

Diversification and Extinction in the History of Life

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Analysis of the fossil record of microbes, algae, fungi, protists, plants, and animals shows that the diversity of both marine and continental life increased exponentially since the end of the Precambrian. This diversification was interrupted by mass extinctions, the largest of which occurred in the Early Cambrian, Late Ordovician, Late Devonian, Late Permian, Early Triassic, Late Triassic, and end-Cretaceous. Most of these extinctions were experienced by both marine and continental organisms. As for the periodicity of mass extinctions, no support was found: Seven mass extinction peaks in the last 250 million years are spaced 20 to 60 million years apart.

All organisms are related to each other and share a single common ancestor. That single ancestor arose during Precambrian times, perhaps 3500 million years ago (Ma) (1). The present-day diversity of some 5 million to 50 million species (2) has clearly been reached by a process of massive diversification. The outlines of the diversification of life are well known in narrative form, but in this article I present a quantitative documentation of the pattern of diversification and extinction for the history of all life, in the sea and on land.

The documentation of the early history of single-celled organisms (microbes, algae, and protists) during the Precambrian (4560 to 570 Ma) is probably too poor to give meaningful continuous information, although current and future work may rectify some of the gaps in information. The fossil record suggests that multicellular life, primarily plants and animals, diversified slowly during the Precambrian, but then ever more rapidly during the past 600 My, the Vendian and Phanerozoic. Multicellular life in the sea (3), land plants (4), and vertebrates (5) showed modest rates of diversification during the Paleozoic (570 to 250 Ma) and then exponential rates through most of the Mesozoic and the Cenozoic, the past 250 million years (My).

The diversification of life was not, apparently, a stochastic process. Substantial bursts of multiplication of major taxonomic groups coincided with their invasion of new habitats, which was often associated with the acquisition of new adaptations (6). The taxonomic groups in such cases are generally clades, that is, groups that have a single common ancestor and that include all descendants of that ancestor. Clade addition, related to the exploitation of new habitats, boosted the overall diversity of life because the new clades generally did not replace preexisting clades. The older modes of life, and many of the older clades, persist to the

present day, and there is no evidence in the fossil record of a limit to the ultimate diversity of life on Earth.

Examples of major clade additions which boosted the overall diversity of life include, in the sea, skeletonized invertebrates such as archaeocyathans, inarticulate brachiopods, and trilobites in the Cambrian; corals, articulate brachiopods, cephalopods, ostracods, crinoids, starfish, and graptolites in the remainder of the Paleozoic; and bivalves, gastropods, malacostracans, echinoids, bony fishes, and marine reptiles in the Mesozoic (3). On land, diversity increased as a result of the evolution of vascularized plants in the Silurian and Devonian, gymnosperms in the Carboniferous, and angiosperms in the Cretaceous (4). Arthropods also contributed to the bursts of diversification, with the first limbed land animals in the Early Paleozoic, insects in the Late Paleozoic, and social insects in the Cretaceous and Tertiary. Among terrestrial vertebrates, major clade additions were often associated with the exploitation of new adaptive zones: the amphibians in the Devonian, the reptiles in the Carboniferous, the pterosaurs and dinosaurs in the Triassic and Jurassic, the birds in the Jurassic, and the mammals in the early Tertiary (5).

Quality of the Fossil Record

There has been considerable debate over the past 25 years about the ability of the fossil record to document the pattern of the history of life. One view (3–5) has been that the patterns recorded from the fossil record may be interpreted directly and without correction. The other view (7) has been that the apparent delay in diversification during the first half of the Phanerozoic is merely an artifact of poor fossil sampling: Fossils were less likely to have survived in ancient rocks than in more modern rocks, and paleontologists are less active in collecting from older rocks.

Tests of preservation and collecting biases (8) showed that the corrected data sets

did not deny the empirical model of Valentine (3). A comparison of results from independent databases (9) confirmed that most of the empirical pattern found from a literal reading of fossil record data was real. These studies demonstrated that geological factors did not fatally damage the evolutionary signal to be read in the fossil record. However, more recent criticisms have focused on aspects of the systematics of the taxa used in the databases.

Systematics and Taxon Counting

It has been argued (10) that taxon-based studies of macroevolutionary patterns are inevitably flawed because of the impossibility of determining (i) that each family or genus is monophyletic and not paraphyletic (that is, the evolutionary source of another taxon), and (ii) that all the taxa under study are equivalent. As yet, the only diagnosable aspect of a taxon may be its origin, which is marked by the acquisition of one or more unique derived characters (synapomorphies). The termination of a taxon is often harder to identify, unless the disappearance was geologically instantaneous. The difficulty arises from the possibility that another taxon evolved from the first, which would render the latter paraphyletic, and the drawing of a line between the two arbitrary.

Another problem is that there is no agreed way of testing the equivalence of taxa: In other words, how can a biologist or paleontologist determine whether a species of ape (for example, *Homo sapiens*) is comparable in evolutionary terms with a species of monkey, or a species of fungus or worm? Is a family of rodents equivalent to a family of flowering plants or a family of dinosaurs? The measure of equivalence among taxa to be assigned the same categorical rank could reside in the time since their origin (11), in the size of the geographic area occupied, in the amount of genetic differentiation, or in some measure of morphometric distinction from other postulated taxa of identical rank (12). At present, the solution is semantic and authoritarian: Families and genera of different taxa are so defined because of the ways in which experts on those groups choose to make taxonomic decisions.

These kinds of problems are true of all uses of systematic data for studies of diversity, whether ancient or modern. It may not be possible to resolve each difficulty in isolation, but one could argue that the individual problems are not fatal to macroevolutionary analyses. The use of data on taxic

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durations from the fossil record could be justified on the basis that (i) statistically systematic biases do not account for all of the empirical pattern (8), (ii) independent databases give comparable results (9), (iii) clade order corresponds to stratigraphic order (13, 14), (iv) substantial revisions to existing databases have not caused dramatic changes to the macroevolutionary patterns detected (14–16), and (v) simulations suggest that fossil higher taxa may reflect patterns of species evolution despite arbitrary definitions, highly variable sizes, incomplete preservation, and paraphyly (17).

Databases

Most recent accounts of the diversification and extinction of marine life (3, 18, 19) have been founded on databases developed by Sepkoski (20). Attention has focused on the fossil record of marine invertebrates, although the Sepkoski databases include marine vertebrates (fishes, reptiles, and mammals). Diversification and mass extinction of land plants (4, 21), of continental vertebrates (5, 22), and of insects (23) have also been studied, but there has been an implicit, if unproven, assumption that the marine fossil record is broadly better than the continental fossil record. Other available data bases (24) have been less often used.

In this article I use a new database, *The Fossil Record 2* (25), which includes all groups of microbes, algae, fungi, protists, plants, and animals that have a fossil record, whether marine or nonmarine, to test broad-scale patterns of diversification and extinction. This record (25, 26) was compiled by 90 contributors who are experts on their own groups. It contains the latest published and unpublished information on the stratigraphic distribution of the 7186 families of marine and continental organisms that have fossil representatives. The data are determined stratigraphically largely to the level of the stage (mean duration of the 77 time units used for the Phanerozoic is 7.4 My). Epochs were used as the time division for analysis for the Ordovician, Silurian, Carboniferous, and Neogene because the stages in these periods are generally much shorter in duration (2.8 My) than the mean length of stages in other periods, and problems of global correlation are severe for the short Paleozoic stages. Taxonomically, the selected level for data recording was the family. Use of the stage (or epoch) and the family divisions were compromises between the need to present data to as refined a level as possible, and the need to ensure some conformity among groups for which precise stratigraphic and taxonomic divisions could be made and those for which they could not. In all analyses, minimum and maximum measures are

given, based on assessments of uncertainty about dates of origin and extinction of families and the broad-scale environmental attributions of those families (27).

The Fossil Record 2 (25) contains 7186 families or family-equivalent taxa [the 1967 version (24) contained 2924]. To some extent, families were assessed for monophyly, but this was only possible for certain groups of angiosperms, sponges, gastropods, arthropods, echinoderms, and vertebrates, where cladistic revisions were available. The ideal would be, of course, a complete listing of monophyletic families for all groups (10), but that is not yet possible.

A database on the marine fossil record to the stratigraphic level of substage and the taxonomic level of genus is under development (3, 16, 19). Genera give a closer view of species-level behavior through time, but the shift of focus to a lower taxonomic level brings with it the likelihood that the record is less complete than one at a higher taxonomic level because of the vagaries of preservation, collection, and study. Hence, data bases, whether at the family or the generic level, and in the future perhaps even at the specific level, offer complementary tests of each other.

Diversification

The diversity of all organisms (Fig. 1A) increased rapidly during the Vendian and Early Cambrian to a global diversity of 280 families, then fell to 120 families in the Late Cambrian, and increased during the Ordovician to about 450. Diversity (Fig. 1A, minimum values, lower curve) rose gradually from 450 to 600 families during the Paleozoic, fell to 420 families at the beginning of the Triassic, then rose rapidly to 1260 families at the end of the Cretaceous and 2150 families in the Pleistocene and Holocene. The difference between maximum (upper curve) and minimum (lower curve) estimates of diversity increases through the Carboniferous and Permian. Maximum diversity was 650 families in the Late Permian, 1350 families in the Late Cretaceous, and 2400 families in the Pleistocene and Holocene. The variations between maximum and minimum values reflect a variety of taxonomic and stratigraphic factors (28).

Diversity inferred for continental organisms (Fig. 1B) increases dramatically from the Silurian to the present day, although the uncertainty, reflected in the divergence between minimum and maximum values, is high. This increase documents essentially the dramatic radiations of land plants, insects, and vertebrates recorded earlier in independent studies of these groups (4, 5, 21–23).

Marine organisms (Fig. 1C) show a more

complex pattern, akin to that identified before on the basis of an independent data set (3, 16, 18). The estimate of minimum diversity (lower curve) is remarkably similar to that obtained by Sepkoski (16). A peak in diversity in the Vendian to Early Cambrian and in the Paleozoic plateau and the Mesozoic-Cenozoic increase in diversity to over 1100 families are indicated in both analyses. The present study shows smaller drops in diversity during the Paleozoic, but this results from a rapid diversification after extinctions;

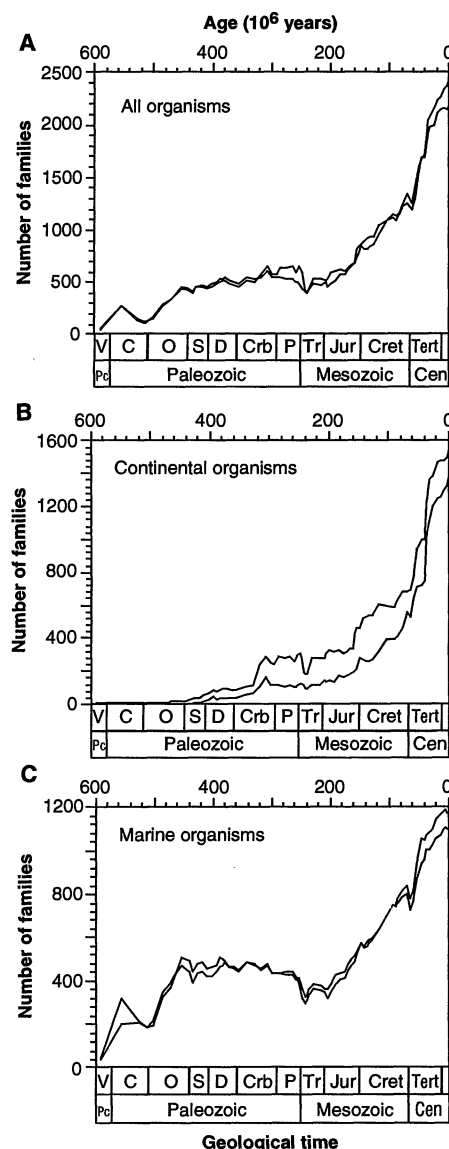


Fig. 1. Patterns of the diversification of life through time plotted for all organisms (A), continental organisms (B), and marine organisms (C) in terms of changes in the numbers of families extant per stratigraphic stage. In each graph, a maximum and minimum curve is shown, based on a combination of stratigraphic and habitat-preference information (27). Abbreviations: C, Cambrian; Cen, Cenozoic; Crb, Carboniferous; Cret, Cretaceous; D, Devonian; Jur, Jurassic; O, Ordovician; P, Permian; Pc, Precambrian; S, Silurian; Tert, Tertiary; Tr, Triassic; and V, Vendian.

in other words, much of the diversity loss is masked by subsequent diversification. The maximum estimate of marine diversity (Fig. 1C, upper curve) is consistent with this pattern, but the uncertainty (divergence from the minimum diversity) is greatest in the Vendian to Early Cambrian, as a result of uncertain range data on Problematica and basal brachiopods and arthropods. The difference of about 100 families between minimum and maximum measures of diversity during the Tertiary is an artifact of the exclusion from the minimum estimates of taxa that certainly, or possibly, occupied both marine and continental realms.

In all three cases (Fig. 1), the increase in diversity from Vendian to Recent is exponential, as indicated by plots of $\log(\text{diversity})$ versus geological time which approximate closely in all cases (Fig. 2) to straight lines. The best fits are for the minimum and maximum estimates of continental diversity (Fig. 2B), perhaps because the initial diversities of nonmarine organisms remain low until the end of the Jurassic. Marine organisms (Fig. 2C) show a more complex pattern of diversification, with apparent initial rapid rises in diversity in the Cambrian and Ordovician, overlain by a strongly exponential pattern of increase in diversity during the Mesozoic and Cenozoic. If diversity increases have been exponential through the Vendian and Phanerozoic, then there is no need to assume equilibrium levels of global diversity, nor to apply logistic models to the investigation of past diversification patterns.

Originations

The numbers of new families that appeared through geological time varied greatly. High measures of origination (Fig. 3) indicate bursts of diversification into new habitats, and many of the high frequencies follow after mass extinction events, when empty ecospace was filled. Maximum (upper curve) and minimum (lower curve) estimates of origination intensity are given, which depend on the certainty of the age assignments of first appearances of families. Most Paleozoic originations (Fig. 3A) were marine, whereas later taxa originated at almost equal frequencies in the marine and continental realms. The record implies that more new terrestrial families (Fig. 3B) arose during the Priabonian (late Eocene) than at any other time. This pattern represents the huge input of first records of extant insect families on the basis of specimens found in the Baltic amber. This peak is a clear example of the Lagerstätten effect, a burst of apparent origination produced by a single exceptional fossil deposit, and the origins should probably smear backwards in time (23). The high peak for marine organisms (Fig. 3C) during the early Cambrian corresponds to the origin

of many families of archaeocyathans, trilobites, brachiopods, and Problematica. Peaks of elevated origination frequencies in the Early Carboniferous, Early Triassic, and Paleocene indicate recovery phases after the preceding mass extinctions.

Extinctions

Major extinctions (Fig. 4A) occurred in the Early Cambrian (Caerfai), Late Ordovician (Caradocian, Ashgillian), Middle and Late Devonian (Givetian, Frasnian, Famennian), Late Carboniferous (Moscovian,

Gzelian), Late Permian (Tatarian), end-Triassic (Rhaetian), end-Jurassic (Tithonian), mid-Cretaceous (Albian), end-Cretaceous (Campanian, Maastrichtian), and late Eocene (Priabonian). During four of these events (in the Late Ordovician, Late Devonian, Late Permian, and end-Cretaceous), the data show elevated extinction measures in two or three stages. In all four of these cases, the second of the two stages shows the higher extinction metric. These findings could be taken to provide evidence for prolonged extinction events, but they more likely represent evidence for the Signor-Lipps effect, that is, the backward smearing of extinction peaks because of inadequate sampling up to an extinction boundary (16, 29).

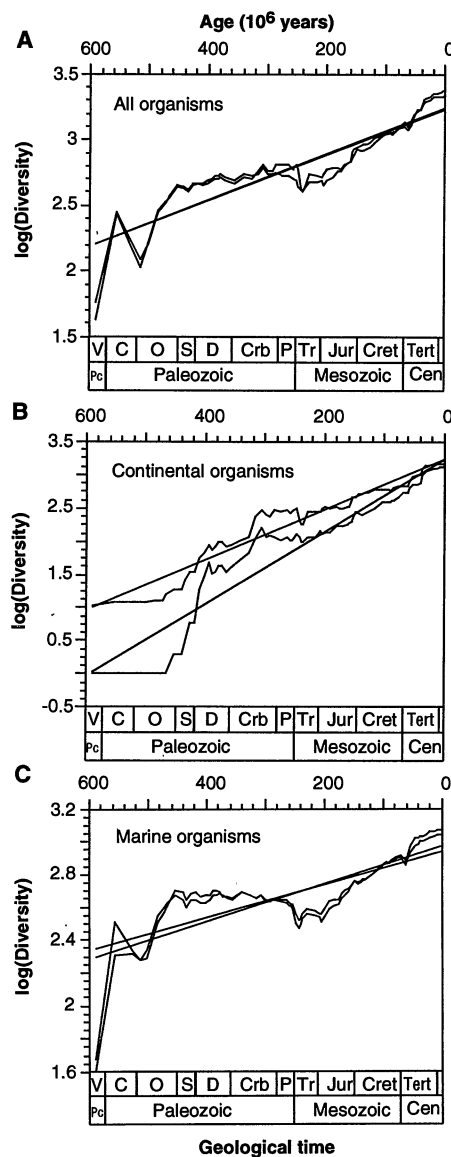


Fig. 2. Patterns of the diversification of life through time plotted as a logarithm of diversity for all organisms (A), continental organisms (B), and marine organisms (C). Diversity increases are exponential in all cases for both minimum and maximum curves because these plots of $\log(\text{diversity})$ versus geological time give straight lines. Maximum and minimum curves are shown, and abbreviations are as in Fig. 1.

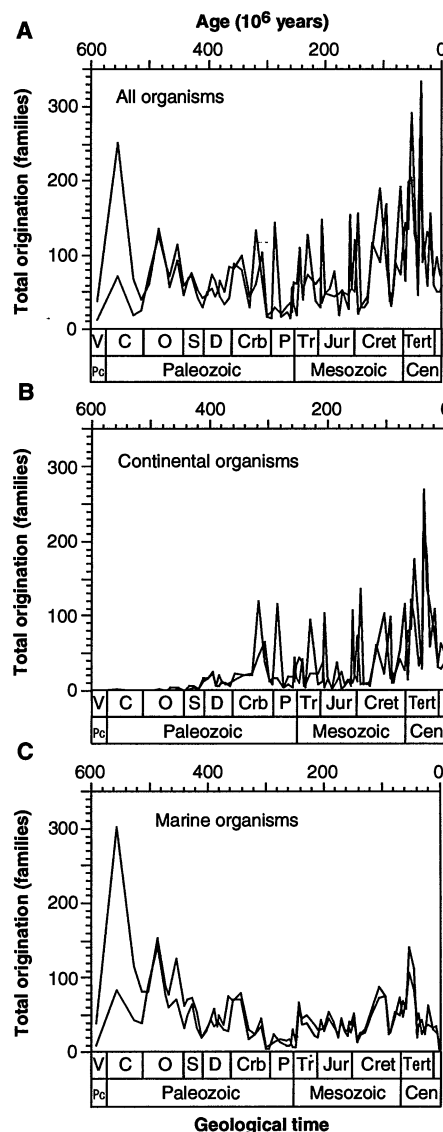


Fig. 3. Patterns of family originations through time plotted for all organisms (A), continental organisms (B), and marine organisms (C) in terms of the numbers of families that originated in each stratigraphic stage. Maximum and minimum curves are shown, and abbreviations are as in Fig. 1.

The same extinction peaks are found for the continental and marine data (Fig. 4, B and C), indicating that the major extinctions affected organisms on land and in the sea at the same time. The Late Carboniferous, end-Jurassic, and Albian (Early Cretaceous) events are more clearly indicated for the continental data than for the marine, and much of the height of each peak consists of taxa excluded from the minimum data set. These peaks probably represent horizons of good preservation, such as the well-known faunas and floras from the Late Carboniferous localities of Mazon Creek, United States, and Montceau-les-Mines, France; the latest Jurassic Solnhofen beds, Germany; and Albian plant and insect beds

in North America. Exceptional fossil deposits followed by poorer parts of the fossil record may produce apparent extinction events. In addition, the imprecise dating of extinctions of many insect families as simply "Early Cretaceous" leads to the artifact of a build-up of such extinctions in the Albian in the maximum estimate. The end-Cretaceous event is more clearly marked for marine groups than for continental, perhaps because most continental plants and animals, except the dinosaurs and pterosaurs, were little affected.

In the Paleozoic (Fig. 4C) the Late Ordovician (Ashgillian), Late Devonian (Frasnian), and end-Permian (Tatarian) events are shared with Sepkoski's analyses

(3, 16, 18, 19). My analysis also confirms smaller peaks located by Sepkoski in the Early Cambrian (Botomian), Late Cambrian (Dresbachian, Trempealeauan), Middle Ordovician (Llanvirnian), Late Silurian (Ludlovian-Pridolian), and mid-Carboniferous (Serpukhovian), but these do not clearly stand out (Fig. 4C).

Magnitude of Mass Extinctions

The magnitudes of extinctions were measured in various standard ways (18, 19), and the results may be compared in Figs. 4 through 7. The magnitudes of individual events are highlighted in different ways depending on the metric used. There is no

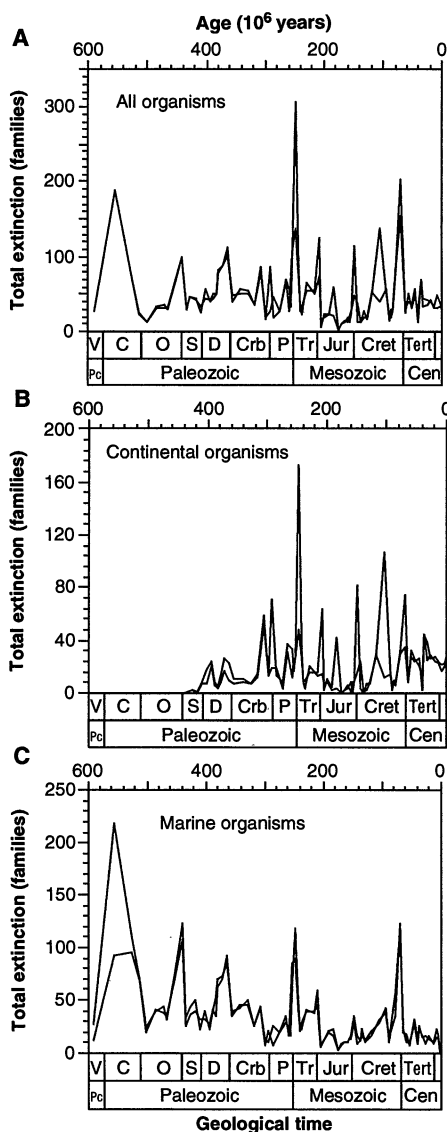


Fig. 4. Patterns of family extinctions through time plotted for all organisms (A), continental organisms (B), and marine organisms (C) in terms of the numbers of families that died out in each stratigraphic stage. Maximum and minimum curves are shown, and abbreviations are as in Fig. 1.

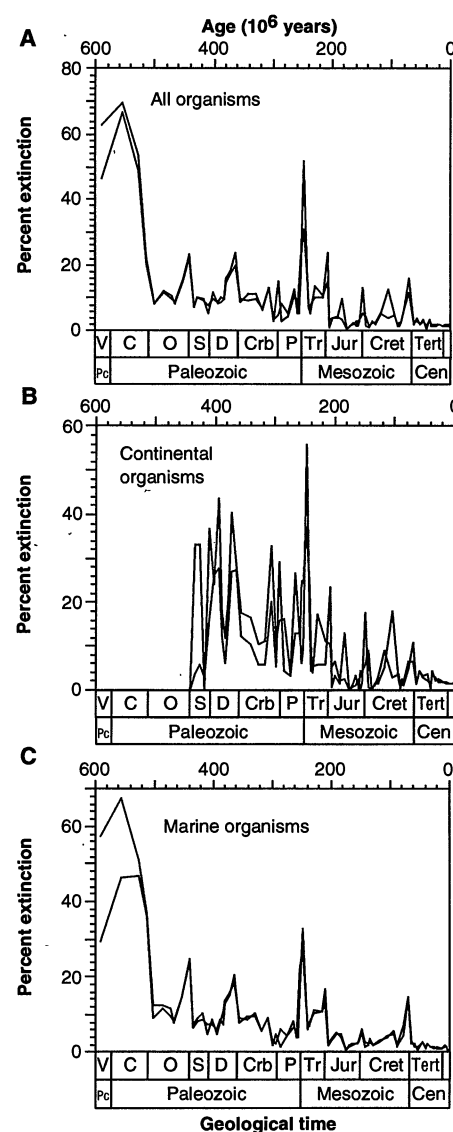


Fig. 5. Patterns of family extinctions through time plotted for all organisms (A), continental organisms (B), and marine organisms (C) in terms of the percent of families that died out in relation to the contemporaneous diversity in each stratigraphic stage. Maximum and minimum curves are shown, and abbreviations are as in Fig. 1.

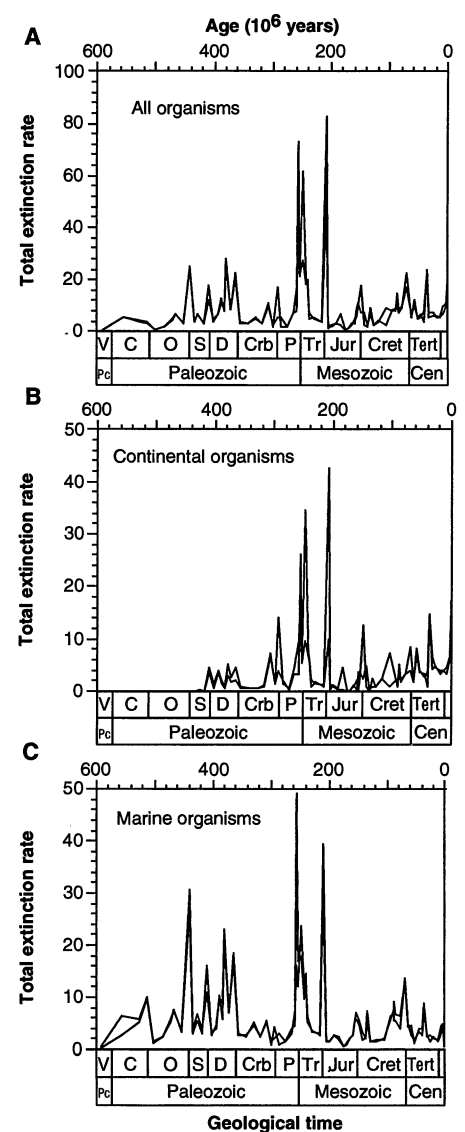


Fig. 6. Patterns of family extinctions through time plotted for all organisms (A), continental organisms (B), and marine organisms (C) in terms of the total extinction rate, that is, the numbers of families that died out in relation to the duration of each stratigraphic stage. Maximum and minimum curves are shown, and abbreviations are as in Fig. 1.

ideal way to measure the importance of extinctions (30). Simple counts of numbers of extinctions (Fig. 4) ignore the effects of varying lengths of time units and varying numbers of taxa. Percent extinction measures (Fig. 5) involve potential errors of estimation of the numbers of extinctions and total diversity. Total (Fig. 6) and per-family (Fig. 7) extinction rates add uncertainties in the estimation of geological time to the equation.

Extinction rates measured relative to the number of families in existence (percent extinction) give unusually high rates when diversities are low: The high percent

extinction rate in the Early Cambrian peak (compare Figs. 4 and 5) results from the relatively low standing diversity at that time, and it is not clear whether this represents a real extinction event. The magnitude of extinctions diminishes proportionately toward the Recent because of increasing familial diversity through time. Percent extinctions for continental organisms in the mid-Paleozoic (Fig. 5B) vary widely because of low familial diversities.

In measures of total extinction intensity [the number of extinctions relative to the stage duration (31)], the Early Cambrian extinction is diminished (Figs. 4A and 6A), as are those at the end of the Jurassic (Tithonian), in the mid-Cretaceous (Cenomanian), and at the end of the Cretaceous (Maastrichtian). The end-Triassic (Rhae-

tian) extinction is much enhanced and is indeed higher than the end-Permian as a result of the short temporal duration of the Rhaetian (1 to 2 My). The Late Devonian and end-Permian events split into two peaks. In terms of total extinction, the end-Triassic extinction is enhanced relative to the end-Permian extinction for continental taxa (compare Figs. 4B and 6B), but otherwise the identity of extinctions based on total counts and on total rates is similar. For marine extinctions (Fig. 6C), total extinction intensities in the Early Cambrian and end-Cretaceous are lower than the total counts (Fig. 4C), but the end-Triassic total extinction rate is higher because of the short estimated time span of the Rhaetian.

The per-family extinction rate (total extinction rate divided by taxic diversity)

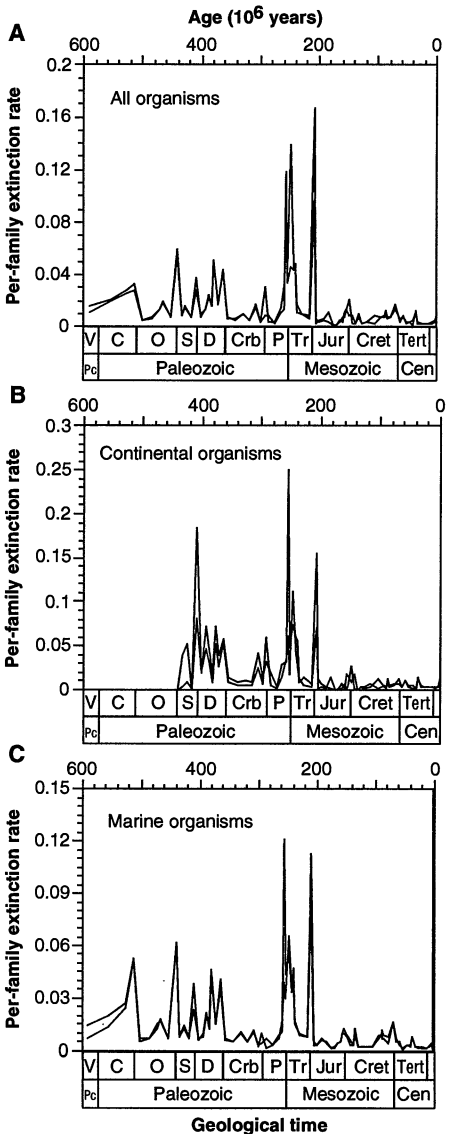


Fig. 7. Patterns of family extinctions through time plotted for all organisms (A), continental organisms (B), and marine organisms (C) in terms of the per-family extinction rate (or probability of extinction), that is, the numbers of families that died out in relation to the duration of each stratigraphic stage and in relation to the contemporaneous diversity. Maximum and minimum curves are shown, and abbreviations are as in Fig. 1.

Table 1. Magnitudes of mass extinctions, indicated as the percent drops in diversity, for different subsets of the data. Minimum figures are based on unequivocal stratigraphic and habitat data (26, 27), whereas maximum figures include less certain assignments. The Late Cambrian values combine data from several extinction events during this interval. The (*) indicates uncertain values that are based on small numbers of families (<100); N, not given.

Stage	Percent extinction					
	All	Continental	Marine	Sepkoski 1982	Raup and Sepkoski 1982	Sepkoski and Raup 1986
<i>Tertiary</i>						
Late Miocene	1.4–2.2	1.3–1.5	1.4–1.9	N	N	1.3
Priabonian	3.5–3.6	2.4–4.3	2.3–2.4	N	N	2.0
Lutetian	2.8–3.4	2.1–3.6	2.9	N	N	<2.2
<i>Late Cretaceous</i>						
Maastrichtian	11.5–16.2	6.3–10.9	14.7–14.8	15	11	13.9
Cenomanian	4.8–5.0	2.2–3.5	4.9–5.6	N	N	6.1
<i>Early Cretaceous</i>						
Albian	3.7–12.6	3.0–17.9	4.0–4.5	N	N	3.4
Hauterivian	2.4–2.9	1.1–1.3	2.8–3.7	N	N	2.7
<i>Late Jurassic</i>						
Tithonian	5.6–13.3	5.8–17.6	5.1–6.1	N	N	6.5
<i>Early Jurassic</i>						
Toarcian	3.6–9.5	2.4–12.8	3.9–5.0	N	N	2.1
Pliensbachian	3.7–4.4	1.6–2.2	4.9–5.2	N	N	5.1
<i>Late Triassic</i>						
Rhaetian	15.2–23.9	10.6–23.4	12.7–16.9	N	N	12.2
Norian-Rhaetian	25.8–34.4	21.7–29.2	23.4–27.6	20	12	23.8
Carnian	10.4–13.5	5.8–17.2	10.2–11.4	N	N	11.3
<i>Early Triassic</i>						
Scythian	17.5–18.1	16.8–23.7	13.3–14.4	N	N	15.9
<i>Late Permian</i>						
Tatarian	31.0–51.8	37.2–56.0	28.1–32.7	N	N	28.1
Kazanian-Tatarian	53.4–68.5	61.5–64.3	47.5–49.8	50	52	63.7
Ufimian	5.5–14.6	6.1–25.0	3.9–12.1	N	N	N
<i>Late Devonian</i>						
Famennian	20.0–23.7	27.4–28.6*	1.2–20.4	N	14	N
Givetian-Frasnian	31.7–34.5	43.6–61.9*	27.8–29.5	21	N	N
<i>Late Ordovician</i>						
Ashgillian	22.5–23.4	0*	24.3–24.6	22	12	N
<i>Late Cambrian</i>						
Merioneth	20.3–22.4	0*	36.4–36.9	N	N	N
<i>Early Cambrian</i>						
Caerfai	66.8–69.5	0*	46.3–67.7	N	N	N

documents the risk (probability) of extinction for any family. By taking account of the time scales involved and the numbers of taxa available to become extinct, the mag-

nitudes of the Early Cambrian extinction and those in the Mesozoic and Cenozoic are reduced (Fig. 7), but the end-Triassic event is enhanced, largely because of the short

duration of the Rhaetian stage. Estimates of per-family extinction rates for mid-Paleozoic continental organisms (Fig. 7B) are suspect because of low diversities.

The "Big Five" Mass Extinctions

The simplest measure of the effect of a mass extinction is the record of the relative decline in diversity, the percent extinction (Fig. 5), a raw statement of the killing effect, that is not dependent on the vagaries of exact age dating. Percent extinction data (Table 1) identify the "big five" mass extinctions in the Late Ordovician, Late Devonian, Late Permian, Late Triassic, and end-Cretaceous. The present figures, assuming a two-stage span, confirm earlier findings (18, 19) that the end-Permian event stands out from the others, with mean familial extinction rates of 60.9% for all life, 62.9% for continental organisms, and 48.6% for marine. These figures for family loss compare with ranges of 11.5 to 34.5%, 6.3 to 61.9%, and 14.7 to 29.5%, respectively, for the other four of the big events, where the lower value is the minimum estimate of percent extinction during the end-Cretaceous extinction and the higher value is the maximum estimate of percent extinction during the Late Devonian event (Givetian, Frasnian).

Only the marine data (Table 1) may be compared directly with previous estimates of extinction magnitudes by Sepkoski (18, 19), and all values are comparable. My estimates of percent extinction are marginally higher than Sepkoski's for the Late Ordovician, Late Devonian, Late Triassic, and end-Cretaceous events, and identical to or slightly lower than his measures for the Late Permian event.

Periodicity of Mass Extinctions

On the basis of various studies of extinction data, Raup and Sepkoski (19) proposed that mass extinctions had followed a periodic pattern over the past 250 My. They were able to identify 9 of the 10 postulated events, which occurred with a mean spacing of 26 My. The present data (Table 2) do not lend strong support to this idea, because only six, or perhaps seven, of the events are evident. These are the three big extinctions in the Late Permian (Kazanian-Tatarian), end-Triassic (Rhaetian), and end-Cretaceous (Maastrichtian), as well as three smaller events in the end-Jurassic (Tithonian), mid-Cretaceous [Aptian (?) and Cenomanian], and Late Eocene (Priabonian). These events are spaced from 20 to 60 My apart, which diverges greatly from a postulated 26- to 30-My spacing. The remaining postulated events (19), in the Pliensbachian

Table 2. Mass extinctions of the past ~250 My, assessed according to four metrics of extinction, and for different subsets of the data (all taxa, continental taxa, and marine taxa). The possibility of a mass extinction is indicated by extinction metrics that are elevated above prevailing background levels. "Background" levels represent the mean of the two stages before and after the stage in question. Only minimum values are used. Stratigraphic stages are listed in reverse order from the present day, and elevated extinction metrics are indicated as 1 if the peak rises above background, as 2 if it is twice the prevailing background measure, and as 3 if it is much higher than that. A, all taxa; C, continental taxa; M, marine taxa.

Stage	Total extinction			Percent extinction			Total extinction rate			Per-family extinction rate		
	A	C	M	A	C	M	A	C	M	A	C	M
<i>Quaternary</i>												
Pleistocene												
<i>Tertiary</i>												
Pliocene									1			
Late Miocene												
Mid-Miocene												
Early Miocene	1											
Chattian												
Rupelian												
Priabonian	2	2	1	1	1	1	3	2	2	1	1	1
Bartonian												
Lutetian	1		1	1	1	1						
Ypresian												
Thanetian	1				1		1	1			1	
Danian			1			1			1			
<i>Cretaceous</i>												
Maastrichtian	3	2	3	3	2	3	3		3	1	1	2
Campanian	2	2	2	2	2	1	1					
Santonian									1			1
Coniacian							1		1			1
Turonian							1		1			1
Cenomanian	2		2	1		1			1			1
Albian	2		1			1						
Aptian	2	2		1	2							
Barremian												
Hauterivian						1			1			1
Valanginian												
Berriasian	2	1		1								
<i>Jurassic</i>												
Tithonian	2	1	2	2	2	1	1		1		1	1
Kimmeridgian					1		1		1	1		1
Oxfordian									1		1	1
Callovian												
Bathonian												
Bajocian												
Aalenian												
Toarcian						1						
Pliensbachian			1			1						
Sinemurian					1							
Hettangian					1							
<i>Triassic</i>												
Rhaetian	3	1	3	3	2	3	3	2	3	3	3	3
Norian	2	1	2	2	2	2						1
Carnian	2	1	2	2	1	2				1		1
Ladinian									1	1	1	2
Anisian				1			2	1	2	2	2	3
Scythian	2	1	2	3	2	2	2	2	2	2	3	2
<i>Permian</i>												
Tatarian	3	2	3	3	3	3	3	2	3	2	3	3
Kazanian	2	1	3	2	2	2	2	1	2	2	1	2
Ufimian	2	1	2	1	1		2	3	3	2	2	2
Kungurian					1					1	1	1

and mid-Miocene, did not appear in the present data, nor was there evidence for a necessary Middle Jurassic event, identified tentatively by Sepkoski (19) in the Cretaceous.

A number of other extinction events are suggested by a variety of extinction metrics in the present data (Table 2). Extinction events that are suggested in five of the analyses occurred in the Late Jurassic (Kimmeridgian) and early Tertiary (Thanetian, Lutetian). Extinction events supported by more of the analyses (Table 2) occurred in the Late Permian (Ufimian), Early Triassic (Scythian), Late Triassic (Carnian), and Late Cretaceous (Campanian). Of these seven events, whether minor or major, only one, the Thanetian, is restricted to a single habitat type, nonmarine in this case. The Lutetian extinction peak could be explained as an artifact resulting from the extraordinary fish fossils of Monte Bolca, Italy, but the high extinction intensities are found in both marine and continental samples. The elevated extinction intensities in the Ufimian and Campanian could be artifacts of backward smearing from the succeeding Late Permian and end-Cretaceous mass extinctions (16, 29). These seven events have not been postulated as part of the periodic signal (19). If the hypothesis of a single periodic cause of catastrophic mass extinctions is accepted, they must be explained by other causes, or they must be shown to be spurious.

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24. The only complete overview of the history of life, *The Fossil Record* [W. B. Harland *et al.*, Eds. (Geological Society of London, London, 1967)], was not used extensively for studies of diversification and mass extinction, partly because it did not provide uniform coverage of all taxa (some groups were treated at the family level, but many were listed at the level of the order), and partly because it was perceived as out of date by the 1980s, when large-scale statistical analysis of the fossil record became commonplace.
25. M. J. Benton, Ed., *The Fossil Record 2* (Chapman and Hall, London, 1993).
26. Data in *The Fossil Record 2* are not entirely uniform in their presentation. Data were not listed to the family level for some groups of scorpions, Paleozoic crinoids, and asterozoans. Stratigraphic data are also rather coarse for some groups, including Foraminifera and pre-Tertiary insects. Certain groups, including some problematic Paleozoic arthropods, are entirely omitted. Likewise, in a small number of cases, relevant experts were not available to complete compilations, and those affected chapters were completed by the editor. These technical problems affect about 10% of *The Fossil Record 2* database, and they arose because of the usual logistical problems in completing a large compilation of data. Only future checking will demonstrate whether these problems affect the macroevolutionary conclusions, although experience suggests [see (15, 16)] that they probably will not.
27. In the analyses reported here, data were coded as far as possible according to the intentions of the authors of each chapter. Hence, definite and questioned age assignments were distinguished. 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 also includes all doubtful stratigraphic attributions of families and all equivocal and shared habitat designations. The sum of the minimum measures for continental and marine organisms is equal to the minimum measure for all taxa together, but the sums of the maximum measures 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.
28. Minimum and maximum estimates of diversity differ to a varying extent at different times. Most of the divergence between minimum and maximum diversity estimates in the continental (Fig. 1B) and marine (Fig. 1C) plots during the Cenozoic arises from the 100 or so families that certainly, or probably, occupied both marine and terrestrial realms. Such families were excluded from the minimum estimates of diversity, but they were included in the maximum estimates. Another major source of difference between both estimates arises from questionable dates of origin and extinction of families. This is particularly acute for continental records, where many insect families have stratigraphically imprecise dates of origin, and where palynological and whole-plant records of angiosperms differ substantially.
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30. Geological time scales are based on W. B. Harland *et al.*, *A Geologic Time Scale 1990* (Cambridge Univ. Press, Cambridge, 1990).
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32. I thank all contributors to *The Fossil Record 2* and M. Benton for compiling the data into a computer-useable format. Also, many thanks to J. Sepkoski and an anonymous referee for their helpful comments on this article. This work was partially supported by the Leverhulme Trust, and compilation of the data was supported by the Royal Society, the Linnean Society (National Environment Research Council Taxonomic Publications Fund), and the Paleontological Association. The data are available in electronic form through the World Wide Web (<http://www.gly.bris.ac.uk/www/research/palaeo/palaeo.html>).