type II superconductor only became strictly zero at $T = 0$. We now know that there exists a finite temperature phase transition at high fields at which the resistance becomes zero. The low-temperature ordered phase is a superconducting vortex glass, which at very low fields has quite long-range orientational (hexatic) order. We are slowly making real progress in our understanding of the vortex–flux lattice statics and dynamics. The oxide superconductors have proven to be a wonderful testing ground for our understanding in this area and have forced us to reexamine, extend, and in some cases discard certain theoretical models. There remain many unanswered questions. These include the role of anisotropy, a microscopic understanding of the critical currents in these systems, and the behavior of the lattices in the very clean limit.

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Paleoceanography of the Tropical Eastern Pacific Ocean

RICHARD W. GRIGG AND RICHARD HEY

The East Pacific Barrier (EPB) is the most effective marine barrier to dispersal of tropical shallow-water fauna in the world today. The fossil record of corals in the eastern Pacific suggests this has been true throughout the Cenozoic. In the Cretaceous, the EPB was apparently less effective in limiting dispersal. Equatorial circulation in the Pacific then appears to have been primarily east to west and the existence of oceanic atolls (now drowned guyots) in the eastern Pacific probably aided dispersal. Similarly, in the middle and early Mesozoic and late Paleozoic, terranes in the central tropical Pacific likely served as stepping stones to dispersal of tropical shelf faunas, reducing the isolating effect of an otherwise wider Pacific Ocean (Panthalassa).

THE TROPICAL EASTERN PACIFIC OCEAN HAS BEEN DESCRIBED as the most effective barrier to dispersal of warm-water shelf fauna in the world (*1*). Ekman named this body of water the East Pacific Barrier (EPB) and defined it as that expanse of ocean where no islands exist in the tropical Pacific separating the Indo–West Pacific (IWP) zoogeographic province from the eastern Pacific province (Fig. 1). Charles Darwin described it as an "impassable barrier" for the migration of coastal marine species (*2*). In terms of coral reef habitats, the EPB exists between the Line Islands in the western Pacific and the western coast of the Americas and several offshore islands in the eastern

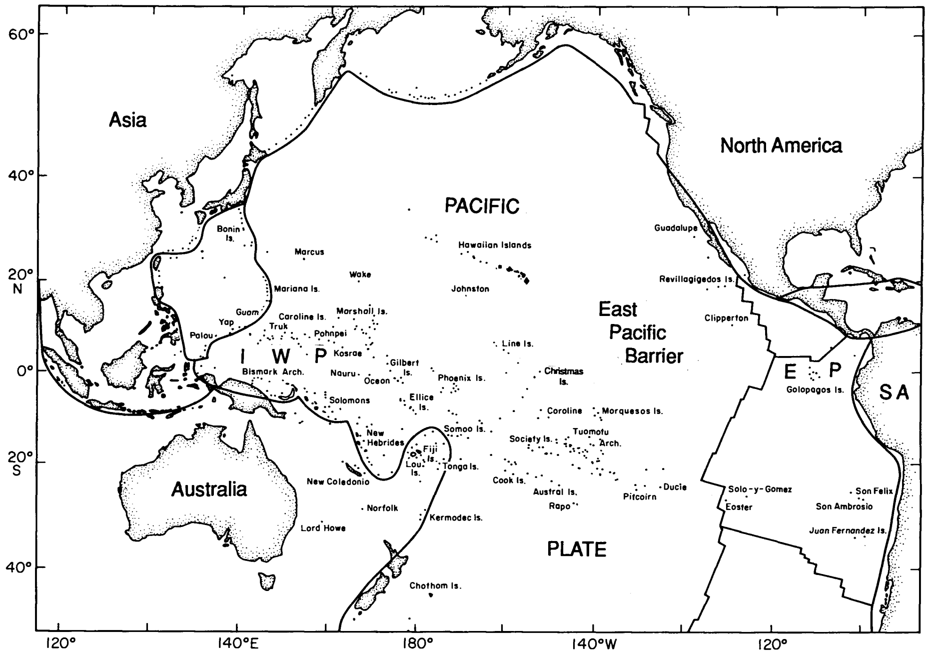

Fig. 1. Pacific Ocean showing location of East Pacific Barrier with respect to the Indo-West Pacific province (IWP) and eastern Pacific (EP) zoogeographic provinces. [After (*40*)]

Pacific including the Galapagos Islands.

While the present geographic limits of the EPB and its effectiveness in limiting the dispersal of tropical shelf fauna are reasonably well understood (*2*), the question of its antiquity has received little attention. How long in the history of the earth has the EPB been a major barrier to dispersal of warm water shelf fauna in the Pacific? We examine this question using several divergent lines of evidence including the fossil record of corals in the eastern Pacific and recent progress in plate tectonics and plate reconstruction. Reef-building corals are particularly well suited to use as sources of information to interpret historical dispersal across the EPB because they are readily fossilized and their larvae are stenothermal warm water organisms capable of long-range dispersal.

Bridging the EPB in the Modern Pacific

Today the EPB is more effective in limiting dispersal westward than eastward across the Pacific (*2*). Why this is true has been attributed to (i) stronger currents periodically running eastward than westward (*3*), (ii) eastern Pacific species being few in number and ill-adapted for long-distance dispersal and adult life in habitats in the IWP (*2*), and (iii) IWP species being high in diversity with many adapted for long-distance dispersal and having eurytypic life history characteristics as attached adults (*4–7*).

The shortest distance across the EPB today is 5400 km between Christmas Island in the west and Clipperton Atoll in the east. On the equator, the shortest distance across the barrier is 7300 km between Christmas Island and the Galapagos Islands. The Marquesas Islands are closer than the Line Islands to Clipperton (3900 km) and the Galapagos (5300 km), but they lie about 10°S of the equator and are situated in a region where a weak westerly flow (~10 cm/sec) is present (the South Equatorial Current). An eastward flowing countercurrent in the region of the Marquesas Islands has been documented (*4*), but it is relatively slow (10 to 30 cm/sec). The Marquesas Islands are therefore unlikely stepping stones for dispersal eastward across the EPB. Hawaii in the north Pacific and Easter Island in the south Pacific are the only other possible islands that might affect the EPB, but both are close to the latitudinal limits of many tropical shelf species and exist in regions of sluggish westerly flow. Thus, neither would serve as likely stepping stones for dispersal from west to east. Other faunal groups such as deep benthic species, temperate or eurythermal species might circumvent the EPB by way of the ocean bottom or by way of islands at higher latitudes in the Pacific.

The distribution pattern of tropical shelf echinoderms illustrates the present-day effectiveness of the EPB across the Pacific. Ekman (*1*) showed that only 2% of the 240 IWP species of echinoderms and 14% (11 or 12 genera) of the 80 genera, have been successful in bridging the entire Pacific from west to east. Genera are probably more widely distributed than species, because they have had more evolutionary time for dispersal, and they are genetically more variable. Ekman (*1*) noted that patterns of distribution of other modern tropical shelf fauna in the IWP are generally the same as those exhibited by echinoderm genera and species.

For reef-building corals, about 500 contemporary species exist in the IWP (*7*), compared to only 21 species reported in the eastern Pacific (*4*), including 13 species in the Galapagos and 14 at Cocos Island. Except for four possible endemic species, all have affinities to the IWP (*4*). Hence less than 4% of the IWP coral fauna are amphi-Pacific. Of 71 species of reef corals found at Fanning Island in the Line Islands (*8*) only about 10% are reported in the eastern Pacific (*4*) and for IWP mollusks, only 14% are successful in bridging the barrier between the Line Islands and the Galapagos Islands (*2*). Even fewer species are successful in reaching the mainland of the Americas (*5*). Sheltema (*2*) has shown that teleplanic larvae are significantly less abundant in the eastern tropical Pacific compared to the central tropical Pacific and argues that the barrier acts as a filter to all species, except those with exceptionally long larval lives.

Present Dispersal Across the EPB

The effectiveness of the EPB can probably be attributed to its great distance relative to the speed of zonal currents and the duration of the larval stage of most tropical shelf species. While the

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The authors are in the Department of Oceanography, 1000 Pope Road, University of Hawaii, Honolulu, HI 96822.

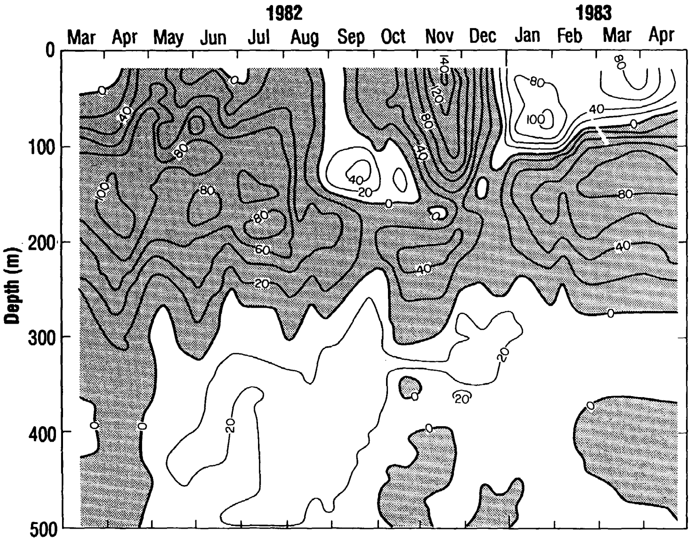

Fig. 2. Zonal velocity of currents on the equator at 159°W. Longitude during the 1982–83 El Niño event. Eastward flow is shaded. [After Firing *et al.* (*19*)]

shortest distance across the EPB is between Christmas Island and Clipperton Atoll (10°N), the shortest time of transport is probably along the equator where stronger currents exist (*3, 9*). The velocity of the core of the easterly flowing equatorial undercurrent (Cromwell Current) along the equator ranges from 100 to 150 cm/sec between the longitudes of 90° and 160°W (*3*). In contrast, the core velocity of the north equatorial countercurrent (NECC) running east between 5° and 10°N is only about 40 cm/sec (*3*). Assuming that larvae remain in core water, the transit time between Christmas and the Galapagos Islands along the equator would be about 70 days with a mean flow of 125 cm/sec and as brief as 55 days at peak flow, 150 cm/sec. This compares to about 155 days for transit from Christmas Island to Clipperton Atoll by way of the NECC (*10*).

While 55 to 70 days is longer than the larval life of most hermatypic corals, a few species are capable of postponing settlement for periods comparable to or in excess of this time (*11, 12*). Atoda (*11*) found the maximum survival time for larvae of *Galaxea aspera* to be 49 days, and Richmond (*13*) has shown that larvae of *Pocillopora damicornis* are able to remain competent for settlement up to 103 days possibly because of fat reserves gained from symbiotic zooxanthellae. Larval competency data for other marine invertebrates is scarce; however, Scheltema (*14*) and Zinsmeister and Emerson (*15*) have all shown that many tropical shallow water invertebrates produce teleplanic (long-lived) larvae.

Larval competency may also be affected by the temperature of the water in which dispersal occurs. Across the EPB during normal years the equatorial undercurrent is about 50 m to 200 m below the surface, and its temperature ranges between 14° to 25°C (*3, 16*). Water of this temperature may restrict the dispersal of warm water stenothermal invertebrate larvae, although the possibility also exists of the metabolism of such larvae being slowed, thereby extending competency and dispersal range (*16*). During El Niño years, equatorial circulation is quite different; the equatorial undercurrent often disappears altogether and is replaced by a warm eastward flowing current on the surface at the equator with core velocities up to 140 cm/sec (*3, 17*) (Fig. 2). This pattern of circulation would transport larvae in warm water (~25° to 29°C) across the barrier in a minimum of about 60 days.

After the 1982–83 El Niño, five species of IWP fishes were observed in the Galapagos Islands and another four at Cocos Island that were previously unknown from the eastern Pacific (*18*). IWP mollusks have also been noted as more abundant in the Galapagos following El Niño years (*19*), suggesting that high rates of recruitment and extinction of IWP forms may generally be associated with El Niño events. Local extinction of two hydrocorals and possibly one reef coral in the eastern tropical Pacific following the 1982–83 El Niño has been recently documented by Glynn and De Weerdt (*20*). Sporadic episodes of transport and recruitment have been termed "dispersal pulses" (*15*) and may also explain anomalous occurrences of tropical species off California and Peru during periods of El Niño (*4*).

Although El Niño currents clearly increase the probability of tropical shelf larvae crossing the EPB, elevated temperatures that accompany strong El Niño events are also known to cause widespread mortality (>95%) of established reefs (*20*) in some parts of the eastern Pacific, particularly in regions like the Galapagos Islands where corals are adapted to cool waters. Elevated temperatures in the Galapagos Islands may persist for almost 1 year (*20*). Hence, the combined result of El Niño–Southern Oscillation (ENSO) events in the Galapagos Islands might be to increase recruitment from the IWP at times when mortality of adult corals is high when more space

Table 1. Fossil coral genera exhibiting apparent successful dispersal between the IWP, the WA, and the EP during the Cretaceous and Tertiary. [After (*24, 25*)]

Time period	WA to EP	WA to IWP	EP to IWP	IWP to EP	IWP to WA	EP to WA
Early Cretaceous						
Middle Cretaceous	Myriophyllia Cyathopora Budaia					
Late Cretaceous					Cyclolites	Siderastrea
Paleocene				Haimesiastrea	Favia	Diploria
Eocene	Trochoseris Stephanocoenia Leptophyllastrea Hydnopora Astreopora			Montipora		Favites
Oligocene			Leptastrea			Oulophyllia
Miocene	Solenastrea	Pocillopora				Manicina
Pliocene				Gardineroseris*		
Pleistocene	Psammocora					
Recent	Agaricia		Stephanaria	Cycloseris		
Totals	11	1	2	4	2	5

From P. W. Glynn and J. Wellington in (*4*) (p. 173, figure 62).

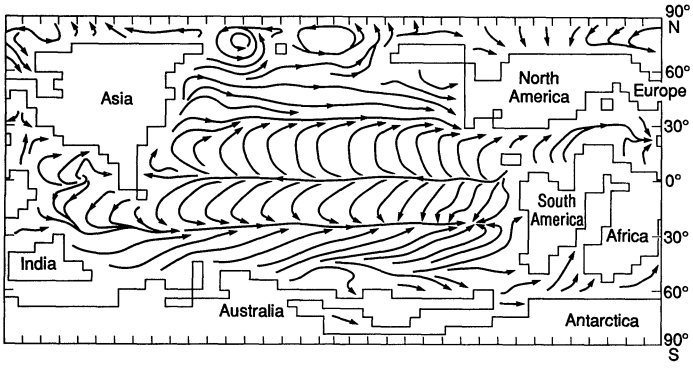

Fig. 3. Model of surface currents of the world in mid-Cretaceous time (~100 million years ago). [After Barron and Peterson (*28*)]

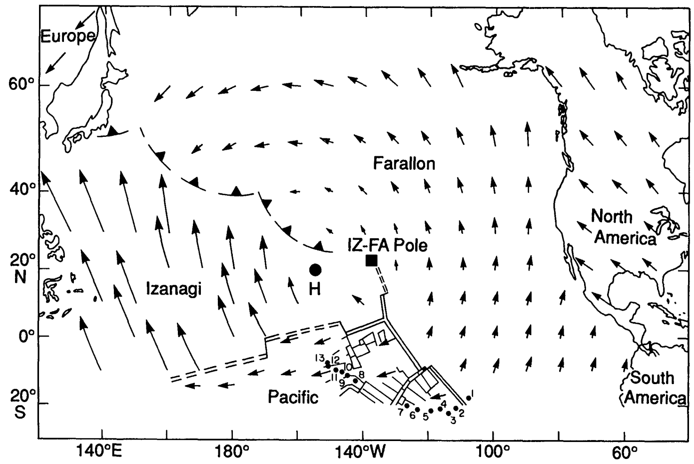

Fig. 4. Position of western Pacific guyots in the Pacific Ocean 110 million years ago. Paleopositions were determined by rotating them from their present positions (Table 2) to positions at 100 million years using the 100-million-year total reconstruction pole of Engebretson *et al.* (*41*, table 2) and then by two-thirds of the total stage pole angle about the 100-million- to 115-million-year stage pole. Poles originally are from Henderson and Gordon (*42*). The technique is described by Cox and Hart (*43*). Base map taken from Engebretson *et al.* (*41*).

is available for settlement. However, for settlement to be successful, newly recruited coral colonies would have to survive post–El Niño secondary disturbances such as high rates of bioerosion (*20*).

ENSO events occur about once every 4 to 9 years and very strong episodes are recorded about once every 50 to 100 years (*6*). The existence of large, old (100 to 350 years) coral colonies in the Galapagos that did not survive the 1982–83 El Niño event suggest events of this magnitude may even be more infrequent (*21*). Thus, in spite of enhanced IWP recruitment, the impacts of extreme ENSO events may combine to actually limit the buildup of reef deposits in the eastern Pacific (*6*). Colgan has argued that development of El Niño events intensified with the closure of the Panamanian Seaway 3.5 million to 3.2 million years ago (*6*). As to the antiquity of ENSO phenomeno in general, the paleoceanography of the source area, the western Pacific, may be even more important than uplift of the Panama Isthmus. Closure of the Indonesian seaway in the early to middle Miocene established a western boundary for equatorial circulation (*22*). While the coupled effect of this change on the ocean-atmosphere system has yet to be analyzed, a western boundary could be expected to assist in the formation of Kelvin surges, which in turn increase eastward equatorial flow of surface water during periods of ENSO. Thus, before the Indonesian seaway closed, the EPB may have been an even more formidable barrier to dispersal than it is today.

A final consideration concerning dispersal across the EPB is the possibility of long-distance dispersal of corals and invertebrates by rafting. Jokiel (*23*) has described colonies of *Pocillopora* up to 7 cm in diameter found attached to floating chunks of pumice which he estimated to be 2 to 3 years old. Clearly pumice rafts of this longevity would have no difficulty in crossing the EPB if situated in eastward equatorial currents. East to west transport of pumice would also be expected to take place in trade wind latitudes. In view of range extensions provided by rafted dispersal, it is surprising the EPB is as effective as it is in limiting dispersal across the Pacific. Perhaps few coral species are adapted to rafting as a mode of dispersal.

Antiquity of the EPB

Evidence of the age of the EPB comes from the following sources of information: (i) the fossil record of reef-building corals in the eastern Pacific (EP) relative to the western Atlantic (WA) and IWP

Table 2. Present location, summit depth, summit age, and paleopositions of Geisha guyots and mid-Pacific mountains. MA, million years ago.

Guyot or seamount	Present		Summit depth (m)	Age of summit fossils (MA)*	Position (91 MA)		Position (100 MA)		Position (110 MA)	
	Latitude	Longitude			Latitude	Longitude	Latitude	Longitude	Latitude	Longitude
Seiko Seamounts (13)†	34.23°N	143.83°E	1359	91	4.59°S	162.2°W	9.96°S	156.09°W	8.6°S	150.9°W
? (12)	34.22°N	144.18°E	1423	91	4.66°S	161.93°W	10.03°S	155.80°W	8.6°S	150.6°W
Winterer Guyot (11)	32.85°N	148.28°E	1405	91	6.55°S	158.75°W	11.93°S	152.60°W	10.4°S	147.4°W
T. Washington Guyot (10)	32.00°N	149.28°E	3567	91	7.50°S	158.02°W	12.89°S	151.85°W	11.4°S	146.6°W
Isakov Seamount (9)	31.55°N	151.22°E	1376	91	8.14°S	156.42°W	13.52°S	150.22°W	12.0°S	145.0°W
Makarov Seamount (8)	29.47°N	153.33°E	1317	91	10.38°S	154.79°W	15.76°S	148.54°W	14.2°S	143.3°W
Darwin Guyot‡ (7)	22.05°N	171.62°E	1253	91–97.5	17.36°S	147.64°W	22.41°S	130.78°W	20.5°S	125.6°W
? (6)	20.73°N	173.45°E	1262	91, 104–112§	18.43°S	135.67°W	23.41°S	128.71°W	21.5°S	123.5°W
Jacqueline Seamount (5)	19.32°N	176.73°E	1609	86.5, 104–112§	19.29°S	132.21°W	24.13°S	125.09°W	22.2°S	119.9°W
Shepard Seamount (4)	19.23°N	179.55°W	1664	86.5, 104–112§	18.63°S	128.56°W	23.31°S	121.36°W	21.3°S	116.3°W
Cape Johnson Guyot (3)	17.17°N	177.32°W	1778	104–112§, 91–119‖	20.11°S	125.84°W	24.65°S	118.52°W	22.7°S	113.4°W
Hess Guyot (2)	17.80°N	174.32°W	1720	91, 104–112§	18.71°S	123.11°W	23.12°S	115.75°W	21.1°S	110.7°W
Horizon Guyot (1)	19.38°N	169.00°W	1416	91, 86.5§	15.63°S	118.63°W	19.77°S	111.35°W	17.8°S	106.4°W

*See Matthews *et al.* in (*29*). †Numbers in parentheses represent the numbers in Fig. 4. ‡Ladd, Newman, and Sohl (*44*). §Winterer and Metzler (*45*). ‖Hamilton in (*29*).

provinces, and inferred routes of dispersal; (ii) zoogeographic affinity of fossil coral genera in the EP to the WA and the IWP province; and (iii) the geophysical history of ancient islands and displaced terranes and their tropical shallow water fossil assemblages.

The record of fossil coral genera in the eastern tropical Pacific throughout the Tertiary and Cretaceous Periods has been compiled by Durham (*24*) and revised by Heck and McCoy (*25*) and Glynn and Wellington (*4*). Durham's revised listing gives the occurrence of these genera in the IWP and WA and EP provinces over this time. The list (*4, 25*) consists of 46 genera of reef building corals.

The chronology of occurrence of these genera in the WA, the EP and the IWP zoogeographic provinces is used here to infer affinity and inter-province dispersal. Our analysis of these data is presented in Table 1, using the following criteria: Co-occurrence of a genus in two provinces at any time is taken as evidence of zoogeographic affinity. Direction of dispersal is determined on the basis of sequence of appearance in different time periods in the different provinces. Source area is determined for genera that first appear in only one province. If two genera appear in two or more provinces in the same time period, the direction of dispersal cannot be inferred. Only genera that exhibit unequivocal sequential appearance in different provinces are used to evaluate dispersal direction. For example, *Montipora* first appeared in the IWP and then in the EP, thus implying dispersal from west to east across the EPB.

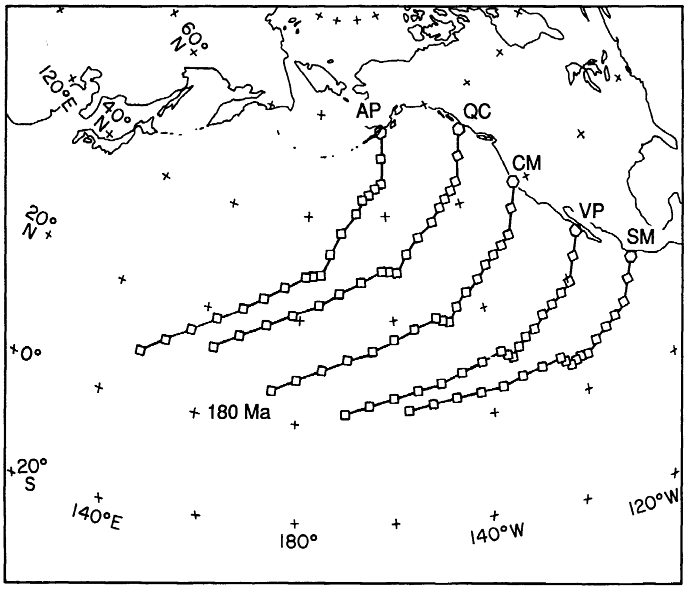

Fig. 5. Trajectories of oceanic plates in fixed North America coordinates determined by modeling motion between 180 million and 90 million years ago. Symbols are plotted at 5-million-year intervals. □, Pacific Plate and Farallon Plate; ○, docking point on North America. AP, Alaskan Peninsula; QC, Queen Charlotte Islands; CM, Cape Mendicino; VP, Viscaino Peninsula; SM, Southern Mexico. [After Debiche *et al.* (*32*)]

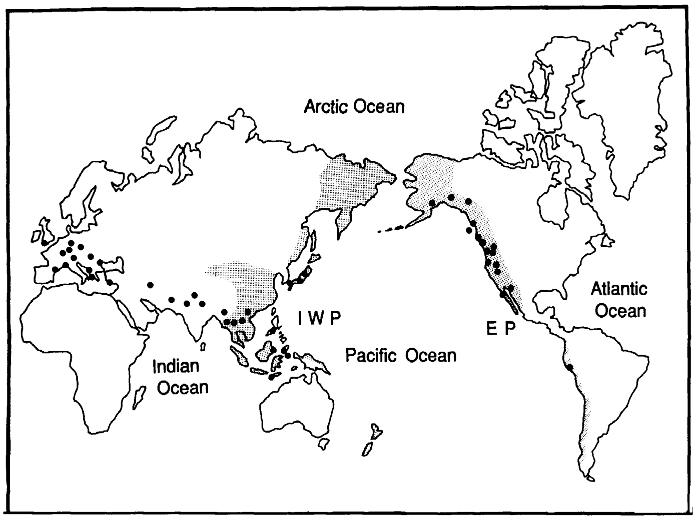

Fig. 6. Mesozoic displaced terranes (shaded) and localities (●) of Upper Triassic fossil coral and reef localities. [After Stanley (*35*)]

As expected, affinity between the EP and the WA between the Cretaceous and Recent period is much higher (0.90) than it is between the EP and the WA or the EP and the IWP (0.61 and 0.53, respectively). This is not surprising given the close proximity of the two American provinces and the open connection that existed between them until late Pliocene time (*6*).

The high rate of dispersal from the WA to the EP is probably also a result of the presence of a historical center of high coral diversity in the Atlantic. The rate of dispersal from the WA to the EP appears to have been particularly high during the Middle Cretaceous and the Eocene. The rate of dispersal between the two American provinces is significantly higher than between either American province and the IWP (Table 1). Durham's fossil record suggests that dispersal between the American provinces occurred 11 times from east to west and 5 times from west to east, compared to only 1 to 4 times between either American province and the IWP in either direction.

Whereas the general trends described above are probably correct, the Durham record is not complete, nor is it without artifacts. For example, the two cases of Atlantic reef-building coral genera (*Psammocora* and *Agaricia*) colonizing the EP in the Pleistocene and Recent (Table 1) must be artifacts of the fossil record because uplift of the Panamanian Isthmus is known to have closed the portal between the two areas before 3 million years ago in the Pliocene (*6, 26*). Dispersal must have occurred before this time even though these two genera do not show up in the pre-Pleistocene record of the EP.

Notwithstanding artifacts such as these, Durham's fossil coral record indicates that dispersal across the EPB has been relatively rare for all of Cretaceous and Tertiary time. Only nine genera from his revised list have been apparently successful in crossing the barrier in either direction between the American provinces and the IWP. These examples are *Haimesiastrea, Montipora, Gardineroseris*, and *Cycloseris* from the IWP to the EP; *Cyclolites* and *Favia* from the IWP to the WA; *Pocillopora* from the WA to the IWP; and *Leptastrea* and *Stephanaria* from the EP to the IWP. No particular time appears more favorable than any other except for higher westerly dispersal between the WA and EP during the Middle Cretaceous and Eocene. In particular, it is surprising that west to east dispersal across the EPB apparently did not increase in the late Tertiary as would be expected with the possible strengthening of ENSO phenomena in the Miocene and northward movement of the Line Islands (stepping stones) in the Miocene and Pliocene (*27*).

In the Cretaceous, the case for greater westerly dispersal in the EP is strengthened by the results of model studies of surface paleocirculation in the Pacific (*28*). Three-dimensional numerical ocean circulation model experiments indicate that flow during the mid-Cretaceous (~100 million years ago) in the central and eastern Pacific was likely dominated by transport producing strong westerly flow near the equator (*28*) (Fig. 3). Although speeds in the model are only indicated qualitatively, the predicted dominant current direction would have produced westward dispersal of tropical shelf species across the Pacific during the mid-Cretaceous.

Westerly transport across the EP in mid-Cretaceous time is also indicated by the presence of Texas-Mexican fossil reef corals (*Astrocoenia, Cyathophora, Diploastrea, Microsolena*, and *Montastrea*) on the summits of western Pacific guyots that drowned about 90 million to 110 million years ago when, as atolls, they were situated at the surface in the eastern Central Pacific near the equator (*29*) (Fig. 4). Shallow water foraminifera 85 million to 65 million years old from the Line and Marshall islands also show Carribean affinities (*30*).

The results of our plate reconstruction model show the paleoposition of the western Pacific guyots [Geisha Guyots, Wake Guyots, and mid-Pacific Mountains (MPM)] when they existed near sea level in the EP, 91 million, 100 million, and 110 million years ago (Table 2 and Fig. 4). A sea-level position of the Geisha Guyots (8 to 13 in Table 2) and MPM (1 to 6 in Table 2) is inferred by presence of the shallow-water corals dredged from their summits that are dated at 86.5 million to 118 million years ago. The model predicts that Horizon Guyot would have been the closest island to the Americas situated at 17.8°S and 106.4°W 110 million years ago (*31*) approximately 5225 km from the nearest land in Central or South tropical America (±10°S of the equator). Thus, at this time horizon even though the Pacific Ocean was about 30% wider than it is today, the distance across the EPB was essentially the same as the present (5400 km). In conclusion, the Texas-Mexican corals on the summits of Pacific guyots and the Pacific foraminifera affinities to the Caribbean indicate that east to west transport was likely stronger during the Cretaceous than it is today. Also the existence of the Geisha Guyots, Wake Guyots, and MPM at sea level in the central equatorial Pacific probably provided many stepping stones to dispersal during the mid-Cretaceous.

During the middle and early Mesozoic, the existence of suspect terranes of oceanic and continental origin in the central tropical Pacific (*32*) may have been another mechanism that assisted dispersal across the EPB. During this time, these terranes may have served a dual role in augmenting the dispersal of tropical shelf fauna across the EP; first, as island stepping stones for larval dispersal [Newton's Pantropic Model (*33*)], and second, by way of tectonic dislocation (displacement) of fossil assemblages (Noah's Arks) (*34, 35*). In the latter case, these terranes may have been fringed by coral reefs that eventually were transported by plate movement as fossil assemblages [Viking Death Ships (*35*)] into more northerly latitudes. Triassic terranes in western North America today contain fossil tropical mollusks and reef-building corals with affinities to western Pacific, in particular, IWP (*33–35*). For example, the Triassic Wallowa terrane, now situated in eastern Oregon and Idaho, contains a diverse assemblage of tropical bivalve species with affinity to Japan (19%), the Tethys (19%), North America (12%), and South America (12%) as well as relatively high (25%) endemic component (*33*). If the Wallowa terrane bivalve fossil fauna is compared to the molluskan fauna of Hawaii today, where only one species of American origin exists (*36*), it is probable that the Wallowa terrane was further east in the ancient Pacific than Hawaii is today, possibly reducing the width of the EPB. The high level of endemism of the Wallowa terrane suggests it was relatively isolated as are the Hawaiian Islands today, while still possibly serving as a stepping stone for the dispersal of teleplanic larvae.

The earliest known terranes present in North America that contain Tethyan fossils are Paleozoic in age (Carboniferous and Permanian) (*37*). During this time (360 million to 285 million years ago), the ancestral Pacific (Panthalassa) was much wider than it is today, and the southern continents (Gondwanaland) were connected with those in the north (Laurasia) in a unified land mass known as Pangaea (*38*). With the breakup of Pangaea, in particular its eastern sector [possibly Pacifica (*38*)], these terranes may have served as numerous stepping stones to dispersal, reducing the isolating effect of the width of Panthalassa (*39*). Better data on the fossil assemblages of North America should greatly improve our knowledge of this early period of earth history and paleozoogeography of the Pacific Ocean.

In summary, the EPB is the most effective oceanic barrier on the earth today to the dispersal of tropical shelf invertebrate faunas. Only about 4% of the modern coral fauna in the IWP is amphi-Pacific. This figure would probably be less were it not for ENSO events that appear to enhance eastward dispersal of tropical shelf fauna. The fossil record of reef-building corals suggests the EPB has been at least as effective as it is today in restricting dispersal throughout the Cenozoic. In the present, dispersal is almost exclusively west to east, whereas in the Cretaceous, fossil evidence and paleocirculation models suggest westward transport was dominant. Westward dispersal in the Cretaceous appears to have been enhanced by the presence of the Geisha Guyots, the Wake Guyots, and the Mid-Pacific Mountains, which were then island stepping stones in the tropical central Pacific. During the early Mesozoic and late Paleozoic, numerous terranes existed in the tropical Pacific. Their fossil assemblages now accreted to the North American cordillera, show they also may have served as stepping stones to dispersal across the Pacific (*33, 34*). Terranes could also have transported fossil reef assemblages across the Pacific (Panthalassa) by way of tectonic dislocation (*34*).

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in our model; and third, Horizon "island" may be younger than 110 million years ago. The third possibility is supported by the age of shallow water fossils (86.5 to 91 million years ago) on the summit of Horizon Guyot.

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Research Article

Response of a Protein Structure to Cavity-Creating Mutations and Its Relation to the Hydrophobic Effect

A. E. ERIKSSON,* W. A. BAASE, X.-J. ZHANG, D. W. HEINZ, M. BLABER,
E. P. BALDWIN, B. W. MATTHEWS†

Six "cavity-creating" mutants, Leu^{46} → Ala (L46A), L99A, L118A, L121A, L133A, and Phe^{153} → Ala (F153A), were constructed within the hydrophobic core of phage T4 lysozyme. The substitutions decreased the stability of the protein at pH 3.0 by different amounts, ranging from 2.7 kilocalories per mole (kcal mol^{-1}) for L46A and L121A to 5.0 kcal mol^{-1} for L99A. The double mutant L99A/F153A was also constructed and decreased in stability by 8.3 kcal mol^{-1}. The x-ray structures of all of the variants were determined at high resolution. In every case, removal of the wild-type side chain allowed some of the surrounding atoms to move toward the vacated space but a cavity always remained, which ranged in volume from 24 cubic angstroms (Å^3) for L46A to 150 Å^3 for L99A. No solvent molecules were observed in any of these cavities. The destabilization of the mutant Leu → Ala proteins relative to wild type can be approximated by a constant term (~2.0 kcal mol^{-1}) plus a term that increases in proportion to the size of the cavity. The constant term is approximately equal to the transfer free energy of leucine relative to alanine as determined from partitioning between aqueous and organic solvents. The energy term that increases with the size of the cavity can be expressed either in terms of the cavity volume (24 to 33 cal mol^{-1} Å^{-3}) or in terms of the cavity surface area (20 cal mol^{-1} Å^{-2}). The results suggest how to reconcile a number of conflicting reports concerning the strength of the hydrophobic effect in proteins.

IT IS GENERALLY AGREED THAT THE HYDROPHOBIC EFFECT IS the major factor in stabilizing the folded structures of globular proteins [see, for example, the recent reviews by Dill (*1*) and Sharp (*2*)]. Until recently, it has also been generally agreed that the strength of the hydrophobic effect, that is, the energy of stabilization provided by the transfer of hydrocarbon surfaces from solvent to the interior of a protein, is about 25 to 30 cal mol^{-1} Å^{-2} (*3*). However, some recent studies in which site-directed mutagenesis and protein denaturation were used suggest that the strength of the hydrophobic effect might be much greater. In a typical experiment, a hydrophobic residue within the core of a protein is substituted by a smaller hydrophobic residue and the resulting change in the stability of the folded versus the unfolded (or denatured) form of the protein is taken as a measure of the difference between the hydrophobic stabilization provided by the two amino acids. Such experiments carried out with different proteins (*4–6*) or at different sites within the same protein (*7*) have, however, given variable results. For example, Shortle *et al.* replaced each of the leucines in staphylococcal nuclease with alanine and found that the decrease in free energy of protein folding ranged from 1.6 to 5.8 kcal mol^{-1} (*7*). The latter value corresponds to stabilization of ~80 cal mol^{-1} Å^{-2}, a value about four times that estimated from solvent transfer experiments (*3, 8–10*). The reason for this discrepancy has not been resolved and remains the subject of debate. A principal difficulty in addressing

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The authors are in the Institute of Molecular Biology, Howard Hughes Medical Institute, and Department of Physics, University of Oregon, Eugene, OR 97403.

*Present address: Department of Molecular Biology, Biomedical Center, Box 590, S-751 24 Uppsala, Sweden.
†To whom correspondence should be addressed.