Reports

Cenozoic High Latitude Heterochroneity of Southern Hemisphere Marine Faunas

Abstract. *Discovery of 11 genera, in five classes within the Mollusca, Echinodermata, and Arthropoda in upper Eocene rocks on Seymour Island, Antarctica, previously known only from Late Cenozoic in mid-latitudes, suggests that the high latitude region of the Southern Hemisphere acted as a center of origin and dispersal for a broad spectrum of taxa. Precursors to modern deep- and shallow-water mid-latitude forms evolved and flourished in the high latitudes until conditions in lower latitudes favored their dispersal. These observations of Antarctic marine invertebrates corroborate those recently made about terrestrial mammals and plants in the Arctic.*

The heterochroneity reported for early Tertiary faunas and floras from the Arctic (*1*) has a parallel in the early Cenozoic marine faunas from the high latitude regions (*2*) of Antarctica. In a number of cases, taxa recently described from high latitude southern polar regions predate their descendants in the middle and low latitudes by as much as 40 million years. The recognition of high latitude heterochroneity within a variety of terrestrial and marine groups in both the Northern and Southern hemispheres indicates that the high latitude regions have played a more important role in the development and diversity of Cenozoic faunas and floras than has previously been recognized. The terrestrial biota described from the Arctic (*1*) imply that the high latitude regions may have acted as areas of biologic innovation rather than merely dispersal corridors between the mid-latitudes. The recognition of similar heterochroneity in a wide variety of taxa in the marine faunas of Antarctica suggests that the sudden appearance of plant and animal groups in the geologic record may reflect major dispersal episodes from the high latitude regions.

The northward dispersal of marine groups from the high southern latitudes was accomplished both by submergence into cooler deeper facies and by passive dispersal as a consequence of cooling associated with the onset of glacial conditions during the Neogene. Although the northward dispersal of many taxa merely reflects the general expansion of cooler sea temperatures, several examples show that some cooler high latitude groups have adapted to warmer habitats during the Late Cenozoic and Recent times.

The Southern Hemisphere has been a fruitful region for biogeographic studies for nearly 200 years. However, the virtual absence of data from Antarctica has hindered explanations of faunal similarities between the southern continents. The anomalous distribution of certain faunal elements of the Southern Hemisphere has been explained either as migrations from the north or passive dispersal by circumpolar circulation (*3–5*).

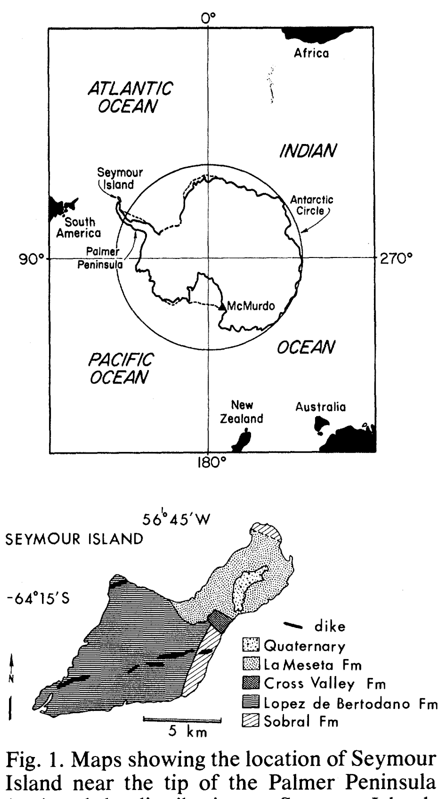

Fig. 1. Maps showing the location of Seymour Island near the tip of the Palmer Peninsula (top) and the distribution on Seymour Island, of the late Eocene La Meseta Formation (bottom) from which the studied specimens were collected.

Although the Upper Cretaceous–lower Tertiary sequence on Seymour Island has been known for about 100 years (*6*), virtually no detailed study of these deposits has been conducted since the early part of the century. During the austral summer of 1974–1975, the first systematic geologic survey of the Seymour Island region (Fig. 1) was conducted by a joint Argentine-American expedition (*7*). The results from this expedition and a second (*8*) during 1982, revealed the existence of a thick, continuous sequence of remarkably fossiliferous rocks of Cretaceous to early Tertiary age (*9*). The sequence contains a nearly complete record from the final breakup of Gondwana to the development of glacial conditions during the early Neogene. Because of its intermediate location along the southern margin of the Pacific, the data provide new insight into the biogeographic history of the Southern Hemisphere and indicate the importance of the high latitudes to the development of mid-latitude Cenozoic faunas and floras.

Analyses of the invertebrate faunas (*10–14*) revealed the presence, in the shallow-water upper Eocene La Meseta Formation, of a number of taxa previously known only from the late Cenozoic (Fig. 2). Many of the late Eocene invertebrates belong to groups that were thought to have evolved only recently or migrated into the southern Pacific at the end of the last glaciation (*15*). These recent immigrants have been referred to as Neoaustral and were believed to have had their origin in the low latitudes (*16*). Because of their high dispersal capabilities, it was assumed that they were spread throughout the Southern Hemisphere by the prevailing west to east circulation of the west wind drift (*4, 5*). Although some of the Neoaustral species may have entered the Pacific basin in this manner, early occurrences in the upper Eocene deposits on Seymour Island indicate that many evolved in the high latitudes of the southern Pacific during the early Cenozoic. Their occurrence on Seymour Island indicates that considerable evolution took place in the high southern latitudes during the Tertiary. Subsequent dispersal of these taxa into lower latitudes suggests that whatever mechanism was acting to prevent their northward migration was no longer operative in the Neogene.

Before final fragmentation of Gondwana during the early Tertiary, the southern circum-Pacific closely resembled the present-day northern Pacific setting, with nearly continuous land extending across the pole from South America to Australia. The southern margin of the

Pacific was isolated by both geography and oceanic circulation from the other major oceans of the Southern Hemisphere (*10*). Climatic conditions in the high southern latitudes during this period were mild in comparison with modern conditions but cooler (*17*) than the mid and low latitude regions of the Southern Hemisphere. As is the case in the high latitude regions today, extreme seasonality was an important feature. The existence of seasonality, together with the isolation of this broad region, is believed to have been the primary cause of the appearance of a number of invertebrate groups during the Late Cretaceous and early Tertiary. Because of the uniqueness of these faunas, the Weddellian Province was proposed for the shallow-water shelf region extending from Australia to southern South America (*18*). With the subsequent breakup of Gondwana during the early Cenozoic, the Weddellian Province was broken into a number of discrete units; each had a different climatic and oceanic history because of changes in geographic location (*19*).

As a consequence of prolonged isolation, new taxa evolved around Antarctica as the climate gradually cooled. Their general absence in Australia, New Zealand, and South America during this period (*15*) is attributed to the absence of suitable, shallow, cool-water facies around those areas (*10*). The region around Antarctica acted like a holding tank for these newly evolved groups. The cool-water fauna would remain within the high latitude holding tank until either suitable cool conditions developed in the lower latitudes or until they migrated into deeper water.

The first record of the cooler water, Weddellian molluscs outside the Antarctic region is in the lower Miocene deposits on the east coast of Isla Grande de Tierra del Fuego (*20*). Their arrival in southern South America before their arrival on the other southern continents reflects both the extreme southern location of Tierra del Fuego and its favorable position relative to southern Pacific circulation patterns. Oligocene and Miocene occurrences of the crab genus *Lyreidus* in Europe (*14*) may provide evidence of more rapid northward dispersal of this group. Southern South America has been a sensitive indicator of Cenozoic climatic changes in the Southern Hemisphere. Because it spans a wide latitudinal range, climatic changes have been felt along the southwest coast of South America earlier than on the other southern continents (*21*). During the Pliocene and Pleistocene, as temperatures declined, the Weddellian species began a general period of northward dispersal through the Southern Hemisphere.

Several groups of invertebrates apparently were able to adapt to deeper water conditions during the Cenozoic. Before their discovery on Seymour Island (*11*), two genera of asteroids (*Ctenophoraster* and *Zoroaster*) were known only from water depths greater than 100 m. The crinoid genus *Metacrinus* also occurs in the shallow-water facies of the La Meseta Formation (*22*). Before its discovery on Seymour Island, *Metacrinus* was known only from the Recent in water depths of 100 m or more. As with the echinoderms, the decapod *Lyreidus* has only been reported from deep sublittoral to bathyal depths (*13, 14*). Its occurrence in a beach facies in association with a land mammal (*23*) indicates that, during the early Tertiary, it was adapted to extremely shallow conditions. The morphologies of species in all these groups are very similar to their modern counterparts, providing a high degree of confidence in the generic determination.

Although the fossil record of these groups is extremely limited or, in several cases, unique to Seymour Island, it is apparent that they have had a long history. Their occurrence in littoral to shallow sublittoral facies on Seymour Island suggests that they probably evolved in shallow environments, an observation reinforced by functional morphological analysis of *Lyreidus* (*13, 14*). As the oceans cooled, groups that were able to adapt to deeper conditions dispersed northward into deeper water along a thermal gradient. If this interpretation is correct, the high latitude region around Antarctica may have been the source for many modern invertebrate taxa known to inhabit outer shelf and slope environs. It has been suggested that most of the shallow marine faunas of Antarctica as well as those in the deep sea originated in place and that unusual morphologic features such as gigantism and dwarfism reflect adaptation to environments of limited resources (*24*). The early occurrence of some groups in high stress, shallow-water environments indicates these groups evolved in shallow-water facies and subsequently moved into deeper water. Comparison of the faunal histories of New Zealand and Antarctica during the early Tertiary (*10*) reveals that as New Zealand gradually moved north into warmer mid-latitudes, most of the cooler water Weddellian elements in the New Zealand faunas became extinct although most survived around Antarctica during the same period (*25*). Although most of the Weddellian groups failed to adapt to the gradual warming of the New Zealand region during the middle Tertiary, several, such as the gastropod family Struthiolariidae, survived and became important elements of the warm temperate fauna persisting to the Recent (*20*). In southern South America similar histories can be seen for the Struthiolariidae, the bivalve family Lahilliidae, and the decapod subfamily Chasmocarcininae. Although both families of molluscs were able to adapt to quite warm conditions during the early Tertiary and are found in central Chile associated with subtropical to tropical Panamic faunas, they became extinct by the middle Miocene (*26*); the Chasmocarcininae have persisted in sublittoral habitats of the subtropics today (*13, 14, 27*).

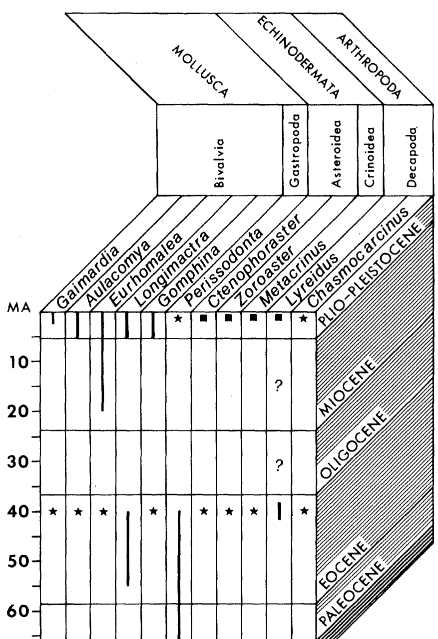

Fig. 2. Geologic record of invertebrate genera that show extreme heterochroneity. Specific range data for each taxon are cited in the text. Stars represent occurrences that are recorded either solely from the Recent or from the La Meseta Formation. Boxes represent Recent occurrences of species from deeper water habitats of the outer shelf and continental slope.

The recognition of heterochroneity displayed by a wide variety of plants and animals in both the Northern and Southern hemispheres during the Cenozoic indicates that the high latitudes have played an important role in the evolution of Cenozoic biotas. Although the sudden appearance of many of these groups in the fossil record may reflect major dispersal events into the lower latitudes as a consequence of the general expansion of cooler conditions during the Cenozoic, some were able to move northward by adapting to warmer habitats. The submergence observed in several groups also suggests that the high southern latitude region was the source for some of the elements of the modern outer shelf and slope communities. The recognition of the importance of the high latitudes to the development of Cenozoic biotas suggests that the high latitudes may have played a more important role in the evolution of the earth's biota throughout the Phanerozoic than has previously been acknowledged.

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25 November 1983; accepted 21 February 1984

Catastrophic Storms, El Niño, and Patch Stability in a Southern California Kelp Community

Abstract. *Strong winter storms in southern California destroyed most of the canopy of the giant kelp* Macrocystis pyrifera *but not the patches of understory kelps in the Point Loma kelp forest near San Diego. Subsequent massive recruitment of* Macrocystis *juveniles and adults that survived the storms had low survival in the summer during the California El Niño of 1983. The combined disturbance may have long-lasting structural consequences for this community because, once established, the understory patches can resist invasion by* Macrocystis.

On 30 November 1982 the first of 11 unusually powerful storms struck the southern California coastline. For 15 days wave heights exceeding 3m were measured at the entrance to Mission Bay in San Diego; some of these waves were the largest measured in 8 years. Seven of the 11 storms had wave periods of more than 20 seconds, the first such occurrence in over a decade (*1*). The storms occurred during an El Niño event, which by many indications appears to be the most extreme yet measured (*2*). Technically, El Niños are periodic events characterized by anomalously warm sea surface temperatures along the coasts of Ecuador and Peru (*2*), but the strength of the California Current correlates to these eastern tropical Pacific Ocean phenomena. The California events were marked by a diminution of the California Current, anomalous poleward flow, and depression of the thermocline (*3*). We now describe the separate and combined effects of the catastrophic storms and the strong El Niño on the structure and stability of the kelp community off Point Loma near San Diego (*4*).

This community is characterized by the giant kelp *Macrocystis pyrifera*, the fronds of which float on the sea surface. There are three other perennial canopy types that occupy areas of various sizes on the sea floor: (i) *Pterygophora californica* and *Eisenia arborea*, whose fronds are held above the substratum by woody stipes and occupy often distinct patches up to several hectares in area; (ii) *Laminaria farlowii*, whose fronds lie prostrate on the substratum and form patches usually less than 100 m^2 in area; and (iii) two types of turf of articulated coralline algae (mostly *Calliarthron cheilosporioides*) or fleshy red algae (often dominated by *Gelidium* spp.), which form patches usually less than 30 m^2 in area. The resistance and resilience stability of these patches were characterized from 1970 to 1981 (*5*). At Point Loma, *Macrocystis* is the competitive dominant, but each of the other patch types has resistance to disturbance or invasion. The winter storms of 1982–1983, however, reduced the surface canopy area from over 600 to less than 40 ha (*6*), and there were periods with essentially no canopy. Our diving surveys covering 960 to 1440 m^2 of subsurface *Macrocystis* plants revealed that the damage was not uniform. Mortality, measured by densities of extant plants and recently killed holdfasts or fresh holdfast scars, was highest (66 percent) in the shallow (12-m) inner margin of the forest, lower (47 percent) at mid depths (15 m) of the central part of the forest, and lowest (13 percent) in the deeper (18-m) central outer margin. Mortality at the northern and southern ends of the forest, 40 and 41 percent, respectively, was higher than that at the central outer station even though these regions are all at the same depth (18 m). Two- and 3-year-old plants survived better than others at Point Loma (*5*). In the winter of 1975–1976, mortality of 2-year-old plants in a 400-m^2 area in the central part of the kelp forest was 6 percent ($N = 84$); during the following winter, mortality of 3-year-old plants was 21 percent ($N = 38$). In the winter of 1981–1982, mortality of 2-year-old plants in the same area was 7 percent ($N = 56$), but the 1982–1983 winter storms resulted in 44 percent ($N = 48$) mortality (*7*).

The observed effects of these storms and the El Niño, combined with the data