Hopping Hotspots: Global Shifts in Marine Biodiversity

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Hotspots of high species diversity are a prominent feature of modern global biodiversity patterns. Fossil and molecular evidence is starting to reveal the history of these hotspots. There have been at least three marine biodiversity hotspots during the past 50 million years. They have moved across almost half the globe, with their timing and locations coinciding with major tectonic events. The birth and death of successive hotspots highlights the link between environmental change and biodiversity patterns. The antiquity of the taxa in the modern Indo-Australian Archipelago hotspot emphasizes the role of pre-Pleistocene events in shaping modern diversity patterns.

One of the most striking patterns in marine biogeography is the tropical center of maximum diversity in the Indo-Australian Archipelago (IAA). Many coral reef groups reach their greatest diversity here (1, 2), a pattern that is also reflected in a wide range of taxa in other shallow marine ecosystems (3–5). This taxonomic richness pattern has been related to a multitude of mechanisms, usually associated with the spatial distribution of modern parameters or processes, and has engendered vigorous debate (3, 6–9). It is the focus of numerous evolutionary and ecological theories (8, 10–13) and has underpinned strategies for current conservation efforts (14). The potential role of the IAA as a museum or cradle for biodiversity has highlighted the importance of the history of the region (12, 15). Moreover, recent discoveries that incorporate the fossil record and evolutionary history of taxa in the IAA hotspot provide an insightful perspective of the history of biodiversity hotspots, that is, geographical areas of maximal biodiversity in a given time interval.

The combination of molecular evidence and the fossil record provides a powerful tool for understanding the spatial and temporal dynamics leading to current biodiversity patterns (4, 16, 17).

Despite the apparent complexity of the IAA, our knowledge of the fossil record of this region is expanding rapidly as new collections clarify taxonomic, paleoenvironmental, and chronostratigraphic relationships. These recent advances have revealed a striking pattern of profound importance for our understanding of the evolutionary history of the IAA hotspot. Its presence has traditionally been attributed to either a speciation pump, as a result of the relationship between Pleistocene sea level changes and the complex geography of the area, or as a result of accumulation, reflecting the exceptional environmental features of the region (1, 3, 7, 13, 18). These hypotheses are derived from analysis of present-day richness patterns. However, this approach is spatially and temporally constrained. Here, we review recent evidence showing that biodiversity hotspots have moved across almost half the globe over the past 50 million years (My) and that the age of the taxa characterizing the modern IAA biodiversity hotspot is much older than previously thought.

Hopping Hotspots

The biogeography of large benthic foraminifera through time shows remarkable similarities with that of other tropical shallow marine organisms (19). This is not surprising but does show that large benthic foraminifera can be used for measuring overall diversity in tropical marine environments, not least because of their high abundance and good fossil record (19). During the Eocene, global α-diversity (number of genera found at a single location) peaked in southwest Europe, northwest Africa, and along the eastern shore of the Arabian Peninsula, Pakistan, and West India (20) (Fig. 1A). Likewise, the fossil record of mangroves and reef corals suggests maximal global diversity in this West Tethyan hotspot during the Eocene, and the diversity of mollusk assemblages was highest at the northwest margin of the West Tethyan region (5, 15, 21–24).

By the Late Eocene, the highest α-diversity is recorded in the Arabian hotspot (20, 25), centered around the Middle East. The Late Eocene Arabian hotspot has an overlapping taxonomic composition with the earlier West Tethyan hotspot, and the Miocene Arabian and IAA hotspots also have broadly overlapping taxonomic compositions (Fig. 1B). For both large benthic foraminifera genera and mangrove pollen types, the Miocene is the most diverse period in southeast Asia, centered around the Philippines–Papua New Guinea region, partly because of the overlapping occurrence of Paleogene and extant taxa (20, 23). Habitat loss, largely due to regional uplift during the Arabia-Eurasia collision, resulted in extensive faunal depletion and the demise of the Arabian hotspot during the Middle to Late Miocene. Similarly, the cowrie gastropods largely disappeared from Europe and the Middle East during the Late Miocene (22). The area of maximal diversity of tridacnine bivalves likewise shows an eastward shift, with a diverse West Tethyan fauna from the Eocene and a modern fauna with highest diversity in the IAA (24).

With the loss of the Arabian hotspot, the modern configuration appeared (Fig. 1C). The fossil record of large benthic foraminifera, mangrove pollen types, gastropods, and corals shows that this high α-diversity was present at least since the Early Miocene [20 million years ago (Ma)]. These patterns indicate the surprising antiquity of the IAA hotspot. To explore this antiquity, we turn to the ages of the modern taxa inhabiting this region (Fig. 2).

Origins of IAA Biodiversity: Heat in the Miocene

Contrary to previous expectations (26–28), the vast majority of extant IAA taxa for which a fossil record is available first occurred before the Pleistocene (Fig. 3). All but one of the 24 extant large benthic foraminifera genera originated during the Pliocene or earlier, with seven genera having an Eocene or earlier origin and two occurring for the first time during the Oligocene (20). Likewise, all modern mangrove pollen types have been present in the IAA since the Late Miocene, with most genera extending back to the Eocene (5, 6, 23) and all mangrove species, where they can be identified on pollen characters, extending to the Miocene (23, 29). In the corals, the modern subgenus *Acropora* (*Acropora*) was represented by the precursors of 9 out of 20 currently recognized morphological groups during the Eocene in the Paris Basin, and the earliest occurrence of this genus in the IAA is from the Early Miocene (21). In the cowries, 9 out of 12 IAA genera with a known fossil record are first recorded from the Miocene (22). Finally, of the 69 extant IAA tonnoid species with a fossil record, 67 have their first occurrence in the Miocene (30). These patterns are particularly striking given the potential dampening effect of the "pull of the recent," causing the extension of stratigraphic ranges of fossil taxa by the relatively complete sampling of the Recent biota (31).
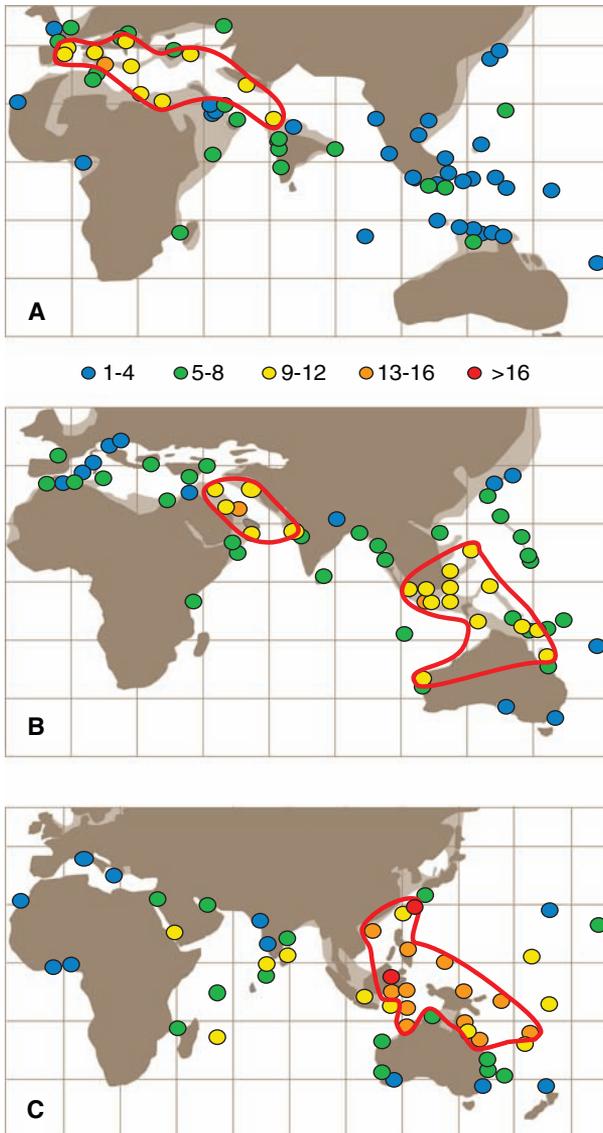
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Fig. 1. Generic α-diversity of large benthic foraminifera in (**A**) the late Middle Eocene (42 to 39 Ma), (**B**) the Early Miocene (23 to 16 Ma), and (**C**) the Recent. Solid lines delimit the West Tethys, Arabian, and IAA biodiversity hotspots (tables S1 to S3). Note the relocation of hotspots across the globe. Where multiple studies occurred at a single locality, the highest recorded diversity is reported. Paleogeographic reconstructions modified after (*41*, *42*).

Legend: 1-4, 5-8, 9-12, 13-16, >16

Fig. 2. Congruent biogeographic patterns are characterized by multiple taxa within the IAA biodiversity hotspot. Evidence exists from the molecular genetics of (**A**) fishes and the fossil record of (**B**) mangroves, (**C**) larger benthic foraminifera, and (**D**) corals.

The pattern of first occurrences provided by the fossil evidence is strongly supported by molecular data. Several recent molecular studies have provided crucial insights into the nature and timing of IAA origins by using a combination of comprehensive species-level phylogenies and geographic distributions. Estimated minimum divergence ages of extant cowrie lineages suggest that the majority of extant species originated in the Miocene, with only a single IAA species arising in the Pleistocene (*32*). Similarly, divergence ages of periwinkle gastropods are estimated to fall in the range of 10 to 47 Ma, with no evidence for speciation in the Plio-Pleistocene (*4*). Most lineages of coral reef fishes arose in the Late Miocene to Pliocene. A few species have been identified that diverged in the Pleistocene, but, as in the cowries, these young species are found throughout the Indo-Pacific and are not concentrated in the IAA (*33–38*). Similar ages of origination have been reported for the symbiotic dinoflagellate *Symbiodinium* (*39*), echinoids (*40*), and corals (*16*).

In summary, the molecular and fossil evidence from a range of taxa contradicts the notion of Pleistocene origins of the modern marine IAA fauna and flora and points to the presence of a high diversity of extinct and extant lineages from at least the Miocene onwards. Fossil data further establish that the IAA has not always been the center of marine biodiversity but that earlier centers of marine biodiversity occurred in at least two additional places during the past 50 My. There appear to have been three distinct hotspot locations. However, the component taxa may shift from one location to another, demonstrating the differences in behavior between hotspots and their component taxa: hotspots hop and taxa shift.

A Role for Plate Tectonics in the Generation and Senescence of Biodiversity Hotspots?

Our review has identified the presence of three spatially distinct biodiversity hotspots with differing biotic and environmental histories through time. Comparisons of these replicate hotspots provide a robust framework for evaluating the wide range of parameters that have been associated with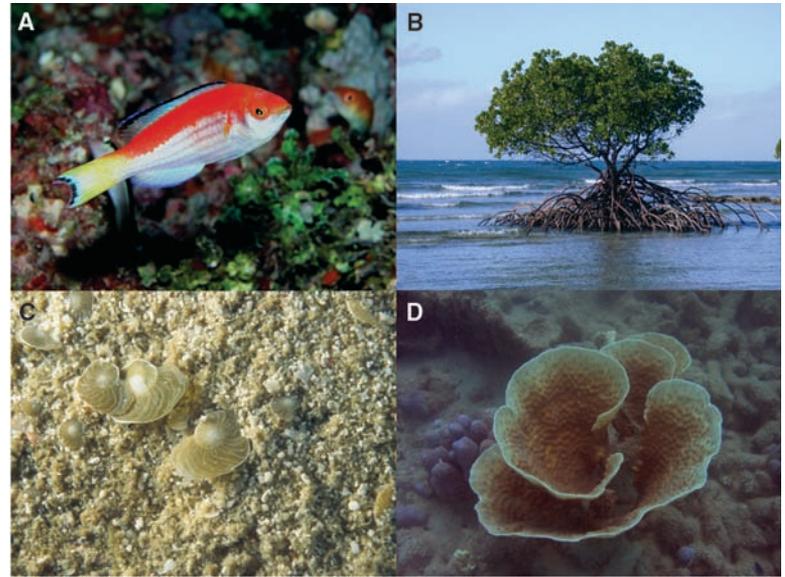 their formation and maintenance. However, because of the temporal sequence now available, we are also able for the first time to examine the relationship between hotspots and factors operating over the past 50 My. One of the most striking features of these three hotspots is that each in turn marks the location of a major collision between tectonic plates.

The Eocene West Tethyan and Arabian hotspots lie within the convergence zone between the African and European continents, separated by the Tethys Ocean and a mosaic of microcontinental fragments (*41*). Important tectonic phases are the onset of counterclockwise rotation of Africa, resulting in the domination of contraction over extension between the Late Cretaceous and Early Eocene (99 to 42 Ma) coinciding with the formation and expansion of the West Tethys hotspot. Continent-continent collision progressed from west to east, resulting in emergence and mountain building in southwestern Europe coinciding with the contraction of the eastern part of the West Tethys hotspot. About 33 to 30 Ma, rifting in the Red Sea region formed the Arabian plate. The progressive rotation of the Arabian plate resulted in collision with Anatolia (*41*), starting ~20 Ma, again coinciding with an increase in diversity in the Arabian hotspot. Mountain building in Anatolia and Iran and the loss of shallow marine habitats terminated the Arabian hotspot. Finally, the IAA hotspot lies in the region of convergence between Eurasia, Australia, and the Pacific/Philippine Sea plates, where there is a complex mosaic of oceanic, arc, and microcontinental fragments. Here, three critical phases are: (i) the onset of subduction of the Australian and Pacific plate below the continental part of southeast Asia ~45 Ma, (ii) the collision of Australia with Pacific arcs and the southeast Asian margin ~23 Ma, and (iii) regional changes of plate motions at the Eurasian continental margin in the
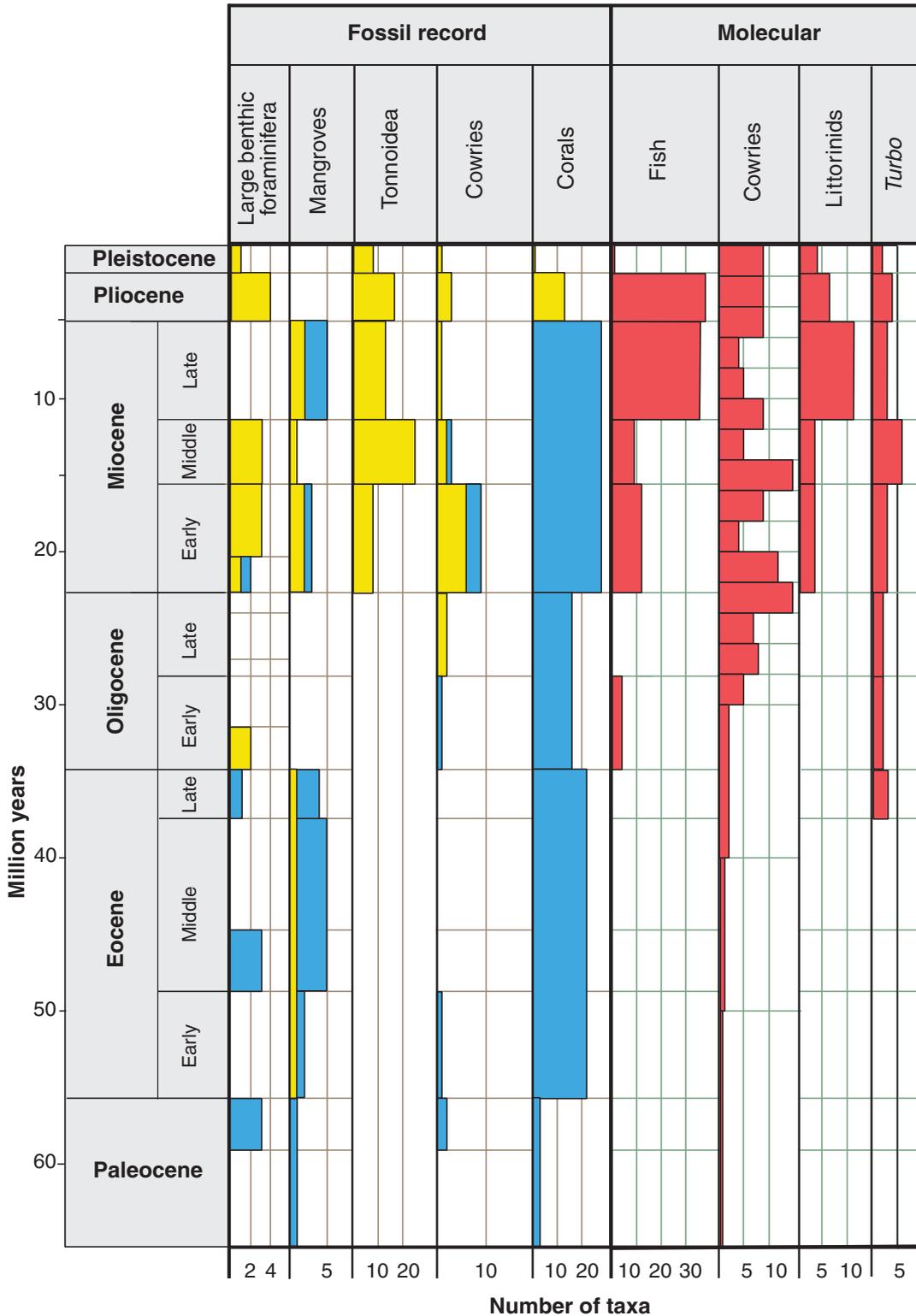
Fig. 3. The earliest records and estimated age of tropical marine taxa occurring in the modern IAA biodiversity hotspot from fossil and molecular evidence, respectively. In all of the taxa examined, numbers of first occurrences are higher in the pre-Pleistocene interval than in the Pleistocene, demonstrating the antiquity of most of the taxonomic diversity in the biodiversity hotspot. The first recorded occurrences of large benthic foraminifera genera (*20*), mangrove pollen types (table S4), tonnoid gastropod species (*30*), cowrie gastropod genera (*22*), and coral genera (*48*) are derived from the fossil record (yellow, first record inside the IAA; blue, first record outside the IAA). In each case, the data are derived from the lowest taxonomic level currently available in the literature. Minimum divergence ages of sister species of fish, cowries, littorinids, and *Turbo* gastropods are based on molecular evidence (*4, 17, 32, 34–38*). Studies were selected where there was relatively complete sampling in the focal clades.

West Pacific about 5 Ma, initiating the recent tectonic regime (*42*). It was in phase (ii) that the most extensive creation of new islands and shallow seas corresponded with the observed formation of the IAA hotspot.

The strong correlation between the presence of hotspots and major tectonic events suggests that the primary drivers may operate over time scales beyond those traditionally used to examine diversity. Nevertheless, the geological processes must be expressed through ecological mechanisms that continue to act in extant ecosystems. Plate tectonic movements control the area and variability of suitable shallow marine habitat. Subject to global climatic constraints, they will modulate ocean circulation, resulting in changes in surface water characteristics as well as altering connectivity between (meta)populations. All of these processes have been identified as key drivers in the origination, maintenance, and extinction of marine taxa (*1–4, 7, 13*). The early phase of plate collision is characterized by the appearance of, and an increase in, new shallow water habitats. The formation of islands will provide new opportunities for isolation and disruption of genetic connectivity. Also, accumulation of diversity as a result of the juxtaposition of communities by accretion of tectonic terranes is most likely to occur in a compressive tectonic setting. All of these changes will serve to increase the biodiversity in the region, either by the origination of new species or through the accumulation of species from elsewhere. For example, in the West Tethys hotspot, the approach of the African plate led to the creation of numerous shallow marine platforms in southern Europe and was associated with a rapid surge in biodiversity throughout the region. High levels of biodiversity were maintained for millions of years while the collision matured, during which habitat area and complexity peaked. The late phase of plate collision is characterized by continent-continent contact, resulting in the rise of mountains, gradual elimination of shallow seas, closure of seaways,

and increased terrestrial runoff. All of these processes provide a mechanism to reduce the regional biodiversity. In the West Tethys hotspot, as the continents of Africa and Europe came closer together, these changes would underpin regional declines in diversity. Acting in concert with climate cooling (*43*) and a decrease in dispersal into the region with the final closure of the Tethyan seaway (*44*), these changes herald the senescence of the West Tethys biodiversity hotspot.

Conclusions

Combined evidence from fossil and molecular studies provides a new perspective on the nature of biodiversity hotspots. The evidence reveals that biodiversity hotspots occurred at different places through time. Today's hotspot in the IAA is not a unique feature but is the latest manifestation of a pattern that has been present for at least 50 My. This long time frame provides a new understanding of the nature of biodiversity hotspots and emphasizes that these phenomena are a product of ecological processes operating over geological time scales. Moreover, hotspots can be studied from their initiation to their termination. The critical role of tectonic events emphasizes the importance of abiotic factors in shaping the world's biotic realm. They drive and underpin the birth, life, and senescence of biodiversity hotspots.

A synthesis of the paleontological and molecular data, interpreted in an ecological context, has enabled us to understand the true antiquity of hotspots and their component species. However, future studies are clearly needed as global threats to marine biodiversity put the spotlight on the vulnerability of coral reef ecosystems. We now realize that human-induced changes are operating on time scales far removed from those that have created these hotspots (*45–47*). An improved understanding of the nature of biodiversity hotspots, be they terrestrial or marine, will require

(i) A clearer understanding of the geographic and environmental context of taxonomic turnover driving the origination, maintenance, and diminution of hotspots over extensive time scales. It is critical to distinguish between the movement of a single hotspot across the globe and the successive origination and extinction of hotspots.

(ii) An understanding of the ecological and environmental processes operating during the natural senescence of biodiversity hotspots to place the current threats to global biodiversity in perspective. It is important to identify the factors that in the past have resulted in the demise of hotspots.

(iii) Multidisciplinary studies integrating large-scale high-resolution data from the geosciences, evolutionary biology, and ecological sciences. This approach can foster the necessary synergies to understand the complexity of global biodiversity patterns over broad spatial and temporal scales.

References

1. B. R. Rosen, in *The Evolving Biosphere,* P. L. Forey, Ed. (Cambridge Univ. Press, Cambridge, 1981), pp. 103–129.
2. D. R. Bellwood, T. P. Hughes, *Science* **292**, 1532 (2001).
3. B. W. Hoeksema, in *Biogeography, Time and Place*, W. Renema, Ed. (Springer, Dordrecht, 2007), pp. 117–178.
4. S. T. Williams, D. G. Reid, *Evolution Int. J. Org. Evolution* **58**, 2227 (2004).
5. A. M. Ellison, E. J. Farnsworth, R. E. Merkt, *Glob. Ecol. Biogeogr.* **8**, 95 (1999).
6. J. C. Briggs, *Evolution Int. J. Org. Evolution* **53**, 326 (1999).
7. D. R. Bellwood, T. P. Hughes, S. R. Connolly, J. Tanner, *Ecol. Lett.* **8**, 643 (2005).
8. S. R. Palumbi, *Coral Reefs* **16**, S47 (1997).
9. P. H. Barber, S. R. Palumbi, M. V. Erdmann, M. K. Moosa, *Nature* **406**, 692 (2000).
10. S. Connolly, T. P. Hughes, D. R. Bellwood, R. Carlson, *Science* **309**, 1363 (2005).
11. R. H. Karlson, H. V. Cornell, T. P. Hughes, *Nature* **429**, 867 (2004).
12. D. Jablonski, K. Roy, J. W. Valentine, *Science* **314**, 102 (2006).
13. P. Jokiel, F. J. Martinelli, *J. Biogeogr.* **19**, 449 (1992).
14. C. M. Roberts *et al.*, *Science* **295**, 1280 (2002).
15. M. E. J. Wilson, B. R. Rosen, in *Biogeography and Geological Evolution of Southeast Asia,* R. Hall, J. D. Holloway, Eds. (Backhuys, Leiden, 1998), pp. 165–195.
16. H. Fukami *et al.*, *Nature* **427**, 832 (2004).
17. S. T. Williams, *Biol. J. Linn. Soc.* **92**, 573 (2007).
18. J. C. Briggs, *J. Biogeogr.* **32**, 1517 (2005).
19. Materials and methods are available as supporting material on *Science* Online.
20. W. Renema, in *Biogeography, Time and Place*, W. Renema, Ed. (Springer, Dordrecht, 2007), pp. 179–215.
21. C. C. Wallace, B. R. Rosen, *Proc. R. Soc. Lond. B Biol. Sci.* **273**, 975 (2006).
22. E. A. Kay, in *Origin and Evolutionary Radiation of the Mollusca,* J. Taylor, Ed. (Oxford Univ. Press, Oxford, 1996), pp. 211–220.
23. R. J. Morley, *Origin and Evolution of Tropical Rain Forests* (Wiley, London, 2000).
24. M. Harzhauser *et al.*, *Zool. Anz.* **246**, 241 (2007).
25. L. Hottinger, *Notebooks on Geology* **CG2007-A06**, 1 (2007).
26. D. C. Potts, *Proc. Fifth Int. Coral Reef Congr. Tahiti* **4**, 127 (1985).
27. P. H. Barber, S. R. Palumbi, M. V. Erdmann, M. K. Moosa, *Nature* **406**, 692 (2000).
28. H. A. Lessios, B. D. Kessing, J. S. Pearse, *Evolution Int. J. Org. Evolution* **55**, 955 (2001).
29. R. J. Morley, in *Tropical Rainforest Responses to Climatic Change,* M. Bush, J. R. Flenley, Eds. (Springer, Dordrecht, 2007), pp. 1–31.
30. A. G. Beu, *Scripta Geol.* **130**, 1 (2005).
31. D. Jablonski *et al.*, *Science* **300**, 1133 (2003).
32. C. Meyer, *Biol. J. Linn. Soc.* **79**, 401 (2003).
33. M. E. Alfaro, F. Santini, C. D. Brock, *Evolution Int. J. Org. Evolution* **61**, 2104 (2007).
34. S. McCafferty *et al.*, *Mol. Ecol.* **11**, 1377 (2004).
35. G. Bernardi, S. J. Holbrook, R. J. Schmitt, N. L. Crane, E. DeMartini, *Mar. Biol. (Berl.)* **144**, 369 (2004).
36. S. O. Klanten, L. van Herwerden, J. H. Choat, D. Blair, *Mol. Phylogenet. Evol.* **32**, 221 (2004).
37. P. H. Barber, D. R. Bellwood, *Mol. Phylogenet. Evol.* **35**, 235 (2005).
38. C. I. Read, D. R. Bellwood, L. van Herwerden, *Mol. Phylogenet. Evol.* **38**, 808 (2006).
39. T. C. LaJeunesse, *Mol. Biol. Evol.* **22**, 570 (2005).
40. H. A. Lessios *et al.*, *Evolution Int. J. Org. Evolution* **53**, 806 (1999).
41. J. Dercourt *et al.*, Eds., *Atlas Peri-Tethys. Palaeogeographical Maps* (Commission for the Geological Map of the World, Paris, 2000).
42. R. Hall, *J. Asian Earth Sci.* **20**, 353 (2002).
43. J. C. Plaziat, C. Cavagnetto, J.-C. Koeniguer, F. Baltzer, *Wetlands Ecol. Manage.* **9**, 161 (2001).
44. M. Harzhauser, W. E. Piller, F. F. Steininger, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **183**, 103 (2002).
45. T. P. Hughes *et al.*, *Science* **301**, 929 (2003).
46. J. B. C. Jackson *et al.*, *Science* **293**, 629 (2001).
47. J. M. Pandolfi *et al.*, *Science* **301**, 955 (2003).
48. J. E. N. Veron, *Corals of the World* (Australian Institute of Marine Science, Townsville, 2002).