

the maximum increases only initially and then levels off, an inhomogeneous dynamic might be a reasonable inference, perhaps an upper boundary of some kind.

Finally, when diversity increases, a rising minimum can be informative. In Fig. 2.3.11.3(a), the rising minimum suggests a driven trend. Importantly, however, a stable minimum, as in Fig. 2.3.11.3(b), does not necessarily indicate passive, because a weakly driven dynamic can produce the same pattern (McShea 1994). (Certain caveats are relevant here, and other methods for distinguishing passive and driven have been devised; see McShea 1994, 1998.)

A final cautionary point is worth making about scale dependence. In a large-scale trend, different dynamical rules and rule distributions may occur at different scales within a clade. For example, Fig. 2.3.11.4(a) shows a case in which the dynamics within the smaller subclades are all passive, but the dynamic at the scale of the entire clade is driven. Figure 2.3.11.4(b) shows the converse case. Thus, for example, in principle, a discovery that changes in relative brain size within various mammalian taxa were mainly driven would not contradict a finding that the increase in mammals as a whole was passive.

References

- Bookstein, F.L. (1988) Random walk and biometrics of morphological characters. *Evolutionary Biology* **23**, 369–398.
- Fisher, D.C. (1986) Progress in organismal design. In: D.M. Raup and D. Jablonski, eds. *Patterns and processes in the history of life*, pp. 99–117. Springer-Verlag, Berlin.
- Gingerich, P.D. (1993) Quantification and comparison of evolutionary rates. *American Journal of Science* **293A**, 453–478.
- Gould, S.J. (1996) *Full house: the spread of excellence from Plato to Darwin*. Harmony Books, New York.
- MacFadden, B.J. (1986) Fossil horses from 'Eohippus' (*Hyracotherium*) to *Equus*: scaling, Cope's Law, and the evolution of body size. *Paleobiology* **12**, 355–369.
- McKinney, M.L. (1990) Classifying and analysing evolutionary trends. In: K.J. MacNamara, ed. *Evolutionary trends*, pp. 28–58. University of Arizona Press, Tucson, Arizona.
- McShea, D.W. (1994) Mechanisms of large-scale trends. *Evolution* **48**, 1747–1763.
- McShea, D.W. (1998) Dynamics of diversification in state space. In: M.L. McKinney, ed. *Biodiversity dynamics*, pp. 91–108. Columbia University Press, New York.
- Raup, D.M. (1977) Probabilistic models in evolutionary paleobiology. *American Scientist* **65**, 50–57.
- Raup, D.M. and Crick, R.E. (1981) Evolution of single characters in the Jurassic ammonite *Kosmoceras*. *Paleobiology* **7**, 200–215.
- Roopnarine, P.D., Byars, G. and Fitzgerald, P. (1999) Anagenetic evolution, stratophenetic patterns, and random walk models. *Paleobiology* **25**, 41–57.
- Trammer, J. and Kaim, A. (1999) Active trends, passive trends, Cope's Rule and temporal scaling: new categorization of cladogenetic body size changes. *Historical Biology* **13**, 113–125.

2.4 Patterns of Diversity

2.4.1 Biodiversity through Time

M.J. BENTON

Biodiversity today

Estimating modern diversity

Estimates of the present diversity of life range over at least an order of magnitude, from perhaps 2–3 million species at the lower end, to 30–100 million at the upper

end. The lower estimates represent summaries of the number of species that have actually been documented. It is estimated (May 1990), for example, that some 1.7–1.8 million species of modern microbes, plants, and animals have been named so far by systematists, and that figure must be a minimum estimate of current biodiversity. Even this assertion, however, must be considered carefully, before proceeding. If synonymy (i.e. the error of naming as new a species that has already been named) is rampant, that total of 1.8 million may be an overestimate.

The roster of named living species clearly includes many synonyms, and the synonymy rate may be as much as 20–40%, based on close study of particular

groups. Synonymy is an inevitable result of the way in which systematists name new species, representing a level of expected error. When erecting a new species, a systematist attempts to establish unequivocally that the purported new form has never been named before, but it is possible to overlook a previous publication, perhaps in an obscure journal, in a language unfamiliar to the systematist, or presented in such a way that its identity is difficult to determine (incomplete description or poor illustrations). Hence, the total of 1.8 million named modern species might be reduced to 1.4 million, if all synonyms were recognized and deleted (Wilson 1992).

Counter to the synonym problem, however, is the constant accretion of newly described species. Each year, on average, systematists add one or two new species of mammals and three new species of birds to the lists (based on estimates of taxonomic activity from 1900 to 1975) as well as dozens of newly named microbes, fungi, plants, and marine animals, and some 7250 new species of insects (Wilson 1992).

The collector curve

These rates of new species descriptions provide one way to estimate the actual diversity of life on Earth. If the additions are the same each year, the pattern of increase would be linear. However, the pattern may be more complex. It could be argued, for example, that the discovery of new species would follow a collector curve, i.e. a pattern of rapid rise when new species were being discovered all the time, followed by a slowing-down of the rate as the number of described species approaches the true diversity (Fig. 2.4.1.1). For birds or mammals, it is likely that the levelling-off phase, the asymptote, was reached about 1900 (Fig. 2.4.1.1a), and that the current slow rate of discovery of new species really means that virtually all species on Earth have been discovered. This evidence could lead to a modest estimate of perhaps 3 million species for true current biodiversity. However, a little reflection suggests that this comfortable impression is probably very far from the truth.

It is wrong to extrapolate from the groups of living organisms that are most fully documented, such as birds and mammals. For insects, microbes, fungi, parasites, meiofauna, deep-sea organisms, and many others, taxonomists find new species wherever they look. If a taxonomist of bacteria takes a random soil sample, he finds many hundreds of previously unrecognized species; if a marine biologist scans a sample of mud scraped from the deep ocean floor, she may find dozens of undescribed species. For these groups, the rates of discovery and description depend only on the time and effort expended by taxonomists. This means that it is impossible to predict ahead when the curve will show an asymptote (Fig. 2.4.1.1b), and consequently final totals

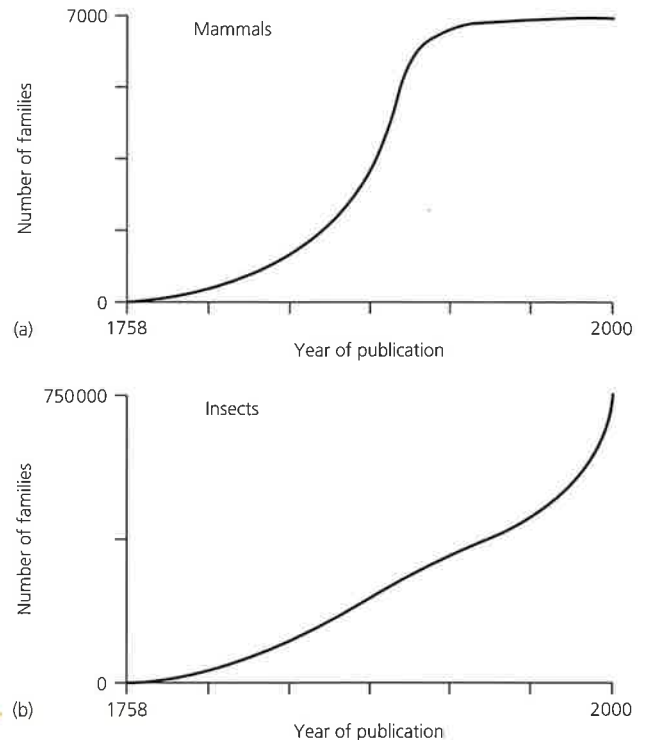


Fig. 2.4.1.1 Collector curves and the estimation of total biodiversity. (a) For well-known groups, such as birds or mammals, apparently nearly all species that exist have been named and described, and the collector curve shows an asymptote to the true biodiversity. (b) For incompletely known groups, such as insects, bacteria, fungi, or parasitic organisms, the rate of discovery is still high, and it is impossible to predict when the rate will slow down and approach the actual total.

for many groups cannot be estimated. These little known groups are highly speciose, and their current diversities must far outweigh those of well-known groups such as birds and mammals. Regrettably, then, estimates of actual global biodiversity based on current records can only work for heavily studied groups like birds and mammals, but not for vast sectors of life where taxonomic work has barely begun.

Extrapolation from intensive local sampling

Biologists have tried another approach in estimating modern biodiversity. For highly speciose groups, it might be more appropriate to carry out a detailed survey in one spot on Earth, find the maximum diversity, and then extrapolate worldwide. A well-known experiment concerns tropical rain forest beetles (Erwin 1982). The entire arthropod fauna was sampled from the canopy of the tree *Luehea seemannii* from Central and South America. This was done by setting 'bug bombs' under the selected trees, devices that pump powerful insecticide. All the dead arthropods which fell to the ground

were collected and classified. Erwin estimated that there are 163 species of beetles living exclusively in the canopies of *L. seemanni*. There are about 50 000 tropical tree species around the world, and if the numbers of endemic beetle species in *L. seemanni* is typical, this implies a total of 8.15 million canopy-dwelling tropical beetle species in all. This figure excludes forms that live in several tree species. Beetles typically represent about 40% of all arthropod species, and this leads to an estimate of about 20 million tropical canopy-living arthropod species. In tropical areas, there are typically twice as many arthropods in the canopy as on the ground, giving an estimate of 30 million species of tropical arthropods worldwide. This estimate came as a considerable surprise when it was published: 30 million species of tropical arthropods must imply a global diversity of all life in the region of 50 million. Some wild-eyed biologists even talked of figures of 100 million or more!

However, mature reflection has suggested that Erwin's (1982) estimate was closer to the truth than more conservative estimates of 2–5 million (May 1990; Wilson 1992). Similar extrapolation exercises have been performed for deep-sea organisms, microbes, fungi, and parasites, and they all point to total global biodiversities of 20–100 million. Such estimates are astounding, and they have profound consequences. Should systematists give up the endeavour to describe and name all species since they will never finish the task? Should governments employ many more systematists in order to do the work properly? How can conservationists and planners begin to estimate the effects of pollution and other human activities on biodiversity since no one has the faintest idea how many species exist today, nor what they are, and where they are?

Biodiversity through time— patterns of increase

Life is unexpectedly diverse today. Indeed, it is assumed that life is more diverse today than it ever has been. This seems in some ways obvious, and yet it could also be construed as extraordinary vanity, somehow akin to the view that all of evolution was planned to lead to human beings, that somehow this instant in the vast span of time is the most important of all. However, it is evident that all living organisms, and all organisms known as fossils, derive from a single common ancestor (based on the evidence of shared complex characters, such as the DNA–RNA system of inheritance, homeobox genes, and the like). That common ancestor, the single species that gave rise to all of life, existed some 3500–3800 million years ago. Biodiversity has, then, expanded from one species to some 5–50 million species.

There are many ways to go from one species to many, and these can be expressed simply in terms of three

mathematical models, represented by a straight line, an exponential curve, and a logistic curve, firstly as an uninterrupted increase (Fig. 2.4.1.2a), and secondly with some mass extinctions superimposed (Fig. 2.4.1.2b).

The linear model represents additive increase: simply the addition of a fixed number of new species in each unit of time. (The increase in this example, and the others, is a net increase, i.e. true increase minus extinctions.) In terms of an evolutionary branching model, additive increase would mean that, through time, speciation rates have declined, or extinction rates have increased regularly at a rate sufficient to mop up the excess speciations. The implied decline in the rate of evolution in the linear model comes about simply because

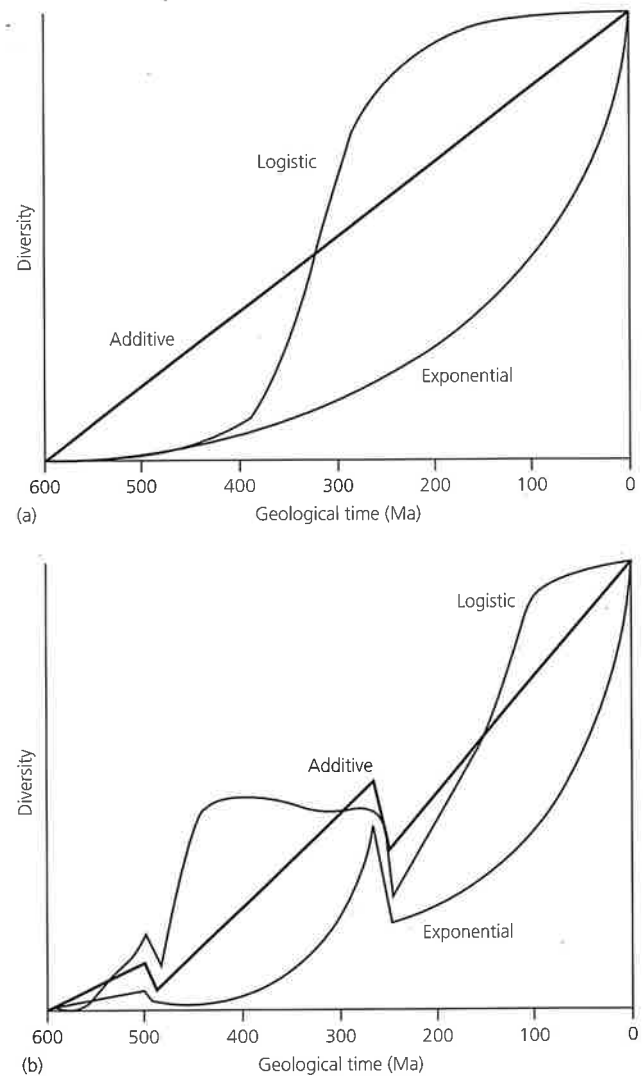


Fig. 2.4.1.2 Theoretical models for the diversification of life: (a) in the absence of major perturbation; and (b) with two mass extinctions superimposed. In each case, the upper curve is the logistic or equilibrium model, the middle curve is the additive or linear model, and the lower curve is the exponential model.

the total number of species is increasing regularly, and yet the *rate* of increase across the board remains fixed; hence, for any individual evolutionary line, the rate or probability of splitting (speciating) must decline. Such a model has generally been rejected as improbable.

The exponential model is more consistent with a branching mode of evolution. If speciation and extinction rates remain roughly constant, then there will be regular doubling of diversity within fixed units of time. A steady rate of evolution at the level of individual evolutionary lines scales up to an exponential rate of increase overall since total diversity is ever-increasing. This model has been applied to the diversification rates of individual clades, and to the diversification of life in general (Benton 1995; Hewzulla *et al.* 1999).

The logistic model involves one or more classic S-shaped curves, each consisting of an initial period of slow diversity increase, a rapid rise, a slowing of the rate of increase as a result of diversity-dependent damping factors, and then a plateau corresponding to a limiting or equilibrium value. The logistic model has been used to explain patterns of diversification of marine organisms (Sepkoski 1984) and of plants.

There is clearly no consensus on which model best explains the diversification of major sectors of life through time, nor on whether all patterns of diversification adhere to the same model of increase. The choice of model is important since each makes profoundly different claims about evolution.

A different approach to the question of diversification through time has been to attempt to estimate the sum total of all species that have ever existed. Three lines of reasoning suggest that 2–4% of all species of plants and animals that have ever existed are alive today (Sepkoski 1992; May 1994):

1 The first argument is based on an assumed pattern of species diversity increase, and the known average duration of a species before it becomes extinct. If species diversity increased roughly linearly (additive model) through the Phanerozoic, and average species duration is 5–10 myr, then living species represent 2–4% of those that existed through the past 600 myr.

2 The second argument is based on the diversification of insects over the past 450 myr. If the average duration of an insect species is 10 myr, and the group has diversified linearly, then 5% of all terrestrial species that ever existed are alive today.

3 The third argument is based on preservability of the fossils. Some 250 000 species of fossil marine animals have been named, similar to the total number of known marine animal species alive today (200 000). Allowing for non-preservation of soft-bodied organisms, and other losses, this could also represent only 2–4% of the total number of fossil species (Sepkoski 1992).

In these discussions, it has only been possible to

examine patterns of diversification for macroscopic organisms, typical plants and animals. Microbes are excluded, because almost nothing is known of their current diversity, and even less is known of their fossil record. If 2–4% of all species that ever existed are alive today (3–50 million), there must have been some 75–2500 million species in the past.

Biodiversity through time — land and sea compared

There are major differences between the patterns of diversification on land and in the sea, and the history of life in each realm may have been rather different. Today, about 85% of described species of plants and animals live on land, and the main groups (plants, arthropods, vertebrates) have reached their present great diversity in the past 450 myr. Plants and animals have been evolving in the sea since at least 600 Ma, and the fossil record is dominated by marine species, which make up some 95% of all described forms. This dominance of marine forms is partly accounted for by the fact that virtually the only organisms known from the Vendian and early Palaeozoic (600–450 Ma) are marine, and that the early history of life on land appears to have occurred at relatively low diversities. Also, fossils in certain marine environments are more likely to be preserved than those in many continental settings. The observation that life on land today is apparently five to six times as diverse as life in the sea, largely because of the insects, could be an artefact reflecting the greater amount of time devoted by systematists to continental than to marine organisms. However, if this difference is even partly correct, then it would imply a much more rapid diversification on land than in the sea.

In studies of the diversification of marine animal families (Fig. 2.4.1.3a), there is evidence for a short plateau in the Cambrian (lasting ≈ 40 myr), and a longer one from the Ordovician to the Permian (≈ 250 myr). This is followed by a long phase (250 myr) of near-exponential increase in diversity through the Mesozoic and Cenozoic, the rising element of a third logistic curve, which shows a hint of a slow-down in the last 25 myr or so, suggesting that a third plateau level may be achieved 125 myr in the future (Sepkoski 1984).

Marine invertebrate diversification has been explained (Sepkoski 1984) as the succession of three major phases of evolution, in which broad assemblages of different phyla ('evolutionary faunas') dominated the oceans, and were then replaced. The Cambrian fauna diversified exponentially at first, and then diversification slowed as the equilibrium level of 85 families was approached. The exponential diversification of the Palaeozoic fauna then began in the Early Ordovician, reaching an equilibrium diversity of 350 families, and

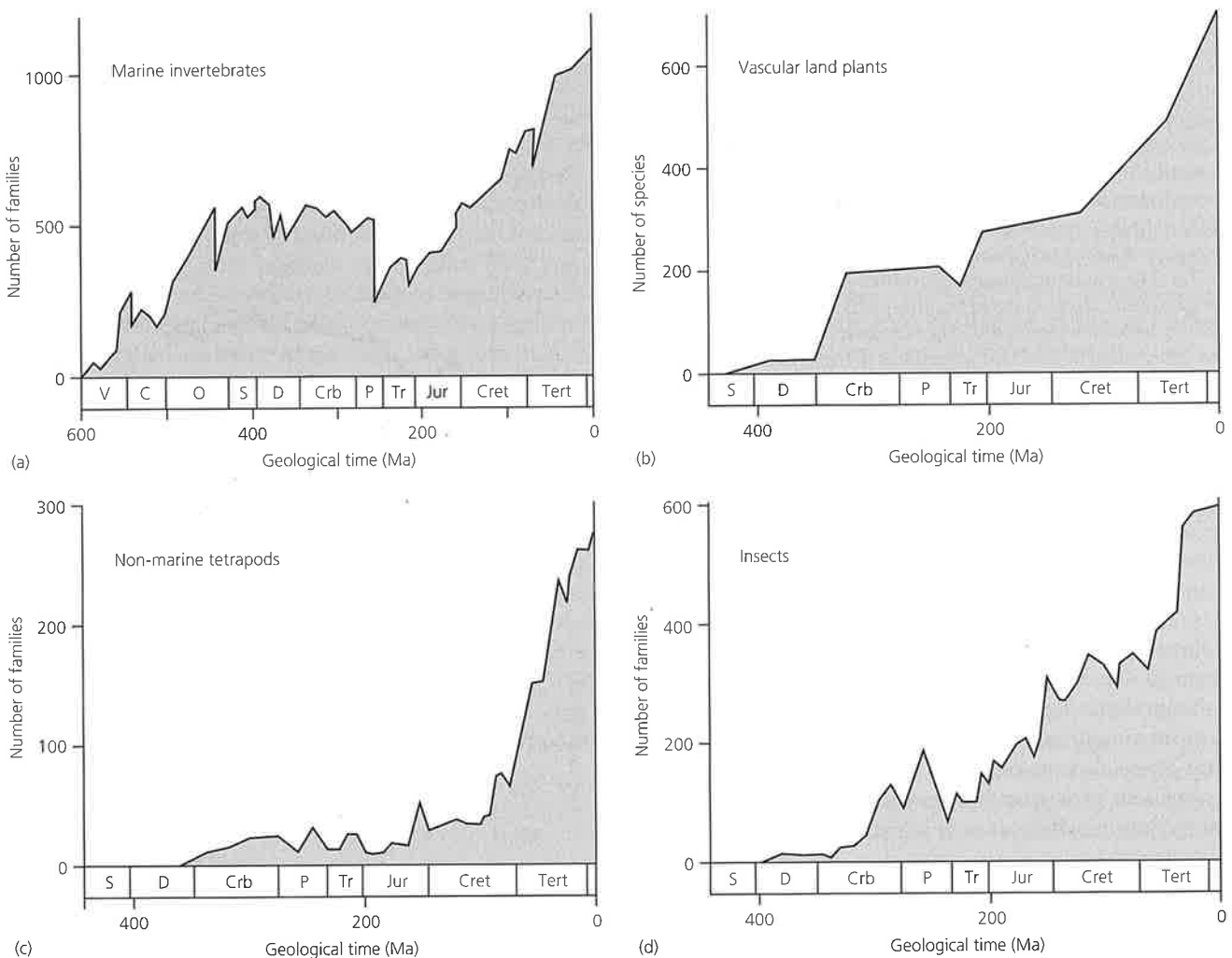


Fig. 2.4.1.3 Patterns of diversification of families of: (a) marine invertebrates; (b) vascular land plants; (c) non-marine tetrapods; and (d) insects. (Based on Sepkoski 1984; Benton 1985; Niklas *et al.* 1985; Labandeira and Sepkoski 1993.)

largely supplanting the Cambrian fauna. Finally, after the end-Permian mass extinction, which reduced the global diversity of the Palaeozoic fauna dramatically, the Modern fauna continued and accelerated its long-term rise in diversity.

In studies of the diversification of vascular plants (Fig. 2.4.1.3b), an equilibrium interpretation has also been given (Niklas *et al.* 1985). There was a succession of major baupläne of plant types: early vascular plants in the Devonian; lycopods, ferns, conifers, and others in the Carboniferous to Permian; gymnosperms in the Triassic to Jurassic; and angiosperms from the Cretaceous onwards. There was evidence for declining speciation rates and increasing species durations during each of the first three radiations, as the new set of clades partially replaced the old. Each new radiation led to an increase in total global diversity, while the diversity of the preceding floras declined. Angiosperms apparently continue to diversify at a high rate. It is hard to identify plateaus in

land-plant species diversification, and it is hard to find evidence for logistic models of diversification. Equally, the total curve of species diversities through time is not obviously exponential and, if anything, the pattern appears to suggest linear increase in diversity through time.

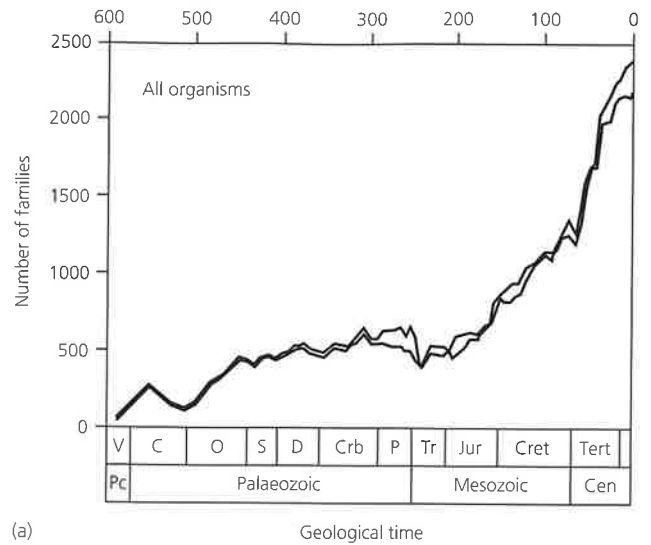
The diversification of continental tetrapod families (Fig. 2.4.1.3c) appears to correspond to an exponential model of increase (Benton 1985). Diversity levels remained low, at some 30–40 families, during the late Palaeozoic and much of the Mesozoic. They then rose to about 100 families at the end of the Cretaceous and, after recovery from the end-Cretaceous (K–T) extinction event, familial diversity increased rapidly towards 330 families, and it shows no sign of a slow-down. The pattern of diversification may be dissected into successive radiations of three global clade associations: basal tetrapods (formerly termed 'labyrinthodont' amphibians) and synapsids ('mammal-like reptiles') in the late

Fig. 2.4.1.4 Patterns of the diversification of life through time in terms of changes in numbers of families extant per stratigraphic stage, plotted for: (a) all organisms; (b) continental organisms; and (c) marine organisms. In each graph, a maximum and minimum is shown, based on a combination of stratigraphic and habitat-preference information. The minimum measure includes only families recorded as definitely present within each stratigraphic stage, or as definitely spanning that stage, and only families designated as restricted solely to the marine or continental realm. The maximum measure includes also all doubtful stratigraphic attributions of families, and all equivocal and shared habitat designations. The sum of minimum measures for continental and marine organisms is equal to the minimum measure for all taxa together. The sums of maximum measures, however, do not equal the maximum measure for all taxa because families with equivocal environmental assignments, and those which occur in both marine and continental settings, are counted as both marine and continental. (Based on Benton 1995.)

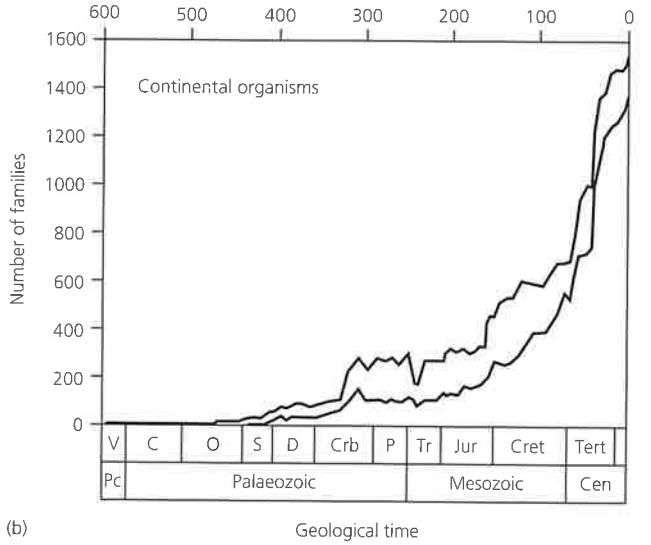
Palaeozoic; archosaurs (dinosaurs, pterosaurs, crocodilians) in the Mesozoic; and lissamphibians (frogs and salamanders), lepidosaurs (lizards and snakes), birds, and mammals from the Late Cretaceous to the present day. These clade associations replace each other, and are associated with ever-higher global familial diversity levels, but it is difficult to fit logistic curves to any of the associations.

The diversification of insects (Fig. 2.4.1.3d) was also apparently exponential, especially in the Mesozoic portion of the curve (Labandeira and Sepkoski 1993). This suggests that insects have had a long and continuous pattern of expansion, perhaps slowing somewhat during the Tertiary. This may indicate that insect diversity is approaching an equilibrium level now.

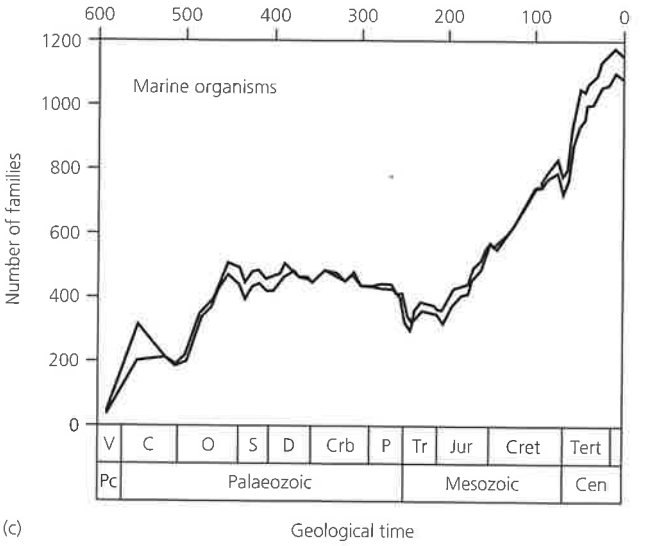
Recent plots of the diversification of families of marine, continental, and 'all' life (Fig. 2.4.1.4) founded on a new database (Benton 1993) confirm these varying models for diversification. The continental curve (Fig. 2.4.1.4b), dominated by tetrapods, insects, and land plants, is exponential. The marine curve (Fig. 2.4.1.4c) retains a Palaeozoic plateau level, and appears to show a slowing-down in diversification towards the Recent, which may indicate that marine diversity levels today are approaching an equilibrium level. The curve combining all marine and continental families (Fig. 2.4.1.4a) could be interpreted as a single poorly fitting exponential curve (Hewzulla *et al.* 1999), but the Palaeozoic plateau, reflecting the contribution of marine invertebrates (compare Fig. 2.4.1.4c), cannot be explained readily. The pattern could be explained equally well by a series of logistic curves, although the post-Palaeozoic portion is harder to fit than the Palaeozoic.



(a)



(b)



(c)

There may be fundamental differences between marine and continental life. Rates of taxonomic turnover in marine invertebrates declined through the Phanerozoic after the initial rapid Cambrian radiation, while vascular land plants show increasing rates of turnover through time (Valentine *et al.* 1991). Terrestrial vertebrates show intermediate patterns. The suggested explanation is that adaptive space was filled early on in the sea, while land plants (and possibly vertebrates) have continued, and may still continue, to conquer new ecospace. The persistence of opportunities for expansion on land may reflect the later onset of diversification here than in the sea, and the fact that new groups of plants invaded unstable habitats and modified them.

Explanations for patterns of diversification

Logistic and exponential models for the diversification of life could be compared directly. However, there is a slight ambiguity in attempting this since the initial phase of a logistic curve is essentially exponential. The key distinction is between equilibrium and non-equilibrium (or expansion) models. The former imply the existence of global equilibria in diversity, while expansion models assume that there is no ceiling to the diversity of life, or at least that such a ceiling has yet to be reached.

Equilibrium models

Equilibrium models for the expansion of the diversity of life were based on an influential body of ecological theory. Logistic modelling of global-scale data on diversification assumes: (1) interactions among species within clades; (2) interactions between clades; and (3) global equilibrium levels. Many studies show that clades may radiate initially at exponential rates, but that the rate of diversification slows at a certain point as a result of diversity-dependent phenomena, such as competitive exclusion, increased species packing, and reduction of species ranges (Sepkoski 1984, 1996). This style of reasoning follows explicitly from classical experiments in competition where the increase of one population suppresses another that depends on the same limiting resource. An initial exponential increase of the successful population is followed by a plateau when the species begins to deplete the limiting resource (usually food); this corresponds to the local carrying capacity.

The pattern of diversification of marine families (Fig. 2.4.1.3a) has been interpreted (Sepkoski 1984, 1996) in terms of a three-phase logistic model which represents the behaviour of the three evolutionary faunas: Cambrian, Palaeozoic, and Modern. The replacing 'faunas' are said to have been characterized by the ability to penetrate ever-wider sets of niches, and hence to achieve

higher diversities. There is some evidence in favour of this idea; for example, later marine animals could burrow deeper, form more complex reefs, and capture prey in ever more ingenious ways. The equilibrium models could be interpreted simply in terms of large-scale competition between major clades, with bivalves outcompeting brachiopods, mammals outcompeting dinosaurs, and so on. Despite its popular appeal, such a view has been generally rejected (Benton 1987; see Sections 2.3.3 and 2.3.4). Sepkoski (1996) attributed the patterns of waxing and waning of clades to diffuse competition between them at the species level, where species in one clade are generally competitively superior to those in another.

A key assumption of logistic modelling is that equilibrium levels exist, i.e. there are steady-state diversities at which speciation and extinction rates are balanced. In the case of global diversification patterns, limiting processes could affect both extinction and origination rates. Origination rates may be more diversity dependent (Sepkoski 1996), however, because: (1) filling of niches could limit opportunities for new species to arise and become established; (2) additional species may intensify diffuse competition and create new directed competition, causing exclusion and thus possible extinction of some species; and (3) increased species packing may cause average local population sizes to be reduced, leaving some rarer species more prone to extinction by adverse environmental challenges.

There are three areas of concern with equilibrium models:

1 There is no independent evidence for equilibria, i.e. for fixed carrying capacities, on the Earth today. In evolutionary terms, equilibrium diversities imply that all available resources are in use and all ecospace is filled. If a new species originates, it must displace a pre-existing one. However, observations of cases where previously isolated floras and faunas come into contact suggest that species are just as likely to insinuate (i.e. enter new niches) and not cause extinction of other taxa.

2 Multiple logistic models imply predictable outcomes of interactions between members of the different 'faunas', i.e. that members of one group will generally succeed where those of another will fail. Where major biotic replacements have been investigated, one group is more likely to disappear due to an extinction event (Benton 1987; see Section 2.3.4) than as a result of interactions.

3 The diversification of the Modern fauna seems more prolonged and slower than predicted by a logistic model. The rising phase of the logistic curve has lasted for 250 myr, with some evidence of a slow-down towards the present. If there is no current plateau, then it would seem that in the second half of the Phanerozoic, the

best-known part of the fossil record, the logistic rules have been forgotten.

Expansion models

The alternative to equilibrium is expansion. Are the aggregate patterns, or at least some of them (Figs 2.4.1.3 and 2.4.1.4), the result of unconstrained expansion? Certainly, some clades (such as insects, angiosperms, birds, and mammals) seem to continue radiating linearly or exponentially for many tens or hundreds of millions of years. Such ever-expanding patterns imply that these groups are highly successful and adaptable. The overall patterns of diversification (Fig. 2.4.1.4) incorporate the numerous constituent clades, some expanding, others diminishing, and yet others remaining at constant diversity at any particular time. From an expansionist viewpoint, there is no prediction of how the individual clades affect each other. New global diversity levels may be achieved by combinations of new adaptations, habitat changes, and extinction events. In the past 250 myr, the diversification of life has been dominated by the spectacular radiations of certain clades, both in the sea (decapods, gastropods, teleost fishes) and on land (insects, arachnids, angiosperms, birds, mammals). There is little evidence that these major clades have run out of steam, and nothing to indicate that they will not continue to expand into new ecospace.

Exponential increase could imply that diversification would last forever. Presumably there is a limit to the numbers of families, or other taxa, that can inhabit the Earth at any time: such a limit would be caused not least by the amount of standing room on the Ark. If a limit of living space were approached, ever-smaller organisms would presumably be favoured by selection. Equally, as has happened so many times during evolution, organisms would take unexpected measures to survive, for example, by occupying the air, burrowing into sediments and, in the case of some bacteria, living deep within the Earth's crust. With size reduction, the ultimate limit to the diversification of life might then become the availability of the chemical components of life, principally carbon.

Equilibrium or expansion?

Five observations might provide a test for distinguishing equilibrium and expansion models of the diversification of life:

- 1 There was an evolutionary explosion of marine animals during the Early Cambrian, and diversification rates slowed after this initial exponential rise. This strongly suggests a logistic/equilibrium explanation.
- 2 The radiation of life on land, and of certain major marine and continental clades, appears to have followed

an exponential pattern, and there is no sign of any slowing down in the rate of increase, nor of the occurrence of any equilibrium levels. These radiations strongly suggest patterns of unfettered expansion.

3 There were rapid rebounds after mass extinctions when local and global diversity recovered to pre-extinction levels during relatively short spans of time. This suggests that ecospace which had been vacated as a result of an extinction event could refill faster than new ecospace. Such rapid rebounds may suggest a logistic/equilibrium model of diversification (Sepkoski 1996). Arguably, they could also be understood in a world of unfettered expansion, especially since most rebounds (mid-Cambrian, post-Ordovician, post-Permian, post-Triassic, post-Cretaceous) were associated with overall rises in global diversity to levels higher than prior to the extinction.

4 Late phases of diversification are associated with an increase in competition, evidenced by declining rates of origination and increasing rates of extinction. This corresponds to the slowing down of diversification rates as the logistic curve approaches the equilibrium level. The marine record generally confirms such expectations, but not entirely. For marine orders, total origination rates decline as a function of diversity, but total extinction rates do not increase as expected. A similar mismatch was discovered for families of marine animals; total origination rates of the Cambrian evolutionary fauna did not show the expected decline in the Late Cambrian, nor did total extinction rates of the Palaeozoic evolutionary fauna clearly increase through the Palaeozoic. These mismatches could indicate serious weaknesses of the equilibrium interpretation, or they could be the result of additional evolutionary factors that were overlaid on a three-phase logistic model (Sepkoski 1984).

5 The Palaeozoic plateau in marine animal diversity (Fig. 2.4.1.3a) is generally taken as strong evidence for equilibrium (Sepkoski 1984, 1996). A second view, however, is that the Palaeozoic plateau is real, but was maintained below any maximum carrying capacity by perturbations, i.e. extinction events of varying magnitude. A third view is that the plateau is an artefact of analyses carried out at high taxonomic level (Benton 1997). A comparison of plots of the diversity of marine life through time, shown at ordinal, familial, generic, and specific level (Fig. 2.4.1.5) shows how the logistic pattern appears to decay into an exponential pattern. At ordinal level, there is a single plateau, lasting for over 450 myr. At familial level, the Palaeozoic plateau lasts for over 200 myr. At generic level, the Palaeozoic plateau is present, but it is relatively lower than the familial plateau, and the post-Palaeozoic diversification of genera is more exponential in appearance. For species, there is no available empirical curve; a suggested consensus plot retains indications of a two-phase Palaeozoic

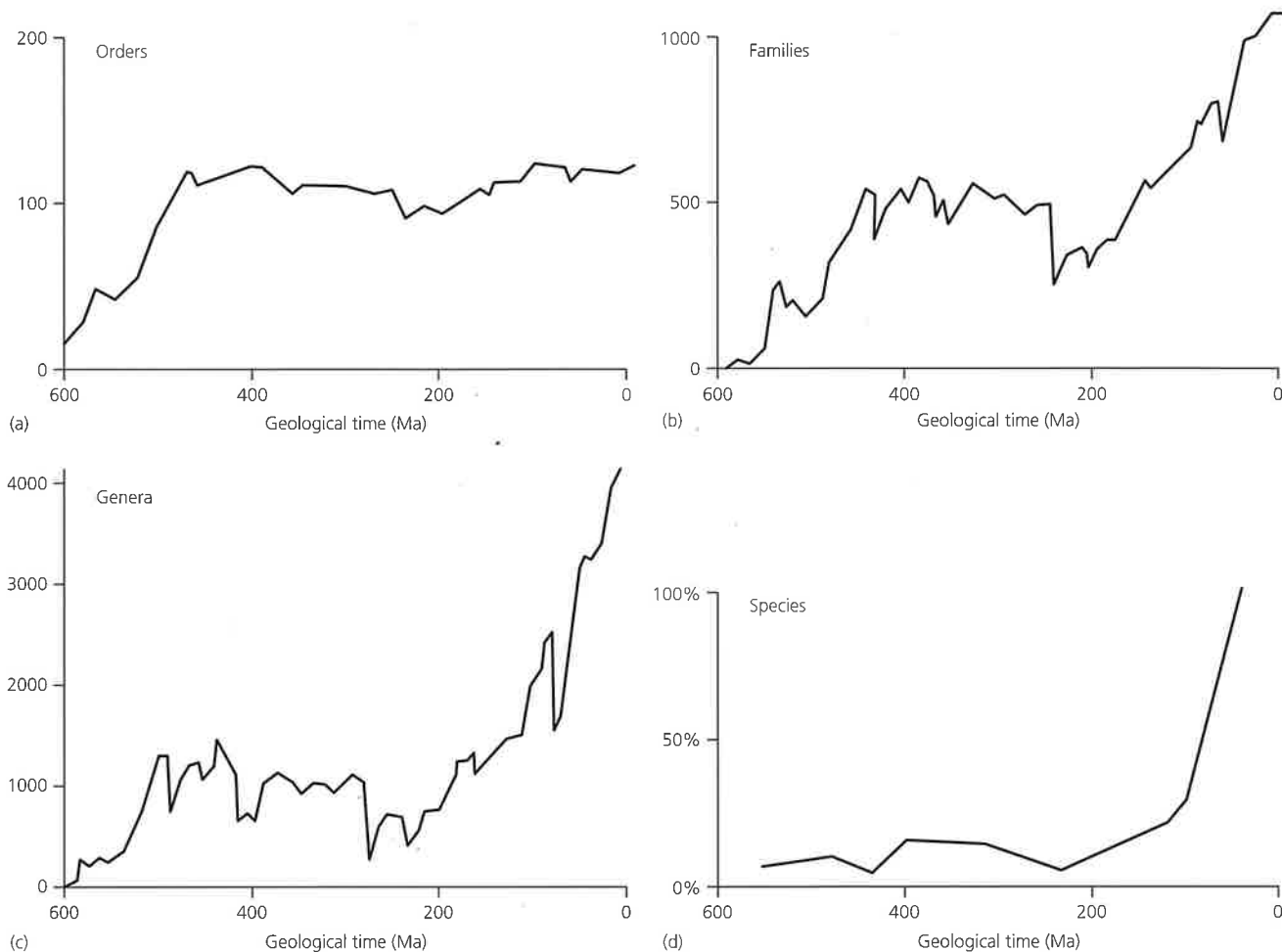


Fig. 2.4.1.5 Patterns of diversification of well-skeletonized marine animals, counted as: (a) orders; (b) families; (c) genera; and (d) species. The ordinal, familial, and generic counts are based on empirical data, while the species curve is based on

real counts and on simulations, and the curve is plotted as percentages of the modern total, set at 100%. (Based on Benton 1997.)

diversification pattern, but the pattern of diversification on the whole is exponential.

Conclusion

Charles Darwin was impressed by the seemingly endless diversity of life, and studies of biodiversity are just as important now as they were in his day. It is hard to establish the current diversity of life, and even harder to estimate past diversities and how life has diversified since its origin. There are two very different models for the diversification of life: equilibrium and expansion. The equilibrium model assumes that specific major ecological realms can accommodate only certain numbers of species, and that when the carrying capacity is reached, net diversification ceases. The expansion model makes no such assumption, and allows for continuing, if episodic, diversification with no ultimate limit in sight.

Palaeobiologists have debated, and continue to debate, which model is correct. Perhaps all of life has diversified according to either an equilibrium or an expansion model. Or perhaps different sectors of life diversified in different ways. Evolution in the sea may have resulted in a greater level of stability, and patterns of increase may have generally been logistic, while life on land may have diversified exponentially since the first plants and arthropods crept cautiously out of the water. The implications of the equilibrium and expansion models are profoundly different, not merely for palaeobiologists, but for everyone concerned about the present and future state of global biodiversity.

References

- Benton, M.J. (1985) Mass extinction among non-marine tetrapods. *Nature* 316, 811–814.

- Benton, M.J. (1987) Progress and competition in macroevolution. *Biological Reviews* **62**, 305–338.
- Benton, M.J. (1993) *The Fossil Record 2*. Chapman and Hall, London.
- Benton, M.J. (1995) Diversification and extinction in the history of life. *Science* **268**, 52–58.
- Benton, M.J. (1997) Models for the diversification of life. *Trends in Ecology and Evolution* **12**, 490–495.
- Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists' Bulletin* **36**, 74–82.
- Hewzulla, D., Boulter, M.C., Benton, M.J. and Halley, J.M. (1999) Evolutionary patterns from mass originations and mass extinctions. *Philosophical Transactions of the Royal Society of London B* **354**, 463–469.
- Labandeira, C.C. and Sepkoski, J.J. Jr (1993) Insect diversity in the fossil record. *Science* **261**, 310–315.
- May, R.M. (1990) How many species? *Philosophical Transactions of the Royal Society of London B* **330**, 292–304.
- May, R.M. (1994) Conceptual aspects of the quantification of the extent of biological diversity. *Philosophical Transactions of the Royal Society of London B* **345**, 13–20.
- Niklas, K.J., Tiffney, B.H. and Knoll, A.H. (1985) Patterns in vascular land plant diversification: a factor analysis at the species level. In: J.W. Valentine, ed. *Phanerozoic diversity patterns*, pp. 97–128. Princeton University Press, Princeton, New Jersey.
- Sepkoski, J.J. Jr (1984) A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* **7**, 36–53.
- Sepkoski, J.J. Jr (1992) Phylogenetic and ecologic patterns in the Phanerozoic history of marine biodiversity. In: N. Eldredge, ed. *Systematics, ecology, and the biodiversity crises*, pp. 77–100. Columbia University Press, New York.
- Sepkoski, J.J. Jr (1996) Competition in macroevolution: the double wedge revisited. In: D. Jablonski, D.H. Erwin and J.H. Lipps, eds. *Evolutionary paleobiology*, pp. 211–255. University of Chicago Press, Chicago.
- Valentine, J.W., Tiffney, B.H. and Sepkoski, J.J. Jr (1991) Evolutionary dynamics of plants and animals. *Palaios* **6**, 81–88.
- Wilson, E.O. (1992) *The diversity of life*. Harvard University Press, Cambridge, Massachusetts.

2.4.2 Late Ordovician Extinction

P.J. BRENCHLEY

Introduction

About 22% of all families became extinct in the Late Ordovician, which makes this one of the largest episodes of mass extinction. The extinction qualifies as a mass extinction in terms of its magnitude, its global nature, the taxonomic breadth of the extinction, the breadth of

the ecological disruption, and the short time span over which the extinction occurred.

Timing of extinction

The extinction occurred in two separate phases, one coinciding with the base of the Hirnantian Stage, and the second in the middle part of the Hirnantian (Fig. 2.4.2.1) (Brenchley *et al.* 1995). The base of the Hirnantian approximates closely to the base of the *Normalograptus*

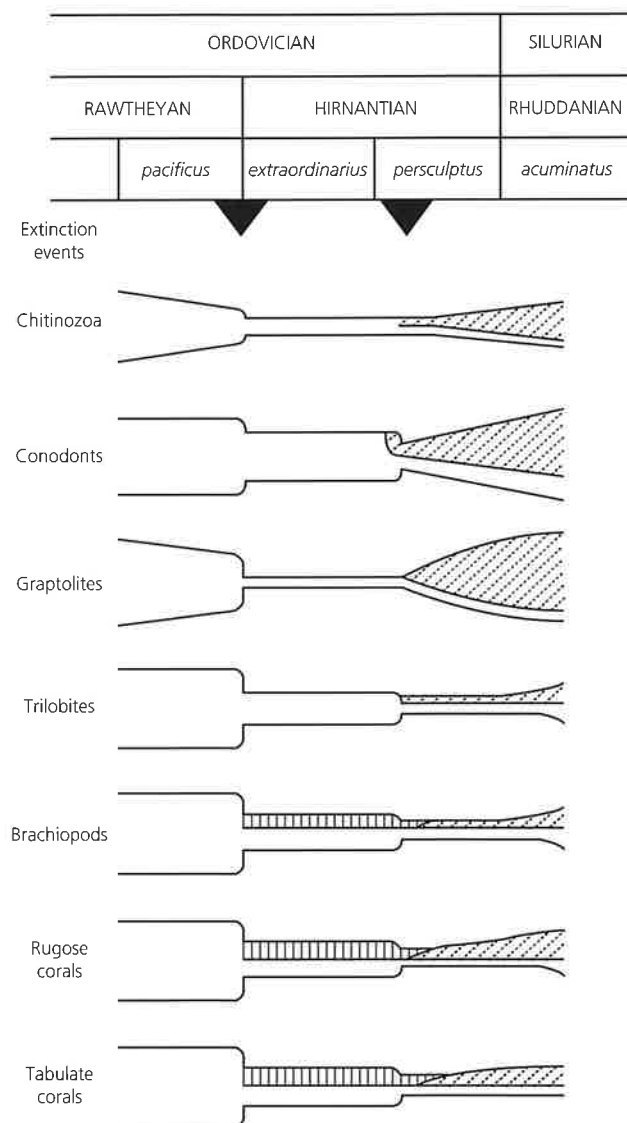


Fig. 2.4.2.1 Schematic representation of the estimated changes in diversity across the two phases of the Late Ordovician mass extinction. Biotas of pre-extinction origin are unshaded; biotas diversifying in the Hirnantian, but mainly confined to that stage, are shown with vertical shading; early representatives of the new faunas typical of the Early Silurian radiation are shown with stippled ornament.