

Mass extinctions among tetrapods and the quality of the fossil record

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The fossil record of tetrapods is very patchy because of the problems of preservation, in terrestrial sediments in particular, and because vertebrates are rarely very abundant. However, the fossil record of tetrapods has the advantages that it is easier to establish a phylogenetic taxonomy than for many invertebrate groups, and there is the potential for more detailed ecological analyses.

The relative incompleteness of a fossil record may be assessed readily, and this can be used to test whether drops in overall diversity are related to mass extinctions or to gaps in our knowledge. Absolute incompleteness cannot be assessed directly, but a historical approach may offer clues to future improvements in our knowledge. One of the key problems facing palaeobiologists is paraphyly, the fact that many higher taxa in common use do not contain all of the descendants of the common ancestor. This may be overcome by cladistic analysis and the identification of monophyletic groups.

The diversity of tetrapods increased from the Devonian to the Permian, remained roughly constant during the Mesozoic, and then began to increase in the late Cretaceous, and continued to do so during the Tertiary. The rapid radiation of 'modern' tetrapod groups – frogs, salamanders, lizards, snakes, turtles, crocodylians, birds and mammals – was hardly affected by the celebrated end-Cretaceous extinction event.

Major mass extinctions among tetrapods took place in the early Permian, late Permian, early Triassic, late Triassic, late Cretaceous, early Oligocene and late Miocene. Many of these events appear to coincide with the major mass extinctions among marine invertebrates, but the tetrapod record is largely equivocal with regard to the theory of periodicity of mass extinctions.

1. INTRODUCTION

Most studies on mass extinctions so far have focused on the fossil record of marine invertebrates (see, for example, Raup & Sepkoski 1982, 1984, 1986; Jablonski 1986; McKinney 1986; Raup & Boyajian 1988). A smaller number of studies have used the fossil record of vascular plants (Niklas *et al.* 1983) and non-marine vertebrates (Benton 1985*a, b*), and there has been an implicit assumption that these records are poorer. Indeed, the fossil record of marine invertebrates generally has the advantages of abundant specimens, good stratigraphic control, closely spaced samples, uniform preservation quality, broad geographic distributions, and a mature taxonomy.

The aims of this paper are to consider the problems and the advantages of the fossil record of the tetrapods, to outline what has been learnt from it about mass extinctions, and to investigate the problems of incompleteness of the fossil record and paraphyly.

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2. THE NATURE OF THE FOSSIL RECORD OF TETRAPODS

(a) The evolution of tetrapods

The first tetrapods, according to most recent classifications (see, for example, Carroll 1987; Panchen & Smithson 1988) are the Ichthyostegalia (Ichthyostegidae, Acanthostegidae), known first from the Famennian Stage (*ca.* 365 Ma BP) of the late Devonian. There are earlier records of tetrapods from the Devonian, based on footprints, but skeletal remains only are considered here. The tetrapods radiated during the Carboniferous into nine or more major lineages of temnospondyl amphibians, which were generally bulky carnivores and piscivores that lived near water, and 'lepospondyl' amphibians, which were often smaller and more varied in their modes of life. Another lineage, the anthracosaurs, led to the amniotes, the clade of tetrapods that moved away from a dependence on the water.

The first amniotes, and thus the first reptiles (see, for example, Carroll 1982; Heaton & Reisz 1986) are the Protorothyrididae (= Romeriidae), known first from the Moscovian Stage (*ca.* 300 Ma BP) of the late Carboniferous. During the remaining 15 Ma or so of the Carboniferous, the early amniotes diversified into a number of additional lineages: the Araeoscelidia and the 'Pelycosauria', the most primitive groups of the Diapsida and Synapsida respectively. These two amniote clades dominated tetrapod evolution from the late Carboniferous to the present day. The Diapsida radiated during the Permian and Triassic, and gave rise to sphenodontians, the ancestors of lizards and snakes, crocodylians and dinosaurs in the Triassic, and birds in the Jurassic. The Synapsida radiated in the Permian and Triassic as the mammal-like reptiles, and gave rise to the mammals towards the end of the Triassic. The mammals remained at low diversity during most of the Mesozoic but began to radiate strongly in the late Cretaceous, well before the end-Cretaceous extinction event.

The temnospondyl amphibians continued, in reduced numbers, through the Permian, Triassic and early to middle Jurassic. The modern amphibians (Lissamphibia) apparently arose in the Permian or early Triassic, and gradually increased in diversity during the Mesozoic, but they never became abundant.

The diversity and importance of the major tetrapod groups are indicated in the phylogenetic tree in figure 1. This is based on recent cladistic analyses, although these leave many doubtful relationships, and familial diversity is indicated.

(b) Size of the data set

In all, there are 858 families of living and extinct non-marine tetrapods, and 58 families of exclusively marine tetrapods (Benton 1987, 1988), giving a total of 916 families. Of these, 352 families are still living (including 157 families of birds and 139 families of mammals) (Table 1).

The total of 916 living and extinct tetrapod families was culled in order to strengthen the data set. Eighty-one of the 916 families have no fossil record (mainly birds and mammals), and they were omitted, reducing the total to 835. A further culling was made to exclude the small number of families that have been based on a single species or genus found in one geological formation ('singletons', a total of 78 families). Indeed, some families have been based on single specimens, and they are best omitted until further finds are made. In effect, a singleton family has zero distribution in time; it arises and disappears in a geological instant, and cannot be

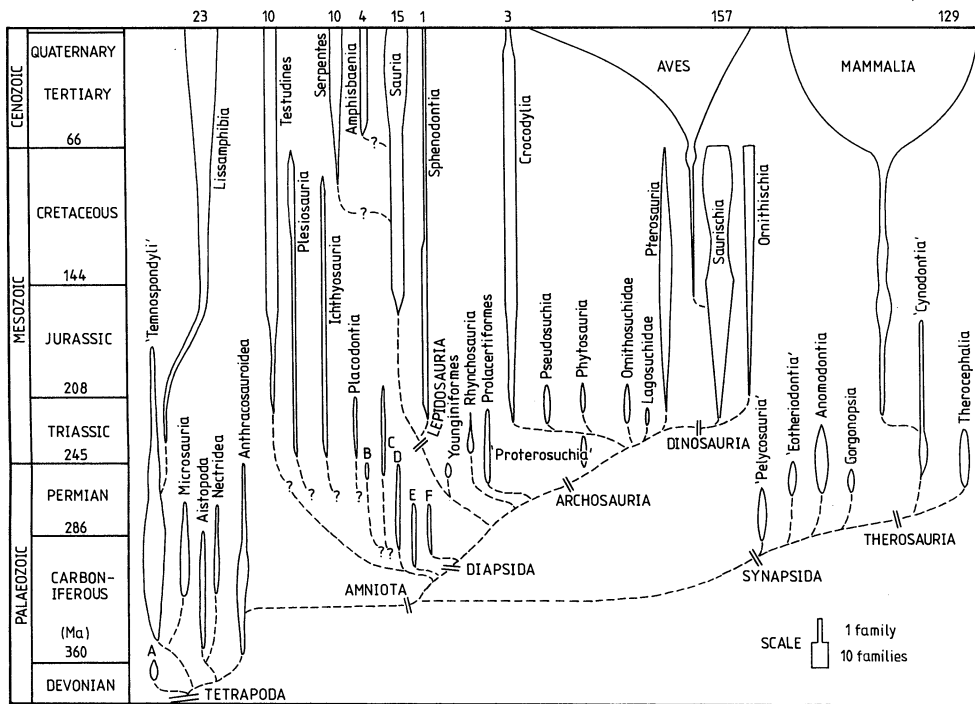


FIGURE 1. Phylogenetic tree of the Tetrapoda, showing relationships, stratigraphic duration and diversity of each group. The major groups are indicated as balloons that show the known stratigraphic range by their height, and the relative numbers of families present by their width (see scale in bottom right-hand corner). Relationships of the groups are indicated by dashed lines on the basis of recent cladistic analyses (see, for example, Benton 1985c; Gauthier 1986; Heaton & Reisz 1986; Gauthier *et al.* 1988; Kemp 1988; Panchen & Smithson 1988). Abbreviations: A, Ichthyostegalia; B, Pareiasauria; C, Procolophonia; D, Captorhinidae; E, Protorothyrididae; F, Araeoscelidia.

TABLE 1. NUMBERS OF FAMILIES OF TETRAPODS

(Based on data in Benton (1987, 1988).)

	non-marine	exclusively marine	total
Amphibia	102	0	102
Reptilia	240	33	273
Aves	202	0	202
Mammalia	314	25	339
total	858	58	916

sensibly included in calculations of origination rates or extinction rates. The final analysed total of tetrapod families was 754.

(c) *Incompleteness*

The incompleteness of the fossil record of tetrapods has been described by many authors (see, for example, Pitrat 1973; Bakker 1977; Carroll 1977; Olson 1982; Padian & Clemens 1985; Benton 1985a, b, 1987). The record of the non-marine tetrapods, which make up the vast bulk of all tetrapods, is particularly poor. Some stratigraphic stages, for example the Aalenian (middle Jurassic), have yielded no identifiable tetrapod fossils at all anywhere in the world, and other stages (e.g. Gzelian (Carboniferous); Toarcian, Bajocian, Callovian, Oxfordian

(Jurassic); Berriasian–Aptian, Cenomanian–Santonian (Cretaceous)) have yielded very few remains.

The incompleteness of the fossil record of terrestrial tetrapods has been characterised in another way by Padian & Clemens (1985, p. 82). Most dinosaur genera are known from only a single stratigraphic stage, which would suggest, in a literal reading of the fossil record, that the dinosaurs experienced total generic mass extinction 24 or 25 times during their history. However, at the family level there is only the one final Cretaceous–Tertiary (K–T) mass extinction event, as dinosaur families generally span more than one stage.

3. ASSESSING THE INCOMPLETENESS OF THE FOSSIL RECORD

Palaeontologists must seek to reduce the incompleteness of the fossil record if its value to macroevolutionary studies is to be enhanced. It is easy to say simply ‘collect more specimens’, but that gives no idea of how complete our knowledge has become. Do palaeontologists know 80% of the main fossil groups, 50%, 20%, or less than 1%? There are two aspects of the incompleteness of the fossil record, relative incompleteness and absolute incompleteness, and ways must be devised of assessing these. Only then can palaeobiologists find out how well founded their hypotheses are.

(a) *Relative incompleteness*

It is often said that, for example, birds and bats have very poor fossil records because they live in the air and in trees, where there is relatively little rock deposition. They can only be preserved out of context when a chance accident leads to the burial of a cadaver under the waters of a lake or in the sea. On the other hand, aquatic organisms, and those that live near to water, are much more likely to be preserved as fossils. Can these assumptions of relative preservability be tested quantitatively?

It is possible to estimate the relative completeness of the tetrapod record in a broad way by examining the numbers of families present per stage. The Simple Completeness Metric (scm) (Paul 1982; Benton 1987, 1988) compares the numbers of families that are known to be present with the numbers that ought to be present. The scm is based on the fact that tetrapod families span several stratigraphic stages. The family may be represented by fossils throughout its entire duration, or there may be gaps spanning one or more stratigraphic stages where fossils are absent. Jablonski (1986) has termed this the Lazarus Effect, where a taxon apparently disappears, and then reappears higher up in the sequence. The more incomplete the fossil record is for a particular stage, the more Lazarus (hidden) taxa there will be. The scm ranges from 0% (no fossils at all, e.g. Aalenian) to 100% (all families represented by fossils, e.g. Viséan, Ufimian, Scythian). Most other stages have scm values between 50 and 100%, but values fall below 50% in the early–middle Jurassic (Toarcian–Bajocian), the late Jurassic (Oxfordian), and the late Cretaceous (Turonian–Santonian).

The scm may also be calculated taxonomically, and it turns out that, among tetrapods, the birds have a 56.9% complete record at the level of the stratigraphic stage, and bats have a surprisingly high value of 75.7% (Benton 1987). The lowest values are for lissamphibians (frogs and salamanders) at 42.0%, and for lepidosaurs (lizards and snakes) at 48.6%. The highest values are for mammal-like reptiles (94.5%), placental mammals (87.0%), and for particular groups of placentals, such as the carnivores (97.1%), artiodactyls (96.6%), perissodactyls (96.2%), and rodents (88.4%).

These figures for relative completeness are calculated at rather coarse levels (families and stratigraphic stages), but they could be estimated at lower levels to make more specific comparisons. They give broad indications of where the gappiness of the fossil record is worst, and where collecting efforts should be concentrated, both stratigraphically and taxonomically. They can also be used to distinguish between episodes of low diversity that may be the result of mass extinction and those that may be the result of collection failure (see below).

(b) *Absolute incompleteness*

The assessment of the absolute incompleteness of the fossil record is much more difficult and it is probably ultimately impossible. However, one interesting approach to this problem stems from the following idea. Some day in the future, palaeontologists will have a perfect knowledge of the fossil record. In other words, our knowledge can be improved in various ways, and we should seek to identify these and to assess their relative importance.

The elements of our present incomplete knowledge may be categorized, and classified into those that may be improved, and those that lie beyond our control.

(a) Some taxa were never fossilized, and can never be known (e.g. they were soft-bodied, lived in the wrong environment, or were geographically very restricted in distribution). No improvement possible.

(b) Some taxa are unknown because of a lack of study. New localities, new collectors, and new study techniques are required. Can be improved.

(c) Some taxa have been incorrectly identified, assigned to the wrong species, to the wrong genera, or to the wrong families. Restudy of the original material, and careful consideration of the characters may resolve these problems. Can be improved.

(d) Some taxa have been incorrectly dated. Re-examination of the original specimens or localities and revisions of stratigraphic schemes may cause changes. Can be improved.

The last three categories are subject to improvement, but it would be useful to determine which is the most crucial source of error in particular cases. Patterson & Smith's (1987) study showed that 38% of Sepkoski's family records of fish and echinoderms were non-monophyletic, and 15% were incorrectly assigned stratigraphically. Thus, according to their assessment, the major problem was taxonomic (category (c)). However, they did not assess the significance of new collecting (category (b)).

The study of the fossil record of tetrapods by Maxwell & Benton (1987) used a historical analysis to attempt some predictions. The idea was that, if the nature and causes of changes in our knowledge over the past 100 years could be determined, they might provide pointers to potential improvements in the future. Over all, the total number of families had increased this century, so that new finds (category (b)) clearly played a part in improving our knowledge. However, comparisons on a shorter timescale, between Romer's (1966) standard compilation of data, and Benton's (1987) effort, showed that this was less important; both lists gave similar total numbers of families. However, in detail, there has been a great deal of change in 50–70% of family records. For particular extinction events, the changes may be categorized as 20–30% owing to new finds, 20–60% owing to taxonomic revision and 20–30% owing to new evidence on dating. The taxonomic element has been crucial.

These figures are only general indications, but they have shown two important facts. Firstly, new fossil finds are not the sole answer to improving our knowledge, and secondly, changes in our knowledge of the fossil record have not occurred in a regular or systematic way. Detailed

analyses of this sort, based on several snapshots of the state of the known fossil record at times in the past decades, may give information on where improvements have occurred and, by extrapolation, where they are likely to occur in the future. The newest idea here is that taxonomic revision may be more important than has been assumed.

4. THE PROBLEMS OF PARAPHYLY

A major problem that is emerging in many macroevolutionary studies is paraphyly. It has been suggested (see, for example, Cracraft 1981; Patterson & Smith 1987; Benton 1988) that a large number of the evolutionary groups used in analyses of evolutionary rates are artificial, either in that they include species that evolved from several different ancestors (polyphyletic groups), or that they do not include all of the descendants of a common ancestor (paraphyletic groups). Polyphyletic groups have long been abhorred by evolutionists, because they are obviously artificial assemblages of superficially similar organisms. However, paraphyly may be a more significant problem. Patterson & Smith (1987) suggested that 20% of the fish and echinoderm families used in the Raup & Sepkoski (1982, 1984, 1986) studies of diversification and extinction were paraphyletic, the largest category in their categorization of incorrect data. They implied that this, or higher figures, probably pertain for the rest of the Sepkoski data set. Similar values were found in a comparison of 'standard' data sets of tetrapod families, where 20–30% were paraphyletic in comparison with modern cladistically analysed classifications (Maxwell & Benton 1987).

It is important to establish clades, or monophyletic groups, for use in macroevolutionary studies (Cracraft 1981; Benton 1988). Such studies generally focus on supraspecific categories, often families or orders. There is no objective way, of course, to determine the rank of a clade in the taxonomic hierarchy, e.g. whether a particular group is a family or an order. However, such groups should, as far as can be determined, include all of the descendants of a single common ancestor, that is be monophyletic (*sensu* Hennig (1966); that is, holophyletic groups, *sensu* Ashlock (1971)).

A paraphyletic group, such as class Reptilia, is descended from one ancestor, but excludes some of the descendants (here, birds and mammals). The starting point of the clade is a real part of the phylogenetic tree, but the terminations of 'Reptilia' along the lines to mammals and to birds is artificial. 'Reptilia', then, is at least partly a human invention. Graphs of the evolutionary rate of reptiles might show, for example, that they enjoyed rapid rates of origination during Permian and Triassic times, but that these rates dropped off in the Jurassic and Cretaceous. This does not necessarily mean that reptiles were evolving in a sluggish manner, but simply that the new hairy reptiles and feathered reptiles have been arbitrarily excluded from the calculations.

The key to identifying monophyletic groups among Tetrapoda is cladistic analysis, in which patterns of relationship are established on the basis of shared derived characters (synapomorphies). Most tetrapod groups have now been tackled by one or more cladists, and attempts are also being made to analyse the links between these major groups. These latter efforts have generated most controversy (e.g. relationships of sarcopterygian fish and tetrapods, birds and reptiles, early mammals) and this has tended to obscure the fact that a great deal of agreement has become evident in smaller-scale cladograms of particular orders or subclasses. In addition, cladistic analyses of tetrapods have generally not affected the composition of

family-level taxa. Even before cladistic methods were widely used, vertebrate systematists defined families on the basis of clear-cut derived characters. It has been in linking the families into orders, then the orders into classes, that character definitions have lost their sharpness, leading to the establishment of artificial taxa on the basis of primitive (plesiomorphous) characters, e.g. Labyrinthodontia, Cotylosauria, Eosuchia, Thecodontia, Prototheria.

Most studies of tetrapod macroevolution have been based on families, and the new classifications have therefore not had as profound an effect as might have been expected. The main changes have arisen in drawing the lower boundaries of families; cladists would tend to exclude 'potential ancestors' from a family unless they display at least one synapomorphy of that family. This has pulled the dates of origin of some families forwards in time. The plesiomorphous taxa are then assigned plesion ranks, possibly equivalent to families. This could potentially give rise to a vast proliferation of new singleton families based on single ill-defined ancestral species. By convention, however, such families are excluded from calculations until a second occurrence is discovered (see above). For example, the family Archaeopterygidae arose and disappeared instantaneously, being represented only by the species *Archaeopteryx lithographica* from rocks of a single age, the Solnhofen Limestone Formation of southern Germany, albeit by several specimens.

The strong rejection of paraphyletic groups by Patterson & Smith (1987) was criticized by Sepkoski (1987). He argued that families are used in palaeobiological studies as convenient proxies for species, which is the level at which macroevolution truly occurs. Use of the family category avoids many of the problems of precise stratigraphic dating and correlation, local effects and gaps in the fossil record that would beset global analyses of species change through time. The Sepkoski (1982) data set of families seems to track species-level patterns of macroevolution even though it includes many paraphyletic families, whereas a culled cladistic data set does not seem to do so. Sepkoski's argument is that the cladistic data set of monophyletic families fails to detect certain mass-extinction events that are well established at the species level, whereas these are clearly indicated in the lists of non-cladistic families. His final argument is that monophyletic families may mask the effects of species-level extinctions, because their temporal shape is biased. He implies that monophyletic groups may actually be inferior to equivalent paraphyletic groups whose upper, arbitrarily established, boundary is determined by some ecological distinction, for example, that corresponds to the loss of many species. For example, one unusual or marginal lineage may prolong a family well beyond a time when all the other included species died out. This notion is testable. It may turn out to have some force, but for vertebrates at least, a rapid survey of non-cladistic and cladistic classifications suggests that the opposite is the case: monophyletic families are generally clearcut packages of species, and their evolutionary fates are closely linked. Paraphyletic families, on the other hand, have few advantages, among vertebrates at least.

5. ADVANTAGES OF USING THE FOSSIL RECORD OF TETRAPODS IN MACROEVOLUTIONARY STUDIES

The fossil record of tetrapods is not as hopeless for studies of mass extinction as has often been assumed. It has a number of advantages over the record of marine invertebrates, and these are noted briefly below.

(a) High probability of identifying clades

Rates of evolution, extinction and origination should be analysed, as noted above, on the basis of monophyletic groups. Tetrapods have proved highly amenable to cladistic analysis, in contrast to fossil invertebrate groups (with the exception of echinoderms and arthropods). This suggests that it may be hard to determine monophyletic families for the bulk of the record of fossil invertebrates. The significance of this problem has been noted above.

(b) Scope for ecological analysis

Many detailed studies of the functional morphology and palaeoecology of single species (autecology) of fossil tetrapods have been carried out, and these often allow detailed reconstructions of their modes of life. Studies have also been made of whole faunas (synecology). This work offers potentially great contributions to detailed palaeobiological interpretation of aspects of extinction events. It may be possible, for example, to compare 'extinction-prone' and 'extinction-resistant' taxa for a broad range of potential ecological correlates: size, diet, position in food chains, locomotory adaptations, reproductive mode, growth rate, habitat preference, geographic distribution and so on. Tetrapods may lend themselves more readily to detailed ecological analysis than many marine invertebrates. This work is facilitated by our knowledge of the ecology of modern terrestrial vertebrates, which is greater than that of modern marine invertebrates.

(c) Maturity of tetrapod systematics

Because *Homo sapiens* is a tetrapod, zoologists have devoted more attention to the species- and generic-level systematics of mammals, birds, reptiles and amphibians than they have to the systematics of brachiopods, annelids, pogonophorans or hyolithids. Our understanding of the relationships and the bounds of living tetrapod species is probably more mature than that of any other group of organisms. This should allow more confident extrapolation of such concepts into the past, and thus better identification of fossil genera and species, better censuses of these taxa and better phylogenetic reconstructions, thereby improving the usefulness of such data for macroevolutionary research.

6. TETRAPOD FAMILY DIVERSITY ANALYSIS

(a) The data

Several authors have recently plotted graphs of the diversity of tetrapod families and orders through time (see, for example, Charig 1973; Pitrat 1973; Bakker 1977; Thomson 1977; Olson 1982; Padian & Clemens 1985; Colbert 1986). However, these graphs have been based largely on data from Romer (1966) and Harland *et al.* (1967), the classic source works. More recent studies (Benton 1985*a, b*, 1988) have been based on a new compilation of data on families of tetrapods (Benton 1987, 1988). These new compilations differ significantly from those derived from Romer (1966) and Harland *et al.* (1967) in several ways.

(a) New records up to the end of 1986 are included. This has affected the date of origination or extinction of as many as 50% of families.

(b) The latest cladistic classifications have been incorporated, as far as possible, and attempts have been made to test that all families are clades. This has caused significant rearrangements

of families of late Palaeozoic and Mesozoic reptiles in particular, by amalgamations and redistributions of genera into monophyletic taxa.

(c) The stratigraphic resolution of family distributions has been improved. As far as possible, the dates of origination and extinction of each family have been determined to the nearest stratigraphic stage, usually by examination of the primary literature. The stage is the smallest practicable division of geological time for this compilation (relevant stage lengths vary from 2 to 19 Ma in length, with a mean duration of 6 Ma). This allows more detailed analysis than simply relying on the Lower, Middle and Upper divisions of geological periods in Romer (1966), Carroll (1987) and elsewhere.

(b) *Diversification of tetrapods*

The diversity of tetrapods has increased through time, with a particularly rapid acceleration in the rate of increase from the late Cretaceous (Campanian) onwards (figure 2) (Benton 1985 a, b). Three major diversity assemblages have been identified (Benton 1985 b), which appeared to dominate for a time, and then gave way to another: I (labyrinthodont amphibians, ‘anapsids’, mammal-like reptiles) dominated from late Devonian to early Triassic times at diversity levels of typically 20–40 families; II (early diapsids, dinosaurs, pterosaurs)

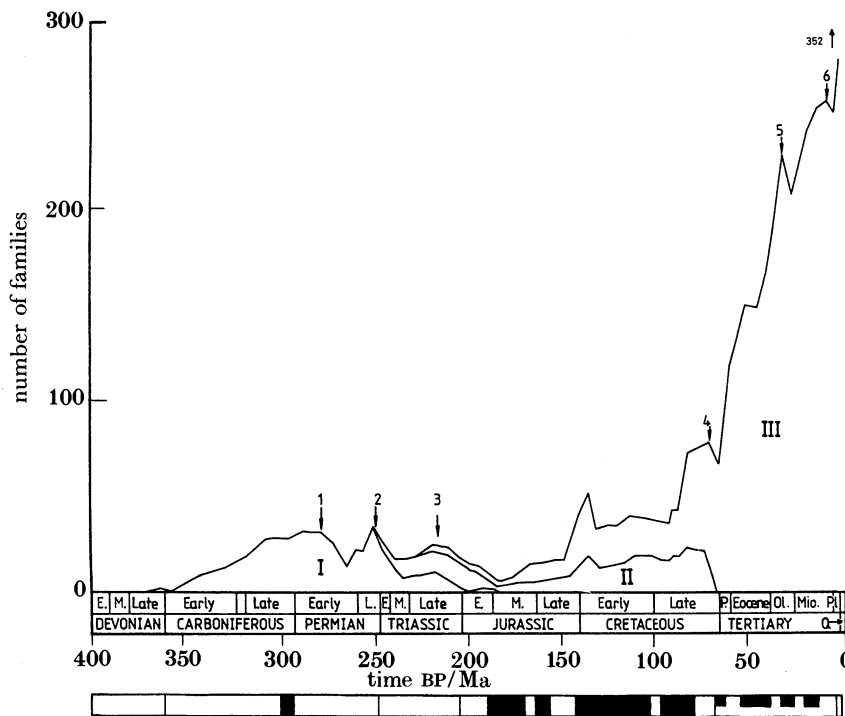


FIGURE 2. Standing diversity with time for families of tetrapods. The upper curve shows total diversity with time, and six apparent mass extinctions are indicated by drops in diversity, numbered 1–6. The relative magnitude of each drop is given in terms of the percentage of families that disappeared. (1) Early Permian (Sakmarian–Artinskian), 58%; (2) late Permian–early Triassic (Tatarian–Scythian), 49%; (3) late Triassic (Carnian–Rhaetian), 22%; (4) late Cretaceous (Maastrichtian), 14%; (5) early Oligocene (Rupelian), 8%; (6) late Miocene (Tortonian–Messinian), 2%. The timescale is that of Palmer (1983). Three assemblages of families succeeded each other through geological time: I, II and III (see text for details). The scm for each stratigraphic stage is indicated in code: values less than 50% (i.e. a poor fossil record) are shown shaded black, values between 50% and 75% are indicated as half black, half blank, and values over 75% are shown fully blank.

dominated during the Mesozoic at diversity levels of 20–50 families; and III (the ‘modern’ groups: frogs, salamanders, lizards, snakes, turtles, crocodiles, birds, mammals) have dominated from late Cretaceous times to the present day, rising rapidly from overall diversities of 50 to 89 in the Maastrichtian, and then successive peaks of 158 in the early Eocene, 234 in the Late Oligocene, and 279 in the late Miocene.

7. MASS EXTINCTIONS

(a) *Methods*

Extinction and origination rates were calculated stage by stage for non-marine tetrapod families based on the new data set. Total extinction (R_e) and total origination (R_s) rates were calculated as the number of families that disappeared or appeared, respectively, during a stratigraphic stage, divided by the estimated duration of that stage (Δt), as $R_e = E/\Delta t$ and $R_s = S/\Delta t$, where E is the number of extinctions and S is the number of originations. Per taxon extinction (r_e) and origination (r_s) rates were calculated by dividing the total rates by the end-of-stage family diversity D (Sepkoski 1978), as $r_e = (1/D)(E/\Delta t)$ and $r_s = (1/D)(S/\Delta t)$. The per taxon rates can be seen as the ‘probability of origin’ or the ‘risk of extinction’. In these calculations, the recent summary geological timescale of Palmer (1983) was used for stage lengths in Ma.

Mass-extinction events are times when large numbers of taxa of diverse taxonomic and ecological position appear to die out in a geological instant (Jablonski 1986). No clear numerical definition of mass extinction has been possible yet, but indications are provided by (a) major drops in overall diversity, and (b) times of unusually high extinction rates.

(b) *Diversity drops*

There appear to have been six declines in diversity (figure 2, 1–6) that are attributable to mass-extinction events. The other drops on the graph (early Jurassic, end-Jurassic, mid-Cretaceous) probably indicate mainly a change in the quality of the fossil record (Benton 1985 *a, b*), and mass extinctions cannot be assumed here. These three episodes correspond to times when the scm described above gives particularly low values (figure 2). Mass extinctions may lurk within the gaps, but they cannot be assumed.

(c) *Extinction and origination rates*

The graphs of total rates (figure 3) for tetrapod families show great fluctuations in both origination and extinction rates. There is no clear correlation of high extinction rates with all mass extinction events. Of the highest rates, those in the Artinskian, Tatarian, ‘Rhaetian’, Maastrichtian, Rupelian, and late Miocene correspond to mass extinctions 2, 3, 4, 5 and 6 (figure 2) respectively. Equally high, or higher, total extinction rates in the Ufimian (late Permian), Tithonian (late Jurassic), Coniacian (late Cretaceous), Thanetian (late Palaeocene), Ypresian (early Eocene), Bartonian–Priabonian (middle–late Eocene), Pliocene and Pleistocene do not match any of the drops in amniote diversity that have been ascribed to mass extinctions.

The total origination rates (figure 3) generally track the total extinction rates quite closely. Both the total extinction and origination rates were found to be dependent on two non-random sources of error, which are noted here.

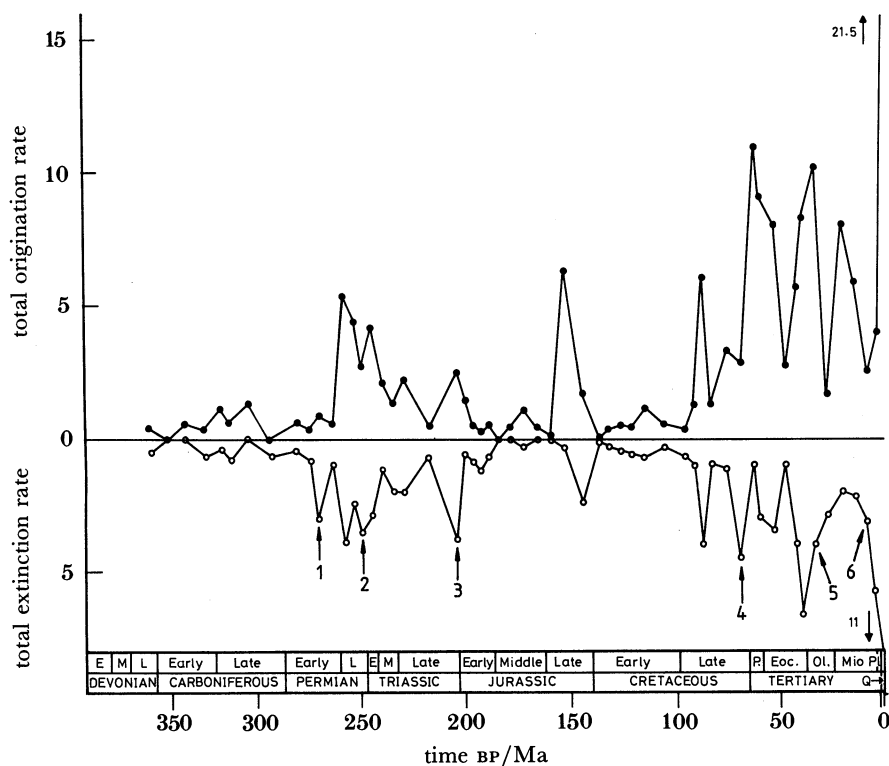


FIGURE 3. Total rates of origination and extinction for families of amniotes, calculated stage by stage for 56 stages between the late Devonian and the Pleistocene. The Miocene was divided into early, middle and late units only, and the Pliocene was treated as a single time unit.

(i) *Variation in the total numbers of taxa available to give rise to new taxa or to go extinct.*

Early parts of both records show very low diversity (1–10 families), whereas the Tertiary portions are two orders of magnitude higher; this must bias the rate values.

(ii) *Lagerstätten effects*

The total origination rates generally track the total extinction rates quite closely; peaks in both rates might have been produced in part by episodes when the fossil record is better than usual, corresponding to particular Fossil-Lagerstätten, such as the Sakamena Group (late Permian), the Solnhofen Limestone (Tithonian), and the Monte Bolca fish beds (Eocene). The improvement in the record boosts the apparent number of family originations and extinctions (Hoffman & Ghiold 1985).

The per taxon rates remove this bias in part. Thus when extinction and origination rates are recalculated relative to the numbers of taxa available (figure 4), the rates do not track each other so closely, although 'Lagerstätten peaks' remain in the Ufimian, Tithonian and Coniacian. There are particularly high per taxon extinction rates at times of mass extinctions corresponding to the Artinskian, Tatarian, and 'Rhaetian' events (1, 2 and 3, figure 2). Per taxon extinction rates are barely elevated at the times of the Maastrichtian, Rupelian, or Late Miocene mass extinctions (4, 5 and 6, figure 2). These mass extinctions correspond to depressed per taxon origination rates (figure 4), as noted by Benton (1985*b*).

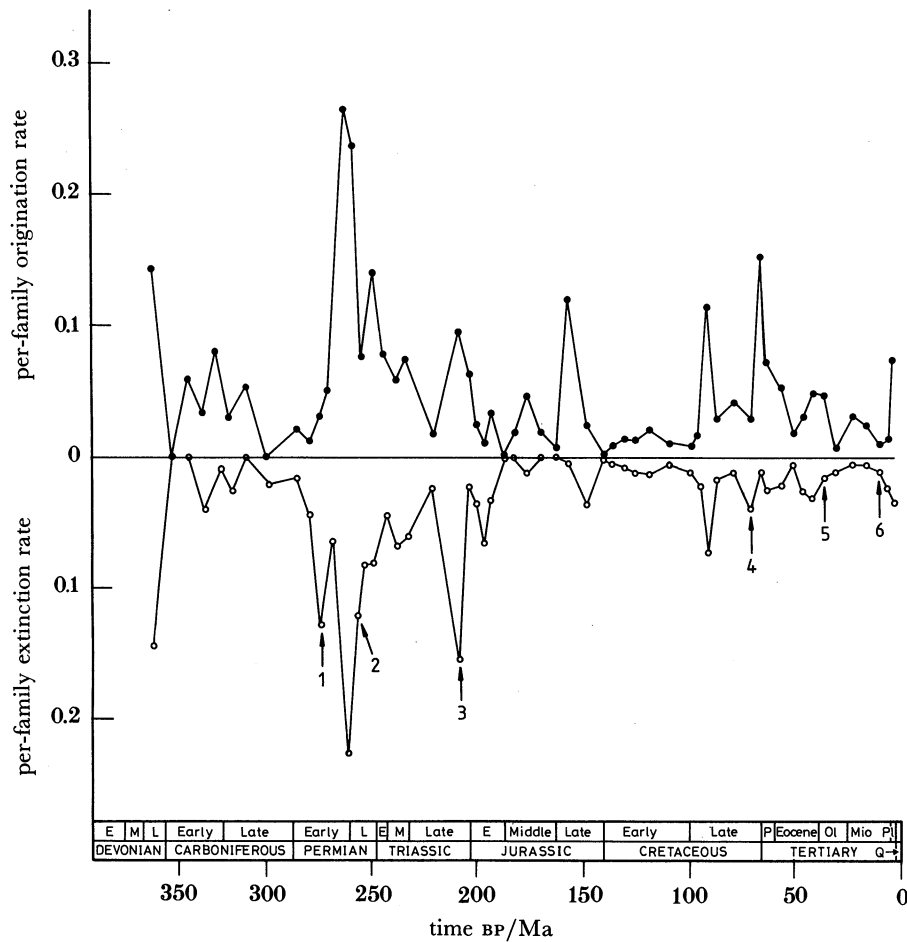


FIGURE 4. Per taxon rates of origination and extinction for families of amniotes. Conventions as in figure 3.

(d) *Mass-extinction events*

The history of tetrapods has apparently been punctuated by at least six mass-extinction events (figure 2) (Benton 1985*b*), together with up to seven other possible extinction events. These had widely differing effects, ranging from a 58% drop in family diversity for the early Permian event to a 2% drop for the late Miocene event. It has already been argued (Benton 1988) that the fossil record of tetrapods is generally not complete enough to test the hypothesis of periodicity of mass extinctions (Raup & Sepkoski 1984, 1986), but the data from the Triassic record appear to contradict the idea (Benton 1986*a*, 1988). The possible tetrapod extinctions are described below.

(i) *Early Carboniferous (Serpukhovian)*

Four families of amphibians died out at the boundary between the early and the late Carboniferous.

'Labyrinthodontia': Proterogyrinidae, Eoherpetontidae;

'Lepospondyli': Adelogyrinidae, Acherontiscidae.

This may correspond to the end-Namurian marine event noted by Sepkoski & Raup (1986,

p. 23), by Saunders & Ramsbottom (1986), and by others. The small number of tetrapod families lost (and each of them is of low diversity) gives lower than normal extinction rates (figures 3, 4). This cannot be regarded as a well-supported tetrapod extinction event.

(ii) *Late Carboniferous (Kasimovian–Gzelian)*

Two families of tetrapods died out.

‘Lepospondyli’: Ophiderpetontidae, Tuditanidae.

The suggested end-Carboniferous extinction event (Sepkoski & Raup 1986, p. 23) is even less convincing for tetrapods. Only two families of rather rare ‘Lepospondyli’ disappeared, and the extinction rates were low during both stages (figures 3 and 4).

(iii) *Early Permian (Artinskian)*

Fifteen families died out during this event (1, figure 2):

‘Labyrinthodontia’: Saurerpetontidae, Trematopsidae, Archeriidae;

‘Lepospondyli’: Urocordylidae, Hapsidopareiontidae, Ostodolepidae, Lysorophidae;

‘Anapsida’: Protorothyrididae, Bolosauridae, Mesosauridae;

Diapsida: Araeoscelididae;

Synapsida: Eothyrididae, Edaphosauridae, Ophiacodontidae, Sphenacodontidae.

Six families of ‘labyrinthodont’ amphibians are known to have survived into the succeeding Kungurian Stage (Trimerorachidae, Eryopidae, Dissorophidae, Archegosauridae, Seymouriidae, Diadectidae), two of ‘Lepospondyli’ (Keraterpetontidae, Gymnarthridae), and only three of reptiles (Captorhinidae, Caseidae, Varanopidae). This extinction then had its greatest effect on the reptiles, and it marked the sharpest decline in the formerly dominant pelycosaurs (early synapsids). Artinskian extinction rates are high, but not excessively so.

(iv) *Late Permian (Tatarian)*

Twenty-seven families of tetrapods died out at the end of the Permian (2, figure 2).

‘Labyrinthodontia’: Dvinosauridae, Melanosauridae, Rhinesuchidae, Kotlassidae, Lanthanosuchidae, Chroniosuchidae;

‘Anapsida’: Captorhinidae, Millerettidae, Pareiasauridae;

Diapsida: Weigeltisauridae, Younginidae, Tangasauridae;

Synapsida: Ictidorhinidae, Gorgonopsidae, Dromasauridae, Endothiodontidae, Cryptodontidae, Aulacocephalodontidae, Dicynodontidae, Pristerodontidae, Cistecephalidae, Diictodontidae, Moschorhinidae, Whaitsiidae, Silphestidae, Procynosuchidae, Dviniidae.

The end-Permian event had a decisive effect on the amphibians, wiping out six families and leaving only three survivors that crossed the Permo-Triassic boundary (Uranocentrodontidae, Benthosuchidae and Brachyopidae). It also caused the end of many major reptilian families, particularly a large number of formerly dominant mammal-like reptiles. The six or seven families that survived into the Triassic rapidly radiated into new forms, but the synapsids had begun to lose their dominance to the diapsids.

The extinction rates for the Tatarian are fairly high (figures 3 and 4), but not as high as those in the Ufimian, the first stage in the late Permian, when there was no drop in tetrapod family diversity.

(v) *Early Triassic (Scythian)*

There was another smaller extinction event about 5 Ma later, at the end of the Scythian Stage, when thirteen tetrapod families died out.

'Labyrinthodontia': Lydekkerinidae, Uranocentrodontidae, Benthosuchidae, Rhytidosteidae, Trematosauridae, Indobrachyopidae;

Diapsida: Proterosuchidae, Euparkeriidae;

Synapsida: Emydopidae, Kingoriidae, Ictidosuchidae, Scaloposauridae, Galesauridae.

The event really affected only the amphibians, as reptilian diversity remained roughly constant as a result of a high origination rate at the time. There was also a small mass extinction of marine invertebrates then (Raup & Sepkoski 1984, 1986).

(vi) *Late Triassic (Carnian–'Rhaetian')*

The three stages of the late Triassic, the Carnian, Norian and 'Rhaetian' (or two, if the 'Rhaetian' is included in the Norian) span 18–25 Ma, depending upon which of the current timescales is employed. Raup & Sepkoski (1984, 1986) have argued that the Late Triassic extinction consisted of a single event, but Benton (1986*a, b*) has identified at least two phases of extinction in the fossil record of tetrapods (3, figure 2), as well as in that of ammonoids and other groups.

The first, and larger, extinction event occurred at the end of the Carnian Stage. Ten families of tetrapods died out.

Diapsida: Thalattosauridae, Trilophosauridae, Rhynchosauridae, Proterochampsidae;

Synapsida: Kannemeyeriidae, Chiniquodontidae;

'Euryapsida': Nothosauridae, Simosauridae, Cymatosauridae, Henodontidae.

The second, smaller, late Triassic extinction event, at the Triassic–Jurassic boundary ('Rhaetian') was marked by the loss of eight families.

'Labyrinthodontia': Capitosauridae, Plagiosauridae;

'Anapsida': Procolophonidae;

Diapsida: Phytosauridae, Aetosauridae, Rautisuchidae, Ornithosuchidae;

'Euryapsida': Placochelyidae.

These extinctions, although few in number, do seem to have some significance. The last of the thecodontians (four families) disappeared on land, as did the last of the placodonts in the sea. Most of the 'modern' groups of amniotes had appeared during the preceding 12–17 Ma of the Norian Stage: the Testudines, the Crocodylia, and the Mammalia, as well as the Pterosauria, and the Dinosauria in the Carnian. At one time it was thought that the end of the Triassic saw the termination of the formerly abundant 'labyrinthodont' amphibians and the mammal-like reptiles, but these two groups continued in greatly reduced diversity until the Bathonian and Callovian (both middle Jurassic) respectively.

Both the Carnian and the 'Rhaetian' events are associated with peaks in total and per taxon extinction rates of tetrapod families (figures 3 and 4), but the peaks are higher for the latter event.

(vii) *Jurassic–Cretaceous events*

Raup & Sepkoski (1984, 1986) and Sepkoski & Raup (1986) have identified three probable extinction events that affected marine animals between the 'Rhaetian' and the K–T events.

These additional extinction events, with dates of the ends of the stages from Palmer (1983), are

- Jurassic: Pliensbachian (193 Ma);
 Tithonian (144 Ma);
 Cretaceous: Cenomanian (91 Ma).

The data on tetrapod families are particularly weak during parts of this time interval (see above). There are indeed declines in family diversity in the tetrapod data (figure 2) after the Pliensbachian, Tithonian, and Cenomanian, with the decline after the Tithonian standing out best. There are also slight peaks in total (figure 3) and per taxon (figure 4) extinction rates in the Pliensbachian and Cenomanian, with a more marked peak in the Tithonian. At present, the tetrapod data are not good enough to decide either way about the occurrence of these postulated extinction events.

(viii) *Late Cretaceous (Maastrichtian)*

The Cretaceous–Tertiary boundary (K–T) event is surely the best-known mass extinction, and not least for its effects on the reptiles (dinosaurs, pterosaurs and plesiosaurs all died out then). However, in relative terms at least, the percentage loss of families of tetrapods as a whole (4, figure 2) was less than for the two Permian events and the late Triassic events already described. The total extinction rate for the Maastrichtian (figure 3) is higher than any before it, but the per taxon rate for tetrapods (figure 4) is not so impressive, being lower than the ‘Rhaetian’, Pliensbachian and Coniacian rates, for example. The decline in tetrapod family diversity at the K–T boundary is caused by a slightly elevated extinction rate, and partly by a low origination rate (Benton 1985*b*).

Thirty-six families of tetrapods died out at the K–T boundary.

Diapsida: Crocodylia: Uruguaysuchidae, Notosuchidae, Goniopholididae;

Pterosauria: Pteranodontidae, Azhdarchidae;

Dinosauria: Coeluridae, Ornithomimidae, Dromaeosauridae, Saurornithoididae, Oviraptoridae, Elmsauridae, Megalosauridae, Dryptosauridae, Tyrannosauridae, Camarasauridae, Diplodocidae, Titanosauridae, Hypsilophodontidae, Hadrosauridae, Pachycephalosauridae, Nodosauridae, Ankylosauridae, Protoceratopsidae, Ceratopsidae

Sauria: Mosasauridae;

Aves: Baptonithidae, ‘Enantiornithes’, Lonchodytidae, Torotigidae;

Mammalia (Marsupialia): PEDIOMYIDAE, STAGODONTIDAE;

‘Euryapsida’: Plesiosauria: ELASMOHAURIDAE, CRYPTOCLEIDIDAE, POLYCOTYLIDAE.

The K–T event was clearly taxonomically selective: certain major groups became completely extinct during Maastrichtian times: the Pterosauria (two families), the Dinosauria (19 families) and the Plesiosauria (three families). Other groups were less affected: turtles, crocodilians, lizards, snakes, birds and mammals (although two out of three marsupial families died out). Indeed, the mammals continued to radiate without any obvious pause right through the K–T boundary.

(ix) *Late Eocene (Priabonian)*

The major late Eocene extinction event identified by Raup & Sepkoski (1984, 1986), and others, among marine animals is not reflected in the global tetrapod data. Of 183 tetrapod families known at the time, 20 (mainly mammals) died out, corresponding to an elevated extinction rate. There was no diversity drop, however, merely a levelling off (figure 2), as

origination rates were also high. This may be a localized, rather than a global, extinction event, corresponding to the 'grande coupure' of French palaeontologists, when numerous species of tetrapods disappeared in Europe.

(x) *Early Oligocene (Rupelian)*

This relatively minor event (5, figure 2) corresponds to a loss of 28 (out of 234) families, mainly of mammals. It has been noted also by Prothero (1985) for North American land mammals, but does not correspond to one of the periodic marine events, even though it was more severe for tetrapods than the late Eocene event. Extinction rates are lower than for the late Eocene event (figure 3), but they are matched by low origination rates, and lead to an overall decline in diversity.

(xi) *Late Miocene (Tortonian–Messinian)*

This event (6, figure 2) also affected the tetrapods, with the loss of 21 families, mainly among mammals, such as certain primates, artiodactyls, notoungulates and cetaceans. It does not match the periodic marine events, where a major extinction occurred earlier, in the Middle Miocene (Raup & Sepkoski 1984, 1986).

(e) *Periodicity?*

In general, the tetrapod fossil record is not adequate to test Raup & Sepkoski's (1984, 1986) theory of extinction periodicity. Most of the extinctions postulated above (?1, ?2, 4, 6, 7, 8, 9) match marine mass extinctions identified by those authors. However, some (1, 2, 4, 6, 9) do not match very well, and others (3, 5, 10, 11) do not fit the 26-million-year cycles at all. Further, many of the 26-million-year extinctions seem to be absent from the tetrapod data (that is, early Jurassic (Pliensbachian), middle Jurassic (Callovian?), early Cretaceous (Barremian–Aptian?), middle Miocene (Langhian–Serravallian)). Note, however, that Sepkoski & Raup (1986) found only limited evidence in the marine data for the middle Jurassic and early Cretaceous events, which are necessary to fill gaps in the 26-million-year periodicity pattern. Overall, the tetrapod data are suggestive, but by no means conclusive, evidence against periodicity.

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