BIOGEOGRAPHY OF CORALS, SEAGRASSES, AND MANGROVES: AN ALTERNATIVE TO THE CENTER OF ORIGIN CONCEPT

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Abstract

McCoy, E. D., and K. L. Heck, Jr. (Department of Biological Science, Florida State University, Tallahassee, Florida 32306) 1976. Biogeography of corals, seagrasses, and mangroves: an alternative to the center of origin concept. Syst. Zool. 25:201–210.—A "center of origin" explanation for the distribution and diversity patterns of the organisms comprising the principal shallow-water habitats in the tropics—hermatypic corals, mangroves, and seagrasses—is highly unlikely, based on fossil data and the dispersal capabilities of the organisms. Instead, these biogeographic patterns are better explained by the existence of a previously widely-distributed biota which has since been modified by tectonic events, speciation, and extinction, in accordance with modern geological and biogeographical theory. [Corals; seagrasses; mangroves; biogeography; vicariance.]

The "center of origin" concept—that a taxon's place of origin is the region in which it is most diverse—is nearly axiomatic (Rotramel, 1973). Briggs (1961, 1966, 1967), Darlington (1957), and Mayr (1965) have all been active proponents of this assumption, although Darlington has warned against its application when a thorough fossil record does not exist to verify it. Other biogeographers (*e.g.* Cain, 1944, Croizat, 1958; Croizat *et al.*, 1974) also have strongly questioned the uncritical application of the center of origin concept. Despite these warnings and criticisms the concept has a facile appeal, and remains viable (for a recent example, see Müller, 1973).

The center of origin concept was originally conceived on the assumption that the positions of the continents remained constant through time. This implied that closely-related organisms inhabiting widely-separated land masses or bodies of water must have somehow dispersed over long distances. Of course, it can no longer be accepted that the continents have remained stationary, and as a result, it is necessary to critically reevaluate the validity of earlier conclusions involving the center of origin concept. In place of the notion that centers of origin can be identified by centers of diversity, we advocate acceptance of the following ideas which take into account current biogeographical, ecological, and geological reasoning: (1) Long-term climatic and tectonic events cause environmental changes with important biotic consequences; hence, present centers of diversity may not have always been so (*cf.* Carson, 1970); and (2) localized ecological processes, such as extinction and species-area relationships, are significant determinants of species diversity independently of where the taxon originated; thus, present distributions and diversity patterns represent more than long-term, monotonous radiation of species from some point of origin. An important ancillary point is that the evidence for long-distance dispersal of widely-distributed organisms is often tenuous, though it is rarely presented as such.

To illustrate how these newer ideas can be applied in explaining biographical patterns, we use three important groups of marine organisms and compare results obtained from them with those generated by the center of origin concept. We have chosen hermatypic corals, seagrasses, and mangroves for a number of reasons: (1) They are the principal shallow-water sessile assemblages throughout the world's tropics; (2) they presently co-occur throughout the tropics, and their diversity patterns and

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[1] Order of authorship was determined by the toss of a coin.

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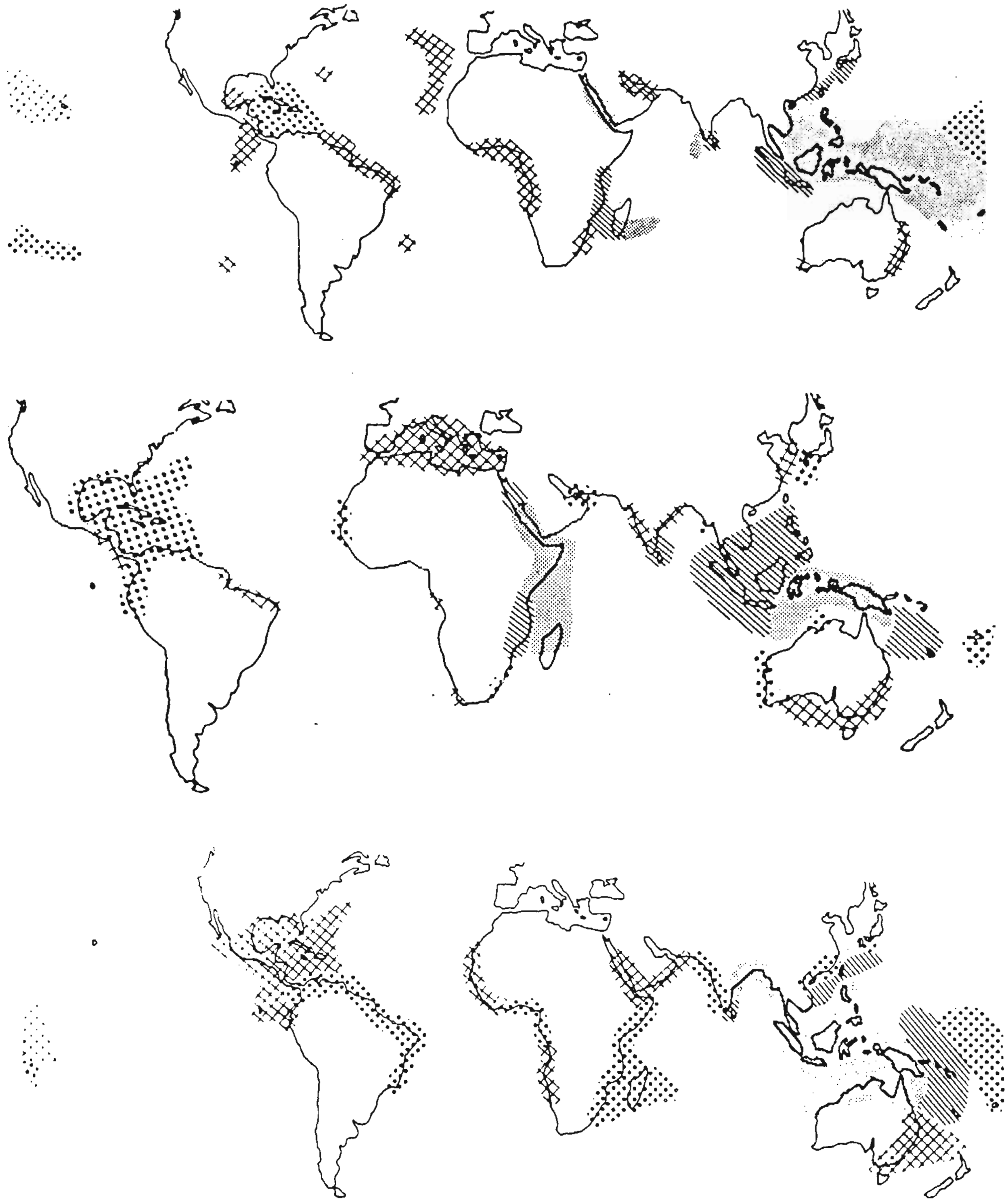

FIG. 1.—Geographical distribution and generic richness for hermatypic corals (above), seagrasses (middle), and mangroves (below). The area where the maximum number of genera occur was taken as 100%, and all other areas scaled as 75–100% of maximum (small dots), 50–75% of maximum (lines), 25–50% of maximum (large dots), 1–25% of maximum (hatching). In the Caribbean there is a maximum of 24 coral genera, 5 mangrove genera, and 4 seagrass genera in any one location; and in the I-WP there is a maximum of 57 coral genera, 16 mangrove genera, and 7 seagrass genera in any one location. Data for corals from Stehli and Wells (1971); data for seagrasses from den Hartog (1970); and data

▒ 75-100%
▧ 50-75%
⁘ 25-50%
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dispersal capabilities are thereby anemable to comparison; and (3) they each have a large number of associated organisms, a situation which allows a further testing of alternatives by evaluating diversity patterns among these additional groups.

We propose that present global distribution and diversity patterns of corals, seagrasses, and mangroves are best explained by the existence of widely-distributed ancestral biotas which have since moved and been modified by tectonic events, speciation, and extinction (*cf.* Axelrod, 1952; Chandler, 1954; Chaney, 1940; Seward, 1934). Although aspects of our proposal have been noted by specialists dealing with each of the groups alone (see Guppy, 1906; Newell, 1971; Ostenfeld, 1915; Setchell, 1935; Vaughn and Wells, 1943), the ideas which we present have not been unified into a synthetic explanation of the current distributional patterns of near-shore tropical biotas. We subscribe to the idea that consideration of a number of distributional patterns simultaneously elucidates relationships that are obscure when individual patterns are considered (*cf.* Croizat, 1964; Croizat *et al.*, 1974).

Generic diversity is used throughout our discussion to facilitate comparison of current distributional data with fossil records, which are not reliable at the species level, and because the taxonomy of both corals and seagrasses is presently unstable at the species level.

CO-OCCURRENCE AND DIVERSITY PATTERNS OF CORALS, SEAGRASSES, AND MANGROVES

Patterns of co-occurrence

There are several references to the fact that mangroves and seagrasses have similar worldwide distributions (den Hartog, 1970; van Steenis, 1962, 1963), and that grass beds and mangrove swamps are often adjacent to coral reefs (*e.g.* Stephenson and Stephenson, 1950; Stoddart, 1969). The extent of this pattern of global co-occurrence is illustrated in Figure 1.

The current association among coral reefs, seagrasses, and mangroves is not fortuitous. Instead, there is a functional, albeit facultative, successional sequence involving the three groups (Chapman, 1940; Price, 1971; Welch, 1962, 1963). This little-known successonal sequence has been described in detail in the Caribbean by Welch (1962). It initially involves the colonization of hard substrates and the development of reef structures by hermatypic corals. Sediment-trapping filamentous algae then colonize the developing reef. These algae are succeeded by mat-forming calcareous algae, especially members of the genus *Halimeda*, which provide a substrate for the invasion of seagrasses. Most often the seagrass *Thalassia* becomes dominant and further sediment accumulation occurs. Gradually the substrate is built upward until it provides a suitable habitat for colonization by mangroves, which eventually shade out the seagrass growing beneath them.

We suggest that this association of corals, seagrasses, and mangroves developed during the Cretaceous, soon after the evolution of mangrove (Raven and Axelrod, 1974) and seagrass (den Hartog, 1970) lineages and the diversification of the scleractinian corals (Newell, 1971); and that these three groups co-occurred through the Tethyan Realm. Figure 2 shows fossil records for corals, seagrasses, and mangroves plotted on maps outlining the position of the continents during the mid-to-late Cretaceous (*ca.* 100–75 m.y.b.p.) and during the Eocene–Miocene

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for mangroves are our own compilation derived from numerous distributional records. The mangrove genera include *Rhizophora*, *Brugeria*, *Ceriops*, and *Kandelia* (Rhizophoraceae), *Sonneratia* (Sonneratiaceae), *Avicennia* (Avicenniaceae), *Xylocarpus* (Meliaceae), *Aegiceras* (Myrcinaceae), *Heritiera* (Sterculiaceae) *Laguncularia* and *Lumnitzeria* (Combretaceae), *Exocoecaria* (Euphorbiaceae), *Scyphiphora* (Rubiaceae), *Aegialitis* (Plumbaginaceae), *Nypa* (Palmaceae), *Pelliciera* (Theaceae), *Camptostemon* (Bombacaceae), *Osbornia* (Myrtaceae), *Machaerium* (Leguminosae), and *Brownlowia* (Tiliaceae).

FIG. 2.—Above, partial Cretaceous fossil record for corals (○), seagrasses (×), and mangroves (●). Coral records from Coates (1973); seagrasses from den Hartog (1970); and mangroves from Chandler (1954), Hackner (references in unpub. m.s.), and Muller (1970). Opposite, partial Eocene–Oligocene–Miocene fossil record. Symbols same as in (a). Coral records from Vaughn and Wells (1943); seagrasses from den Hartog (1970); and mangroves from Fuchs (1970), Gray (1960), Hackner (references in unpub. m.s.), Langenheim *et al.* (1967), Moore (1973), Muller (1970), and Reid and Chandler (1933). Maps redrawn from Smith *et al.* (1973).

interval (*ca.* 54–10 m.y.b.p.). These data show that the three groups had a pan-Tethyan distribution, although they do not necessarily imply that these occurrences were contemporaneous. Van Steenis (1962) has proposed that the fossils of mangroves found outside the present tropics are "allochthonous drift material," rafting their way from the tropics to their temperate resting places, and similar proposals could be advanced to explain the occurrence of fossil corals and seagrasses. Such suggestions are not necessary in view of the paleoclimatic data which are now available for these areas.

In summary, there is reason to suspect a long-standing pattern of co-occurrence of corals, seagrasses, and mangroves that may

FIG. 2.—Continued.

be explained, in large part, as arising from modification of the environment by one group providing an opportunity for colonization by another. Differences in the frequency of co-occurrence through time may, however, be modified by local extinctions resulting from tectonic and climatic changes. The point we stress here is that regardless of how long the close association among hermatypic corals, seagrasses, and mangroves has existed, it is important to note how wide-spread they were at a time predating wide dispersal of the continents.

Patterns of diversity

The similar patterns of current generic richness for the three groups are demonstrated in Figure 1. The strength of the relationship can be better appreciated, however, if the numbers of genera in each of the three groups are correlated at the 44 locations world-wide for which data on all three groups are available. Table 1 shows that all of these correlations are highly significant ($P < .001$).

The most parsimonious explanation of the similar global patterns of diversity among the three groups in that they are the result of areal effects and differential probabilities of isolation that affect the three groups in a similar manner. Two examples will show how this explanation of the biogeographic patterns differs from previous interpretations.

Van Steenis (1962), in attempting to explain patterns of mangrove diversity based on the assumption that the I-WP was the center of origin for the group, has postulated that there was radiation from the I-WP accomplished by currents which spread the propagules westward to East Africa and eastward across the Pacific, and finally across the Atlantic to the west coast of Africa. Stehli and Wells (1971) show that in the I-WP center of diversity, the average generic age of hermatypic corals is lower than anywhere else. In addition, there are more or less concentric circles spreading out from the I-WP which delimit areas of greater average age [similar patterns are also shown by mangrove genera (Muller, 1964)]. Stehli and Wells interpret these patterns as showing a rapid

TABLE 1. CORRELATIONS OF GENERIC DIVERSITIES AMONG THE THREE GROUPS.[1]

Variable Pair	Spearman's Corr. Coeff.	Signif.	Kendall's Corr. Coeff.	Signif.
Coral with Grass	0.6252	< 0.001	0.5003	< 0.001
Coral with Mangrove	0.6108	< 0.001	0.4769	< 0.001
Grass with Mangrove	0.5079	< 0.001	0.3839	< 0.001

[1] $N = 44$. Locations are from Stehli and Wells' (1971) sample sites for which current numbers of genera present for all three groups were known.

evolution of coral genera in the I-WP, with subsequent outward radiation. Both of these explanations call for some emigration from a diversity center, often involving very long distances. It has been proposed (Briggs, 1961, 1966, 1967) that this outward radiation occurs as a result of young (in the geologic sense), strong competitors forcing older taxa out of the "optimal" habitats. An alternative hypothesis is that outward radiation is simply the result of passive dispersal over time. Regardless of the driving mechanism, it is very difficult to conceive of long-distance dispersal by currents for any of the three groups considered here. Most genera of tropical seagrasses do not have buoyant fruits, and those that do have the most restricted distributions (den Hartog, 1970). Although Guppy (1906) discounted any possibility that mangrove seedlings make transoceanic crossings, the main evidence which allowed the possibility of long-distance dispersal, the presence of *Rhizophora mangle* in Fiji, Samoa, and Tonga, was difficult to refute. It now appears more likely, however, that the presence of *R. mangle* on these islands is a result of introductions by man (Chapman, 1970; Heyerdahl, 1963). Even corals, which possess planktonic larvae, do not appear to disperse routinely over long distances (Connell, 1973 and included references), although the presence of I-WP genera on the western but not the eastern coast of the Americas would seem to counter this suggestion (Dana, 1975; Newell, 1971). However, many extant I-WP genera occurred throughout the Caribbean and Eastern Pacific regions prior to the closure of the isthmus of Panama (Stoddart, 1969). It has been assumed that most I-WP genera became extinct in the Eastern Pacific early in the Tertiary, and that some have reestablished themselves here since the Eocene by larval dispersal from the I-WP (Dana, 1975; Newell, 1971). In view of the poor dispersal abilities of coral larvae, and the lack of extensive fossil data from the Eastern Pacific, the contention that I-WP coral genera have reimmigrated into the Eastern Pacific region is tenuous. Our alternative explanation is that the formerly widespread coral biota has since been largely eliminated in the Caribbean, but that some refuges existed on the western coast of the Americas, which allowed the continued existence of the I-WP associated genera (Heck and McCoy, in prep.). These refuges were probably located on offshore islands where the effects of climatic, tectonic, and sea-level changes would have been less drastic. An analogous situation in which a widespread taxon has become a western American relict since the joining of North and South America is the mangrove genus *Pelliciera* (Fuchs, 1970; Langenheim *et al.*, 1967). As well, many other groups, such as foraminiferans, echinoids, and molluscs, exhibit similar biogeographic patterns (Durham and Allison, 1960; Woodring, 1966).

Our explanation for the above distributional and age patterns differs from that of Stehli and Wells and van Steenis in that it does not require the invocation of unproven long-distance dispersal or competitive superiority. Instead, we suggest that the

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older groups of genera around the I-WP diversity center represent a formerly widespread biota which became established by a series of small range extensions throughout the continuous Tethys Seaway. We also suggest that genera (as well as species) are accumulating in the I-WP area now, rather than necessarily having originated there with subsequent outward dispersal. This accumulation is due, we propose, to the simple fact that the present-day centers of diversity contain many islands which provide greater shoreline area for colonization and increased chances for isolation and diversification (*cf.* Newell, 1971; Stehli and Wells, 1971).

In summary, there is no good evidence for long-distance dispersal of the three groups. As well, the fossil record indicates the existence of a formerly widespread biota. Hence, we stress evolutionary diversification resulting from an interplay among speciation, extinction, and tectonic events to account for current diversity patterns. This explanation is dynamic and invokes processes known to operate currently. It does not, as do previous explanations, rely upon unlikely processes that produce patterns unchanged over vast stretches of time.

PREDICTIONS

Below we test some predictions that follow from our model.

Prediction 1. Corals, seagrasses, and mangroves provide habitats for characteristic species assemblages (associates). Thus, there should be a number of globally-distributed organisms associated with the three groups which are likely a remnant of Tethyan distributional patterns.

Ideally, the fossil record would be used to verify the generic ages of associates which are currently widespread throughout the tropics. However, since the fossil record is not sufficiently complete to permit this we must use present-day distributions, and evaluate our prediction indirectly. It is not enough that genera of mangrove, seagrass, or coral associates presently co-occur on a global scale since this could conceivably be the result of transoceanic dispersal. To minimize this problem we exclude from consideration all circumtropical congenerers that are also conspecifics, thereby reducing the chances of mistaking long-distance dispersers for remnants of a Tethyean biota. This follows from the work of Scheltema (1971) who found that, for marine organisms which disperse routinely over long distances, little morphological differentiation occurs between populations on either side of the intervening span of ocean, and such populations are usually considered members of the same species. There is the possibility that some species which are good long-distance dispersers and are circumtropically distributed may actually be remnants of a previously widespread biota and are examples of the phenomenon we are considering. Thus, because we do not consider conspecifics our evaluation is likely conservative.

With this restriction in mind, fishes associated with coral reefs contain many generic similarities on either side of the isthmus of Panama which represent remnants of widespread Tethyean ichthyofaunal assemblages (Rosenblatt, 1963). Myers (1940) has pointed out the large number of generic similarities that lack specific identity between Old World and New World fish faunas (*eq. Chaetodon, Pomacentrus, Abudefduf*), and actually considers the Caribbean ichthyofauna to be a depauperate subset of the I-WP fish fauna. The crab fauna associated with mangroves also shows several shared circumtropical genera without species identity, including *Uca, Sesarma,* and *Cardiosoma* (Warner, 1969 for Caribbean genera; McNae, 1968 for I-WP genera), as do a number of plant genera associated with mangroves, such as *Acrostichum* (Filices), *Derris* and *Entada* (Leguminosae), and *Sporobolus* (Gramineae). Among grass-bed associates there are many genera of decapod crustaceans which are common to Old and New World areas, including *Alpheus, Portunus, Callianassa, Hippolyte,* several hermit crab genera, and others (Thomassin, 1974 for Indian Ocean genera; Heck, 1976 for Caribbean genera). Several genera of infaunal molluscs are also shared between the I-WP and the Caribbean, including *Codakia, Anodontia, Ctena, Pinna, Atrina*, and others (Kira, 1962 for I-WP genera; Jackson, 1972 for Caribbean genera). This large number of similarities, which is by no means exhaustive, substantiates our first prediction. If these generic similarities are due to long-distance dispersal, it is a very infrequent dispersal, with gene transport so rare subsequent to the original introduction that speciation has occurred. It seems more likely that they are cases of classic allopatric speciation (Mayr, 1963).

Prediction 2. Since it is known that mangroves and corals are more diverse and have a lower average generic age in the large I-WP (data not available for seagrasses, see above), the same should be true for the associates of the three groups.

This second prediction is partially confirmed by the well-known pattern of maximal richness in the I-WP for the coral reef ichthyofauna (Myers, 1940) and the mangrove crab fauna (MacNae, 1968), for example. As noted previously, the fossil record is not complete enough to evaluate whether I-WP associates are of lower average generic age, and we have not been able to devise an indirect assessment of this question. Until the appearance of more fossil data this must go unevaluated.

Prediction 3. Areas other than the I-WP which provide large amounts of habitable area and relatively high chances of isolation should also have higher diversities than areas not possessing such characteristics.

The final prediction is verified for corals, which have a secondary center of diversity in the island-rich Caribbean area (Figure 1). Although the Caribbean does not *appear* to be as prominent a center of diversity for mangroves and seagrasses as for corals, this is due to the fact that there are absolutely fewer genera of mangroves and seagrasses than corals (see legend of Figure 1), and that mangroves and seagrasses are more widely distributed. For example, there are no genera of seagrasses endemic to the New World and only one endemic genus of mangrove, while there are a large number of endemic corals. The entire problem may simply reflect a taxonomic bias in that the apparently slow rate of taxic evolution among the seagrasses and mangroves could be an artifact arising from the small chance of observing changes in their relatively simple morphology when compared to the morphologically complex corals (*cf.* Schopf *et al.*, 1975), or may reflect an actual slow rate of evolution, at least for the seagrasses (den Hartog, 1970).

There are some areas of high diversity which are not explained by the mechanisms we have proposed to operate in the I-WP and Caribbean. These areas are along the eastern coast of Africa, the southern tip of India, and the Red Sea (Figure 1). The high diversities there may reflect the proximity of these areas to one another and to the I-WP during a large part of their geologic history (Figure 2). In fact, the entire region encompassing these areas can be considered a part of the I-WP during the Cretaceous and shortly thereafter. The depauperate regions now occurring between these diversity centers are probably a result of extinctions of tropical species concomitant with the northward movement of the continents (*cf.* Hughes, 1973).

The predictions outlined above are not necessarily inconsistent with a center of origin concept. To the advantage of our model, however, we have not been forced to invoke numerous, identical chance movements over long distances by organisms with different means of dispersal (an untestable proposal); nor have we been forced to contrive mechanisms to explain radiation from some ancestral center of origin. Additionally, some situations which appear to contradict our model (see prediction 3) are explained by internally consistent mechanisms: we have not had to resort to invoking unlikely "chance events" as have many proponents of the center of origin concept.

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