

## Paleoceanography of Coral Reefs in the Hawaiian-Emperor Chain

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The fossil record of shallow marine organisms in the Hawaiian Archipelago and Emperor seamount chain indicates that reef corals were absent during the first half of the Tertiary. Their appearance during the early Oligocene, 34 million years ago, is associated with several paleoceanographic events that appear to have combined to intensify gradually gyral surface currents in the north Pacific. This association suggests that corals were absent in the early Tertiary because of isolation of the Hawaiian Archipelago from the Indo-West Pacific (IWP), the center of reef coral abundance and diversity in the Pacific. Today, the number of species of reef corals in Hawaii is less than 10 percent of the number of species in the IWP. Since their initial colonization, reef corals have been present continuously in the Hawaiian Archipelago, although not without taxonomic change. Episodes of extinction and recolonization are the most likely cause of change in species composition. Recolonization from the IWP may also explain the low rate of endemism (about 20 percent) in the present-day coral fauna.

NUMEROUS STUDIES HAVE SHOWN THAT REEF-BUILDING corals are geographically restricted to tropical shallow marine environments (1). Although some species can tolerate average minimum temperatures of 18°C, most reef corals flourish at temperatures between 25° and 29°C and few reefs occur poleward of the 20°C winter isotherm, which marks the limit of tropical world oceans (2). The distribution of fossil reef corals suggests that similar temperature limits have constrained hermatypic corals since their origin in Early Triassic time (3). The distribution of reef corals is also determined by the ability of their larvae, which are transported by surface currents (4) to propagate and disperse across open oceans. The distribution patterns of reef corals is therefore useful for interpreting the paleoceanography of a region and oceanic paleocirculation. In this article, I consider these biological attributes and use the available fossil record of reef corals throughout the Hawaiian-Emperor (H-E) chain to investigate the paleoceanography of the Pacific Ocean and coral reef zoogeography.

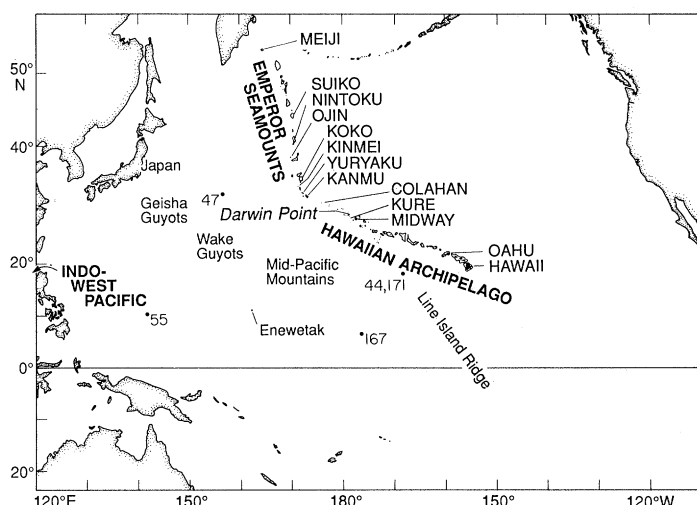
Abundant geophysical evidence has established that the islands, seamounts, and guyots in the H-E chain (Fig. 1) all formed over a hot spot in the mantle, located near 19°N and 155°W in the North Pacific (5). Motion of the Pacific Plate over the hot spot has resulted in the formation of a linear chain of volcanic islands and seamounts that progressively increase in age to the northwest (6, 7) (Fig. 1). The oldest volcanic edifice in the chain is Meiji Guyot, which has

been dated isotopically (K-Ar) at  $61.9 \pm 0.5$  Ma and biostratigraphically (Maastrichtian nannofossils) at 68 to 70 Ma (8). The K-Ar date is a minimum estimate of age because some Ar may have been lost during alteration of the rocks (8). The youngest island, Hawaii, has been dated at less than 1 Ma (K-Ar) and is currently located over the hot spot. The northernmost island in the archipelago is Kure Atoll [located 90 km northwest of Midway Island which is isotopically dated (K-Ar) at 27.7 Ma (9)]. Kure Atoll is situated at 29°N near the present-day northern limit of coral reef formation, defined as the Darwin Point (Fig. 1) (10). Northwest of Kure Atoll the chain continues underwater as a series of drowned atolls (guyots) and seamounts.

Fossil reef corals and other shallow marine organisms have been collected from Oahu (20°30'N) to Meiji (53°N), the entire length of the H-E chain. Samples are from raised (11) and drowned (12) reef terraces on Oahu, drill core holes on Oahu (13) and Midway Island (14), dredged limestones from a number of southern Emperor seamounts and guyots (15), and deep-sea drilling cores from the northern Emperor seamounts collected during Legs 19, 32, and 55 of the Deep Sea Drilling Project (6). Coral ages and species are given in Tables 1 to 4 (16-19).

### Hawaiian-Emperor Biostratigraphy

On the basis of the fossil record (distribution and ages) of shallow marine organisms collected in the H-E chain, reef corals were absent



**Fig. 1.** Map showing location of major Hawaiian Islands, Emperor seamounts, and other areas referred to in the text. Numbered circles refer to Deep Sea Drilling Project (DSDP) sites for which temperature data are plotted in Fig. 2.

**Table 1.** Pleistocene fossil reef corals from elevated terraces on Oahu, Hawaii (11), and Pliocene corals dredged from a drowned terrace at 500 to 520 m off Oahu, Hawaii (12).

| Pleistocene corals                     | Pliocene corals                 |
|----------------------------------------|---------------------------------|
| <i>Acropora</i> sp.*                   | <i>Fungia</i> sp. nov.          |
| <i>Gardineroseris planulata</i> * (52) | <i>Leptastrea</i> sp. nov. A    |
| <i>Porites lobata</i> *                | <i>Leptastrea</i> sp. nov. B    |
| <i>Porites compressa</i> *             | <i>Pavona</i> sp. nov. A        |
| <i>Montipora patula</i> *              | <i>Pavona</i> sp. nov. B        |
| <i>Pavona duerdeni</i> *               | <i>Acropora</i> sp.             |
| <i>Cyphastrea ocellina</i> *           | <i>Pocillopora molokensis</i> * |
| <i>Leptastrea purpurea</i> *           | <i>Porites lobata</i> *         |
| <i>Fungia scutaria</i> *               | <i>Platygyra</i> sp.            |
| <i>Pocillopora damicornis</i> *        |                                 |
| <i>Pocillopora eydouxi</i> *           |                                 |
| <i>Pocillopora ligulata</i> *          |                                 |
| <i>Pocillopora meandrina</i> *         |                                 |
| <i>Psammocora</i> sp.*                 |                                 |

\*Present in the Hawaiian Islands today.

in the chain before the early Oligocene (34 Ma) (Fig. 2). The oldest reef corals that have been recovered are five species from Koko, Yuryaku, and Kanmu seamounts (35°25'N to 32°10'N) (Tables 1 to 4). They include species of *Platygyra*, *Favites* (Fig. 3), *Porites*, and *Astropora* and range in age between 30.5 and 34 Ma. The isotopic ages of Koko and Yuryaku average 48 Ma and 43 Ma, respectively (6), which indicates that reef corals may not have populated these volcanic pedestals until 9 to 17 million years after their formation. Reef corals are absent in all of the samples from the older northern Emperor seamounts (Ojin, Nintoku, Suiko, and Meiji) (6) (Tables 1 to 4).

The biostratigraphy of cores from the northern Emperor seamounts consists primarily of a tropical biofacies of shallow water coralline algae, bryozoa, benthic foraminifera, ostracods, spirorbids, echinoid spines, bivalves, and brachiopods (6, 20) (Table 4). The only corals in these cores are non-reef-building solitary species, and these are scarce. Seismic evidence indicates that reef structures occur on Suiko, Nintoku, and Ojin, but the thinness of their carbonate caps (100 to 200 m) suggests that these structures may be bryozoan-algal mounds instead of coral reefs. Although bryozoa and coralline algae can occur in subtropical environments (21), they are also common in tropical climes and are abundant in the Hawaiian Islands today (10, 22). The presence of keeled planktonic foraminifera, large foraminiferans, and broadly attached spirorbids in the cores from the northern Emperor seamounts is strong evidence of a warm tropical environment (20). Because all of the northern Emperor seamounts are guyots and contain shallow, warm water fossils, there is little doubt that they all once were at sea level in a warm tropical environment.

A second important conclusion revealed by the fossil record of reef corals in the H-E chain is that, once established, corals appear to have persisted in the chain continuously to the present, although not without some taxonomic change (Fig. 2). For example, <sup>87</sup>Sr-<sup>86</sup>Sr dates for ten samples of reef corals from Koko, Yuryaku, and Kanmu guyots indicate that corals continuously inhabited the guyots from early Oligocene to early Miocene time (the ages of these ten corals are: 34.0, 33.0, 30.7, 30.5, 27.7, 27.0, 27.0, 25.7, 24.7, and 21.0 Ma, Table 3). The genus *Porites*, in particular, apparently existed on Kanmu for at least 12 million years.

The degree of taxonomic change in reef corals that has occurred in the H-E chain through time is difficult to quantify. This is particularly true for the species level in older sections of the record. For example, the *Porites* that was identified by J. W. Durham from Kanmu (Table 3) may not be the same species of *Porites* that was

identified by J. W. Wells in the Midway core (Table 2). Identification of samples of even living scleractinian corals can be difficult because of ecotypic variation within species. For these reasons I used the degree of similarity between reef-building coral genera to estimate taxonomic change among epochs. The equation used for the calculation of generic similarity is Jaccard's index of similarity, where GSI (generic similarity index) =  $c/(a + b - c)$ , where  $a$  and  $b$  equal the number of genera in two successive epochs and  $c$  is the number of genera that is shared in common (23).

## Taxonomic Changes in Hawaiian Corals

Although the number of species of fossil reef corals in the Hawaiian chain has been fairly constant (12 to 15 species) since their first appearance in Oligocene time, a moderate amount of taxonomic change has taken place both in and between epochs (Fig. 2). Perhaps the clearest record of this is in the Midway core. Wells (24) has identified 14 species of reef corals in the Miocene and 6 in younger rocks. Of these 20 species, three groups can be identified. Five species that form the earliest group near the bottom of the core all disappear together at a core depth of 275 m. Species in the second group first appear at different depths in the core but mostly drop out at about 170 m. A third group appears about 115 m and then drops out at 20 m. Wells identified the first two groups as Miocene corals and the third group as post-Miocene in age (24). This record of discontinuities may represent repeated colonization events and at least three periods of extinction, perhaps because of rapid rises in sea level or other disturbance events. The second extinction event coincides with a solution unconformity at 169 m (25) and therefore may appear sharper than what actually occurred.

The generic similarity between epochs in which corals are present ranges between 0.38 and 0.20 up to the Miocene-Pliocene boundary after which it rises steeply (Fig. 2), reaching 1.00 at the

**Table 2.** Fossil reef corals from cores drilled at Midway Island (18).

| Species                                           | Depth in core (m) |
|---------------------------------------------------|-------------------|
| <i>Post-Miocene corals</i>                        |                   |
| <i>Pavona clavus</i> Dana*                        | 21–30             |
| <i>Pavona maldivensis</i> (Gardiner)              | 18–113            |
| <i>Pocillopora ligulata</i> † (Dana)              | 21–27             |
| <i>Porites lobata</i> Dana†                       | 21–60             |
| <i>Cyphastrea ocellina</i> †                      | 37–56             |
|                                                   | 70–73             |
| <i>Leptoseris</i> cf. <i>incrustans</i> (Quelch)  |                   |
| <i>Miocene corals</i>                             |                   |
| faunal break                                      |                   |
| <i>Galaxea</i> cf. <i>heligena</i> Felix          | 146–150           |
| <i>Pocillopora</i> cf. <i>hempriche</i> Ehrenberg | 175–256           |
| <i>Favia</i> sp.                                  | 177–179           |
| <i>Stylophora pistillata</i> (Esper)              | 174–326           |
| <i>Stylophora pistillata</i> Mordax               | 174–300           |
| <i>Stylophora gemmans</i> Gerth                   | 192–300           |
| <i>Porites</i> sp. A                              | 180–350           |
| faunal break                                      |                   |
| <i>Plesiastrea</i> cf. <i>curta</i> (Dana)        | 224–238           |
| <i>Porites</i> sp. B                              | 236–243           |
| <i>Acropora</i> sp.                               | 274–279           |
| <i>Favia</i> sp. A                                | 275–329           |
| <i>Favia</i> sp. B                                | 276–282           |
| <i>Seriatopora</i> cf. <i>hystrix</i> Dana        | 275               |
| <i>Favites</i> cf. <i>chinensis</i> (Verrill)     | 275–305           |

\*May be *Pavona duerdeni* (52).

†Present in Hawaiian Islands today.

Pleistocene-Holocene boundary. The rise in recent time is probably an artifact because epochs since the Miocene were increasingly shorter in duration. If taxonomic change is examined at the species level in the Pliocene and Pleistocene (younger material being easier to identify), about 30% of the Pliocene species exist in Hawaii today, and all Pleistocene corals are currently extant (Tables 1 and 2). Evolutionary change at the species level, whether caused by speciation in the archipelago or from immigration, appears to require between 1.6 million years (beginning of the Pleistocene) to about 5.0 million years (beginning of the Pliocene). The rate of change in the Hawaiian Islands may be slower than in the eastern Pacific and Caribbean region where no species of coral are shared in common today. Closure of the Panamanian seaway isolated these two regions about 2.5 to 3.6 Ma (26). In contrast, the Hawaiian Archipelago is not currently isolated from the IWP and recolonization is probably a sporadic but continuing process (27). Hence, recolonization may dilute or swamp the speciation process within the Hawaiian chain. This may explain the moderately low incidence (~20%) of endemism in the present Hawaiian coral biota (28).

## Paleoceanographic Implications

At least five hypotheses might account for the absence of reef corals in the Hawaiian Archipelago before the early Oligocene: (i) older reef corals may occur but have not been sampled; (ii) the sea surface temperature may have been too low during the early Tertiary; (iii) the Hawaiian hot spot in the early Tertiary may have been located at a more northerly position than at present; (iv) rapid changes in sea level or other frequent disturbances may have prevented coral reefs from forming in Hawaii during the early Tertiary; and (v) patterns of ocean circulation in the early Tertiary may have been different or too weak to transport coral larvae from the center of their abundance and diversity in the Indo-West Pacific (IWP) to islands in the Hawaiian Archipelago.

The first hypothesis cannot be dismissed altogether but is unlikely because the biostratigraphy is similar in eleven cores from different seamounts in the northern Emperors and all are dominated by a warm, tropical, shallow-marine biofacies (Table 4) (6). The second hypothesis, absence due to low temperature, is also unconvincing. McKenzie, Bernoulli, and Schlanger (21), on the basis of oxygen isotope analyses of bryozoan-algal sand, carbonate muds, algal nodules, and cemented calcarenites from Suiko, Nintoku, Ojin, and Koko seamounts, have suggested that water temperatures were cool (11° to 16°C) at the time of deposition. However, these carbonates could have formed on insular shelves at depths of 50 m or more (29). The interpretation of McKenzie *et al.* is also countered by the recovery of eight species of fossil reef corals, which require warm water, from Koko Guyot (Table 3). Butt and Hagn *et al.* (20), in contrast to McKenzie *et al.*, hypothesized that the bryozoan algal biofacies in the northern Emperors were evidence of a warm, tropical environment. Oxygen isotopes in planktonic foraminifera from numerous deep-sea drilling sites also indicates that the sea-surface temperature was warm at high latitudes in the Eocene and Paleocene on a global scale (30). Data representing four low-latitude drill sites (Fig. 1) are plotted in Fig. 2. At the two stations that are now closest to the Hawaiian Archipelago (44 and 167), sea-surface temperatures are well above 20°C during parts of the Eocene and Paleocene. Surface temperatures at these sites did not drop close to 20°C until the Oligocene, but this is the time when corals first appeared in the Hawaiian Archipelago. The lack of a relation between a steep rise in sea-surface temperature at these stations during the Miocene and diversity of coral species in Hawaii (Fig. 2)

further weakens the case that temperature is a significant controlling factor of coral diversity in Hawaii. This conclusion is supported by CLIMAP data that show that sea-surface temperature was nearly stable in the central gyres of the subtropical North Pacific during glacial minima (18,000 years ago) even though average global surface waters cooled on the order of 2.3° and thermal gradients steepened along polar fronts (31).

The third hypothesis, that of a more northerly hot spot during the early Tertiary, is important because, if true, temperature limitation is more likely. There is considerable controversy over this question in the literature. Although some geophysical data suggest that hot spots are fixed relative to each other (32), other analyses indicate that hot spots move relative to each other and relative to the earth's spin axis (33, 34). Sager and Bleil (34) argued that the Hawaiian hot spot was located slightly to the north of its present position during the early Tertiary. Also the paleolatitude of at least one Emperor seamount, Suiko, has been backtracked by Kono (35) to  $27.0^\circ \pm 3.5^\circ\text{N}$  which is almost  $8^\circ$  (~800 km) north of the present position of the hot spot. However, both of these interpretations rest on the assumption that the earth's magnetic field is a dipole. If nondipole components are taken into account, their calculated paleolatitude is shifted farther south, closer to the present position of the hot spot (36). Also the paleolatitudes of other Emperor

**Table 3.** Fossil reef corals dredged from Emperor seamounts (15).

| Species                                       | Guyot or seamount | Depth of dredge (m) | $^{87}\text{Sr}/^{86}\text{Sr}$ age (Ma) |
|-----------------------------------------------|-------------------|---------------------|------------------------------------------|
| <i>Platygyra</i> sp.*                         | Kanmu             | 411–645             | 21.0, 27.7, 33.0                         |
| <i>Porites</i> (?)*                           | Kanmu             | 411–645             |                                          |
| <i>Stylophora</i> sp.*                        | Kanmu             | 411–645             |                                          |
| <i>Astreopora</i> sp.*                        | Yuryaku           | 645–947             | 34.0                                     |
| <i>Fungia</i> sp. (?)*                        | Yuryaku           | 645–947             |                                          |
| <i>Porites</i> sp.*                           | Yuryaku           | 645–947             |                                          |
| <i>Stylophora</i> sp.                         | Yuryaku           | 645–947             | 24.7                                     |
| <i>Favia</i> sp. 1*†                          | Koko              | 624–823             |                                          |
| <i>Favia</i> sp. 2*†                          | Koko              | 624–823             |                                          |
| <i>Favia</i> sp. 3*†                          | Koko              | 624–823             | 25.7, 30.7                               |
| <i>Favites</i> sp. 1*†                        | Koko              | 624–823             |                                          |
| <i>Favites</i> sp. 2*†                        | Koko              | 624–823             |                                          |
| <i>Platygyra</i> sp.*†                        | Koko              | 624–823             | 30.5                                     |
| <i>Psammocora</i> ( <i>Stephanaria</i> ) sp.* | Koko              | 624–823             |                                          |
| <i>Seriatopora</i> sp.*                       | Koko              | 624–823             |                                          |

\*Identified by J. W. Durham.

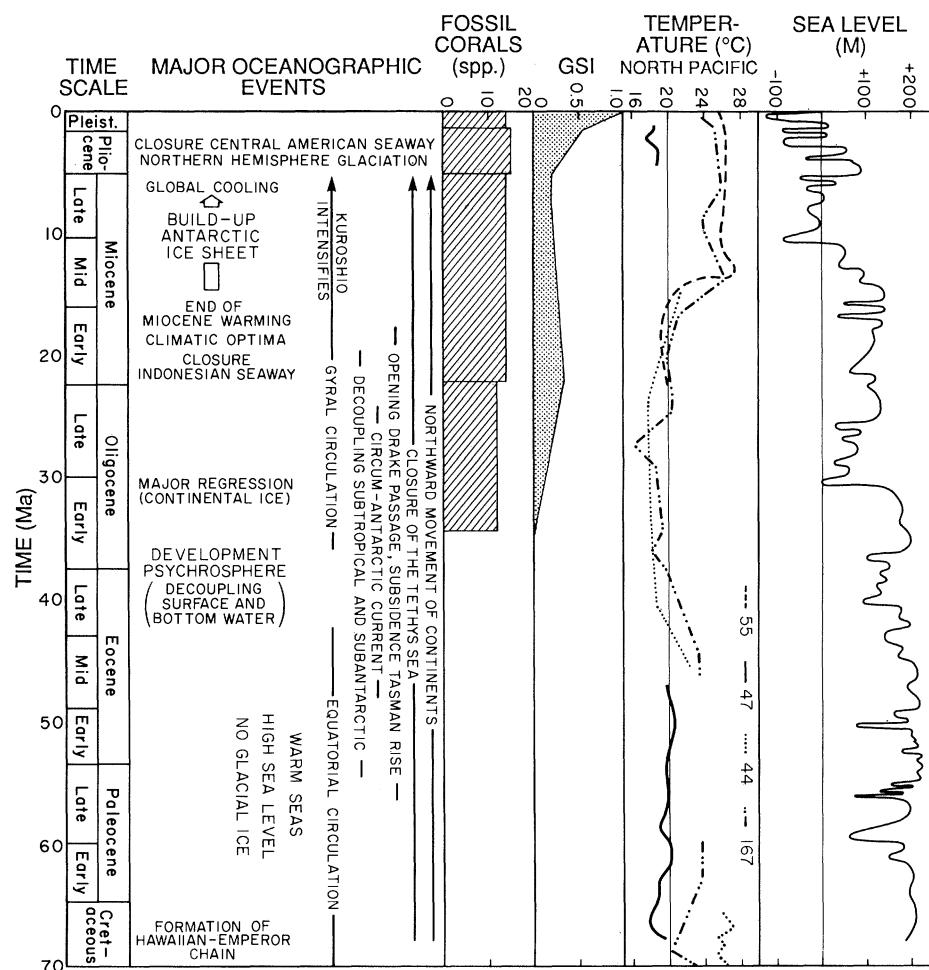
†Identified by J. W. Wells.

**Table 4.** Biostratigraphy of Deep Sea Drilling Project cores from northern Emperor seamounts; reef corals are absent in all samples.

| Biostratigraphy (21)                                                                                 | Guyot or seamount | Depth of summit (m) | Age of edifice (Ma) (6)  |
|------------------------------------------------------------------------------------------------------|-------------------|---------------------|--------------------------|
| Coralline algae, bryozoa, bivalves, echinoids, benthic foraminifera, lagoon deposits, no reef corals | Ojin              | 899                 | $55.2 \pm 0.7$           |
| Coralline algae, bryozoa, bivalves, echinoids, brachiopods, ostracods, foraminifera, no reef corals  | Nintoku           | 1003                | $56.2 \pm 0.6$           |
| Coralline algae, bryozoa, echinoids, ostracods, foraminifera, no reef corals                         | Suiko             | 1062                | $64.7 \pm 1.1$           |
| Basalt overlain by 1044 m of diatomaceous ooze and clay, no reef corals                              | Meiji             | 2851                | $61.9 \pm 0.5$<br>68–70* |

\*Age determined by biostratigraphy. Other ages are K-Ar ages.

**Fig. 2.** Fossil record of Hawaiian reef corals, sea-surface temperature at four DSDP sites in the North Pacific (55) (Fig. 1), global sea level (53), and major paleoceanographic events (54) in the Pacific Ocean during Cenozoic time. GSI = Generic Similarity Index (see text).



seamounts and islands in the Hawaiian Archipelago back-calculate to the present position of the hotspot (6, 35). Perhaps it is best to leave the question of hot spot fixity open, although to have caused the absence of coral reefs in the archipelago during the first half of the Tertiary, the hot spot would have to have been farther north for 35 million years and then quickly move south (8°) at about 34 Ma.

The fourth hypothesis, that reef corals were absent in the first half of the Tertiary because of rapid changes in sea level or other frequent disturbances, can be dismissed because evidence regarding changes in sea level and other environmental variables indicate that climate was more stable in the early Tertiary than at later times (sea level and temperature curves, Fig. 2).

The last hypothesis, that absence of reef corals in the H-E chain before 34 Ma was a result of isolation caused by insufficient speed and direction of surface currents, must be tested against what is known of the paleoceanography of the Pacific Ocean. Even though data are limited, a number of large-scale changes are known to have taken place during the Cenozoic that collectively may have led to a gradual strengthening of gyral circulation in the North Pacific (Fig. 2).

The world's oceans have gradually cooled during the past 70 million years (30, 37). This global cooling trend is attributed to the combined effect of gradual northward movement of several continents or land masses, closure of the Tethys Sea, and the isolation of Antarctica (Figs. 2 and 4). Collectively, these events may have caused a major change in oceanic circulation from predominantly equatorial to a strongly meridional (north-south) or gyral pattern in the Pacific (Figs. 2 and 5).

During the early Cenozoic, the oceans were warm and poorly

stratified with weak latitudinal temperature gradients and sluggish circulation patterns (38). This time was most likely the warmest period of the entire Cenozoic (39) and probably represents a continuation of late Cretaceous conditions when high sea level may have drowned the Mid-Pacific Mountains and Geisha guyots (Fig. 1) (40). This transgression may have been the last great flooding of the continental shelves in Phanerozoic time, and it may have greatly enlarged the shallow Tethys Sea (37).

During the Tertiary, particularly in the Pacific Ocean, three major paleoceanographic events are thought to have completely altered patterns of ocean circulation (41). First, the Tethys Sea (Indonesian and Panamanian seaways, Fig. 4) gradually closed during the middle and late Tertiary. This would have enhanced meridional (north-south) circulation patterns, which in turn would have increased transport of warm water toward the poles. Evaporation at the poles would have increased precipitation leading to the buildup of glacial ice. The second event, the development of the psychrosphere (bottom water), may be connected to the first event in that the buildup of ice on Antarctica may have triggered the formation of Antarctic bottom water. The psychrosphere, which developed about 36 Ma, decoupled surface water from the deep ocean water and created a new thermohaline circulation pattern in the world's oceans. The third event was the opening of the Drake Passage between South America and Antarctica (Fig. 4) and the subsidence of the Tasman Rise about 25 to 30 Ma. These changes led to the development of a strong circumpolar current around Antarctica that isolated the southern continent. All three of these changes would have produced stronger latitudinal temperature gradients than existed earlier, as well as stronger winds and currents. Thus a current

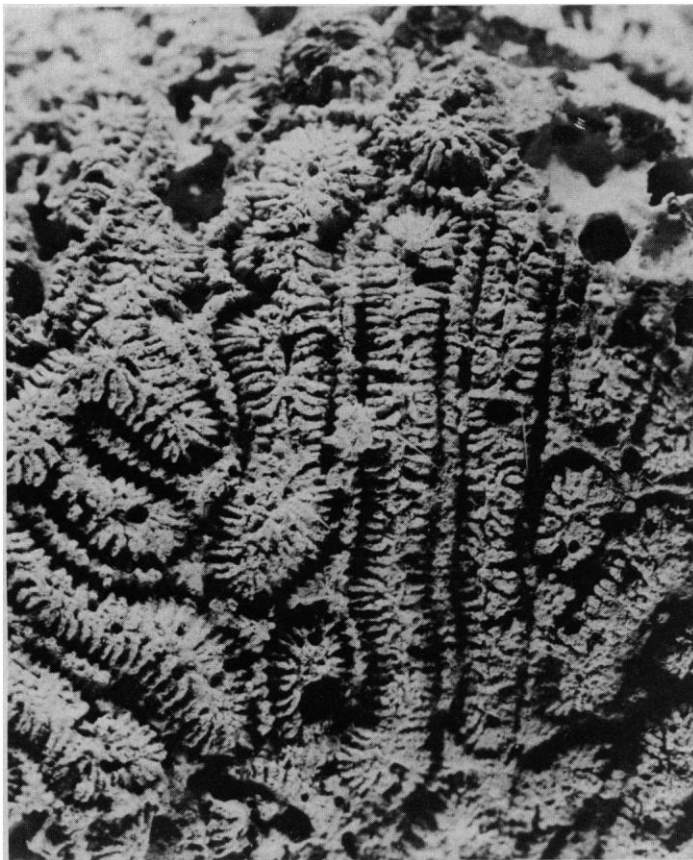
regime in the North Pacific may have been produced that was strong enough to transport coral larvae from the IWP to the Hawaiian Archipelago. Certain islands in the western Pacific may have served as stepping stones to dispersal, as they do today (42).

The appearance of reef corals in the Hawaiian Archipelago at a time that approximately corresponds with the above paleoceanographic changes provides evidence that the Hawaiian islands may have been completely isolated from the IWP region before the early Oligocene. Even with the existence of a strong pattern of gyral circulation in the North Pacific today (Kuroshio and North Pacific drift, Fig. 5), there are only 43 species of reef corals in the Hawaiian Archipelago (43). All exhibit taxonomic affinity with species in the IWP. In contrast there are about 500 species in the IWP (2), which indicates that reef coral diversity in Hawaii today is attenuated by as much as 90% or more of the diversity in the IWP. A weak pattern of gyral circulation during the early Tertiary could have prevented any corals from reaching Hawaii.

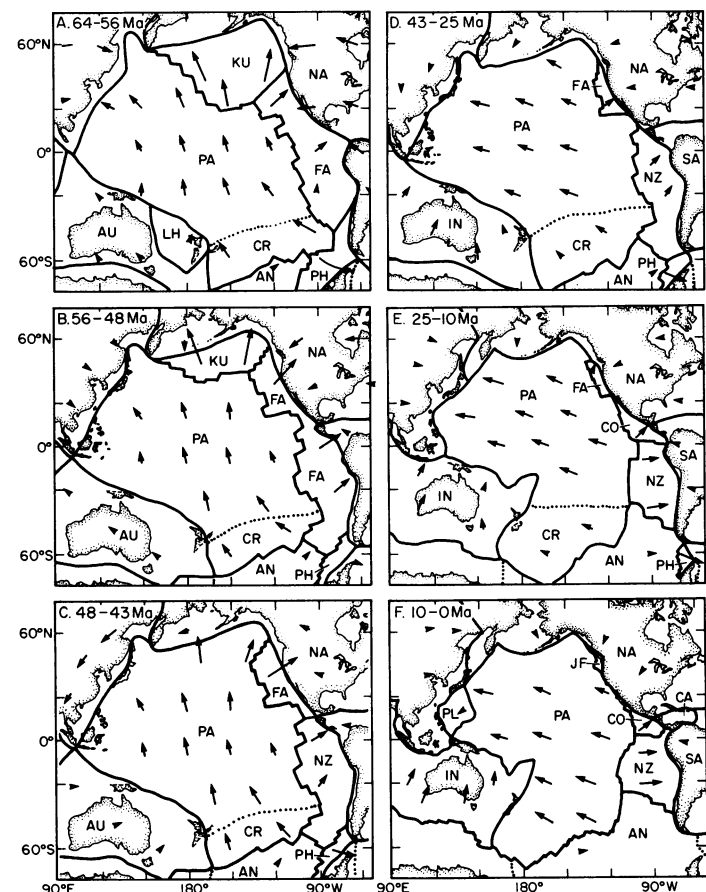
Biogeographic isolation from the IWP due to paleocirculation may have prevented the development of coral reefs in other parts of the Pacific besides Hawaii during the Cretaceous and early Tertiary. Reef corals were apparently absent in the Line Islands at the end of the Cretaceous and beginning of the Tertiary (Paleocene) (44). These islands were then situated much farther south and east but were still probably in tropical waters. Cross Seamount, which is currently situated 160 km south of Oahu and has a summit depth of 360 m, is a guyot that subsided near the equator about the end of the Cretaceous (45). In seven recent (1987) submersible dives to its summit my colleagues and I have not found any evidence of fossil reef corals. A large number of other islands drowned in the central

Pacific near the equator during Albian to Cenomanian time (91 to 119 Ma, in the Cretaceous) (40, 46). Today, these volcanic pedestals make up the Geisha guyots, the Wake Guyots and the Mid-Pacific Mountains (Fig. 1). Evidence of reef corals from dredge hauls taken from these guyots is fragmentary (46, 47); however, six genera of fossil reef corals have been identified in calcareous fossils dredged from the summit of Hess and Cape Johnson guyots (near 18°N, 177°W) in the Mid-Pacific Mountains (46). Interestingly, all of these have a zoogeographic affinity with a Texas-Mexican part of the Tethys Sea (46). Upper Cretaceous (Campanian-Maastrichtian, 84 to 65 Ma) shallow water foraminifera from the Line and Marshall Islands also have Caribbean affinities (48). These faunal links suggest that circulation in the Tethys Sea was east to west and that there was a major colonization route from the Caribbean to the Pacific during the Cretaceous.

Reef corals with an IWP affinity first appeared in the northwestern Pacific in the Marshall Islands during the Eocene; they are present in the bottom of a deep core drilled at Enewetak (49). Apparently by the Eocene, currents were sufficiently developed in the western Pacific to transport larvae from the IWP northeast to the Marshall Islands but were not strong enough to allow larvae to reach Hawaii. In the eastern Pacific during the early Tertiary, reef corals extended well north along the coast of North America (50). Of 15 fossil coral genera in the eastern Pacific Eocene, 13 show taxonomic affinity to the Caribbean-Atlantic, which suggests that these corals were transported by way of the Central American seaway up the west coast of America (51).



**Fig. 3.** Fossil hermatypic corals *Platygyra* sp. (elongated calices) and *Favites* sp. (circular calices) contained in limestone rocks dredged from Koko Guyot in the Emperor seamounts. Strontium isotope age of corals is 30.5 Ma. K-Ar isotopic age of Koko Guyot is about 48 Ma (6).



**Fig. 4.** Cenozoic plate reconstructions, from 64 Ma (A) to present (F) modified from (56). Arrow lengths are scaled for a constant time interval of 15 million years. Plate abbreviations are: AN, Antarctic; AU, Australia; CO, Cocos; CR, Chatham Rise; FA, Farallon; IN, Indian; JF, Juan de Fuca; KU, Kula; LH, Lord Howe; NA, North America; NZ, Nazca; PA, Pacific; PL, Philippine; PH, Phoenix; and SA, South America.

## Conclusions

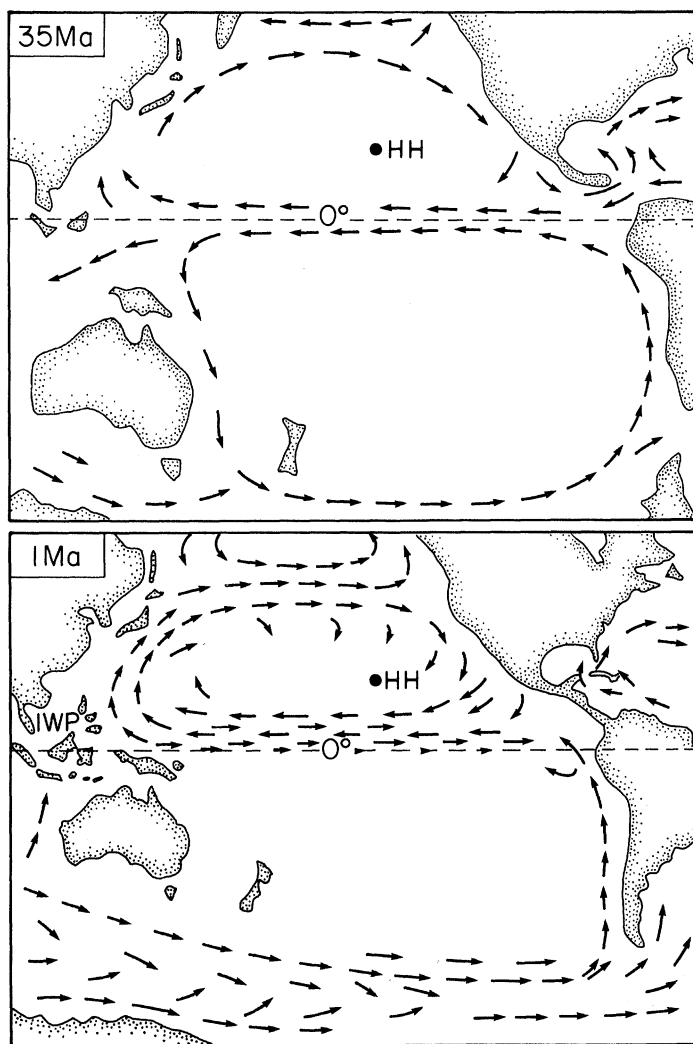
The fossil record of shallow water marine organisms in the H-E chain indicates that reef corals were absent during the first half of the Tertiary. Before the Oligocene, the shallow biota consisted of a warm, tropical, coralline algae-bryozoan biofacies. The absence of reef corals in the early Tertiary could be attributed to a more northerly position of the Hawaiian hot spot in combination with cooler sea-surface temperatures. However, the evidence for a more northerly hot spot is controversial and cooler temperature is inconsistent with biostratigraphy of the northern Emperors and oxygen isotopic compositions of pelagic foraminifera which indicate warm sea surface temperatures at high latitudes in the Eocene and Paleocene. The most likely explanation is that insufficient transport of coral larvae by surface currents during the early Tertiary isolated the Hawaiian Islands from the IWP. This hypothesis is supported by past and present patterns of ocean circulation. During the middle Tertiary, a series of gradual but interconnected paleoceanographic events including closure of the Tethys Sea, development of the psychrosphere, isolation of Antarctica, and intensification of latitudinal temperature gradients may have combined to produce gyral currents in the North Pacific of sufficient strength to transport coral larvae from the IWP to the Hawaiian Islands. Even today, with

vigorous western boundary currents in the North Pacific, the coral fauna of Hawaii is highly attenuated and consists of less than 10% of the species now present in the IWP.

Since initial colonization, a moderate degree of taxonomic change has occurred in the reef coral biota of Hawaii. Episodes of extinction and recolonization are the likely cause of this change in species composition. Such a pattern is not surprising, given the northerly position of the Hawaiian Islands near the current latitudinal limit of reef-building corals. Recolonization episodes may also explain the moderately low rate of endemism of reef corals (~20%) in Hawaii today, which suggests that modern species are of recent origin.

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**Fig. 5.** Postulated surface circulation of the Pacific Ocean at 35 Ma (above) and 1 Ma (below). Modified from (39). Number of arrows indicates relative strength of currents.

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# Mixing in Stars

GEORGE WALLERSTEIN

**Analysis of the chemical and isotopic composition of stellar surfaces reveals the types of nuclear reactions that have occurred in the stellar interiors as well as the timing and depths from which material once deep in the star has reached the surface. Mass loss from the stellar surface and, in some cases, mass transfer from a companion enhance the opportunity to observe material that is the product of internal nuclear reactions. Detailed studies show substantial deficiencies in current models with the timing and depth of convective and other forms of mixing.**

**A**LMOST 35 YEARS AGO MERRILL (1) ANNOUNCED THE discovery of the lines of the unstable element technetium in the spectrum of the star R Andromeda (abbreviated R And). Because the half-life of the longest lived isotope of Tc is  $2.6 \times 10^6$  years it was evident that the Tc seen on the surface of R And was produced by nuclear transformations within that star and mixed to the surface. For the first time a way had been found to test the theory of stellar interiors.

The basic theory of the structure of stars was worked out by Sir Arthur Eddington and others in the 1920s (2). Stellar structure is described by four first-order differential equations that use the conservation of mass, conservation of energy, hydrostatic equilibrium, and energy transport. In addition, the equation of state, the opacity of the material to radiation, and the rates of nuclear reactions that generate energy must be known (3). With reasonable boundary conditions the equations can be solved for a spherical star in a few seconds with a modern computer (although it took Eddington months with a desk-top calculator to solve them 60 years ago).

It is not so easy to verify our calculations. Since the opacity of stellar material is very high no radiation emitted except by the surface layers can reach us. Only neutrinos can travel from the center of a star to an external observer and even these may suffer a conversion that permits only a fraction of the emitted neutrinos to emerge from the stellar surface unchanged (4). Solar neutrinos are barely detectable with modern instrumentation and only from supernovae can we detect neutrinos from any other stellar source within our galaxy or the Local Group (5). Checks on the correctness of the theory of stellar structure and evolution can be made if one uses the integral properties of stars such as the radius and luminosity. These checks are not very critical, however, because the solutions of stellar structure may predict an observed radius and luminosity even though the internal structure is not unique, especially for evolved stars.

The latter have converted their internal hydrogen to helium and hence are now generating energy by helium burning. The best test of our calculations for such stars is to determine the chemical composition of the visible layers of a star and endeavor to relate the composition to events in the interior revealed by the mixing of previously deep layers to the surface. In some cases we are greatly assisted in this process by the loss of material from the stellar surface. Extensive mass loss may be driven by the absorption of radiation by the outer atmosphere of the star. For hot stars highly ionized species of light elements such as carbon, nitrogen, and oxygen are the absorbers, whereas for the coolest stars the absorbing agent is dust. In binary stars mass loss may be induced by the gravitational field of a companion. In some situations significant amounts of mass may be transferred to a companion so the star with peculiar atmospheric abundances may be the recipient, rather than the producer, of the anomalous material.

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