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Generation and Maintenance of Gradients in Taxonomic Diversity

Abstract. *Latitudinal gradients in diversity of organisms represent an equilibrium distribution for at least the last 270 × 10⁶ years. Faunas endemic to tropical regions evolved significantly faster than extra-tropical faunas. The latitude-dependent difference in rates of evolution also represents an equilibrium condition for at least the last 270 × 10⁶ years and has consequences for paleontological correlation of rocks because the attainable resolution depends on rate of evolution and will thus be greater in tropic regions than in extra-tropical ones.*

Latitudinal gradients in taxonomic diversity of organisms have recently been accorded attention by geologists because of their implications about past environments and possible continental movements. For such geological studies it is sufficient to know that an empirical relationship exists between diversity of organisms and latitude. The associated problem of identifying mechanisms by which diversity gradients are generated and maintained is biological rather than geological. It appears, however, that the perspective of geological time, permitting consideration of the evolutionary history of organisms, may constrain the number of possible mechanisms.

Strong diversity gradients sloping poleward from the equator are characteristic for widely distributed, large groups of living organisms having a good distribution potential. Such gradients characterize diversity among genera and families, as well as among species (*1*). The fact that gradients are strongly expressed among higher taxa suggests but does not prove that they have existed for a long time. In considering the equilibrium condition of this biological pattern the realm of geology is entered, for the problem is dependent on the scale of geological time.

The equilibrium condition of this pattern can be tested by examining the diversity of well preserved, adequately collected, and extensively studied fossil groups. We have chosen for this purpose two widely distributed invertebrate groups, Permian brachiopods and Cretaceous planktonic foraminifera.

In the region for which we have data (Northern Hemisphere) for the Maestrichtian interval of the Cretaceous (about 70 to 80 × 10⁶ years B.P.) a typical diversity gradient existed among species of Cretaceous planktonic foraminifera (Fig. 1). This gradient existed despite the fact that climatic belts in the Cretaceous apparently were ill-defined, and world climate was milder than at present with a concomitant reduction in slope of the

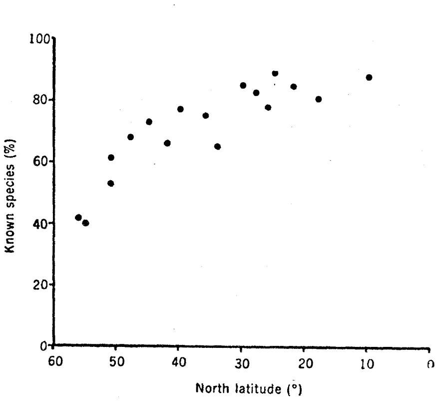

Fig. 1. Diversity among species of Maestrichtian planktonic foraminifera in the Northern Hemisphere as percent of total number of species known plotted against latitude. The gradient in diversity is similar to that typically found in living organisms.

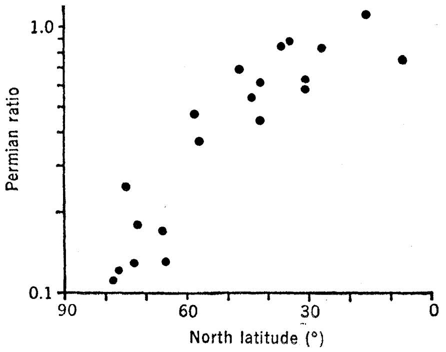

Fig. 2. Diversity among families of Permian brachiopods in the Northern Hemisphere as shown by the Permian ratio. This ratio is Tethyan Endemics : Cosmopolitan Dominants and tends to normalize for the sampling inequities common in the geologic record. The gradient in diversity is similar to that typical of living organisms and Cretaceous planktonic foraminifera.

thermal gradient between the equator and the poles. A second test can be made with Permian brachiopods, using a measure of diversity among families normalized for sampling efficiency (*2*) (Fig. 2). Permian brachiopods show a typical gradient in the latitudes for which we have data despite the peculiar Permian climate characterized by intense Southern Hemisphere glaciation which apparently left the Northern Hemisphere untouched (*3*).

Typical diversity gradients existed during intervals of time climatically somewhat like the present in the occurrence of glacial conditions (Permian) and strongly contrasting with the present in the existence of broadly distributed equable conditions (Cretaceous). Thus, a gradient in diversity sloping poleward from the equator has existed for at least the last 270 × 10^6 years; this gradient represents an equilibrium condition for large groups of organisms with wide distribution.

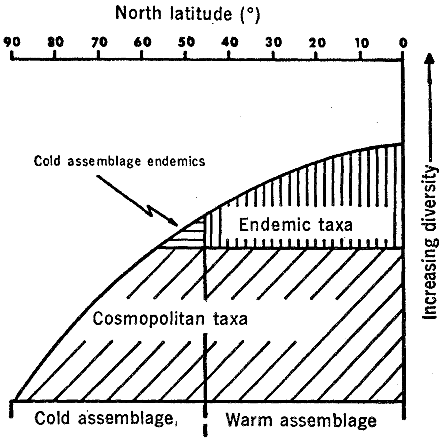

Fig. 3. Composition of "warm" and "cold" assemblages of families in terms of cosmopolitan and endemic elements. The "cold" assemblage is seen to consist almost entirely of cosmopolitan elements, while the "warm" assemblage contains the cosmopolitan elements and many endemic forms as well.

More than a simple change in diversity along the gradient is involved—populations at the high and low ends of the diversity curve differ widely in a taxonomic sense and are generally divisible into "warm" and "cold" assemblages, respectively. A cluster analysis (*4*) has been used on data for the distribution of families of living clams which objectively separates stations characterized by the warm-water and cold-water assemblages (*2*, *5*). The cold-water assemblage virtually lacks endemic families and consists of families cosmopolitan in their distribution (Fig. 3). Stations comprising the warm-water assemblage have cosmopolitan families, but they have many endemic families as well (*2*).

We may examine separately the cosmopolitan and endemic warm-water subsets in the distribution of bivalve mollusks. Of particular significance is any difference in evolutionary history of the subsets which might be related to generation or maintenance of an equilibrium condition characterized by a diversity gradient sloping from the equator poleward.

One possibility is to consider the relative antiquity of the families comprising the two subsets by plotting percent of clam families against the time of their origin (Fig. 4). While the data lack precision (*6*), they are adequate to show that cosmopolitan elements (which comprise virtually all of the cold-water assemblage) are relatively old and in particular include few families evolved in the last 50 million years. The curves shown in Fig. 4 are modified survivorship curves (*7*) which, as Simpson has noted, should be reciprocals of evolutionary rates. Thus, among living clams the families found in cold water are evolving slowly relative to families endemic to warm water.

It is suggested by the data that typical diversity gradients owe their form to higher evolutionary rates in warm than in cold regions. It is conceivable that rates have generally been equivalent the world over, but that the rigors of Pleistocene and Recent climates have created a temporary bias by systematically excluding more recently evolved families from the colder regions.

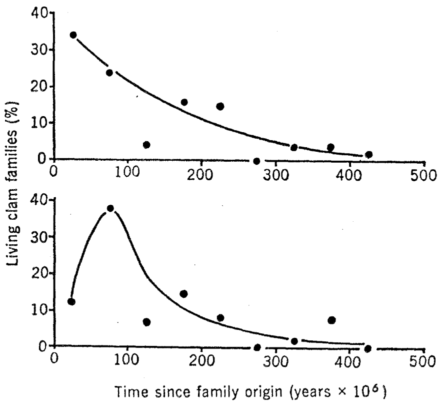

Fig. 4. Modified survivorship curves for families of living clams belonging to the warm-water endemic (top) and cold-water (cosmopolitan) groups (bottom). While the data lack precision, it appears clear that evolution has been considerably faster in the warm assemblage than in the cold assemblage.

To determine whether or not relative differences in evolutionary rates between warm- and cold-water areas represent an equilibrium situation, recourse again can be made to the fossil record. Cretaceous planktonic foraminiferal genera which occur at sample stations north of 50°N are ancient relative to those at stations between the equator and 50°N (Fig. 5). Clearly, high rates of evolution were concentrated in the tropical realm of Cretaceous time and were notably lacking at high latitudes. Stehli performed a similar analysis of longevity in Permian brachiopod families (*2*) and found a pattern in which endemic Tethyan (warm water) families appear to have evolved at high rates while cosmopolitan forms appear

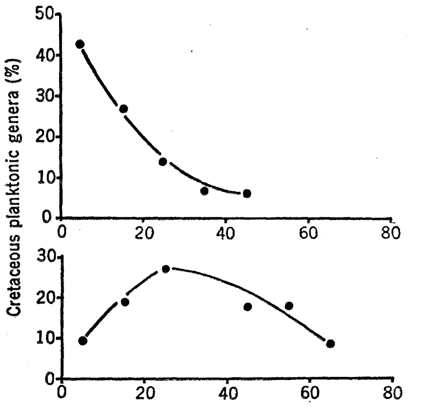

Fig. 5. Modified survivorship curves for Cretaceous planktonic foraminiferal genera taken between 0° and 50°N (top) and those from north of 50°N (bottom). Again evolution has clearly been faster in the warm-water region close to the equator than elsewhere.

to have evolved at much slower rates.

These three examples show that rapid evolution in tropical areas is an equilibrium situation as is slow evolution in extra-tropical regions. Both the generation and the maintenance of diversity gradients are due to this relative difference in evolutionary rates (Fig. 2). It may also be seen that, at least among the taxa here employed, adaptations which permit the occupation of major new niches and thus lead eventually to the development of higher taxa take place in the tropics and some of the more successful groups later contribute representatives to the cosmopolitan fauna (and thus to cold-water regions). Although species and perhaps some genera do evolve in the cold regions, they do not seem to have the potential for crossing major adaptive thresholds, or else major thresholds are not available in this region, and new lower taxa thus do not lead to the establishment of new families. The potential for threshold-crossing adaptations of major significance is evidently high in the tropics, and such adaptations frequently develop there and are exploited with the concomitant development of groups whose success and diversity lead to their recognition as families.

The three groups used to document the existence of rapid evolution in the tropics are all marine invertebrates, and thus are all poikilotherms; they are all strongly influenced by the ambient temperature. It might be supposed that the more rapid evolution found among tropical forms might simply be due to a thermodynamic effect on reaction rates and a resultant higher mutation rate. As a check on this possibility we have examined a homoiothermic group—the mammals—which should be independent of such an effect. It is evident that the effect is as strongly expressed among mammals (Fig. 6) as among the poikilotherms (*8*). We conclude therefore that the more rapid evolution in the tropics is not simply a matter of reaction rates. We believe that the cause of rapid evolution in the tropics is to be found ultimately in the greater capture of solar energy in this region and secondarily in the response of organisms to this higher and more constant energy level, but we are not yet able to furnish proof.

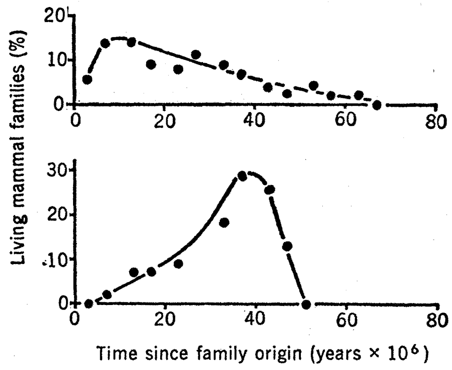

Fig. 6. Modified survivorship curves for living mammal families of warm (central-west Africa) (top) and cold (northern Eurasia) regions (bottom). This homoiothermic group shows the same latitude-dependent variation in evolutionary rates seen among the other groups examined.

The existence of evolutionary equilibria in which there are demonstrably higher rates in warm than in cold regions has significant geological implications. Foremost among these are the consequences for the correlation of rocks by means of the fossils they enclose. Paleontological correlation is, of course, most effective in establishing the synchrony of rock units when it can make use of distinctive fossils belonging to rapidly evolving groups. Conversely, paleontological correlations based on relatively staid and slowly evolving forms provide minimum precision. The high rates of evolution characteristic of the tropics favor stratigraphic correlations of sediments deposited in this environment. The low evolutionary rates of colder regions militate against precision in dating and correlating sediments deposited there.

One may further generalize that east-west correlations (within the tropical climatic belt) will be more facile and precise than north-south correlations which must of necessity deal with the slowly evolving elements (cosmopolitan forms) that are common to both assemblages. East-west correlations in extra-tropical regions must also deal with the unfavorable cosmopolitan elements and may be expected to yield minimum precision. It has been noted (*2*) that this effect is probably the cause of some of the notorious confusion regarding correlation between the Tethyan (warm) and Boreal (cold) faunal realms during the Permian period.

For the geologist interested in evolution, the rapid evolution of the tropics suggests that it is in this climatic zone that "missing links" should be sought, for, as noted above, it is here that threshold-crossing adaptations of major significance occur.

Our model suggests a mechanism by which the gross form of the typical diversity gradient is generated and maintained. This model does not account for variation in slope of the diversity gradient of a given group as a function of time, but this is clearly shown in the fossil record. For instance, the diversity of genera and species of planktonic foraminifera increases in the mid-Cretaceous, wanes in the early Senonian, increases toward the end of the Cretaceous, and then suddenly undergoes a drastic reduction at the end of the Cretaceous. A similar situation has been noted among Cenozoic members of this group of protozoans (*9*).

Variations such as these must be biological as well as physical in origin, but causes cannot as yet be confidently identified. Considerable evidence does seem to exist, however, that climatic change is the most important single cause of time-dependent variation in the slope of diversity gradients.

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6. The "noise" level is high because true ranges are rarely accurately known and because there is considerable uncertainty involved in assigning absolute time limits to the relative time scale.
7. These curves are termed modified survivorship curves because the total survivorship is unknown for the living families and cannot be known until all become extinct. See, for instance, G. G. Simpson, *The Major Features of Evolution* (Columbia Univ. Press, New York, 1953).
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