

## A Review of the Tectonic History of New Guinea and its Significance for Marine Biogeography

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**Abstract.** Advances in our understanding of the geological history of the Indo-West Pacific Ocean during the past 20 years have provided new insights to build a framework to test hypotheses concerning distribution patterns of marine taxa. New Guinea, including Irian Jaya and Papua New Guinea, is located on 5 lithospheric plates. The southern part of New Guinea has been located on the northern part of the Australian plate at least since the Australian craton began rifting from eastern Gondwana during the late Triassic to Middle Jurassic (230–160 MA). The northern part of New Guinea comprises at least 32 separate tectono-stratigraphic terranes that collided throughout the late Cenozoic. These terranes along with the regional tectonic history of the region, have important implications for the biogeographic distribution patterns of marine taxa.

Marine distribution patterns can best be interpreted by incorporating the geological history of the biogeographic areas under study. In New Guinean tectonics and biogeography, a striking co-existence of a tectonic zone composed of many independent parts with a marine biosphere of high diversity is apparent. Three hypotheses which help account for such high diversity in a geologically complex area are: 1) longitudinal displacement of whole faunas passively by plate tectonic motion; 2) emergence of land barriers during the great Miocene collision event between Gondwanic Australia/New Guinea and Laurasian SE Asia; and 3) the Plio-Pleistocene sea level fluctuations which produced land barriers and fragmented island archipelagos.

A correlation exists between biogeographic pattern and geological history in modern reef corals. An hypothesis of successive isolation is presented to explain the biogeography of reef corals and illustrates the potential of geological history to shed

light on biotic distribution patterns in New Guinea and elsewhere.

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### Introduction

The geological complexity of the Indo-West Pacific Ocean can probably best be visualized by considering the occurrence of at least eight island arcs (New Hebrides, Solomons, New Ireland-Manus, New Britain, Yap, Halmahera, Banda, and Sulawesi-Sangihe) and three oceanic plateaus (Euripeik and Caroline rises, Onton-Java plateau) between the Tonga Arc and Borneo (Silver and Smith 1983). Indeed New Guinea (Irian Jaya and Papua New Guinea) rests on no less than 5 lithospheric plates (Fig. 1) (Crook 1989). Such geological complexity is bewildering to biogeographers searching for congruence between geological pattern and tropical marine faunal and floral distributions. Recent work on the geology of the Indo-West Pacific has resulted in a coherent, if still incomplete, picture of the tectonic history of the region. The first goal of this paper is to simplify and summarize the major geological events of concern to tropical marine biogeographers in general and New Guinea marine biogeographers in particular.

The island of New Guinea, along with other centrally located Indo-Pacific islands, has long been known to have a high diversity of marine taxa. The high diversity has been generally explained by a center-of-origin hypothesis, but more recent workers have noted that that hypothesis is basically untestable as an historical explanation of distribution patterns (McCoy & Heck 1976, 1983; Rosen 1984). Other hypotheses of Indo-West Pacific tropical ma-

rine biogeography are based on either dispersal capability of the adult and/or larval planktonic stage of marine animals and their relationship to oceanic current patterns (Jablonski and Lutz 1983; Scheltema 1986), reliction (Newman 1991), or vicariant events which rely on relating present distribution patterns to past geological events (Pandolfi 1992; Springer 1982; Rosen 1984; Wallace et al. 1991). The second goal of this paper is to relate the geological information to possible mechanisms for distribution patterns of New Guinea marine taxa.

### Geological Setting of New Guinea

#### *Paleozoic, Mesozoic, and Early Cenozoic History of Australia and New Guinea*

The geological history of the southern portion of New Guinea has been intimately allied with that of Australia since the Paleozoic. The Australian craton (the stable part of the continental crust) was part of eastern Gondwana through the Paleozoic until the mid-Mesozoic. The southern portion of New Guinea is and has been a part of the Australian plate at least since the Australian craton began rifting from eastern Gondwana during the Late Triassic to Middle Jurassic period (230–160 MA—million years before present). The rifting formed the continental margin of Australia and was a contin-

uous event which migrated southwestwards from Papua New Guinea through Irian Jaya into Western Australia, where it is related to the opening of the Indian Ocean (Pigram & Panggabean 1984). The close tectonic association between Australia and southern New Guinea continued throughout the remainder of the Mesozoic and Cenozoic.

The progressive break-up of Gondwana, referred to as the Jurassic rifting event, started at about 160 MA (Late Jurassic/Early Cretaceous) when India separated from Antarctica/Australia (including part of New Guinea, part of East Indonesia, and some of the Pacific Islands) and from Africa and South America. A change occurred during the Eocene, in which India and Australia, originally on separate plates, coalesced (McGowran 1978). The northward drifting of the Indian continental fragment resulted in a collision with Laurasia about 55 MA (mid-Eocene). Meanwhile at about 53 MA, Australia/New Guinea separated from Antarctica where a new ocean ridge developed which continues spreading to this day.

As Australia and the southern autochthonous portion of New Guinea belonging to the Australian craton drifted northward, the edge of the craton collided with a complex subduction system, including several island arc complexes, oceanic plateaus and micro-continents (Pigram & Davies 1985, 1987) during the middle to late Oligocene

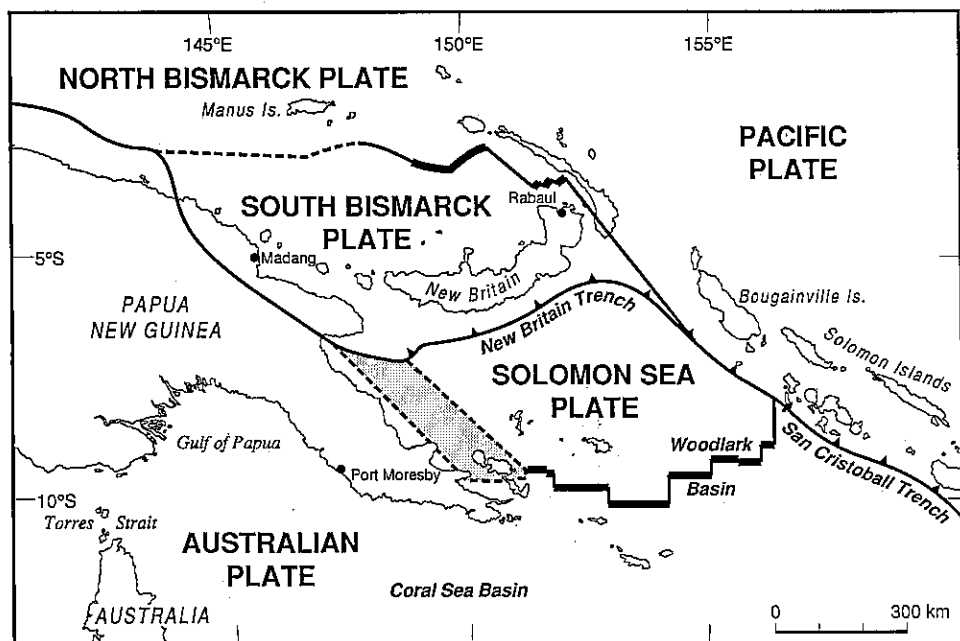


Fig. 1. Plate boundaries in Papua New Guinea. New Guinea is an area of complex tectonism where 5 lithospheric plates converge (after Crook, 1989).

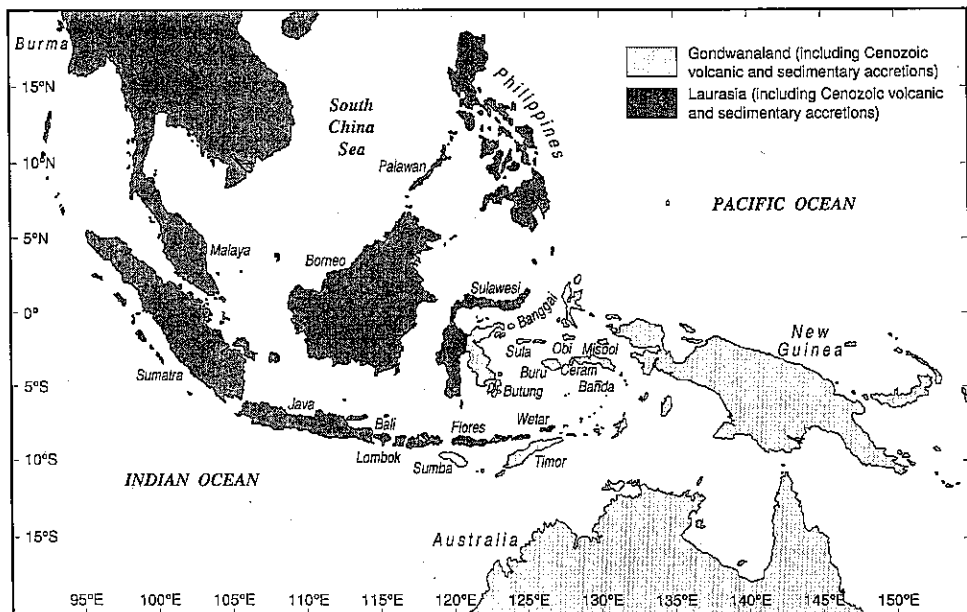
(Pigram et al. 1989). In the north, this arrival initiated development of the New Guinea Orogen, which consists of a southern para-autochthonous portion (Papuan Fold Belt) and a northern allochthonous portion comprising numerous terranes that collided throughout the late Cenozoic (Pigram & Davies 1985, 1987). In the south, the result was the development of the southern Papua New Guinea carbonate platform which lasted from the Late Oligocene to Middle Miocene (Pigram et al. 1989).

#### *Southeast Asia, the Malay Archipelago and the Miocene Collision Event*

Southeast Asia (Fig. 2; South Tibet, Burma, Thai-Malay Peninsula and Sumatra) was attached to northern Australia/New Guinea during the Late Paleozoic. It was rifted apart during the Jurassic rifting event (160 MA). From 200 MA (Early Triassic) to 50 MA (Middle Eocene) the two halves of the Malay Archipelago remained far apart (Audley-Charles 1981). Then, from the mid-Miocene (15 MA) to the Pliocene (5 MA) a progressive collision, the great mid-Miocene collision, started between the Australian/New Guinea component of Gondwana and the Asian component of Laurasia. East Indonesia

was largely created by this great mid-Miocene collision.

Convergence probably started as the Sula Platform/Peninsula portion of Australia/New Guinea collided with the rest of Sulawesi at around 15 MA (Fig. 2). The Sula Platform may have been rifted from New Guinea sometime between the Cretaceous and late Miocene (Pigram et al. 1985; but see Hamilton 1979, Norvick 1979, and Pigram & Symonds in press for alternative views). The Moluccan Islands are sinuous due to a continuous 10 MA interval of collision between the irregular northern edge of the Australia/New Guinea continent and the Banda Island Arcs to the northwest (Audley-Charles et al. 1981), or simply because the original microcontinent was long and narrow (Pigram, pers. comm 1992). Subduction of sub-ocean lithosphere belonging to the Australian/New Guinea plate occurred beneath the Banda Arc (Fig. 2). The subsequent collision of Australia with the islands of Alor and Wetar to create Timor occurred in the early Pliocene after all the oceanic lithosphere had been consumed by subduction (Fig 2). Post-collision land has also arisen in the collision zone. In the islands east of Java the oldest rocks are Miocene and great uplift occurred during the Plio-Pleistocene (see below).



**Fig. 2.** Southeast Asia, the Malay Archipelago and Australia/New Guinea. The great Mid-Miocene collision event brought together elements of Gondwana (stippled) with Laurasia (shaded). Convergence probably started as the Sula Peninsula of Gondwanic Australia/New Guinea collided with the rest of Sulawesi at around 15 MA. The Australian/New Guinea lithosphere was subducted beneath the Banda Arc (Inner Laurasian: Flores and Wetar and north to Banda; Outer Gondwanic: Timor around to Ceram and Buru). This was followed by a continuous 10 MA interval of collision between these two areas (after Audley-Charles 1981).

*Australia/New Guinea and the Indian Ocean*

McGowran (1978) discussed the evolution of the Indian Ocean in the area between India, Australia, and Antarctica in terms of three historical phases: 1) A spreading ridge develops with a NE/SW trend from the Middle-Late Jurassic to the Late Cretaceous; 2) from 70–85 Ma the spreading system now strikes East-West and lasts until the Eocene; and 3) from the Eocene, development of the present NW/SE strike spreading ridge. During the Cretaceous and earliest Tertiary India was moving rapidly northward. During this time, the crest of the Ninetyeast Ridge on the Indian Plate was marked by a line of small islands that had become submerged by the Miocene (Kemp & Harris 1975).

*New Guinea Terranes: Oligocene to Pliocene*

Pigram & Davies (1985, 1987), in a comprehensive discussion of the tectonic history of New Guinea throughout the Cenozoic, identified 32 tectono-stratigraphic terranes of both continental and oceanic affinities within the New Guinea Orogen (Fig. 3). Some terranes were amalgamating, forming composite structures in ocean basins far from the edge of the craton as early as the Eocene, but did not dock until the late Oligocene. Pigram & Davies

(1987) suggested that although no terrane accretion has occurred to the east of Sarera Bay (northwestern Irian Jaya) since the Pliocene (2 MA), the opening of the Woodlark Basin is currently dismembering the eastern end of the East Papua composite terrane (Fig. 1). Crook (1989) suggested that the collision between the Finisterre Terrane and the New Guinea Orogen was likely to be Pleistocene in age, but Abbott & Silver (1991) placed this collision in the Pliocene (3 MA).

Approximately 45% of the New Guinea terranes have continental affinities. Many of these were displaced portions of the northern edge of the Australian craton and would never have been very far away from it; others, however, were formerly parts of Gondwana that were detached early in the Mesozoic and had a subsequent history wholly independent of the Australian craton before docking in the mid- to late-Oligocene. Some of the oceanic terranes were plateaus, seamounts, or parts of island arc complexes, whilst others are composed of deep-water chert or carbonate.

*Quaternary Tectonics and Sea-level Fluctuations*

Glacial sea-level lows resulted in drier and more seasonal climates than exist today as well as increased land area in the area between Malaysia,

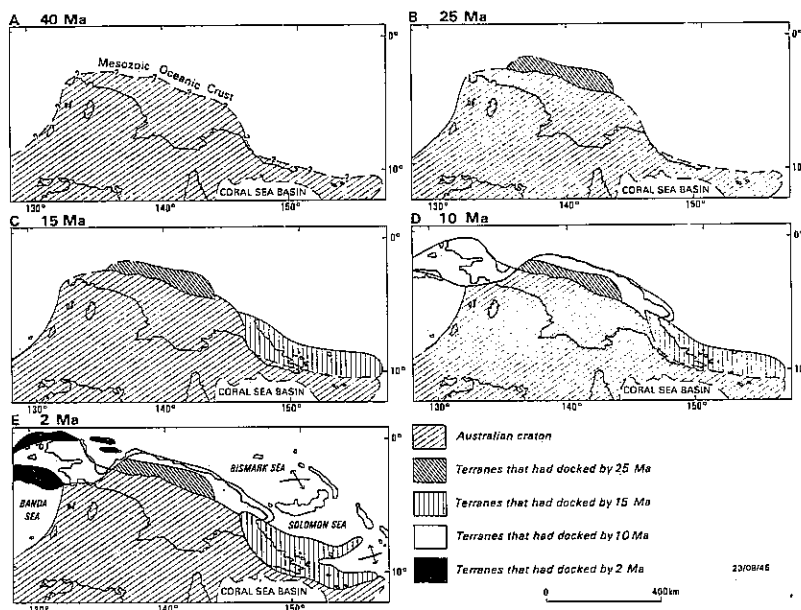


Fig. 3. Accretionary history of the New Guinean terranes according to Pigram & Davies (1987). The terranes are shaded according to the time of docking. Pigram & Davies (1987) have identified 32 tectono-stratigraphic terranes in New Guinea. Some of the terranes are composite, having amalgamated far from the edge of the craton as early as the Eocene. Docking commenced in the late Oligocene and terminated in the Pliocene. Reproduced with permission of C. Pigram and the Geology & Geophysics Branch, Bureau of Mineral Resources, Australia.

Indonesia and Australia/New Guinea. Morley & Flenley (1987) reported that during the past 140,000 years, major sea level lows have ranged from about 50–150 m lower than today and 18,000 years ago sea temperatures dropped by 2° C. They also believe the Quaternary minimum sea level was as low as 200 m below present sea level. While such estimates might be locally possible during glacial maxima, estimates around 120–130 m maximum are probably more likely (Chappell & Shackleton 1986; Shackleton 1987). Regardless of maximum lowering levels, during the Pleistocene low sea level stands there was almost continuous land between Australia and Asia. Both the Sunda Platform and the Sahul shelf between Australia and New Guinea would have been exposed (Fig. 2). Sea level fluctuations would also have united Sumatra, Malaya, Java and Borneo, all of which lie in the shallow seas of the Sunda continental shelf and could have exposed extensive tracts of land, for example at Ceram and Buru (Fig. 2). These changes in sea level could also have united Borneo with Sulawesi where the seaway is < 180 m deep.

### Geological History and Biogeography

Given the present level of understanding of its geological history, it is now appropriate to begin interpreting the marine biogeography of the Indo-West Pacific in terms of past geological events. How do present marine Indo-West Pacific distribution patterns reflect that history? Many marine taxa display a high diversity in the tropics, and, of these, many show an elevated diversity in the Indo-West Pacific region where New Guinea and the Malay Archipelago are situated. Whilst dispersal may be a primary influence over the numbers of species in the area, explanations congruent with past geological events will be discussed here. Rosen (1984) discussed the biogeographical implications of geological events to reef corals in terms of tectonic, eustatic, climatic and oceanographic (TECO) processes. Three types of geological/biogeographical events are discussed here: 1) longitudinal displacement of whole faunas passively by plate tectonic motion; 2) the emergence of land barriers; and 3) the relationship between sea level and speciation patterns.

1) Longitudinal displacement. Displacement of faunas may have occurred in relation to the microcontinents rifted from eastern Gondwana that now compose SE Asia, and through motion of the numerous terranes that now compose the northern portion of New Guinea. The SE Asian microcontinents, regardless of whether they are actual mi-

crocontinents detached from the northern margin of the Australia/New Guinea continent (Pigram and Panggabean 1984) or they are merely part of the continental margin of Australia/New Guinea (Audley-Charles 1988), are significant because they may have transported tropical marine faunas as they moved north and westward. McKenna (1973) coined the term 'Noah's Arks' for faunas which have been transported passively on geotectonic plates. Although such Noah's Arks may not have been responsible for transporting SE Asian faunas to New Guinea, they may have acted to transport New Guinea marine faunas to SE Asia.

Of more relevance to New Guinean biogeography is the accretion of terranes onto the northern New Guinean coast as Australia/New Guinea collided with the island arc complexes in the Oligocene. Species which occupied formerly narrow regions could have expanded their ranges as passive migrants on each moving tectonic terrane. Such Noah's Arks have been postulated for explaining biogeographic patterns in the northwestern North America, where a similar number of terranes have docked since the Cretaceous (Stanley 1988; but see Newton 1988 for alternative view). As the terranes neared and coalesced with each other and with Australia/New Guinea, an integration of biotas might have enriched diversity (Rosen 1984; Rotondo et al. 1981). Rosen (1984) proposed a diversity pump effect caused by repeated vicariance and merging of species through time in closely clustered archipelagic regions. Sea level fluctuations may have increased diversity even before the terranes docked onto the New Guinea Orogen, and this is discussed below.

2) Land connections and sea barriers. The presence of land barriers in the Indo-West Pacific is significant from two standpoints; first they impede dispersal of marine taxa with planktonic larvae and second they may enhance speciation by providing a mechanism for isolating populations of marine taxa by fragmenting species ranges. The microcontinents of SE Asia and the New Guinean terranes in the Early Tertiary might have provided a filter to dispersal since the availability of substrates and/or niches could have a role in determining the successful establishment of planktonic larvae. There appears to be at least two pre-Quaternary events which could have isolated populations between the Indian and Pacific Oceans in the vicinity of Wallace's line (Whitmore 1987).

The first is the creation, due to the directions of movement, the northward drift, and the rotation of both Australia/New Guinea and the SE Asian microcontinents of a substantial land barrier from

Laurasia to Australia by the Cretaceous (Audley-Charles 1987). The SE Asian microcontinents may have acted as small scale barriers which fragmented species ranges and acted as an in situ diversity pump. In addition, this barrier could have acted as a filter between the Pacific and Indian Oceans as early as the Late Cretaceous and through the Tertiary (Audley-Charles 1987; Burret et al. 1991; George 1987).

The great mid-Miocene collision between Sulawesi and the Sula Peninsula appears to be the second direct connection between the Australian continent and SE Asia. As a result of this collision, there was either continuous land or only narrow sea gaps between Laurasian Borneo and Gondwanic New Guinea from sometime between the late mid-Miocene (ca. 12 MA) to late Pliocene. In fact, shallow water Early to Middle Miocene carbonates occur on most of the eastern Indonesian microcontinent and northern island arcs (Pigram, pers. comm 1992). Because of this, and the fact that Late Miocene to Quaternary reefs occur on the western part of the Sula Peninsula, the collision zone between Australia/New Guinea and Sulawesi probably had land above the sea. The presence of Pleistocene terraces of raised-fringing-reefs in East Sulawesi and Timor suggests that these areas also remained above sea level after their post-collision emergence in the mid-Miocene (Fig. 2). In fact, the mid-Miocene orogenesis might have meant land connections were well established then as well.

Audley-Charles (1981) discussed the probable land areas emergent as a consequence of the Mid-Miocene collision event. In New Guinea, huge tracts of land up to 2,000 km long had probably emerged above the sea by the Early Miocene (Pigram, pers. comm 1992). West Sulawesi might have been intermittently linked to Borneo by exposure of parts of the Makassar Strait. Buru, Ceram, and Misool appear to have been submerged, but Banggai, Sula and Ceram possibly began to emerge by late Miocene or early Pliocene and certainly by late Pliocene (Fig. 2). Buru may also have been exposed by late Pliocene (Audley-Charles 1981). Based on Audley-Charles (1981) interpretations, both a migration route for the terrestrial biota and a barrier for the marine biota could have been established between Sulawesi and eastern Australia/New Guinea by the latest Miocene or early Pliocene and by the late Pliocene, it was probably as well established as at present. Later, Audley-Charles (1987) noted that "it's exceedingly difficult to determine how much of the present land area of Malesia was above sea level during the Plio-Pleistocene [but there was always some exposed land (Pigram, pers

comm 1992)], but land area has substantially increased since the great mid-Miocene collision". The almost continuous land barrier between New Guinea and Asia thus formed twice due to tectonism in the Indo- West Pacific, perhaps completely isolating the Pacific marine fauna from the Indian Ocean marine fauna.

Transient land may also have existed in the Indian Ocean (Audley- Charles et al. 1981). The Ninetyeast Ridge of the Indian Ocean was exposed during the Eocene and Oligocene (Kemp & Harris 1975). This may have provided a stepping stone between populations living on both sides of the Indian Ocean. When it became submerged, however, it may have created a broad oceanic barrier which disrupted previously mixed marine populations (see below). The significance of these events to New Guinean biogeography would have been the isolation of previously widespread marine taxa.

3) Sea level history and speciation. Sea level changes in the Mesozoic and Cenozoic need to be considered in interpreting the biogeography of tropical marine taxa. Most parts of the SE Asian microcontinents (South Tibet, Burma, Thai-Malay Peninsula and Sumatra) were above sea level during the Jurassic rifting event and the late Cretaceous rise in sea level seemed to have had minimal effects on their emergence. The mid-Oligocene onset of Antarctic glaciation caused a marked lowering of global sea levels (Morley & Flenley 1987). The Plio-Pleistocene sea level fluctuations resulted in a sea level minimum during the mid- Pleistocene. Land would have been emergent between Australia and New Guinea, and between Australia/New Guinea and SE Asia for long periods during the Quaternary low sea level stands.

Plio-Pleistocene glacio-eustatic sea level fluctuations would have resulted in changing configurations of fragmented island regions. The abundance of terranes and their accretionary history in New Guinea would have provided an ideal setting for speciation in marine invertebrates, many of which are sessile benthic space occupiers and competition for diminishing space as sea level lowered could have been a factor in driving up their diversity. Sea level changes resulting in fragmented island regions provide ideal conditions for rapid and independent speciation and island areas influence the number of species that can be accommodated (George 1987; McManus 1985; Myers 1989; Rosen 1984).

Wallace's Line was first recognized by Wallace in 1858 based on the striking difference between plants and animals on either side of the Makassar Strait separating Sulawesi from Borneo. The line is based, as is most Indo-Pacific biogeography (but see

Briggs 1987), on the terrestrial biota, and two recent monographs discuss its significance in some detail (Whitmore 1981, 1987). Fleminger (1986) attempted an explanation of Wallace's line by suggesting the high diversity of marine copepods in its vicinity (including New Guinea) was due to repeated vicariant events during Pleistocene glacial stages. He argued that the increased area of land in the boundary between the Indian and Pacific Oceans during Pleistocene sea level lows would have resulted in a greater incidence of coastal upwelling, depressing surface water temperatures by as much as 5° C, resulting in thermal barriers in the form of chilled surface waters. Springer & Williams (1990) believe that these lower sea levels with increased coastal upwelling and loss of marine habitats could have led to the extinction of continuously distributed Indo-Pacific marine populations and led to the formation of widely separated Pacific plate endemics.

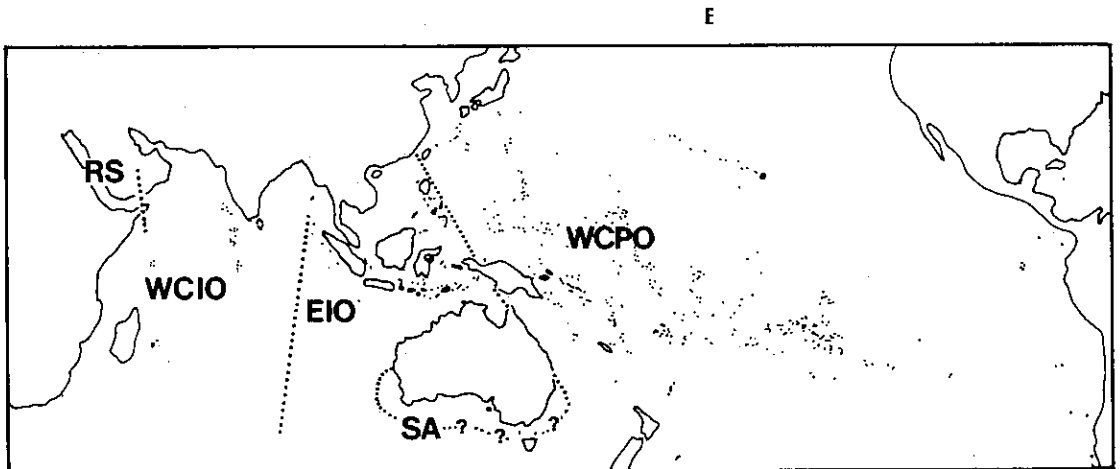
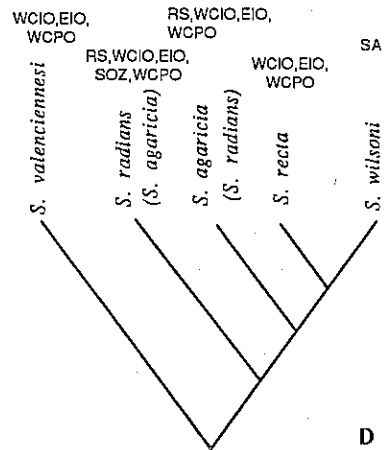
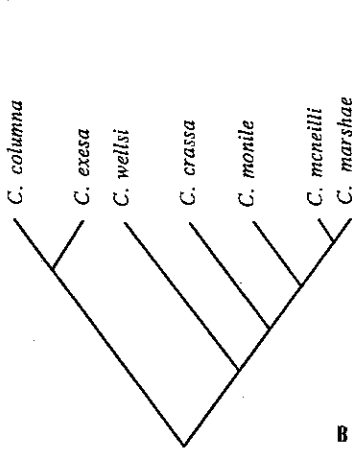
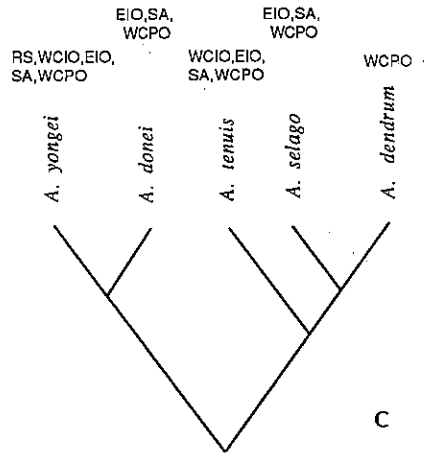
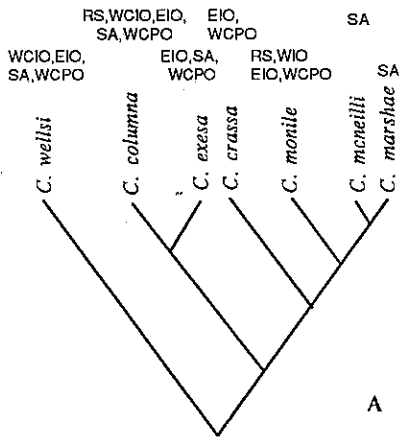
Widely distributed species also may have given rise to new species after the formation of either the oceanic or land barriers which characterized glacial stages. Myers (1989) used such a model to explain the high diversity of Indo-Australian fishes and the occurrence of many endemic species in the Indo-Pacific. As glacial sea level lows create land barriers, widespread populations are isolated into groups, with subsequent speciation. During inter-glacial periods remixing occurs, re-establishing overlapping species boundaries (see also Rotondo et al. 1981 for example in Hawaii). McManus (1985) put forth a similar scenario to explain high speciation in Indo-West Pacific corals, and Potts (1985) proposed ap-

propriate tests for such models. In an additional phylogenetic test of these models in acroporid, muscid, and siderastreid corals, these speciation models would also appear to be applicable (see below and Pandolfi, 1992). Potts (1983, 1984), however, suggested that in corals with long generation times, such speciation events would be suppressed because the corals would not have experienced enough generations in isolation to differentiate sufficiently to become new species.

#### An Example from the Historical Biogeography of Indo-Pacific Reef Corals

Indo-Pacific biogeographic area relationships based on phylogenetic analysis of modern reef coral species show a predominantly stepwise progression from west to east with adjacent biogeographic areas more closely related to each other than to areas further apart (Pandolfi, 1992; Wallace et al. 1991). This progression is consistent with past geologic events related to the submergence of the Ninetyeast Ridge in the Early Miocene, to the separation of the Indian and Pacific Oceans as a consequence of the great Mid-Miocene collision between Gondwanic Australia and Laurasian SE Asia, and to Quaternary sea level and temperature fluctuations associated with glacial intervals. An hypothesis of successive isolation congruent with past geological events has been proffered to explain the evolutionary history of Indo-Pacific reef corals (Pandolfi, 1992).

**Fig. 4.** Phylogenetic trees and distributions of *Symphyllia*, *Coscinaraea*, and the *Acropora selago* species group. a,b) *Coscinaraea*. Two equally parsimonious trees were obtained; c) *Acropora selago* group; d) *Symphyllia*. Two topologies were found; in the second tree, the position of *S. agaricia* and *S. radians* is reversed. Biogeographic areas are shown above terminal taxa. e) Map of biogeographic areas: RS, Red Sea; WCIO, west to central Indian Ocean from the east African coast to the Ninetyeast Ridge; EIO, east Indian Ocean from the Ninetyeast Ridge to the Malay Archipelago and the Philippines; SA, southwest (Shark Bay southeast to Reserche Archipelago) to southeast (Solitary Islands) Australia; WCPO, western to central Pacific Ocean. The phylogenetic program Hennig86 (Farris 1988) was used. The outgroup comparison method was used to root the trees. For *Symphyllia* and *Coscinaraea* a phylogenetic analysis (Pandolfi, 1992) of the genera of the entire family (Mussidae and Siderastreidae, respectively) was conducted first using Lundberg rooting. All species of the sister genus in the family level analysis were used as the outgroup in the species level analysis. Characters and states were derived from recent taxonomic monographs (Veron and Pichon 1980) and specimens housed at the Australian Institute of Marine Science. The characters included valley and colline size and shape; septal density, orders, ornamentation and exsertness; growth form; and columellae characteristics for *Symphyllia*, and colline size and shape; growth, arrangement, size, and number of rows of corallites; and septal, wall and columellae characteristics for *Coscinaraea*. For the *Acropora selago* species group, *A. millepora* was considered to be the closest related taxon to the ingroup (Wallace et al. 1991). Characters and character states include: 1) a set of morphometric characters derived from populations from Britomart Reef, on the Great Barrier Reef, which included the density, diameters, branching angles, and lengths of the first two orders of branches; the density of radial corallites; and the exsertness of axial corallites and diameters of radial corallites; and 2) a set of qualitative characters, in part derived from a recent taxonomic monograph (Veron & Wallace 1984), which described colony growth form, branching, symmetry, determinate vs indeterminate growth; radial corallite shape and density; and wall structure. Distribution patterns were compiled from presence/absence data in distributional papers (Wallace et al. 1991; Veron and Marsh 1988, Veron 1993), and from collections housed at the Museum of Tropical Queensland, Townsville.





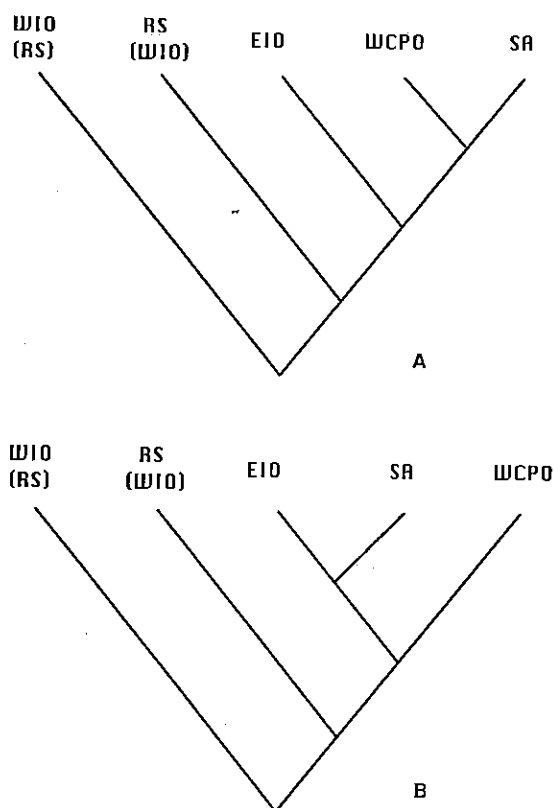


Fig. 5. Five area statements of relationships of the Red Sea, the west/central Indian Ocean, the East Indian Ocean, the west/central Pacific Ocean, and SW/SE Australia. The biogeographic program COMPONENT (Page 1989) was used to generate the area cladograms congruent with the three area cladograms derived from the phylogenetic analysis. The area cladograms shown represent trees shared by the coral taxa. *Symphyllia* and *Coscinaraea* shared trees with West Indian Ocean as the basal area, whilst the *A. selago* group and *Coscinaraea* shared trees with the Red Sea as the basal area (see Pandolfi 1992; and Wallace et al. 1991 for data and analyses).

Two patterns emerge from a comparison of species-level phylogenetic relationships and distribution patterns of *Symphyllia* and *Coscinaraea* (Pandolfi, 1992) and the *Acropora selago* species group (Wallace et al. 1991) (Fig. 4): 1) biogeographic area relationships show a predominantly west to east stepwise progression, and 2) species of reef corals from different genera show congruent biogeographic relationships which can be correlated with past geological events.

Area cladograms were derived by replacing the terminal taxa of the phylogenetic cladograms by the area(s) in which the taxa occur (Humphries et al. 1988). Two area cladograms were shared by *Sym-*

*phyllia* and *Coscinaraea* and five area cladograms were shared by *Coscinaraea* and the *A. selago* group. Congruence of patterns among components of the shared area cladograms results in two reduced area cladograms (Fig. 5a,b).

The area cladograms show firstly the separation of a component comprising the East Indian Ocean (EIO), southwest to southeast Australia (SA) and the western to central Pacific Ocean (WCPO) from the west to central Indian Ocean (WCIO) and the Red Sea (RS). In one of the area cladograms a component comprising southwest to southeast Australia and the western to central Pacific Ocean is then separated from the East Indian Ocean, and is followed by the separation of southwest to southeast Australia from the western to central Pacific Ocean (Fig. 5a). In the second area cladogram the west central Pacific Ocean is separated from the East Indian Ocean and southwest to southeast Australia before the latter two areas become distinct (Fig. 5b). Thus, species ranges overlap in a predominantly west to east stepwise fashion with the closest biogeographic relationships occurring between adjacent areas.

The area cladograms show congruence with particular geologic events and lead to an historical explanation of how and where reef coral species may have originated (Fig. 5). Palaeocene or earlier ancestral taxa occupied a broad distribution in the Tethys Ocean from the present day Mediterranean Sea to the Pacific Ocean. The Ninetyeast Ridge in the central Indian Ocean (Kemp and Harris 1975), emergent in the Eocene and Oligocene, became submerged and may have acted as a wide oceanic barrier between western and eastern Indian Ocean taxa whose populations had earlier used the Ninetyeast Ridge as a stepping stone for maintaining genetic continuity across the Indian Ocean. The great mid-Miocene collision between Gondwanic Australia and Laurasian SE Asia would have separated, either as a barrier or a strong filter, the east Indian Ocean fauna from the Pacific plate fauna (Audley-Charles 1987; Pigram & Davies 1987). A separation of faunas may also have occurred during Quaternary sea level fluctuations (Fleminger 1986). The separation of southwest and southeast Australia from the remainder of the biogeographic areas may have occurred in response to lower sea temperatures during Pleistocene glacial sea level minima. Such times were accompanied by an increase in upwelling, further depressing surface temperatures (Fleminger 1986) thus providing a thermal vicariant barrier. Individual speciation events may have been followed by dispersal to broaden the range of individual taxa. Thus, the presence of the Red Sea on the left side of the general area cladogram was prob-

ably due to dispersal of west/central Indian Ocean taxa to the Red Sea when it opened to the Indian Ocean in the early Pliocene (Girdler & Styles 1974).

### Conclusion

In order for meaningful biogeographic analysis to proceed, distribution patterns must be evaluated with respect to geological events (Michaux 1991). The geological complexity of New Guinea and the Indo-Pacific is well established and has been used in various dispersalist explanations, especially for the interpretation of terrestrial faunal and floral range expansions (Burret et al. 1991). For marine biogeographers, the terrestrial biogeographers' land bridge becomes a barrier to dispersal and we must acknowledge the affects of such barriers on the evolutionary history of the marine realm. The main hypotheses for distribution patterns are longitudinal displacement of marine organisms on continental and oceanic fragments throughout the Cenozoic, the isolation of populations of marine taxa during tectonic collision events, and the extinction and speciation of marine faunas in conjunction with glacio-eustatic sea level changes. The strong propensity for marine organisms to disperse can easily blur events which occurred due to geological processes. Thus it is strongly recommended that biogeographic studies utilize species relationships in evaluating hypotheses about how and where marine species in the Indo-West Pacific originated. Michaux's (1991) call for the collaboration of biogeographers and geologists to work together to tackle biogeographic problems in Indonesia can reasonably be echoed for those working in New Guinea.

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