

WIDELY DISTRIBUTED PACIFIC PLATE ENDEMICS AND LOWERED SEA-LEVEL

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ABSTRACT

Glacial sea-level lowerings resulted in greatly increased land area in the Malayan, Indonesian, southern New Guinea-northern Australian region. During the glacial lows, cold, coastal upwelling greatly increased in the region and depressed surface water temperatures significantly. We propose that loss of marine habitats and cooler seawater temperatures resulted in extinction of Indonesian-Malayan populations of continuously distributed Indo-Pacific marine organisms, and contributed to the existence of widely distributed Pacific plate endemics.

Springer (1982) made special note of endemism among the shore fishes and other organisms of Pacific plate islands. In particular he called attention to widely distributed endemics, such as the halfbeak fish *Hyporhamphus acutus* (Günther) (Fig. 1) and the gastropod *Strombus maculatus* Sowerby (Fig. 2). Springer was unable to explain the factors that might have contributed to the evolution of widely distributed Pacific plate endemics.

Herein, we wish to call attention to a type of distribution pattern that offers clues to the origin of widely distributed Pacific plate endemics.

During the course of our ongoing revision of the marine, shallow-dwelling (often intertidal), blennioid fish genus *Istiblennius* Whitley, we noted that the distributions of two species, *I. gibbifrons* (Valenciennes) and *I. bellus* (Günther), exhibited disjunct distribution patterns (Figs. 3, 4). For each species, one portion of the distribution was confined to the Pacific plate (including margins) and the other to the Indian Ocean. On cursory examination of the literature, we found several fishes and mollusks that exhibit similar, although not always quite as sharply delimited, distributions (literature references refer to distribution maps). Among the fishes are: *Stegastes albifasciatus* (Schlegel and Müller) (Allen and Emery, 1985: fig. 1); *Pervagor aspricaudus* (Hollard) (Hutchins, 1986: fig. 10); *Liopropoma lunulatum* (Guichenot) and *L. tonstrinum* Randall and Taylor (Randall and Taylor, 1988: figs. 3, 7); *Cirripectes perustus* Smith (Williams, 1988: fig. 10). Among the mollusks are: *Strombus haemastoma* Sowerby, *S. dentatus* Linné, and *S. terebellatus* Sowerby (Abbott, 1960: figs. 57, 59, 62); *Littorina pintado* (Wood) (Rosewater, 1970: pl. 348); *Chlamys coruscans* (Hinds) (Waller, 1972: fig. 2); *Rhinoclavis diadema* Houbriek (Houbriek, 1978: pl. 35); *Clypeomorus nympha* Houbriek (Houbriek, 1985: fig. 59; reproduced here as Fig. 5).

It is readily apparent from these fish and mollusk examples that a widely distributed Pacific plate endemic (or an endemic almost entirely restricted to the Pacific plate) would result if the disjunct Indian Ocean portion of the taxon became extinct or differentiated taxonomically. The reverse is also true: an Indian Ocean endemic would result if the Pacific population became extinct or differentiated taxonomically. A possible example of this circumstance is illustrated by the distributions of the blennioid fishes *Cirripectes fuscoguttatus* Strasburg and Schultz, a widely distributed Pacific plate endemic, and *C. gilberti*, an Indian Ocean endemic (Fig. 6), which Williams (1988 and in prep.) hypothesized cladistically to be sister taxa prior to our recognizing the significance of Pacific plate-Indian Ocean disjunct distributions.

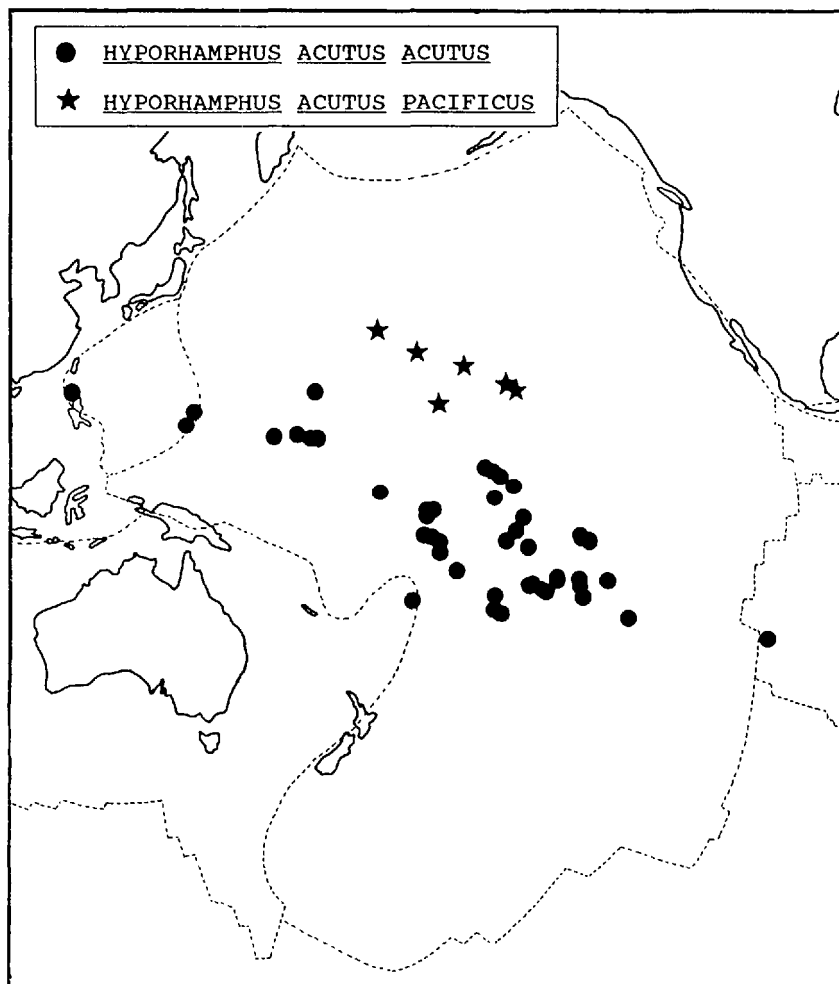


Figure 1. Distribution of the halfbeak fish *Hyporhamphus acutus*, a widely distributed Pacific plate endemic (updated from Springer, 1982: fig. 22).

What are the possible explanations for such a disjunct distribution pattern? There are three.

1. Jump dispersal, which requires that the distributional hiatus was unoccupied by the species (or ancestor of the sister species on either side of the hiatus), and that the species or ancestor dispersed (skipped) across the hiatus and occupied the area on the other side.

We can neither falsify nor corroborate jump dispersal, but intuitively we find it objectionable as an explanation. It raises the question of how a species could travel the great distance between the Pacific plate and Indian Ocean, dodging the labyrinth of land masses that lie between these two areas, without establishing populations along the way. However, if jump dispersal did occur and the original population was a widely distributed Pacific plate endemic, we remain without an explanation of the causes producing that type of endemic.

2. Formation of as yet uncolonized new coastlines and seafloor in the midst of the distribution of a continuously distributed taxon (effectively a bilateral spreading apart of a continuously distributed population).

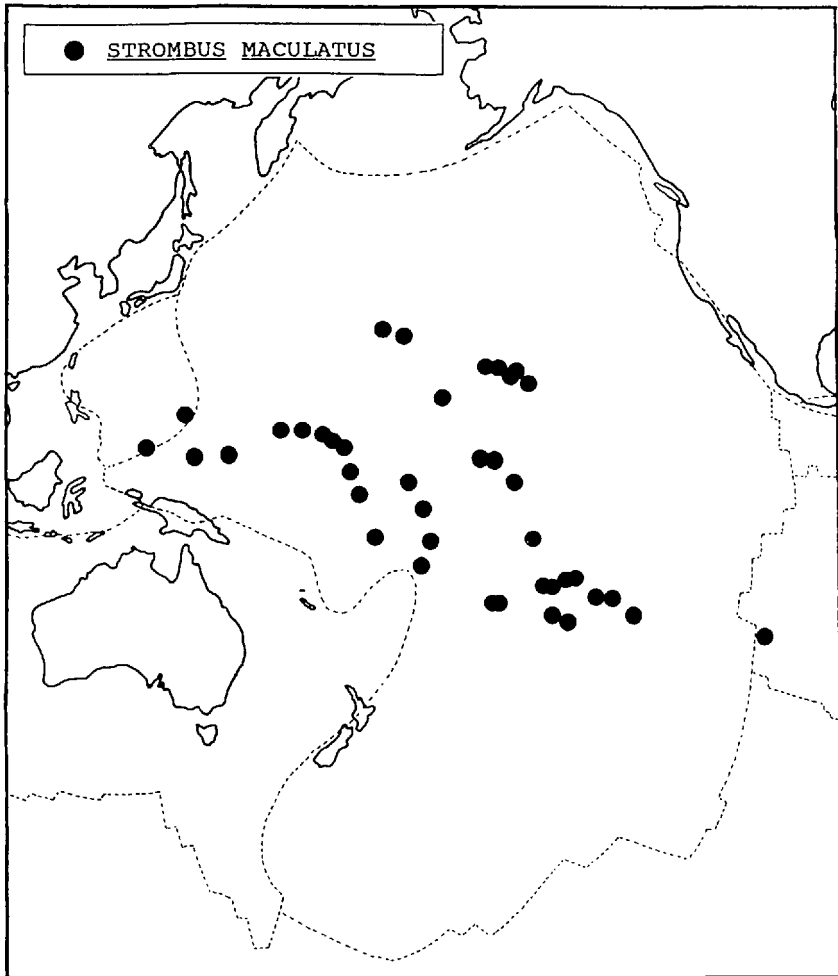


Figure 2. Distribution of the gastropod mollusk *Strombus maculatus*, a widely distributed Pacific plate endemic (after Springer, 1982: fig. 47).

There is geological evidence for this possibility. Since the collision of Australian Gondwana with Asia, beginning in middle Miocene and continuing to Pliocene, 15 to 3 mya (Audley-Charles, 1981; 1987), considerable island-arc volcanism has occurred in the collision zone (now includes much of eastern Indonesia), creating new islands and seas. If the ecological conditions of these new areas were unsuitable for the organisms whose distributions had been split, colonization of the new area would be precluded. Another possibility is that there has been insufficient time for colonization, but we believe this is unlikely.

We cannot falsify these possibilities, but again we are disinclined to believe they explain the distribution patterns of interest to us.

3. Extinction of previously continuous populations in the area of disjunction. Potts (1983: fig. 3; 1984: fig. 3) and Myers (1989: fig. 8) have noted graphically the effect of glacial sea-level lowering on the emergence of land in the Malaya-Indonesia-Australia-New Guinea area during the Pliocene-Pleistocene. During the past 140,000 years, major sea-level lows have vacillated from about 50–150

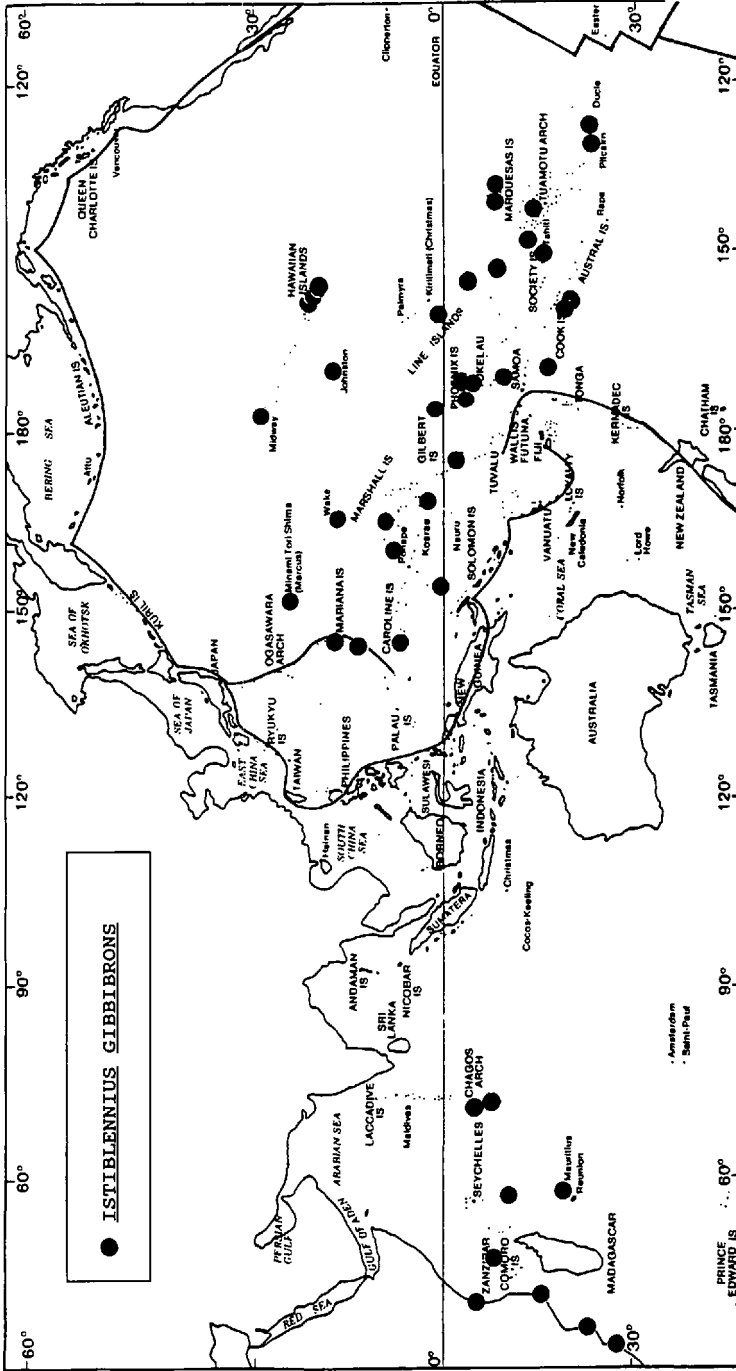


Figure 3. Distribution of the blennioid fish *Istiblennius gibbifrons* (only Pacific and Philippine plate margins shown for Indo-west Pacific).

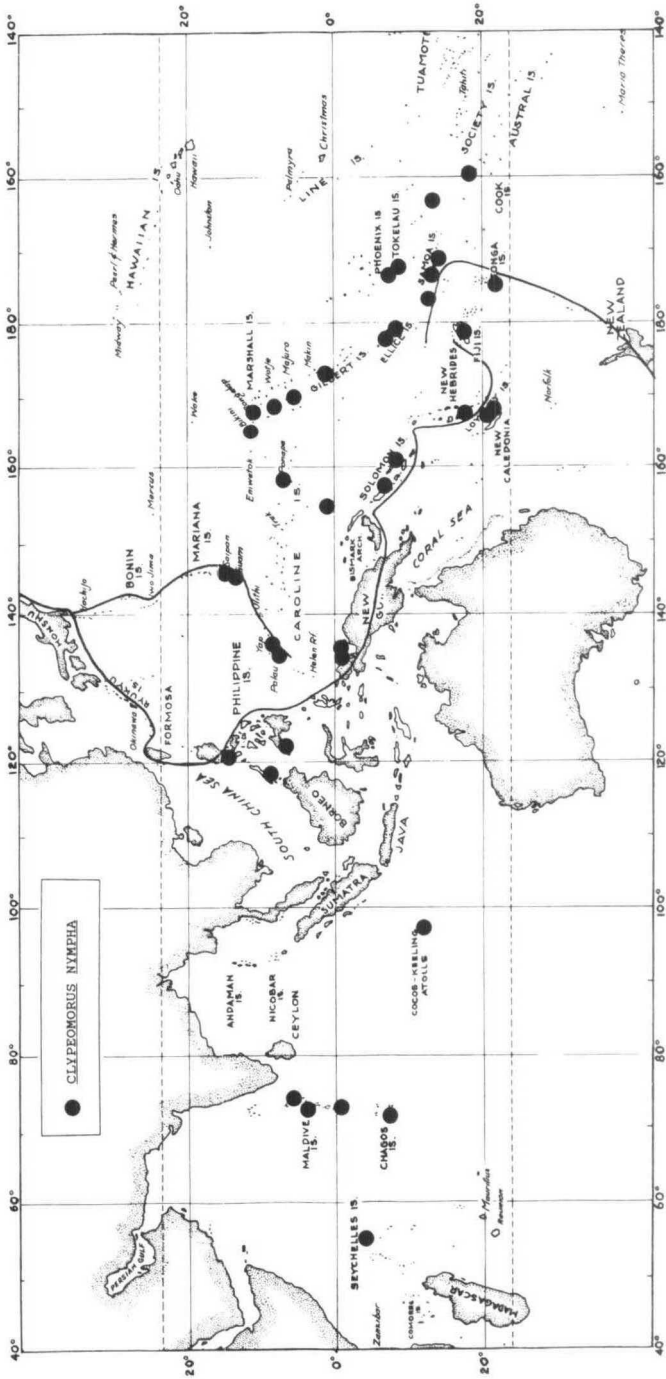


Figure 5. Distribution of the gastropod mollusk *Clypeomorus nympha* (Houbrick, 1985: fig. 59; only Pacific and Philippine plate margins shown for Indo-west Pacific).

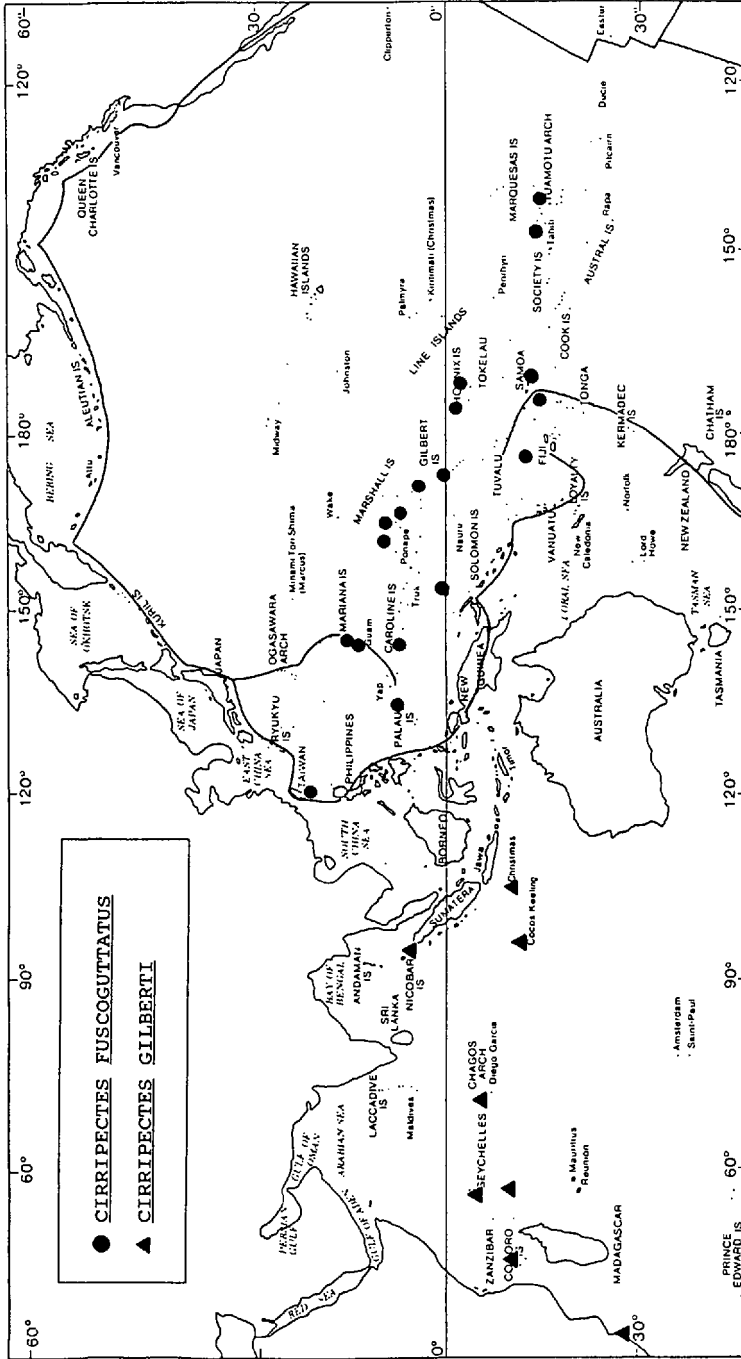
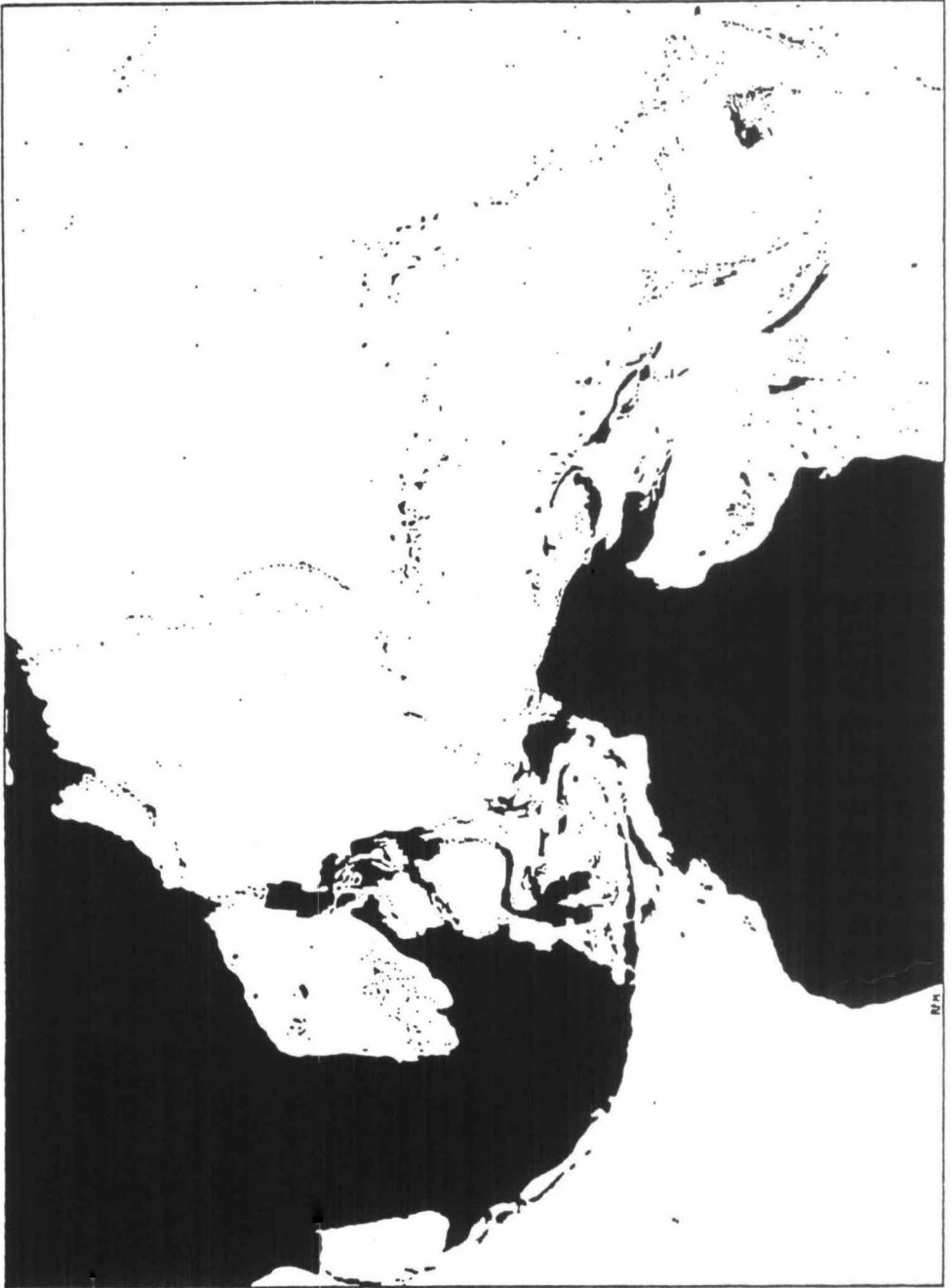


Figure 6. Distribution of two species of the blennioid fish genus *Cirripectes* hypothesized to form a monophyletic group (only Pacific and Philippine plate margins shown for Indo-west Pacific).



m lower than sea level today (Potts, 1984: fig. 1). During the last low, about 18,000 years ago, sea level was about 150 m lower than today (Fig. 7; some authors have proposed that sea level was 200 m lower than today; the additional 70 m would make scant change in Fig. 7). Land replaced much of the sea in the Indo-Malayan region, and an almost complete land barrier was created between the Indian and Pacific oceans. River runoff from the land masses into the reduced passageway between the Indian and Pacific oceans would have enhanced the barrier for stenohaline species by creating turbid, hyposaline conditions. Undoubtedly, there was considerable elimination of marine forms from the area.

Fleminger (1986) skillfully showed that the increased land masses in the area under consideration resulted in increased upwelling of cool water. The cool water depressed surface water temperatures in the area by as much as 5°C (Fleminger, 1986: fig. 5), eliminating many shallow-dwelling species and enhancing the effect of the land barrier.

Potts (1983; 1984) was interested in the effects of the oscillations of sea-level on the evolution of corals. He concluded that the long generation times of corals essentially prevented them from speciating as a result of the extinction and barriers created by lowered sea level in the Indo-Malayan area because there was not enough time. He proposed, however, that fishes and other organisms that have much shorter generation times could well evolve in response to the fluctuations. Fleminger (1986), who did not reference Potts' papers, detailed examples of copepods that support Potts' ideas.

Myers (1989) was interested in the barrier to dispersal of marine organism that the newly emergent land created: "The draining of the continental shelves results in the near separation of the tropical Indian and Pacific Oceans and the isolation of certain Indo-Australian seas. This isolates populations of widespread species into two or more groups, enabling some to differentiate into distinct species. Remixing and recolonization occur during interglacial periods, sometimes blurring the faunal boundaries established during periods of glaciation. Some species that evolved in small areas may eventually become extinct, but ecological factors that tend to reduce competition could allow many species to remain. This is one of the processes that resulted in the enormous diversity of Indo-Australian fishes found today with many endemic species of limited distribution" (Myers, 1989: 12-13).

Myers wrote in general terms and did not cite specific examples of organisms, nor did he consider the effects of cold upwelling and the kinds and implications of disjunct-distribution patterns of concern to us.

We favor a hypothesis of extinction together with the formation of a barrier resulting from glacial sea-level lowerings (including cold upwelling) as the cause of Indian Ocean-Pacific plate disjunct distribution patterns and the evolution of widely distributed Pacific plate endemics.

Note

An anonymous reviewer commented that if so much extinction occurred as we have suggested, why is species diversity in the area the highest in the world. (Fleminger, 1986, and Myers, 1989—see our quotation above—address, at least in part, the reasons for the high diversity of the area.) The reviewer offered as an alternative to our explanation for disjunct distributions that sea-level fluctuations

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Figure 7. Distribution of land in a portion of the Indo-Pacific about 18,000 years ago when sea-level was more than 130 m lower than today (from Myers, 1989: fig. 8).

stimulated speciation in the area and that the newly formed species competed successfully with their older relatives and supplanted them. Aside from the fact that we reject sympatric speciation as an important evolutionary process (as opposed to allopatric speciation, which we believe is the main process), if this were the case, it seems logical that the closest relative of the disjunct taxon would be the one excluding the taxon from the area. As a contraindicative example, our present studies (in progress) suggest, in the case of *Istiblennius gibbifrons*, that *I. chrysopilos* is its sister species. *Istiblennius chrysopilos* does occur in the East Indies, but it is also sympatric with *I. gibbifrons* over most of the latter's range. If *I. chrysopilos* outcompeted *I. gibbifrons* in the East Indies, why has it failed to do so throughout the remainder of their joint range?

On a highly localized scale, competitive exclusion of one species by another may be complete, but on the grand scale of so large an area as we are dealing with, one with a tremendous variety of habitats and ecological conditions, we would expect competitive exclusion to result in patchy distributions of both species.

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