barred to most of the massive or elaborately foliate or branching forms. It has been confined to the Indo-Pacific since its small beginnings in the eastern Tethys during the early Tertiary, and it seems fairly clear that it has expanded from its site of origin, which has remained the site of evolution of new and more complex forms, while the earliest fungiid, *Cycloseris*, has spread to the limits of the subtropical zone and even ventured into depths a little beyond those of most other hermatypes. This relatively recent evolutionary pattern seems to exemplify the general pattern of other reef corals. The most important, quantitatively, of the modern reef-builders, confined to sites where there is at least initially some kind of hard, stable, substrate, which may be a floating object such as a piece of pumice, a much more efficient distributional mechanism over great ocean deeps than short-lived planulae, are the pocilloporid, poritid, and acroporid corals, marked by rapidly-growing colonies of massed individualized polyps producing huge, fixed, branching, foliaceous, or encrusting, very porous and seemingly but not really delicate, wave-resisting skeletons. Although generic differentiation has been very slow or conservative in these groups (13 genera, only 2 of them extinct) from slow beginnings in the very late Cretaceous and early Tertiary in the Tethys, they have proliferated since the Miocene in species, as has already been mentioned, and in sheer quantity they are at present the main constructors of Indo-Pacific reefs as well as being the most widely distributed. These very widespread genera, such as *Pocillopora, Porites, Acropora,* and *Montipora,* although amongst the geologically oldest, did not become the dominant forms until after the Miocene.

This radiation, with the evolution of groups with high growth-rates and wide adaptation to varied conditions of water movement and substrate within the tropics, has been especially marked in the central and eastern Tethys and its biotopic descendant the tropical Indo-Pacific since the Miocene. Routes between the western Atlantic-Caribbean and eastern Pacific were open at various times during the Tertiary but few genera characteristic of the western Tethyan (Caribbean) fauna penetrated into the extreme eastern Pacific and only one (*Cladocora*), scarce and unimportant, has survived. Enrichment of the eastern Pacific reef coral fauna from the western Atlantic has not occurred, apparently due to the narrowing of the tropical zone in the Tertiary and unfavorable environments. It has been pointed out that "it would be a serious departure from reality to regard marine climates as stable", and while marine climates acceptable to hermatypic corals existed during much of the Tertiary in the Pacific basin beyong the present limts, there is no evidence that these extra-limital areas were sources of new forms and all data now point to the Tethys and central Indo-Pacific as the center of radiation.

Any measure of the rate of radiation from the old Tethyan province at present can certainly be only hypothetical for the fossil record in the Indo-Pacific is not only very spotty but also because there is no reason to suppose that most of the reported occurrences are even subadequate samples of the reef faunas. The wider extent of the tropical zone during the Tertiary is emphasized by the occurrence in early and middle Tertiary sediments of hermatypic corals far north of their present limits, and while these marginal faunas are small they suggest that reefs were more widely spread than at present although it is doubtful that any were like the lush and richly-speciated growths of the Quaternary and recent.[3]

[3] The most widely distributed reef coral genera have the longest paleontological record. Of the 85 now living in the Indo-Pacific, 35 have no fossil record, the rest dating back to the Late Cretaceous and Early Tertiary. The Miocene coral fauna of the Tethys was fairly uniform over its extent; today 7 Tethyan genera survive in the Caribbean (*Isophyllastraea, Isophyllia, Montastrea, Mussismilia, Mycetophyllia, Solenastrea* and *Stephanocoenia*) but not in the Indo-Pacific. On the other hand 20 Tethyan genera (*Alveopora, Astreopora, Cyphastrea, Diploastrea, Favites, Galaxea, Goniastrea, Goniopora, Hydnophora, Leptoseris, Montipora, Pavona, Pocillopora, Psammocora, Pseudocolumnastrea, Stylocoeniella, Stylophora, Synaraea, Trachyphyllia, Antillophyllia*), and the alcyonarian *Heliopora* are common in the Indo-Pacific but became extinct in the Caribbean in the Late Tertiary. Surviving Tethyan genera common to both provinces are few: *Acropora, Favia, Porites,* and *Siderastrea,* but these are much less richly speciated in the Caribbean.