BIOGEOGRAPHY AND EVOLUTION OF INDO-PACIFIC MARINE MOLLUSCA: PATTERNS, PROGRESS, PROBLEMS AND PROSPECT

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ABSTRACT

High species diversity with high species:genus ratios, geographic distributions ranging from narrowly endemic to province-wide, and ecological specialization by species but broad ranges of resource use by higher taxa characterize marine molluscan assemblages of the vast tropical Indo-West Pacific region. Evidence from historical-biogeographic syntheses, paleoecology, larval ecology and dispersal ability, and cladistic hypotheses of phylogeny and distribution have recently advanced understanding of how lithospheric plate movements and their effects on earth topography, and global climatic change, especially since the Cretaceous-Tertiary transition, have profoundly affected modern biogeographic patterns. Integrated studies of recent and fossil members of the same taxon are suggested as a promising source of new insights.

Marine biogeographers seek to describe the geographic distribution patterns of the earth's marine biotas, to understand the physical and biotic factors that generate and maintain these patterns, and to understand their development through evolutionary time. The latter aspirations are the more interesting: they help us to understand why modern organisms are found where they are, and why they are not where they are not. How can analyses of present and past biogeographic patterns inform us of the processes that have led to these patterns? Can they distinguish causes intrinsic to the organisms from those imposed by external environments? The study of modern assemblages provides only a snapshot of dynamic, constantly and actively changing processes, but the durable shells of most molluscan taxa preserve well as fossils and permit direct access to the historical record of evolutionary and distributional change.

Patterns

Marine molluscs of the Pacific Ocean basin exhibit biogeographic and evolutionary patterns that are of general interest and importance to evolutionary biology. The tropical and subtropical central and western Pacific region shares an extremely diverse but homogeneous fauna with the Indian Ocean, forming the vast Indo-Pacific (IP) province that covers more than one-fourth of the world ocean area. Unusual combinations of attributes characterize many of its marine taxa: high species diversity due to the concentration of many very similar species in some families; a spectrum of geographic distributions from narrow endemism on isolated islands to the apparent maintenance of gene flow throughout the entire IP region; and ecologically specialized species but broad ranges of resource use and life history patterns at higher taxonomic levels (Kohn, 1983; 1987; Kohn and Nybakken, 1975; Taylor and Reid, 1984; Perron and Kohn, 1985). Striking differences among species in some of these attributes and gradients in others invite comparative analysis and provide dependent variables for hypothesis testing.

Progress

At the preceding Symposium in this series, I suggested three likely sources of enhanced understanding of Pacific marine biogeography and evolution: new par-

adigms in the earth sciences, resolution of conflict in biogeographic theory, and new syntheses of data in historical biogeography and paleoecology (Kohn, 1983). At this third Symposium, it is appropriate to evaluate these suggestions, based on what we have learned during the past six years.

Current Paradigms in the Earth Sciences.—PLATE TECTONICS. Early in the plate tectonics revolution Valentine (1973: Ch. 8) recognized that the major barriers to distribution for marine organisms are related to earth topography and hence to plate tectonic processes. While the marine biogeographic implications of several recent advances in knowledge of Pacific basin tectonic history (Charlton, 1986; Colley and Hindle, 1984; Leitch, 1984) remain to be explored, others have been pursued. A major recent application of plate tectonic history to Pacific molluscan biogeography involves the Late Cretaceous-Early Cenozoic break-up of Gondwanaland. This altered shallow marine environments at high southern latitudes from a more or less continuous but isolated southern circum-Pacific coast to the separate, geographically isolated southern land masses that have persisted and dispersed since the early Tertiary. Zinsmeister (1982; 1984; Zinsmeister and Feldmann, 1984) has combined this analysis with a historical-biogeographic synthesis, and I discuss it more fully below.

Other recently revealed and potentially biogeographically important consequences of the northward migration of the Indo-Australian plate throughout the Cenozoic are the increasing age and thickness of coral reefs of the Great Barrier Reef system from south to north (Davies et al., 1987) and the mid-Tertiary impingement of the Indo-Australian plate against the Eurasian and Philippine plates to the north. This undoubtedly altered western Pacific current flows and the dispersal possibilities of planktonic larvae (Zinsmeister, 1982). During the last 3 million years especially, global climatic fluctuations of large amplitude have altered sea level by 100–200 m. Improving documentation of these events (Haq, Hardenbol and Vail, 1987) provide new data important to historical biogeographic analysis. The effects of global eustatic sea level change and of plate movements in the Pacific region on molluscan distribution patterns remain to be elucidated.

THE IMPACTS OF IMPACTS. During the past six years, the theory that the impacts of large extraterrestrial objects have catastrophically altered environmental conditions, caused mass extinctions, and effectively redirected the course of evolution on earth has at least stood its ground, despite alternative hypotheses advanced to explain each proposed effect (Raup, 1986; Hartnady, 1987). Perhaps more significantly, the impact theory and its predicted effects have challenged thinking about the evolutionary role of infrequent, very large-scale catastrophic perturbations of the earth's biosphere (Olsen, 1986; see also Raup and Jablonski, 1986; Jablonski and Flessa, 1986).

At the Cretaceous-Tertiary transition, molluscan species diversity along the southeastern coast of North America decreased by 80%, from Late Maestrichtian to Early Danian. Hansen (1988) has tracked the subsequent recovery from this mass extinction: an initial radiation, then widespread extinction in Late Danian, and a secondary, major radiation with a four-fold increase lasting more than 25 million years to late Middle Eocene. I am unaware of any attempts at comparable analyses of Paleogene Pacific molluscan faunas.

Biogeographic Theory.—Three types of hypotheses are advanced to explain observed patterns in the geographic distribution of animals. Dispersal hypotheses state that ranges depend on the dispersal ability of a distributive phase in the life history. In the case of benthic molluscs, this is typically the ability of a planktonic larva to traverse areas of ocean unsuitable for adult habitation, usually passively

via currents. Vicariance hypotheses hold that extrinsic barriers that prevent dispersal along geographic pathways determine biogeographic patterns. The barriers separate evolutionarily most closely related taxa, and congruent patterns of distribution are shared by different, unrelated groups of organisms endemic to the same areas. Ecological hypotheses hold that environmental requirements are more important than either dispersal or vicariance in determining ranges of species. It should be noted that these hypotheses are not mutually exclusive, not equally applicable to biogeographic processes at the same time scales, and not easily refutable. Next, I review evidence collected during the last six years on specific marine molluscan distributions, with reference to these theories.

Jablonski and Lutz (1983) provide the most up-to-date review of evidence relating larval dispersal to biogeographic and paleobiogeographic patterns of benthic invertebrates, mainly molluscs. In a comparative study of larval development and ecology among about one-fourth of the some 250 IP species of the gastropod genus *Conus,* Perron and Kohn (1985; Kohn and Perron, in prep.) demonstrated that species with greater potential for larval dispersal have broader geographic ranges. Other species-rich IP molluscan taxa with gradients of larval developmental mode have not yet been examined. Reid (this symposium) has adopted a historical biogeographic approach, combining phylogenetic information derived from a cladistic analysis with data applicable to the possible roles of both vicariant and dispersal processes in cladogenesis within the genus *Littorina.*

Although molluscan larvae are generally distinguished as either planktotrophic or lecithotrophic, that is with or without a dispersing, pelagic feeding larval stage, recent studies show that some may be more flexible (Hoagland and Robertson, 1988; Reid, ms.; Kempf and Hadfield, 1985; Kempf and Todd, 1989). The latter authors showed that some lecithotrophic opisthobranch larvae have not lost the ability to feed and that they benefit from feeding. This could affect planktonic survivorship and enhance dispersal ability, and it raises the possibility that the evolutionary loss of planktotrophy may not be irrevocable (Strathmann, 1985).

Historical-biogeographic and Paleoecologic Data. — Extensive study of Eocene molluscan assemblages on Seymour Island has provided a new synthesis of major changes in species composition and distribution patterns through the Cenozoic in the southern circum-Pacific, particularly its southwest corner. Zinsmeister (1982; 1984; Zinsmeister and Feldmann, 1984) relates faunal shifts both to tectonic events and to climatic change. Sequential fragmentation of Gondwanaland and the northward migration of New Zealand and Australia and westward migration of South America away from Antarctica fostered differentiation in isolation of, e.g., struthiolariid gastropods. These dispersals of continental fragments into lower latitudes ameliorated the environments of New Zealand and Australia in the Eocene, causing an environmental crisis for their temperate marine faunas and exposing them to colonization by tropical IP elements. Marked cooling at the Eocene-Oligocene transition reduced diversity in Australia and New Zealand, especially of their IP components, caused marked extinction in the paleoaustral fauna, and restricted survivor taxa to southern circumpolar distributions. Molluscan diversity of New Zealand increased again with warmer conditions during the Oligocene and Early Miocene but later cooling episodes associated with Neogene glaciation permitted northward dispersal of southern forms to lower latitudes. Effects of the Eocene-Oligocene transition persist in the modern molluscan faunas of the temperate southern Pacific (Zinsmeister, 1982).

This synthesis of southern circum-Pacific Cretaceous and Tertiary paleogeography explains discoveries of bivalve and gastropod as well as echinoderm and

crustacean genera in the Eocene of Seymour Island, Antarctic Peninsula, that were previously known only from the late Cenozoic in mid latitudes. It offers a mechanism for two major historical-biogeographic changes in the composition and distribution of shelf faunas: 1) increased isolation of the faunas of individual plates and local provincialism from early Tertiary on as the southern continents separated, in contrast to the broadly distributed but highly endemic prior southern marginal or austral Pacific fauna, and 2) alterations in composition and distribution of faunas in response to changes in ocean circulation patterns as well as sea temperatures caused both by drift of land masses and by abrupt cooling at the beginning of the Oligocene (Zinsmeister, 1982; 1984; Zinsmeister and Feldmann, 1984).

At the eastern margin of the Pacific basin, westward plate movement has resulted in encroachment of the North American continent onto the Pacific plate, and this has split the formerly continuous spreading ridge into the Juan de Fuca and Gorda Ridge system in the north and the East Pacific rise near the equator. A 3,000-km discontinuity now separates their hydrothermal vent faunas, and their molluscan and other components have differentiated at the species and genus levels (Tunnicliffe, 1988).

Valentine (1984a, 1984b) has related new knowledge of Tertiary climatic change, especially since the warmest Eocene, and of accompanying latitudinal and seasonal sea temperature differences, to the temporal regulation of diversity. During the Neogene, the latitudinal thermal gradient steepened, enhancing provincialization resulting from plate movements and fostering diversification, especially in molluscs with basically linear distribution patterns along north–south-oriented continental coasts. This analysis also indicates that the present highly diverse tropical marine biotas are probably not older than Neogene (Valentine, 1984a; Crame, 1986).

At a finer temporal scale, Plio-Pleistocene climatic change and concomitant marked eustatic sea level shifts (Haq et al., 1987) have also exerted profound effects on tropical IP molluscan distribution patterns (Paulay, 1988, in press). Paulay combined study of habitat requirements of bivalve species across the reef systems of tectonically stable islands, comparisons of these assemblages with those of locally uplifted islands, and comparisons of faunal change on an uplifted island from the time when it was an atoll until its present condition, with the shells of the former lagoon assemblage preserved as a rich fossil assemblage. The results indicate that bivalves face severe extinction as reef platform and lagoonar environments are stranded during sea level falls, while re-establishment of these reef habitats with rising or stable sea level leads to recolonization but often with a fauna differing in species composition. This study also provides new understanding of apparently anomalous patterns of bivalve diversity across southern Polynesia. While bivalve species richness decreases from west to east in the South Pacific islands, as in other taxa, the decline is steep from Fiji (probably about 200 species) to Niue (78 species), more gradual within the Cook Islands (61 in the west to a minimum of 43 in the east), and is then reversed in the Society Islands, due to the ecological factor of the reappearance of more complex inner reef environments (Paulay, 1988, in press).

CONTRIBUTIONS OF THIS SYMPOSIUM. Vermeij (1987) has recently demonstrated that barriers to dispersal of gastropods between continental islands of the eastern Eurasian plate and the oceanic islands of the Philippine and Pacific plates are selective with respect to ecology and morphology. They more effectively block sand-dwelling species than rock-dwellers, smaller than larger sand-dwellers, and rock-dwellers with less armored shells. Bivalves with different ecological attributes

are also differentially susceptible to such barriers (Vermeij, 1990). Vermeij's and Paulay's results emphasize the importance of examining interactions among dispersal ability, ecological requirements, and morphological attributes as well as treating the hypotheses separately.

During the Middle and Late Miocene and Pliocene in subtropical and subtemperate Japan, more marked temperature fluctuations occurred as well as associated habitat loss and gain due to regressions and transgressions. Shuto (1990) has now shown that relatively few survivor species evolved from indigenous ancestors during cool periods, while speciation from southern invaders characterized warm periods. Also at extra-tropical latitudes, Reid's historical biogeographic analysis of *Littorina* (1990) relates speciation events both to climatic changes that may have caused vicariance and to the opening of the Bering Strait, which permitted transarctic migrations between the Atlantic and Pacific oceans in late Pliocene time. These studies also provide new results that can also be applied to enhance understanding of the roles of different modes of speciation in the sea, for which prior data have been inadequate (Valentine and Jablonski, 1983).

Sampling difficulties have long shielded deep-sea faunas from yielding critical information relevant to biogeographic hypotheses. Recent collections of deep-sea Aplacophora are, however, beginning to provide enough information to support the hypothesis of an ancient, widespread deep-sea fauna and more derived taxa in peripheral, geographically more restricted shelf, slope, and hydrothermal vent environments (Scheltema, 1990).

Problems and Prospect

At the earlier symposium, I posed the basic question, what historical-geographic, ecologic, and evolutionary processes produced the biogeographic patterns that characterize modern Pacific marine molluscs, particularly high species diversity combined with very broad geographic ranges, some encompassing the entire events and changes in physical oceanic environment and climate. The important ecological factors must include food and living space requirements, interactions with predators, prey and competitors, and physical environmental variables. All of these differentially affect planktonic larval stages and benthic juveniles and adults.

A second problem, clarified and sharpened to some extent since the last symposium, concerns whether modern Pacific molluscan distribution patterns are essentially Cenozoic phenomena, developing afresh on a nearly clean slate created by the Cretaceous-Tertiary mass extinctions, as Hansen (1988) has documented in southeastern North America. To what extent can evolutionary changes such as taxonomic diversification and the radiation of taxa into new adaptive zones be traced in the more limited fossil record of the Pacific region? Within the Cenozoic, how important to modern patterns are long-term Tertiary processes such as plate migrations and oceanic change? Were they rendered insignificant by the profound, glacially induced climatic changes of the latest Tertiary and Quaternary? At the shortest relevant time scales, are ecological processes and interactions more important than any long-term, geomorphic processes and events?

CONTRIBUTIONS OF THIS SYMPOSIUM. Kay (1990) has begun to address these questions by examining cladogenesis in the species-rich gastropod family Cypraeidae, in order to determine the temporal and geographic origins of infrageneric-level taxa and their subsequent diversification history. This approach could profitably be extended back in cypraeid evolution, as the family is of Early Cretaceous or Late Jurassic origin (Kay, 1985).

Reid's study (this symposium; in press) of the historical biogeography of *Littorina*, using a phylogeny determined by cladistic analysis, shows that the biogeographic pattern shown by this genus in the Pacific is best explained by vicariance caused by climatic change, while trans-Arctic migration is a clear case of dispersal. This emphasis on historical processes contrasts with that of Kohn and Perron (in prep.; Perron and Kohn, 1985) on short-term dispersal capability and ecological factors. These different views may reflect different patterns of speciation along linear, continental margins and over two-dimensional oceanic provinces (Valentine and Jablonski, 1983). In *Littorina* species on the essentially continuous margin of the northern Pacific there is a clear correspondence between the spatial pattern and the proposed phylogeny, and the range of the species is independent of their type of larval development. In the North Atlantic, however, there is no clear spatial pattern, but rather a suggestion that species with the potential for wider dispersal have larger ranges, as in IP *Conus*.

The present preliminary and unsettled state of knowledge of how molluscan dispersal ability relates to geographic distribution indicates that pursuit of studies in additional taxa both of comparative larval ecology and dispersal ability, and of cladistic phylogenetic analysis and its relationship to present geographic distributions of sister taxa, should be encouraged, as they are complementary approaches.

Finally, a particularly advantageous attribute of most Mollusca for biogeographic and evolutionary study is the durable external shell. Shells not only protect their makers in their lifetimes, but their persistence in the fossil record preserves considerable biological information about those lifetimes and, in some cases information about lifestyles and population and community paleoecology (Kohn, 1985). Comparisons of fossil and recent molluscs have been particularly informative, e.g., in elucidating larval modes and their dispersal capabilities (Jablonski and Lutz, 1983) and how these change over time within lineages (Shuto, 1983). Integrated studies of recent and fossil members of the same taxon could more fully apply comparative biological knowledge of extant taxa to hypotheses of historical biogeography as well as other aspects of paleobiology. Perhaps the next symposium in this series will present new insights derived from this additional direction.

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