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Phanerozoic Taxonomic Diversity: A Test of Alternate Models

Although the fossil record forms our only direct evidence of the course of evolutionary and ecological history, it is notoriously incomplete (*1*). Many of our historical interpretations must be based on interpolations between scattered datum points; in effect we construct historical models that explain the data at hand and that are tested as new data appear. Two such models are available to describe the course of taxonomic diversity of marine biota during the Phanerozoic (*2, 3*). The purpose of this comment is to show that the fossil data are adequate to falsify one of them.

1) *Empirical model.* Although the processes of evolution and ecology operate chiefly on species, the fossil record of species is far too incomplete to serve as an adequate basis for the interpretation of many paleoecological patterns. Taxa in progressively higher categories, however, are represented by progressively more individuals over progressively broader geographical and temporal ranges and thus have increasingly better chances of being discovered in the record. For diversity estimation the family level is commonly employed. As diversity regulators apparently operate on species rather than directly on higher taxa, however, it is important to estimate the species diversities associated with the family data.

Figure 1 depicts the Phanerozoic diversity trends of well-skeletonized marine benthic phyla, classes, orders, and families as known from the fossil record (*2*); note that each category has a separate vertical scale. The diversity of taxa in increasingly lower categories is increasingly volatile. Below the phylum level, late lower Paleozoic to early middle Paleozoic diversity levels were high, but they declined in late Paleozoic to a low at the beginning of the Mesozoic. Classes have remained at this low level, but orders increased somewhat during the Mesozoic and families underwent a great increase during the Mesozoic and Cenozoic. Genera of the best-known higher taxa that have contributed most to the post-Paleozoic rise in family diversity show an increase even more spectacular than that of the families. From such data it has been inferred that marine species diversity (Fig. 2B) rose to a mid-Paleozoic high, declined to a low at the close of the Paleozoic, and then underwent a Mesozoic-Cenozoic rise that raised species diversity by at least an order of magnitude over the early Mesozoic level (*2, 4*).

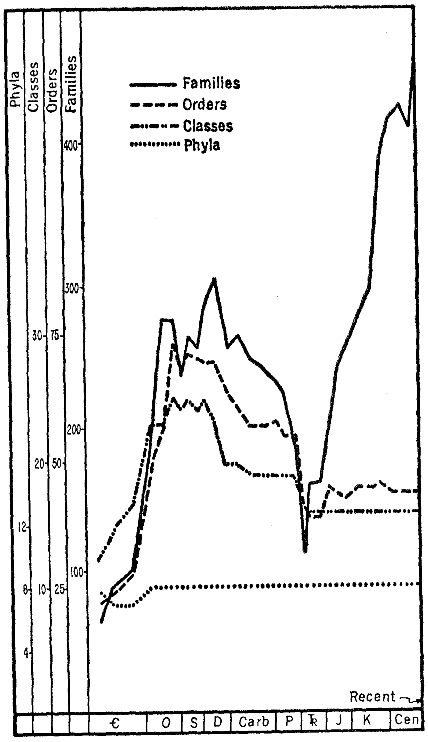

Fig. 1. Diversities of higher taxa of well-skeletonized benthic marine invertebrates as actually described from the Phanerozoic fossil record, plotted by period from Cambrian to Recent.

2) *Bias simulation model.* Our knowledge of diversity patterns and levels for living species far exceeds our knowledge of these factors for any time in the past. In general it is expected that preservation of ancient biotas would become successively poorer in successively older rocks, since the chances of destruction of fossils should increase with the time available. Raup (*3*) examined the main sources of bias in the fossil record in some detail, and while some of his points are arguable, it certainly seems clear that time-dependent biases do exist. Since higher taxa have a better chance of being recorded than lower taxa, higher categories should be proportionately better represented than lower ones at times when the record is poor. Therefore as the record improves through time the taxa in successively lower categories should display proportionately larger gains in diversity, even if diversities in all categories were temporally constant.

From such considerations, Raup (*3*) erected a model of Phanerozoic species diversity trends that is quite different from the empirical one (Fig. 2). He assumed an early species diversity maximum, presumably to correspond with the Ordovician to Devonian peaks in higher categories displayed in Fig. 1, and then a decrease to an intermediate species diversity plateau. He then employed a time-dependent bias to determine by computer simulation the diversities of genera and of species that would be registered in the fossil record. These resultant diversities rise toward the present, naturally, and the genera are proportionately better preserved than the species in progressively older rocks.

These two models imply radically different species diversity levels at certain times in the past (Fig. 2), so that if there were a way to obtain an estimate of actual diversity at one of these times it should be possible to falsify at least one of the models. In fact there is a way, and although it is indirect and does not involve actual species counting it nevertheless provides a strong test of these hypotheses.

The test revolves around our knowledge of how species diversity is accommodated in the marine biosphere at present. The regulators of diversity within habitats are still uncertain, though environmental stability is commonly considered to be a major factor. However, there is no question as to the way in which marine benthic diversity is chiefly accommodated on a planetary scale; the world's shelves, which contain more than 90 percent of the world's benthic marine species, are partitioned into provinces by major dispersal barriers—primarily by changes in thermal regimes in latitudinal directions, and by deep-sea or land barriers in longitudinal directions. The average species difference between latitudinally contiguous provinces with a common boundary is well over 50 percent (*5*), and between provinces separated by longitudinal barriers it is much higher. As a result, the more provinces that exist, the more species that are present. Allowing for diversity gradients, it has been conservatively calculated that marine species diversity levels associated with the present degree of shelf provincialization (over 30 marine provinces) is over ten times the level that would be accommodated in a single extensive tropical province, even one of high intraprovincial diversity (*5*).

The empirical model predicts that diversity in the early Mesozoic following Permian-Triassic extinctions was low, while the bias simulation model predicts that it was approximately the same as today but that the fossil record is so poor, especially for Permian-Triassic time, that the fauna appears to have been depauperate. Now, if the species diversity of Permian-Triassic time was anything like that of today, there must have been numerous marine provinces then. The amount of species packing required to accommodate such a diversity within the communities of a single province cannot be justified, especially in view of the sorts of invertebrate species that are known to have existed at the time. If, on the other hand, early Mesozoic diversity was quite low, then numerous provinces are not required and indeed would be difficult to account for.

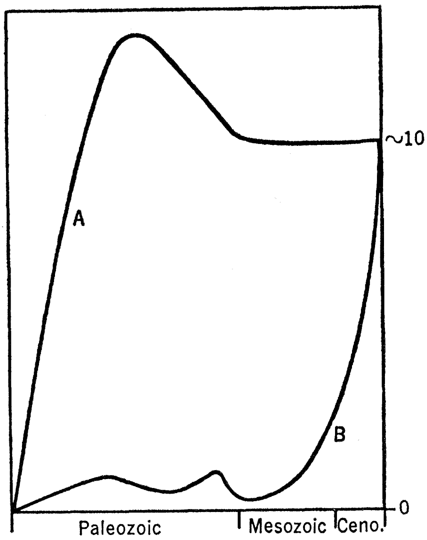

Fig. 2. Contrasting Phanerozoic species diversity trends as predicted by the bias simulation model (A) and the empirical model (B). The point where the curves meet on the right represents about 100,000 species of well-skeletonized benthic marine invertebrates.

The detection of a whole biotic province in the fossil record is far more likely than the detection of a fossil lineage or of a fossil community (*6*) for the same general reason that higher taxa are more easily detected than lower. Even for times when the record is poor, it is difficult to miss an entire province, considering the geographic extent of provinces and the density of fossil sampling even at worst. For early Mesozoic times, even well into the Jurassic, provinciality appears to have been quite low, for at times many fossil species are found on numerous continents while the number of species endemic to local regions is relatively low considering the nature of the fossil record. A good example is documented for the Lower Jurassic, for which sampling is reasonably abundant and is widespread; provinciality is nearly absent (*7*). In Late Jurassic and Early Cretaceous times provinciality increased, but compared with today it was still very low (*8*). It is conceivable that a province or two has been overlooked at times in the Mesozoic, but one or two provinces would not much affect the general picture. It is difficult indeed to escape the conclusion that early Mesozoic diversity was very low, and that as provincialization increased, diversity rose, eventually to its present level. In fact, these sorts of biogeographic considerations were implicit in the establishment of the empirical model (*2, 4*).

Most other objections to the bias simulation model require extended discussions and add little to the conclusions. Two objections that require no preamble are: (i) the fossil associations that are found in the fossil record during times of low recorded diversity, such as the Early Triassic, have consistently low diversities themselves; and (ii) the time-dependent bias does not appear to operate during the Paleozoic, although this era encompasses the first 400 million years of Phanerozoic time.

Finally, we must ask why time-related biases, which must exist (*3*), do not play a larger role in the fossil record than is accorded them by the evidence reviewed here. Probably a major reason is that at the family level the record is good enough so that the temporal biases are greatly reduced, and in fact the empirical model was based chiefly on the family level for just this reason. Coupled with this is the possibility that short-term natural fluctuations in diversity together with episodic nontemporal biases in the record frequently outweigh the time-related biases on the family level. And finally, the progressive provincialization of late Mesozoic and Cenozoic times must have resulted in a progressive shrinkage of the average geographic range of species (and of genera and families to a lesser extent). Thus, the chances of discovery of a certain proportion of taxa in these categories were decreasing. And while Upper Cretaceous seas were widespread on continental platforms, Cenozoic seas were much more restricted, which further lessened the chances of discovery of taxa. How such decreases compare with an imputed increase in chances of discovery due to better sampling in younger rocks is not known, but they might well mask it completely.

It is concluded that the diversity trends suggested for the bias simulation model are not historically correct. Probably the general trends suggested by the empirical model are real. Nevertheless, it would be a mistake to suggest that the species diversity levels inferred from the empirical model are any more than very rough estimates (indeed it is probable that the Paleozoic levels were underestimated by a factor of 2 or so, owing to an underestimate of Paleozoic provinciality). Clearly, paleontologists should work to develop improved estimates of biases and incompletenesses of all types in the record, as Raup has done.

JAMES W. VALENTINE
Department of Geology,
University of California, Davis 95616

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