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Taxonomic Diversity during the Phanerozoic

The increase in the number of marine species since the Paleozoic may be more apparent than real.

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The evolution of taxonomic diversity is receiving increasing attention among geologists. The immediate reason for this is that diversity data may have a direct bearing on problems of plate tectonics and continental drift. The tantalizing possibility exists that diversity may be a good indicator of past arrangements of continents or climatic belts, or both. Valentine (*1*, *2*) has related temporal changes in fossil diversity to changes in climate and to the evolutionary consequences of continental drift. Stehli (*3*) and others have used spatial differences in diversity to interpret paleoclimates and paleolatitudes for single intervals of time.

Diversity information from the fossil record is also important because of its bearing on general models of organic evolution. Is the evolutionary process one that leads to an equilibrium or steady-state number of taxa, or should diversification be expected to continue almost indefinitely? Has equilibrium (or saturation) been attained in any habitats in the geologic past? If mass extinction has led to a significant reduction in diversity, what are the nature and rate of recovery? The answers to these and comparable questions depend in part on theoretical arguments, but their documentation must come ultimately from the fossil record itself.

The large-scale analysis of taxonomic diversity has been facilitated in the past few years by several important publications. The American *Treatise on Invertebrate Paleontology* (*4*) and the Russian *Osnovy Paleontologii* (*5*) are particularly valuable in having brought together vast amounts of taxonomic data with a minimum of inconsistency. Also, the British publication *The Fossil Record* (*6*) provides a useful synthesis of the geologic ranges of the higher taxa. This new literature, plus advances in data-processing technology, makes possible a more sophisticated study of diversity problems than has been possible heretofore (*7*).

Valentine (*1*, *2*) used the newly published data to estimate temporal changes in diversity during the Phanerozoic, the geologic time since the end of the Precambrian. His conclusions were not dramatically different from those of earlier workers, but the breadth of documentation was far greater.

My purpose in this article is to investigate the nature of the diversity data to determine if more can be learned from it. In particular, I will examine the proposition that systematic biases exist in the raw data such that the actual diversity picture may be quite different from that afforded by a direct reading of the raw data. My study will be limited to the major groups of readily fossilizable marine invertebrates (as was Valentine's) and to changes in their worldwide diversity through time.

Traditional View

Figure 1 shows three histograms of taxonomic diversity for the Phanerozoic. The three sets of data differ somewhat in scope. Those of Valentine (*1*) and Newell (*8*) are principally tied to the family level, whereas Müller's (*9*) are numbers of genera. All three are limited mostly to the major groups of fossilizable marine invertebrates: Protozoa, Archaeocyatha, Porifera, Coelenterata, Bryozoa, Brachiopoda, Arthropoda, Mollusca, and Echinodermata, but Newell's data also include vertebrates. All three sets of data inevitably include some nonmarine and terrestrial taxa, but in none is this influence numerically significant.

The important fact is that all three show essentially the same picture and the one that has constituted the consensus for many years. The overall pattern is one of (i) a rapid rise in the number of taxa during the Cambrian and Early Ordovician, (ii) a maximum at about the Devonian, (iii) a slight but persistent decline to a minimum in the Early Triassic, and (iv) a rapid increase to an all-time high in diversity at the end of the Tertiary. Valentine (*1*, *2*) has suggested that the rise in diversity at the species level in Mesozoic to Tertiary time was an exponential one, with the late Tertiary having up to 20 times more species than the average for the mid-Paleozoic. This rise would appear even greater if insects, land plants, and terrestrial vertebrates were considered. These are particularly "noticeable" groups, important to man, and the history of their diversity has influenced thinking on the general subject.

It should be emphasized that the Phanerozoic diversity pattern yielded by the published taxonomic data depends on the choice of taxonomic level. As Valentine has pointed out, diversities at the levels of phylum, class, and order have behaved very differently from those at the lower levels. The number of phyla has been essentially constant since the Ordovician, for example.

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Sedimentary Record and Diversity

It has been established that the general quality of the sedimentary rock record improves with proximity to the Recent (*10, 11*). That is, the younger parts of the record are represented by larger volumes of rock (per unit of time), and the amount of metamorphism, deformation, and cover by overlying rocks is generally less. This is usually interpreted as resulting from the fact that the younger rocks are closer to "the top of the stack" and that, being younger, they have had less chance to be destroyed by erosion, metamorphism, and the like.

Figure 1 includes a graphic display of Gregor's estimate (*12*) of change in the sedimentary record through the Phanerozoic. The vertical coordinate in the lower graph is what Gregor calls the "survival rate" and is expressed as cubic kilometers of sediment per year now known and dated stratigraphically. This shows, for example, that the Devonian is represented by about twice the volume of sediments as the Cambrian (after adjustment for the relative durations of the periods). Gregor's survival data are comparable to estimates made on quite different bases by others (*10, 13*).

There is unquestionably a strong similarity between the patterns of taxonomic diversity at the genus and family levels and the pattern of sediment survival rate. This similarity suggests that changes in the quantity of the sedimentary record may cause changes in apparent diversity by introducing a sampling bias.

In spite of the fact that the patterns in Fig. 1 are correlated, a causal relationship is by no means demonstrated. Furthermore, the correspondence is not perfect, and both the diversity and sedimentary data are subject to many errors and uncertainties. The remainder of this article is devoted to a more detailed assessment of these relationships.

Gregor's data (Fig. 1) are estimates of survival rate for all sedimentary rocks, without distinction between marine and nonmarine. This detracts from the comparison with diversity because the biologic data are nearly free of nonmarine elements. Also, with the exception of the interval from the Devonian through the Jurassic, Gregor's numbers are derived from estimates of maximum sediment thickness (*14*). This part of the data is suspect because of the logical problems involved in going from the maximum known thickness (in a local section) for a geologic system to the total volume of rock in that system (*11*). Furthermore, Gregor's rates are all sensitive to errors in estimates of the absolute time durations of the periods.

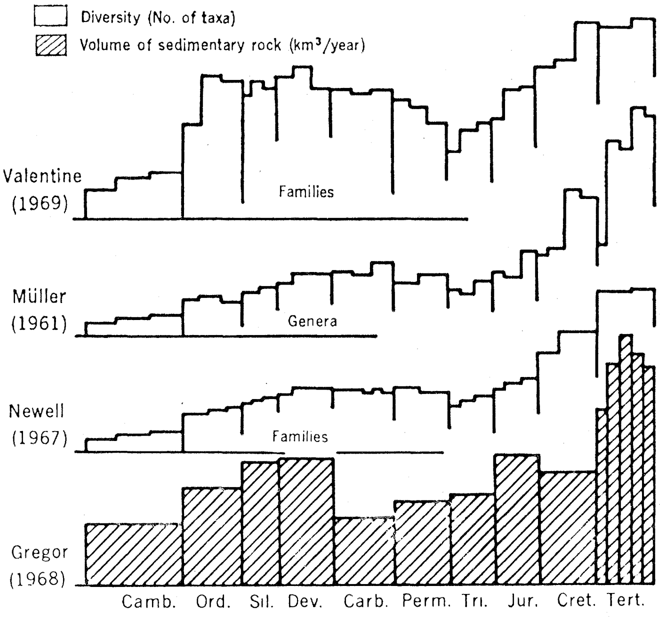

Fig. 1. Comparison of the number of taxa and the volume of sedimentary rock during the Phanerozoic. The diversity data are based mainly on well-skeletonized marine invertebrates (*1, 8, 9, 12*).

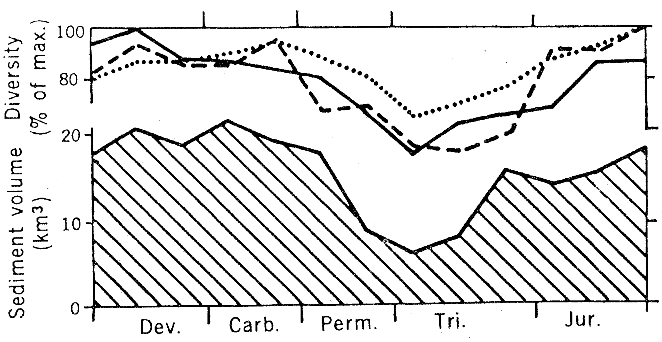

Fig. 2. Apparent taxonomic diversity compared with estimated volume of marine and lagoonal clastic and carbonate sediments. The diversity data are from Fig. 1. (Solid line) Valentine (*1*), (dotted line) Müller (*9*), (dashed line) Newell (*8*).

Thus, although there is little doubt about the general validity of Gregor's pattern, the inherent weaknesses prevent its use in more rigorous analysis.

By far the best data for sediment volumes are those published by Ronov (*15*). They are based on the results of a 10-year project of compiling lithological-paleogeographic maps and must be considered the most comprehensive data available. They are limited, however, to the Devonian-Jurassic interval. Ronov's data were used by Gregor where possible, but were modified by his calculation of survival rates. Ronov carefully distinguished between continental clastics, marine clastics, evaporites, marine and lagoonal carbonate rocks, and volcanics.

In Fig. 2, the taxonomic diversity data of Newell, Müller, and Valentine are compared with Ronov's estimates for the total volume of marine and lagoonal clastics and carbonates. Absolute time does not enter in because for each stratigraphic series total number of taxa and total sediment volumes are used. The diagram is thus free of most of the effects of errors in radiometric dating.

The correspondence between diversity and quantity of sediments is much stronger than indicated in Fig. 1. In particular, it should be noted that the Early Triassic diversity minimum coincides with a sediment minimum, which was not the case when Gregor's data were used. This is primarily because Gregor used Ronov's data for all sedimentary facies and because of the effect of Gregor's rate calculation.

It could be argued that the similarity between the patterns in Fig. 1 is due simply to a broad but independent increase in both sediment volume and diversity from the Cambrian through the Tertiary and that similarity in detail is quite accidental. Figure 2 largely denies this interpretation because the Carboniferous-Permian interval shows the reverse trend in both measures. Thus, although a causal relation is not proved, the empirical relation appears to be strong enough to justify further investigation.

There is no disagreement on the proposition that the number of taxa known from the fossil record is less than the number that actually lived. This stems simply from the fact that some taxa (particularly at the species level) are rarely or never preserved. The effect is most striking when late Tertiary diversity is compared with the diversity of living organisms. There is no evidence for widespread extinction in the late Tertiary yet most groups have much smaller Tertiary records than would be predicted from neontological data. Furthermore, it is agreed that some biologic groups show fossil diversities closer to their actual diversities than do other groups because of inherent differences in preservability. Crustaceans, for example, are clearly underrepresented as fossils when compared with brachiopods or bivalves. The real problem, however, in the present context, is to evaluate relative changes in diversity over time, using the fossil record as the only available measure.

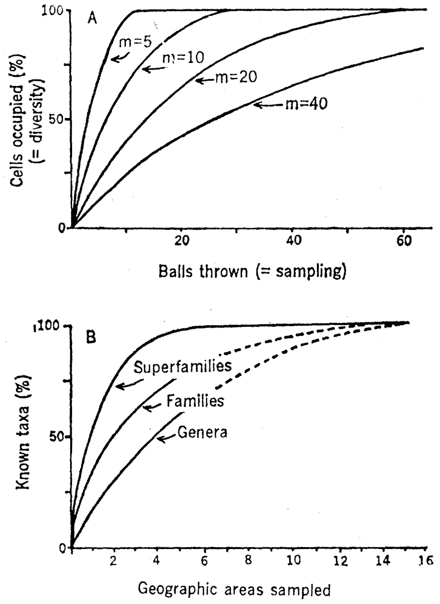

Fig. 3. Diversity as a function of sampling. (A) Illustration of cell occupancy problem. The average waiting time for cell occupancy varies with the number of cells to be occupied (m). (B) Effect of sampling on apparent diversity in fossil ammonoids of the *Meekoceras* zone (Triassic).

Sampling Problems

Many fossil taxa remain to be discovered. At the species level, this number probably exceeds even the number that have been described, although this would vary greatly from group to group. The diversity problem is thus in the realm of sampling theory and can be attacked from a mathematical viewpoint.

Exploration for fossils is analogous to problems in probability theory known variously as cell occupancy and urn problems. Consider a wooden tray which is divided into small compartments or cells, and assume that small balls are thrown randomly at the tray in such a way that each ball falls into a cell, without being influenced by the position of the cell or whether it is already occupied. The first ball thrown will inevitably result in the occupancy of one cell. The second ball may fall in the same cell and thus not add to the number of cells occupied: The probability of this event will be greatest if the total number of cells is small. At some point, all the cells will be occupied by at least one ball, and the waiting time necessary to accomplish this (measured in number of balls thrown) will depend only on the number of cells in the tray.

As noted above, the waiting time for occupancy of one cell is equal to 1 (one ball thrown). It can be shown (*16*) that the average additional waiting time for occupancy of a second cell is:

$$\frac{m}{m-1}$$

where m is the total number of cells in the tray. The additional waiting time for the third occupancy is:

$$\frac{m}{m-2}$$

and so on. The total waiting time for complete cell occupancy then becomes:

$$m\left(\frac{1}{m}+\frac{1}{m-1}+\frac{1}{m-2}+\ldots+\frac{1}{2}+1\right)$$

Calculated curves for the expected waiting time for various values of m are shown in Fig. 3A.

The appropriate paleontological analogy is as follows: Let m be the total number of taxa available for discovery (thus, one cell equals one taxon), and let the balls thrown be the number of fossils found and identified or described. The first fossil discovered inevitably means recognition of one taxon. The second fossil may be the same or it may be from a second taxon (second cell occupied). Groups with fewer subgroups will require less sampling to be completely discovered.

This reasoning can be applied directly to the influence of taxonomic level on observed diversity. In any fossiliferous rock unit, the number of families represented is inevitably equal to or greater than the number of phyla, the number of genera is equal to or greater than the number of families, and so on. Thus, much less sampling is required to find all or nearly all the phyla (low m) than the families or genera (higher m values). At any point in the sampling process, a larger percentage of the phyla will be known than of the lower taxa. In Fig. 3, the curves of low m are what would be expected for discovery of high taxa, and the curves of high m would be representative of lower taxa. It should be noted that as sampling progresses, the ratio of the numbers of lower to higher taxa (genera per family, for example) steadily increases.

Figure 3 also shows a paleontological analog of the calculated curves. It is based on published data for ammonoids of the *Meekoceras* zone (Lower Triassic) (*17*). The data include the known occurrences of 58 genera in 15 geographic assemblages around the world. The ammonoid data (Fig. 3B) show the relationship between sampling and apparent diversity. Sampling is in this case expressed as the number of sites or areas sampled and is analogous to the number of balls thrown in the cell occupancy problem. The number of taxa found at one site in the *Meekoceras* case depends, of course, on which site is used. China, for example, yields well over half the genera and about three-quarters of the families; at the other extreme, the assemblage from the Caucasus has only two of the genera. The curves in Fig. 3 are therefore based on average expectations. For each taxonomic level, some of the values could be calculated directly; other values were determined by simulation based on a random selection of the published distributional data. The remainder (dashed lines) were extrapolated.

The ammonoid example demonstrates that apparent diversity is severely controlled by (i) the extent of sampling and (ii) the taxonomic level. At the order level (Ammonoidea) any one of the 15 sites is sufficient to yield 100 percent of the known diversity. At the generic level it requires (in this case) an average of 5 sites to exceed 50 percent. It should be emphasized that the leveling off of the curves at 100 percent does not mean that the 15 sites yield all of the ammonoid diversity in the *Meekoceras* zone: New genera and new localities are still being found.

As noted above, an increase in sampling is accompanied by predictable increases in the apparent number of genera per family, and so forth, and the effect is seen in the *Meekoceras* zone data. That this is a general phenomenon was noted by Simpson (*18*) as follows: "Sampling at few, restricted localities certainly reveals a much higher percentage of the genera than of the species that existed at any one time."

The sampling problem need not be analyzed only in the context of geographic extent of collecting. The sampling axes of Fig. 3 could be replaced by various measures of the intensity of collecting or study (such as number of paleontologists or years of study) or by measures of the quality of the fossil or rock record (extent of outcrops, type of preservation, and even accessibility of outcrops). The fact that new taxa are constantly being defined or discovered means that the fossil record is still in a relatively early stage of sampling and thus may be represented by the steeper parts of the curves in Fig. 3.

Sources of Error in Diversity Data

In the following numbered sections I consider seven major sources of error that may affect any set of diversity data. All of them certainly have influenced published diversity data of the type shown in Fig. 1.

1) *Range charts.* When the objective of a diversity study is to estimate how many taxa lived during a given interval of geologic time, the primary source of information is usually a range chart drawn at the appropriate taxonomic level. If a family has a range from the base of the Silurian to the top of the Lower Devonian, for example, it is assumed that the family lived throughout the entire range. Thus, the family is registered for the Upper Silurian even though the Upper Silurian fossil record may not actually contain species of the family.

This procedure is valid biologically as a means of estimating actual diversity, but it does have the effect of overestimating "observed" diversity for relatively unfossiliferous intervals. In fact, an interval can be completely unfossiliferous yet still be credited with having considerable fossil diversity. This source of error becomes important when one is assessing the biasing effect of low sediment volume, as in the Permian-Triassic of Fig. 2. In this instance, the drop in fossil content of Permian rocks may be greater than it appears from the range chart data.

More important, the use of range charts introduces a systematic, time-related bias, as follows. Many (or most) range charts are incomplete in that the true first and last occurrences have not yet been found. In fact, the fossil record may not even contain the first or last occurrences (due to nonpreservation). Ranges of taxa may be truncated at either end, but truncation at the older end (first occurrence) has a higher probability because the older rocks have a greater chance of nonexposure or destruction by erosion and metamorphism. This means that the Phanerozoic diversity data are inevitably biased toward an increase in observed diversity through time.

2) *Influence of "extant" records.* Cutbill and Funnel (*7*) have already noted the biasing effect of the fact that ranges of fossil taxa are generally said to include the Recent if the taxa have living representatives. A not uncommon example would be a living group which has only one fossil occurrence, let us say in the Jurassic. Its range would be listed as Jurassic-Recent which, again, is valid for many purposes but causes problems in the present context. If the group had the same sparse fossil record but had not survived to the Recent, its range would be given as simply Jurassic. Cutbill and Funnel concluded that truncation at the "last occurrence" end of a range through nondiscovery is less likely if the group has living representatives, and since younger rocks contain more extant forms, the late Mesozoic and Cenozoic diversity data are consistently biased toward larger diversity and fewer extinctions than older parts of the column.

3) *Durations of geologic time units.* Consider the effects of the durations of periods and epochs on the diversity data in Fig. 1. The horizontal axis in the diagram is roughly adjusted for relative durations—albeit with little justification in many cases—but the vertical axes showing numbers of taxa are not. The height of each bar on the histograms indicates the total taxa which are found anywhere in the system or series or which have ranges that include those rocks. All things being equal, a long time interval will show a higher diversity than a short one. The effect of the bias is probably to overestimate diversity in the early Paleozoic, where period and epoch durations are generally greater (*7*). This bias thus operates in a direction opposite to that of the two discussed above.

Furthermore, the bias is not easily corrected. The calculation of a simple ratio, such as families per million years, is valid when working with, for example, extinction rates, but only makes matters worse in the present context, where "standing crop" is the objective.

4) *Monographic effects.* The effects of the quality and quantity of taxonomic activity on apparent diversity are well known. It has been noted, for example, that the peak number of brachiopod genera shifted from Devonian to Ordovician largely as a result of the publication of one monograph (*19*). It is interesting to note that the generic peak has since shifted back to the Devonian.

Some of the monographic effects stem from the stratigraphic distribution of taxonomic specialists and taxonomic and phylogenetic philosophy, and perhaps even from the geographic distribution of taxonomists. Fossiliferous rocks in western Europe and eastern North America are more likely to be fully studied and thus to show higher diversity than rocks in other parts of the world.

If monographic effects are randomly distributed among the major phyla and throughout the stratigraphic column, then the consequences for overall trends in Phanerozoic diversity are minimal. Whether this lack of systematic bias exists is difficult to prove. If more families and superfamilies have been defined in the lower Paleozoic than in other parts of the geologic time table, it is impossible to say whether the difference reflects a tendency of lower Paleozoic paleontologists to be quick to erect such taxa, or whether it results from different kinds of diversity and states of preservation. At the very least, the monographic factors make highly precise studies of diversity impossible.

One special type of monographic effect is surely time dependent. If a group of organisms has many living representatives, and if biologists have subdivided it into many higher taxa, fossil representatives of these higher taxa are more likely to be recognized than if living forms are absent. This says in effect that it is easier to recognize a fossil taxon as distinct if the classification has already been established on the basis of the more complete morphological information afforded by living species. This bias has the effect that diversity is underestimated in extinct groups relative to nonextinct groups. For example, the discovery in Japan of a bivalved gastropod led to the reassignment of its Eocene counterpart from the Bivalvia to the Gastropoda. This greatly extended the stratigraphic range of the gastropod order Sacoglossa and thus increased the apparent gastropod diversity of the Tertiary (*20*).

5) *Lagerstätten*. Our knowledge of the history of life would be very different were it not for the occasional instances of spectacular preservation of large assemblages (Lagerstätten). Individual formations such as the Solnhofen, the Burgess shale, and the Baltic Amber as well as unusually fossiliferous groups of rocks such as in Timor and Madagascar have significant effects on diversity curves. In some cases, the lack of Lagerstätten is also significant. For example, the observed diversity of insects during the Cretaceous is essentially zero, but this is presumably only an artifact resulting from the lack of the special conditions required for good insect preservation during that period.

The distribution of Lagerstätten through time does not appear to be systematic although they are probably more common in younger rocks. To the extent that this is true, there will be a bias toward high diversity in younger rocks. The greatest effect, however, is to add "noise" to the diversity data in much the same way that monographic bursts produce irregularity in diversity trends in the affected groups.

6) *Area-diversity relationships.* When a new geographic region is opened to exploration, new taxa are almost inevitably discovered. This is due in part to increased sampling, but it also results from the fact that taxa tend to be geographically restricted because of either climatic factors or barriers to dispersal. Also, diversity has been shown empirically to be area dependent (*21*).

Many instances of geographic effects could be cited. One example comes from Mortensen's tabulation of distributions of living cidarid echinoids, which shows that the 148 species and subspecies of the 27 genera are distributed among 18 geographic regions (*22*). Only one genus, *Eucidaris*, is found in as many as half the 18 regions, and 63 percent of the genera are confined to fewer than four regions. No single region contains even one-third of the species. This is in spite of the fact that most cidarids have a free-swimming larval stage.

If the cidarid distribution is looked at in terms of the probable fossil record it will leave, the potential effect of geographic restriction becomes greater. The biogeography of living echinoids is based on a reasonably good sampling of three-quarters of the earth's surface—that is, the oceanic areas. In the fossil record, sampling is limited for all intents and purposes to one-quarter of the earth's surface (the continents and islands), and a significant part of that quarter has remained out of the marine realm by being emergent during most of the Phanerozoic. Thus, the paleontologists can examine only a small fraction of the ocean area for any point in the geologic past. If one were to look at only 5 percent of the present ocean area (or even 5 percent of the present continental shelf area), the apparent diversity in groups such as echinoids would be greatly reduced at all taxonomic levels. This is particularly true since, in most geologic systems, the bulk of the record is usually concentrated in a few areas—rather than being randomly scattered over the world.

The effect of biogeography on diversity is greatest at the species level and decreases upward in the taxonomic hierarchy. Most modern phyla have worldwide distributions but even so are missing in some large regions, mainly due to climatic factors. At the family level, endemism becomes much more common, although this varies greatly from group to group.

The net effect of the biogeographic factor in the present context is to make the observed fossil diversity dependent not only on the area of rock exposure but also on the nature of the world distribution of exposures. Relatively small exposures on several continents are likely to yield a higher overall diversity than the same total exposure concentrated on one continent.

Although Gilluly has demonstrated a clear increase in area of exposure through the Phanerozoic column (*10*), no studies have been made on the manner in which these rocks are distributed spatially. However, because the probability of finding older Phanerozoic rocks is less than that of finding younger ones (assuming equal time durations) it would seem reasonable that geographic coverage improves toward the Recent. This should produce higher observed diversities in younger rocks.

7) *Sediment volume.* This article started with the empirical correlation between sediment volume per unit of time and diversity of major marine groups. It is clear from sampling considerations that more sedimentary record should produce more diversity. The correlation shown in Fig. 2 is thus quite plausibly a causal one. But the strength of the resulting bias depends on (i) the taxonomic level and (ii) the kinds of differences in sediment volume from one part of the column to another. A figure for sediment volume for one geologic system [such as used by Ronov (*15*)], may be higher than the figure for another geologic system for many reasons. Discontinuous sedimentation may mean that many short-lived taxa are not preserved, but the fossil record of longer-lived taxa, characteristic of families and orders, may not be much affected. Thus, for example, if the Paris Basin had twice the volume of sediments, species diversity would be higher but family diversity little if any different. If sediment volume figures are influenced by differences in area of sedimentation, then the biogeographic relationships discussed above become significant, even at high taxonomic levels.

Postdepositional destruction or covering of sediments is the most widely accepted explanation for the temporal trends in sediment volume. Such losses of record are likely to have a spotty geographic distribution. That is, loss of the sedimentary record from one or more whole regions is more likely than small-scale reductions in all areas. This suggests that loss of biogeographic coverage is the important factor for diversity and that the sediment volume bias is closely tied to the geographic bias discussed earlier.

Models for Phanerozoic Diversity

Figure 4 shows in generalized form Phanerozoic diversity patterns at several taxonomic levels for shelf invertebrates with well-developed skeletons. The illustration is a composite of several from Valentine (*1*) and one from Müller (*9*). Minor irregularities were removed in making the composite, and vertical scales were adjusted. Valentine based the species curve on inference, but all the others were drawn directly from observed diversities.

Valentine concluded that the patterns are a plausible result of a combination of the evolutionary process of diversification and certain events in the physical history of the Phanerozoic. The basic biologic process envisioned requires that diversification take place first at high taxonomic levels (phylum, class, order) and later at successively lower taxonomic levels. The number of phyla (not shown) reached a maximum during or before the Early Ordovician, classes and orders later in the Ordovician, families in the Devonian, and genera and species in the Carboniferous or earliest Permian. According to Valentine, the diversity of the higher taxa (except phyla) declined after the initial peaks because as high taxa became extinct, they were replaced not by equally distinct groups but rather by specialized lower taxa (genera and species) within the surviving groups.

Still following Valentine's interpretation, the Permian-Triassic mass extinctions sharply reduced the diversity at all levels, and this was followed by a dramatic rise in diversity at the family, genus, and species levels, leading to the present-day array. Valentine argues that the driving forces behind this Mesozoic-Cenozoic rediversification were (i) continental drift and (ii) an increase in latitudinal temperature gradients. The diversity increase would presumably have taken place anyway—but to a lesser degree—as a continuation of the trend to specialization that was interrupted by the Permian-Triassic extinctions.

Figure 4 and its interpretation represent, therefore, one model for Phanerozoic diversity. It is an appealing one in that it is based largely on a "face value" use of empirical data and because it is biologically and ecologically plausible.

The foregoing interpretations are subject to several problems. The patterns in Fig. 4 contain elements that are qualitatively those which would be predicted from the biases discussed in this paper, as follows:

1) If the quality or quantity of sampling increases through time, it is inevitable that the ratios of species to genera, genera to families, and so on, will also increase.

2) Time-dependent biases should produce a rise in diversity at the lower taxonomic levels as the Recent is approached. The post-Paleozoic increase in numbers of families, genera, and species seen in Fig. 4 may be due to this factor.

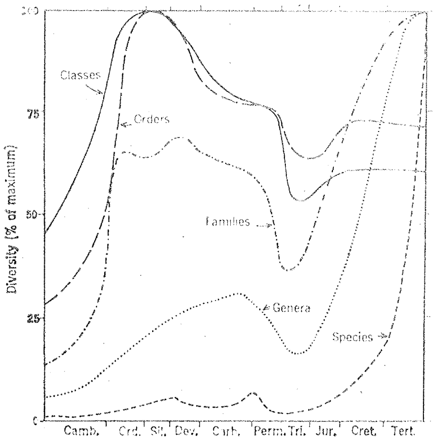

Fig. 4. Variation in apparent taxonomic diversity for several taxonomic levels of well-skeletonized marine invertebrates during the Phanerozoic.

3) Time-dependent biases should also shift any diversity peak toward the Recent (to the right in Fig. 4), and the amount of shift should be greatest at the lowest taxonomic levels. The fact, noted by Valentine (*1*), that diversities at lower taxonomic levels appear to have peaked after those at higher levels may actually be due to the effects of biases.

The last point deserves more consideration. From an evolutionary viewpoint, it is certainly plausible that diversity maxima for species and genera should occur after those for higher taxa in the same group. The question is whether the time lag is large enough and sufficiently universal to produce distinct offsets when diversities of several major animal groups are plotted together as in Fig. 4. If this were the case, periods of widespread extinction should be followed by recognizable intervals of low diversity, during which rediversification takes place. But the fact is that most major extinctions are not followed by periods of low diversity. Lowered diversity must have occurred at such times, but it evidently did not last long enough to be noticeable on the time scale used here. Valentine points out that the Permian-Triassic extinction is the only one which is followed by a diversity drop. Figure 2 indicates that in that interval the diversity drop may be an artifact of sampling.

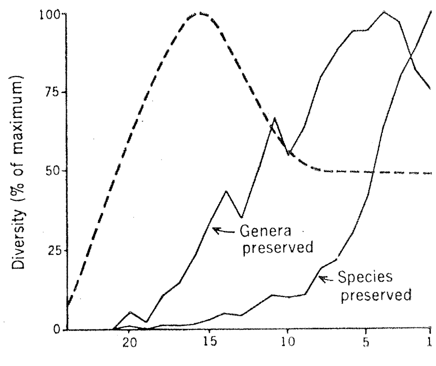

Fig. 5. Computer simulation of taxonomic diversity. The dashed line is a hypothetical diversity distribution before fossilization and is based on simulated ranges of 2000 species constituting 100 genera. The solid lines indicate the diversity trends after biases are applied to the range data.

An alternate model for Phanerozoic diversity is suggested by the dashed line in Fig. 5 and consists of a diversity maximum followed by a decline to an equilibrium level. The time scale in Fig. 5 is arbitrary, but a mid-Paleozoic position for the maximum is implied: The curve was suggested by the curves in Fig. 4 for classes and orders (where effects of biases should be least). The alternative model makes no distinction between taxonomic levels and thus is meant to apply to all levels below phylum. Thus, the assumption has been made that the offset of diversity peaks caused by gradual diversification either is not large enough to be observed at this scale or is masked by noise resulting from the fact that many animal groups with different evolutionary histories are plotted together. The proposed model is, of course, valid only if the biases described in this article are quantitatively significant.

The plausibility of the alternative model was checked by a computer simulation. By using random numbers, hypothetical first and last occurrences were generated, and a range chart was constructed showing the distributions in time of 2000 hypothetical species (segregated into 100 genera). The dashed diversity curve in Fig. 5 was computed from the simulated range chart. The curve thus represents a hypothetical diversity pattern before biasing factors are applied.

Next, information was removed from the range chart by a random process designed to simulate the biasing factors. For each species, portions of the record were "destroyed," with the probability of destruction increasing back in time. Record losses occurring only inside a range had no effect. If, however, a loss included the beginning or end of the range, the range was shortened accordingly. In many cases, species were completely removed by this process. The Recent was made immune from these information losses to stimulate the biasing effect of "extant" records.

Finally, a new range chart was constructed from what was left after the information removals. The diversity curves computed from this are also shown in Fig. 5. Species diversity increases sharply toward the Recent whereas generic diversity shows a maximum, offset to the right of the original maximum. When genera are grouped into hypothetical families (not shown), the diversity maximum is offset to the right but not as far.

The simulation demonstrates that diversity patterns such as are observed in the fossil record can be produced by the application of known biases to quite different diversity data. The simulation does not, of course, prove the alternative model for Phanerozoic diversity because of our present ignorance of the actual impact of the biases. The simulation does suggest, however, that the model proposed in Fig. 5 is a plausible one for the Phanerozoic record of marine invertebrates.

The alternative model cannot be applied literally to land-dwelling forms because the exploitation of terrestrial habitats started much later in geologic time and may be still going on. The fossil record of terrestrial organisms is subject to the same biases, however, and so should be read with caution.

Summary

Apparent taxonomic diversity in the fossil record is influenced by several time-dependent biases. The effects of the biases are most significant at low taxonomic levels and in the younger rocks. It is likely that the apparent rise in numbers of families, genera, and species after the Paleozoic is due to these biases. For well-skeletonized marine invertebrates as a group, the observed diversity patterns are compatible with the proposition that taxonomic diversity was highest in the Paleozoic. There are undoubtedly other plausible models as well, depending on the weight given to each of the biases. Future research should therefore be concentrated on a quantitative assessment of the biases so that a corrected diversity pattern can be calculated from the fossil data. In the meantime, it would seem prudent to attach considerable uncertainty to the traditional view of Phanerozoic diversity.

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Maize and Its Wild Relatives

Teosinte and *Tripsacum*, wild relatives of maize, figured prominently in the origin of maize.

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The close relatives of maize, teosinte and the genus *Tripsacum*, have assumed increasing importance in the understanding of the evolution under domestication of the New World's most important plant food. *Tripsacum* hybridizes with maize under experimental conditions, and teosinte crosses with maize in its native habitat, Mexico and Central America. Much of the heterotic vigor of maize is attributed to introgressive hybridization from its closest relative, teosinte. Today, the maize crop is the single largest harvest in the United States and is the staple food for most of the inhabitants of Latin America.

Considering the importance of the hybridization of maize (*Zea mays* L.) with its wild relatives (Fig. 1) teosinte [*Z. mexicana* (Schrad.) O. Ktze.] (*1*), an annual grass looking very much like maize, and *Tripsacum* (*2*), perennial grasses quite distinct from maize in appearance, it is startling to realize how little is known about this phenomenon in the wild. Maize and teosinte are genetically compatible and hybridize freely with each other in places where the isolating mechanisms between the two have broken down, as in the Sierra Madre Occidental of northern Mexico, the Central Plateau and Valley of Mexico in central Mexico, and in Heuhuetenango of northern Guatemala. *Tripsacum* does not hybridize readily with maize in the field, but hybrids can be produced under experimental conditions. There is reason to be alarmed by the rapid extinction of these wild relatives in and around maize fields where teosinte is known to have hybridized with maize for at least three millennia. This extinction of the native populations of teosinte is disastrous from the standpoint of future introgression, since it

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