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The Fossil Record: A Sampler of Life's Diversity [and Discussion]

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The fossil record: a sampler of life's diversity

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SUMMARY

The fossil record is adequate to determine the general patterns of diversity of genera and higher taxa across geological time, for most groups of organisms. The Linnaean hierarchy, in which most of the fossil groups have been classified, is ideally suited for such studies. Marine invertebrates are represented by three successive faunas that display increased diversities, but lower evolutionary turnovers; perhaps increasing specializations favoured lineages with higher extinction resistance. Tetrapods are also represented by three faunas that display increasing diversities and similar though more complex patterns of decreasing evolutionary turnovers. Tracheophytes have been placed in four Phanerozoic floras with generally increasing diversities, but by contrast with animals display increased species turnover with increasing diversity, perhaps in response to competitive requirements imposed by the successive origination of major clades.

1. INTRODUCTION

The only direct evidence of the diversity of life through geological time is contained in the fossil record. It is clear that the record is incomplete and biased, so that in interpreting past diversities these difficulties must be kept in mind and their effects minimized as far as possible. Evaluation of the nature of the fossil record, and of the stratigraphic record in which it is contained, have led to strategies of interpretation aimed at deriving the most information possible while minimizing the risks of overinterpretation. However, there are no precise ways of testing the extent to which these aims are realized, at least for the present. Instead, we must rely chiefly on the plausibility and coherence of our interpretations when viewed in the light of biological knowledge of today's world.

2. QUALITY OF THE FOSSIL RECORD

The completeness of the stratigraphic record varies with the resolution required (Schindell 1980; Sadler 1981). That is, the record is less complete if one wishes to resolve intervals of 1 Ma than if one can settle for intervals of 5 Ma; there is simply a far better chance of finding sediment in a long interval than in a short one. On the other hand, if one actually has a sedimentary column, the rocks in shorter timespans will tend to be more complete than those in longer spans. This is because in an average section, most stratigraphic gaps are of short durations, but there are nevertheless many gaps of intermediate duration and a few that are quite long. The longer the timespan studied, the more chance of encountering larger gaps, and it happens that they render the longer spans increasingly less complete. These relations have been quantified by Sadler (1981) for an average section. For example, an average 30-million-year section of shelf carbonates and detrital sediments (from which the vast bulk of Phanerozoic marine fossils come) is of the order of 33% complete for one million year resolution intervals. Non-marine deposits tend to be less complete and more variable. As many sediments are unfossiliferous, the fossil record is usually less complete than the stratigraphic record; some exceptions may occur in cases of condensed sections or of reworked fossils.

Usually there are many stratigraphic sections scattered across the world to represent some span of geological time such as an Epoch (a subdivision of a Period, such as the Cambrian Period) or an Age (a subdivision of an Epoch, averaging around 8 million years). If the stratigraphic gaps are random from section to section, then for resolution intervals as long as 1 Ma the chance of finding contemporaneous sediment in two average 30-million-year sections is on the order of 0.11, and in five sections, 0.004 (Sadler in Valentine *et al.* (1990)). Faunas that appear to be roughly contemporaneous, then, and that are common and widespread, must either represent times when deposition among sections was not random, as during extensive transgressions, or times when the gross composition of a fauna persisted over many 1 Ma intervals. There is evidence that numbers of transgressive episodes correlate globally, though how common this may be is still under debate. At any rate, to the extent that gaps and depositional episodes correlate widely, stratigraphic correlations will be better than in a random model but, on the other hand, the faunal record will contain more global gaps.

A single faunal locality can hardly represent the global biota of the times. Species diversity may be accommodated by the number of provinces in the biosphere, and/or by the number of communities in provinces, and/or by the number of species in communities. How many samples are required adequately to represent the global biota depends

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partly upon the biotic heterogeneity at provincial and community levels. The present day may represent nearly or quite the peak of biotic heterogeneity during the Phanerozoic. The accumulation of potential fossils at present, or of actual fossils in the near past, should provide a good test of fossil completeness. A study of the extent to which the durably skeletonized portion of the living fauna is represented in the fossil record of an entire marine shelf province has been based on the living Californian Province fauna as contrasted with its fossil record during the past million years (Valentine 1989*b*). The record proved surprisingly complete; about 85% of the living species were captured by the fossil record, and a single locality yielded over 50% owing to intermixture of species from a variety of shallow-water habitats. The implications are that most species with durable skeletons are recruited into the fossil record, and that the spottiness and gaps found in the record are chiefly because of subsequent loss of sediments via erosion, or of fossils via diagenesis. However, when rich fossil localities or locality clusters do occur there is a good chance that a large fraction of the easily fossilized fauna that was present is represented. Of course, the more localities in the more varied sediments, the greater the completeness of the fossil fauna is likely to be. As there are literally hundreds of rich fossil localities in the Phanerozoic record, there are likely to be many local faunas that are rather complete with respect to durably skeletonized forms. For diversity studies, this situation is far better than having, say, five times as many localities that average only one fifth as complete, for it provides us with data points that suggest the general mangitude of the standing faunal diversities, or at least of a rather constant fraction of the fauna (we hope). It is thus posible to extrapolate geographically between roughly contemporaneous localities and stratigraphically between successive faunal samples. To be sure, many of the finer-scale fluctuations are missed, but on the other hand the coherence of the data appears to indicate that the broad patterns revealed by palaeodiversity studies are real. This point has long been taken on faith, but studies leading to quantitative assessments of the record, that are improving steadily, suggest that the faith is by and large justified.

A final consideration is that the available diversity record does not simply deteriorate in a linear fashion with geological time, although it does seem certain that as the ages pass, more and more fossils are lost to erosion and diagenesis. At the same time, however, buried fossils, a sort of fossil 'bank', are constantly being brought into the realm of the collectible by erosion. Whether the available record of any given period is being improved or degraded, then, depends partly upon structural and erosional history. For example, Sadler (in Valentine *et al.* 1990) points out that because Cambrian cratonic and mioclinal rocks are being well-exposed now to erosion, because of the timing and extent of structural uplifts, the present is a better time to study Cambrian faunas than the faunas of some later Periods, such as the Carboniferous. Exposure of Cambrian rocks is not yet optimal; the future will probably be an even better time to be a Cambrian palaeontologist (say, in 20 Ma).

3. NATURE OF THE TAXA

Most research on fossil diversity patterns has used the taxa of the familiar Linnaean hierarchy as units of diversity. Such usage has been criticized as inappropriate by proponents of cladistic classification (Wiley 1981; Eldredge & Salthe 1984; Vrba & Eldredge 1984; Patterson & Smith 1987). However, Linnaean taxa seem on the contrary to be the most appropriate for diversity studies, a contention that requires a brief justification.

The Linnaean taxa are monophyletic clusters of species (or a single species) that share a polythetic assemblage of characters; higher and higher taxa are clusters of such clusters that share polythetic assemblages of characters. (Polythetic units have many defining features in common, but not unit has all such features, and no such feature is found in all units; they share a 'family resemblance'.) Linnaean taxa at any level have arisen from a species that branched from an ancestral taxon of the same level; indeed they must have done. Therefore, the only Linnaean taxa that are not paraphyletic are those that have never given rise to daughter taxa of the same rank. For Linnaean families in the fossil record, between about the third and one half seem to be paraphyletic, the others becoming extinct without daughters (Valentine 1990). Paraphyly provides a nested aggregational hierarchy of taxa with similar ranks. Probably no system of classification has as much organizing power as a properly nested hierarchy (see Simon 1962).

An important feature of such a nested Linnaean hierarchy is that it provides a clear strategy to cope with the incompleteness of the fossil record. As taxa in each successive higher category have generally many individuals, a wider distribution and a longer geological range than lower taxa, their completeness of representation as fossils increases at each succeeding level (it may remain the same as a limit). If species records are too spotty and incomplete, we may simply employ generic records, which involve the same species, but clustered. Most Phanerozoic marine diversity studies have been prosecuted at the family level (see papers in Valentine 1985), but generic data are being compiled by Sepkoski, and some preliminary uses of this generic data set have appeared (Sepkoski 1986; 1988; Raup & Boyajian 1988).

The Linnaean hierarchy is particularly useful in considering the changing relative and absolute diversities of individual clades, whereby the taxonomic composition of the biosphere is altered. For such studies it is possible to consider a taxon of a given level as a unit (an 'individual' see Ghiselin 1974) in the macroevolution of a higher level; to consider genera as units within a class, for example. Such usage implies that taxa above the species level have certain properties: they must be able to reproduce, some of their features must be heritable and subject to sorting, and they must nevetheless suffer some changes that are themselves heritable and subject to sorting. As holophyletic taxa do not reproduce by definition, they cannot contribute to macroevolution among clades. In classifcations that admit only holophyletic taxa, families (for example) cannot derive from other families. If paraphyly is permitted, however, then there is no problem with clade evolution in principle (Valentine 1990). Families do emanate from other families. Of course a family arises from within a particular genus of its ancestral family, and moreover from a particular species within that genus. Indeed families arise, not from an entire species, but from some sample of a species population, a vicar or founder population, that may be as small as two genetic individuals (or even one in some cases), a sample that need have no effect whatsoever on the biology of the species (genus, family) from which it came. It seems that either species no more give rise to families than do other families, or that, units in both categories may be considered ancestral.

A Linnaean hierarchical system emphasizes the pattern of adaptive radiation that is so common at every evolutionary level, and in the fossil record it permits the employment of taxa above the species level to measure and to trace the tempo of evolutionary activity across the biosphere or of large realms within it, the clear strategy to best combat a spotty record. Furthermore, descendant Linnaean taxa do inherit features from ancestral ones, while still other features are derived; cladistic methods show this. The differential success of taxa with different derived features, then, constitutes macroevolution. A final objection posed to such use of taxa above the species level as evolutionary units is that they do not interact the way individuals do within populations, in particular that they do not interbreed (Wiley 1981). However, there are entire prokaryote Kingdoms that do not interbreed, yet such organisms certainly do evolve. I shall proceed to use Linnaean taxa here, for they are best suited to the present purpose.

4. MODEL LINNAEAN TAXA

Modelling of the behaviour of taxa in a Linnaean-style hierarchy has suggested how some of their interrelations and trends may be interpreted. Species lineages are permitted to grow within a model biosphere with finite resources represented as adaptive 'addresses', with attempted randomly chosen speciations or origins of higher taxa at stochastically constant rates. Each species occupies one adaptive address exclusively; attempted speciations onto occupied addresses fail. Random extinctions of species occur at a 'background' rate, so that species diversity reaches a stochastic equilibrium when successful speciations slow to the extinction rate. The success of originations is thus density-dependent (diversity-dependent). Progressively higher taxa requiring increasingly large, unoccupied blocs of adaptive addresses to originate. At speciation (S) and extinction (E) rates inferred from the fossil record, trees may be generated that resemble, in the frequency distributions of branches at all levels, many phylogenetic trees of living taxa (Valentine & Walker 1987). An interesting feature of this model is that with average E and S estimated from the fossil record, about one third of the adaptive addresses remain unoccupied (Walker & Valentine 1984). Three distinctive behaviours are exhibited by higher taxa during and subsequent to the rise of species diversities to a (stochastic) equilibrium at which S comes to equal E. The first behaviour occurs during the growth of species diversity towards an equilibrium; the diversities of higher taxa rise also. Secondly, when species reach a stochastic equilibrium with speciation and background extinctions approximately balanced, most higher taxa tend to decline in diversity; it is easier then to extinguish higher taxa than to originate new ones, for adaptive space is vacated by declining taxa piecemeal and it is usually taken over by surviving groups. Thirdly, those taxa that happen to become quite large relative to the capacity of the model biosphere become relatively immune to background extinction levels; it is taxa on the higher levels that first achieve such size, of course.

If two independent clades that have different ratios of E and S are both present in the same adaptive space, then the clade with the higher stochastic equilibrium will eventually exclude the other clade from that space (Walker 1984; Valentine 1990). If two clades have equal E/S ratios, but have different species turnover rates, then the clade with the lower turnover rate will eventually exclude the other (Valentine 1990).

5. MARINE INVERTEBRATE RECORD

Marine invertebrates furnish the longest and most complete fossil record. Marine invertebrate diversity displays three main phases, as identified faunally by Sepkoski (1981): a late Precambrian–Cambrian fauna I, during which species diversity rose from the earliest records of animals to a possible Late Cambrian 'plateau'; a fauna II that includes the remainder of the Paleozoic Era when species diversity rose again from the Late Cambrian levels to perhaps the end of the Ordovician, and thereafter fluctuated about a fairly constant or perhaps slightly rising mean until terminated at the severe Permian–Triassic extinction; and a Mesozoic–Cenozoic fauna III after the extinction, when diversity climbed to an all-time high during a rise that shows no evidence of slackening (mankind's depredations aside, that is). These Faunas were originally established at the family level, but are convenient for discussion of diversity trends across the entire taxonomic hierarchy (figure 1).

Phase I can be subdivided into two main portions. The late Precambrian ('Upper Vendian') fauna contains body fossils, most of which appear to be of cnidarian grade (see, for example, Jenkins 1984; Norris 1989). Bilaterians are chiefly represented by epifaunal creeping traces and horizontal shallow semi-infaunal or infaunal burrows that show a variety of behaviours but from which no very accurate diversity estimate may be drawn. Possible bilaterian body fossils include sprigginids and vendomiids that may represent segmented, haemocoelic and scleritized worms (Valentine 1989*a*) but that have also been considered to represent an extinct non-metazoan clade (Seilacher 1989). The Early Cambrian record contains evidence of an explosive radiation of higher invertebrate body plans that probably raised the number of phylum-level

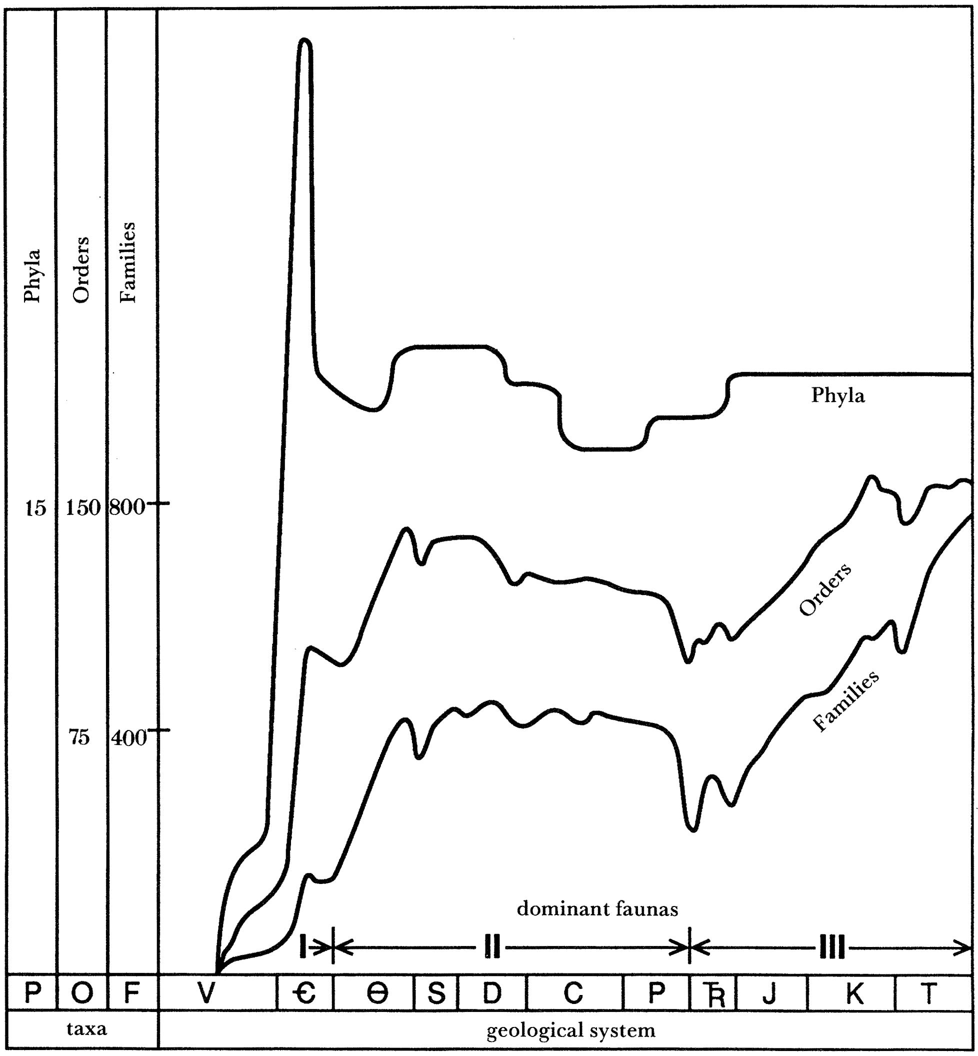

Figure 1. Observed diversity record of phyla, orders and families of marine invertebrates across the late Precambrian and the Phanerozoic. The Precambrian–Cambrian boundary is placed at 540 Ma ago; the remaining time divisions are as in Sepkoski (1981). Intervals of measurement are geological stages, which are not of equal lengths, and there are slight differences in the taxa used from level to level; neither of these features strongly biases the trends, however. The peaks in the Cambrian are from Lagerstätten, which include poorly skeletonized forms. Fauna I is dominated by trilobites, fauna II by articulate brachiopods and crinoids, and fauna III by molluscs. Families after Sepkoski (1981); Orders after Sepkoski (1978), amended by Valentine *et al.* (1990).

clades to the highest point in their history (Valentine 1969; Valentine *et al.* 1990), although species diversity must have been many times lower then than at present (Valentine 1969; Bambach 1977).The first two stages of the Lower Cambrian are particularly characterized by the appearance of novel body plans, and of 'skeletal plans' of extinct forms that have proved to represent unique body plans whenever their gross body morphology is discovered (e.g. wiwaxiids (Bengston & Conway Morris, 1984) and *Microdictyon* (Chen *et al.* 1989)). Perhaps between 35% and 50% of the phylum-level taxa and over 90% of the ordinal-level taxa have become extinct. The record of body fossil diversity at three taxonomic levels is shown in figure 1.

The Middle and Late Cambrian diversity decline that can be inferred for the class and ordinal levels can be interpreted as accompanying a stable or even somewhat increasing species diversity, a situation that occurs when species' S and E are approximately equal (Valentine & Walker 1987). The Vendian part of Fauna I, then, can be regarded as recording a radiation of diploblastic and acoelomate bilaterian grades, the establishment of segmentation, and a build-up of body-plan complexity that culminated in the establishment of several lineages of higher invertebrates near the Cambrian boundary. During Early Cambrian time the earliest coelomates appear (brachiopods), vertically penetrating burrows were established (the timing and extent of which are still in dispute) and higher invertebrates radiated explosively; some of the body plans involved durable skeletons to create the Precambrian–Cambrian boundary.

Fauna II began with a decided rise in diversity, nearly doubling at the Ordinal level (figure 1). In a study of this diversification, Sepkoski (1988) concluded that it resulted chiefly from a partitioning of resources on the community level, although accompanied also by a less important increase in species packing within communities. Provinciality was not believed to be a significant contributor. The reason that the shelf environment became the site of an important increase in habitat specialization at this particular time is not understood, although it may be associated with the faunal dynamics of the clades that rose to dominance at that time (see later). Phylum, class and ordinal diversity apparently declined through the remainder of the Paleozoic, probably punctuated at mass extinction events (Valentine 1969). There is some indication that familial and generic diversities, increasingly more volatile than higher taxa, fell slightly through that Era (Sepkoski 1981, 1988). Species diversity, even more volatile than generic diversity, may have increased somewhat overall during the Middle and Late Palaeozoic, with higher taxa becoming increasingly speciose (Valentine 1969), possibly one of the reasons that high-level diversities do not decrease markedly (Flessa & Jablonski 1985).

Following the Permian–Triassic extinctions, Fauna III began with few marine invertebrate species, perhaps fewer than at the beginning of Cambrian time (Valentine *et al.* 1978), but so far as we know with at least as many phyla and classes as exist now. A few new orders appear. At lower taxonomic levels, however, high rates of diversification continued right into the Quaternary, nearly doubling the number of families from their fauna II levels, and implying greater increases in genera and still greater ones in species. Species packing within communities is thought to have doubled from fauna II to fauna III (Bambach 1977), and this estimate may be conservative. There are as yet no quantitative estimates for increases (if any) in the numbers of communities within provinces. The number of provinces, however, began to increase following the Mesozoic breakup of Pangaea and this has probably been an important contributor to global marine diversity during fauna III, especially at the species level (Valentine 1967; Valentine *et al.* 1978).

Data from all Faunas may be synthesized into a generalized description of the dynamics of marine invertebrate diversity changes. The earliest (Vendian) faunas seem to consist of creeping vermiform and segmented haemocoeloic bilaterians, together with diploblastic sessile and pelagic forms. As the fauna is soft-bodied, taxonomic diversities cannot be estimated with confidence, although they appear to be relatively low at all levels and to have a far lower ratio of low- to high-level taxa than exists today. This fauna presumably records the rise in complexity of bilaterians

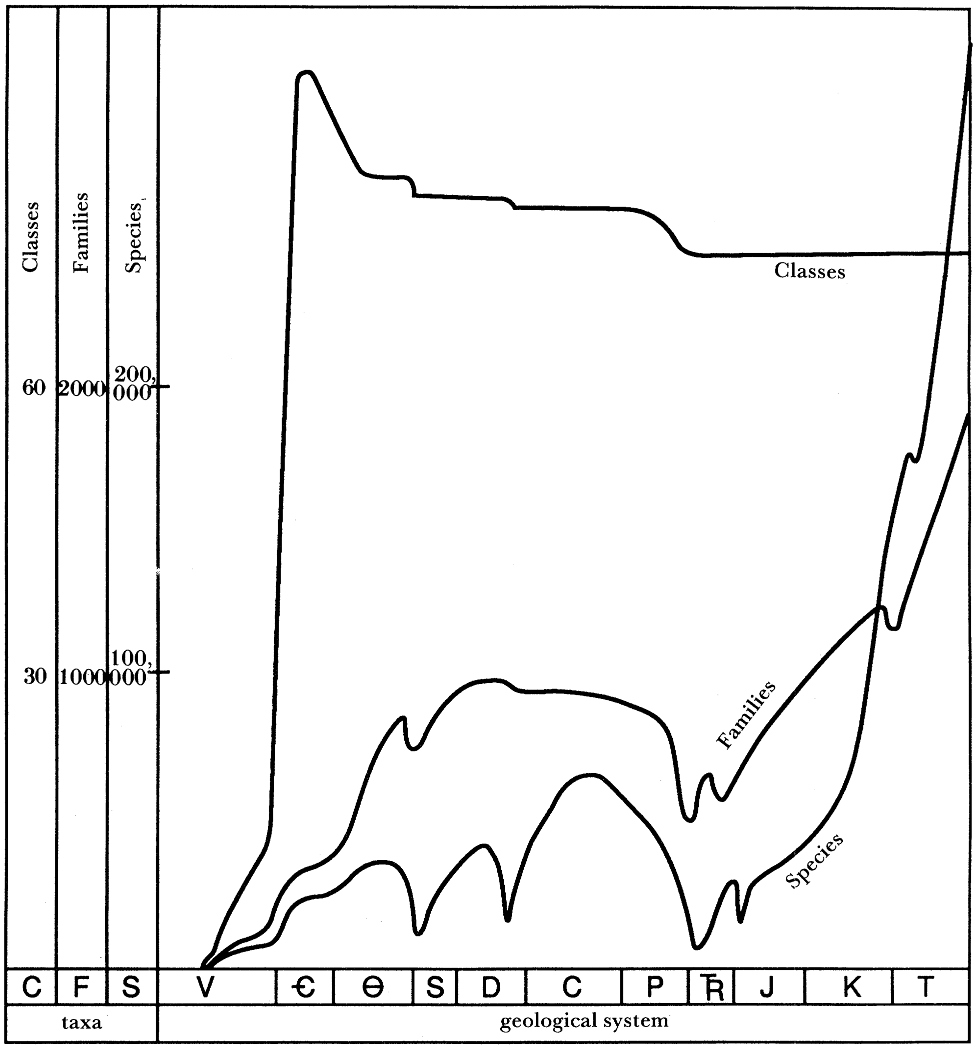

Figure 2. Estimates of actual standing diversities of marine invertebrate classes, families and species based on fossil diversities, trends in fossil diversities among taxonomic levels, and ratios of easily to poorly fossillized taxa at present and in Lagerstätten.

from simple acoelomate beginnings to rather complex segmented forms with hydrostatic skeletons. As the level of complexity appropriate to higher invertebrates is achieved, secondary body cavities appear in some lineages and both arthropod and annelid ancestors explode into a variety of body plans, chiefly segmented (Jacobs 1990). Probably the ratio between low-level and high-level taxa was never lower than during the middle to late Early Cambrian. Those lineages that happen to have a high speciation rate diversified rapidly in the relatively empty adaptive space of the times; the Cambrian fauna was eventually dominated by trilobites, which have high rates of *S* and *E* for invertebrates (Stanley 1979), especially the earlier lineages (Foote 1988), and which had relatively wide distributions across the Cambrian shelves. These broad associations were replaced by benthic communities dominated by brachiopods and crinoids, the members of which were more narrowly distributed and possessed slower turnover rates (see Stanley 1979; Walker 1984; Valentine 1990).

That a general increase in specialization should correlate with a general slowing of taxonomic turnover, requiring a concomitant lowering of extinction rates, seems contradictory at first glance: shouldn't more specialized organisms be at greater extinction risk? However, I argue here that in fact those lineages that are endowed for some reason with relatively high extinction resistance are more likely to produce successful specialized taxa (in macroevolutionary terms, those of longer durations). A clade with high extinction rates that produces specialists may practically commit suicide, and this has no doubt happened often. The specialists with the best chance to persist, then, may be precisely those that are the most extinction-resistant. So the high-turnover, generalized taxa dominating fauna I are replaced by lower-turnover, more specialized taxa of fauna II.

The reign of fauna II was brought to a spectacular close by the end-Permian extinctions. From the Cambrian example, one would expect the rediversification to be dominated by faster-turnover clades, and indeed this is observed (Van Valen 1984). The early Mesozoic success of higher-turnover ammonoid lineages is a case in point. More successful in the long run, however, are the gastropods, bivalves, and other important members of fauna III that have even lower turnover rates than the fauna II dominants (see rates in Stanley (1979); Raup & Sepkoski (1982); Raup & Boyajian (1988)). Furthermore, the fauna III organisms appear to be still more specialized than those of fauna II, since species packing within communities rises significantly. The same generalities that apply to the fauna I–II shift apply to the fauna II–III shift. In addition, the effects of high species diversities achieved within communities have been multiplied by provincialization to reach a great Quaternary diversity high (Valentine 1967). Figure 2 shows estimates of actual standing diversities of classes, families and species of the marine realm during the Vendian and the Phanerozoic.

6. TERRESTRIAL TETRAPOD RECORD

Perhaps because the terrestrial record seems less complete, fewer diversity studies involve terrestrial than marine organisms. Some of the problems involved in such analyses are reviewed in Padian & Clemens (1985), who present Phanerozoic patterns at the generic and ordinal levels. Tetrapod diversities at the family level have been considered by Benton (1985), who has tabulated family geologic ranges (Benton 1987). These sources provide the chief basis of the following discussion.

Three assemblages of tetrapod families are recognized: a primitive assemblage I of chiefly late Palaeozoic dominance; a Mesozoic assemblage II (early diapsids, dinosaurs, pterosaurs); and assemblage III, including mammals and birds, that began in the early Mesozoic but assumed dominance only in the Late Cretaceous (figure 3). A metric that estimates completeness (the ratio of all stages in which a taxon is found to all stages that it spans) suggests that faunal completeness is not particularly time-dependent for the tetrapod groups; for example, the record of the small lepidosaurs and lissamphibians of assemblage III is poor, while the record of mammal-like reptiles is judged to be rather complete (Benton 1987). The strong Tertiary diversity rise, then, is presumably real. Per-taxon extinction rates have been calculated for families from within various tetrapod groups from Benton's data (Valentine *et al.* in preparation). Early amphibians display faster turnover rates than late amphibians, early reptiles than later reptiles and dinosaurs, and mammal-like reptiles (therapsids) than mammals, even though the mammalian record includes short-lived families associated with the early Cenozoic radiation. However, dinosaur turnover rates are only a little faster than those for mammals.

The contributions of various forms of diversity accommodation to the increased Cenozoic tetrapod diversity has not been studied, except that biogeographic endemism must play a role. The work of

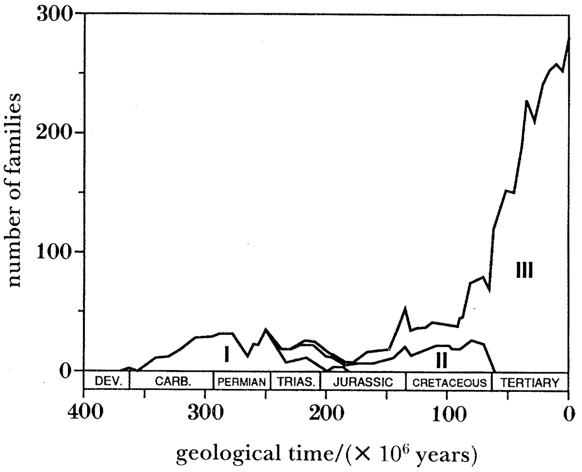

Figure 3. Observed Phanerozoic diversity record of terrestrial tetrapod families. Fauna I includes early amphibians, anaspids and mammal-like reptiles; fauna II, early diapsids, dinosaurs and pterosaurs; fauna III, 'modern' amphibians, reptiles, birds, mammals. After Benton (1987).

Flessa (1975) and Flynn (1986) make it clear that the distinctiveness of regional faunas contributes significantly to mammalian diversity at both generic and familial levels. These studies conclude that the arrangement and number of land regions is a primary control on diversity, while latitudinal environmental variation has also been important. As continental separations have increased and climatic zonation has been enhanced during the Cenozoic, geographic factors must have become increasingly important as diversity controls both intercontinentally and in terms of habitat patchiness intracontinentally. Estimates of the extent to which tetrapod species packing within environments has increased or varied seems not to have been attempted. Whether increasing specialization has accompanied slowing in tetrapod taxonomic turnover rates cannot be addressed as yet. The data thus suggest possible similarities with marine faunas but are hardly conclusive at this time.

7. VASCULAR PLANT RECORD

Data from land plant (tracheophyte) diversities have been summarized by Niklas *et al.* (1980, 1983, 1985) for species within major plant groups. Four floras were recognized (figure 4), which tend to be composed chiefly of groups that are successively freed from dependence on moisture for reproduction. It is the experience of palaeobotanists that the later local floras are more speciose than the earlier except during the Permian and Triassic, so that increased species packing within plant associations is probably important (Niklas *et al.* 1980). That habitat patchiness has increased as Cenozoic climates have developed seems likely also (Tiffney & Niklas 1990) although habitat evolution has not been thoroughly studied in this context. On the larger geographic scale, the increased climatic zoning of Cenozoic time was probably quite important, but there seems to be no clear signal that plant diversity is tied to the number of land regions (Tiffney & Niklas 1990).

A striking feature of vascular plant evolution, at least to one accustomed to marine invertebrate history, is that the pace of evolutionary turnover has increased from flora to flora (Niklas *et al.* 1983, 1985), precisely opposite to the turnover trajectory of marine forms and certainly different from tetrapods also. Elements of the later floras display faster rather than slower turnover rates; the dependence on extinction resistance (low E) for long-term success in invertebrate faunas is replaced by a dependence on high speciation rates (high S).

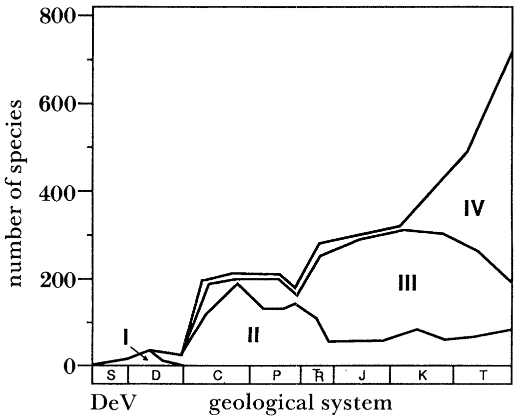

Figure 4. Observed Phanerozoic diversity record of vascular land plants at the species level (excluding spore and pollen floras). Flora I embraces early vascular plants; flora II, pteridophytes; flora III, gymnosperms; flora IV, angiosperms. After Niklas *et al.* (1983).

It would seem that, among the best-known groups of organisms, trachaeophytes are contrarians. If their increasing diversity and presumably increasing partitioning of adaptive space indicates increasing specialization, the response to any accompanying increase in extinction rates has been to favour lineages with higher S. This is a possible strategy, but why animals seem to have adopted low E and plants high S strategies is not clear. One possibility is that animal radiations have tended to produce the major clades early, and then those taxa are sorted out in favour of slow turnover groups over tens to hundreds of millions of years. In plants, by contrast, the major groups have appeared sequentially, invading new environments over hundreds of millions of years. The incoming floras may have favoured high speciation rates so as to cope with colonization of increasingly hostile environments (Valentine *et al.* in preparation). Why plants have not been able to increase their extinction resistance, and thus allow a lowering in turnover rates, is not at all clear, but at least these studies permit the question to be posed.

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Discussion

P. J. GRUBB (*Botany School, University of Cambridge, U.K.*) What is the order of magnitude of the differences in longevity of particular genetic lines of animals or plants early and late in the record? Is there any evidence on whether the shorter-lived lines of animals found early on were made up of shorter-lived individuals?

J. W. VALENTINE. Average extinction rates for marine invertberate species appear to fall by nearly an order of magnitude between fauna I and fauna III, though data are spotty and there is considerable variation among clades. Land plant species increase extinction rates by about the same amount (a factor of 8 or so) between flora I and flora IV.

Unfortunately, data on individual lifespans are so spotty for early animals that they can't be meaningfully compared with the spans of living forms. Incidentally, Bruce Tiffney tells me that with land plants, much of the increase in turnover in flora IV is because of angiosperms of herbaceous habit and that as herbs have shorter lives than plants with secondary growth, the average generation and species turnovers are positively correlated in this case.