

MASS EXTINCTIONS IN THE FOSSIL RECORD OF LATE PALAEOZOIC AND MESOZOIC TETRAPODS



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Abstract: The fossil record of tetrapods is very patchy because of the problems of preservation in terrestrial sediments, 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 (many characters; 'fast' evolution), and there is the potential for more detailed ecological analyses (greater knowledge of modern tetrapod ecology).

The diversity of tetrapods increased during the Devonian, the Carboniferous, and the Permian, but it remained generally constant during the Triassic, the Jurassic, and the Early Cretaceous. Overall diversity 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, crocodiles, birds and mammals - was hardly affected by the celebrated end-Cretaceous extinction event.

Major mass extinctions amongst tetrapods took place in the Early Permian, Late Permian, the Early Triassic, Late Triassic, and at the end of the Cretaceous. Many of these events appear to coincide with the major mass extinctions amongst marine invertebrates, but the tetrapod record is largely equivocal with regard to the recent theory of cyclicity of mass extinctions. Some data, on the Permo-Triassic events, is very much against the cyclical model, because the events are irregularly spaced in time. However, the absence of documented mass extinctions amongst Jurassic and Cretaceous tetrapods, apparent evidence against cyclicity, may be explained by the relatively patchy fossil record during those periods.

INTRODUCTION

Most studies on mass extinctions so far have focussed on the fossil record of marine invertebrates (e.g. Raup & Sepkoski, 1982, 1984, 1986; Jablonski, 1986; McKinney, 1986). A smaller number of studies have used the fossil record of vascular plants (Niklas et al., 1983) and non-marine vertebrates (Benton, 1985a, b), and there has been an implicit assumption that these records are relatively poorer. 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 objectives of this paper are to consider the problems and the advantages of the fossil record of tetrapods of the late Palaeozoic and Mesozoic, and to outline what has been learnt from it about mass extinctions.

THE NATURE OF THE FOSSIL RECORD OF TETRAPODS

Scope

The first tetrapods, according to most recent classifications (e.g. Romer, 1966; Carroll, 1977; Smithson, 1985; Panchen & Smithson, 1988) are the Ichthyostegalia (Ichthyostegidae, Acanthostegidae), known first from the Famennian Stage (c. 365 Myr.) 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

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during the Carboniferous into nine or more major lineages of labyrinthodont amphibians which were generally bulky carnivores and piscivores that lived near water, and lepospondyl amphibians that were commonly smaller and more varied in their modes of life. One labyrinthodont lineage 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 according to most recent classifications (e.g. Romer, 1966; Carroll, 1982; Heaton & Reisz, 1986) are the Protorothyrididae (= Romeriidae), known first from the Moscovian Stage (c. 300 Myr.) of the Late Carboniferous. During the remaining 15 Myr. or so of the Carboniferous, the early amniotes diversified into a number of additional lineages within 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, crocodilians 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 event.

The labyrinthodont 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 Fig. 1. This is based on recent cladistic analyses, although these leave many doubtful relationships, and familial diversity is indicated.

In all, there are 858 families of living and extinct non-marine tetrapods, and 58 families of exclusively marine tetrapods (Benton, 1987), totalling 916 families. The figures for late Palaeozoic and Mesozoic families are 338 non-marine, and 32 exclusively marine, giving a total of 370 (Tab. 1).

Table 1

Numbers of families of Late Palaeozoic and Mesozoic tetrapods, based on data in Benton (1987a, b). Note: some of these families cross cut the Tertiary.

	<u>non-marine</u>	<u>exclusively marine</u>	<u>total</u>
Amphibia	85	0	85
Reptilia	205	32	237
Aves	13	0	13
Mammalia	<u>35</u>	<u>0</u>	<u>35</u>
TOTAL	338	32	370

Quality of the fossil record of tetrapods

The relative incompleteness of the fossil record of tetrapods has been described by many authors (e.g. 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 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.

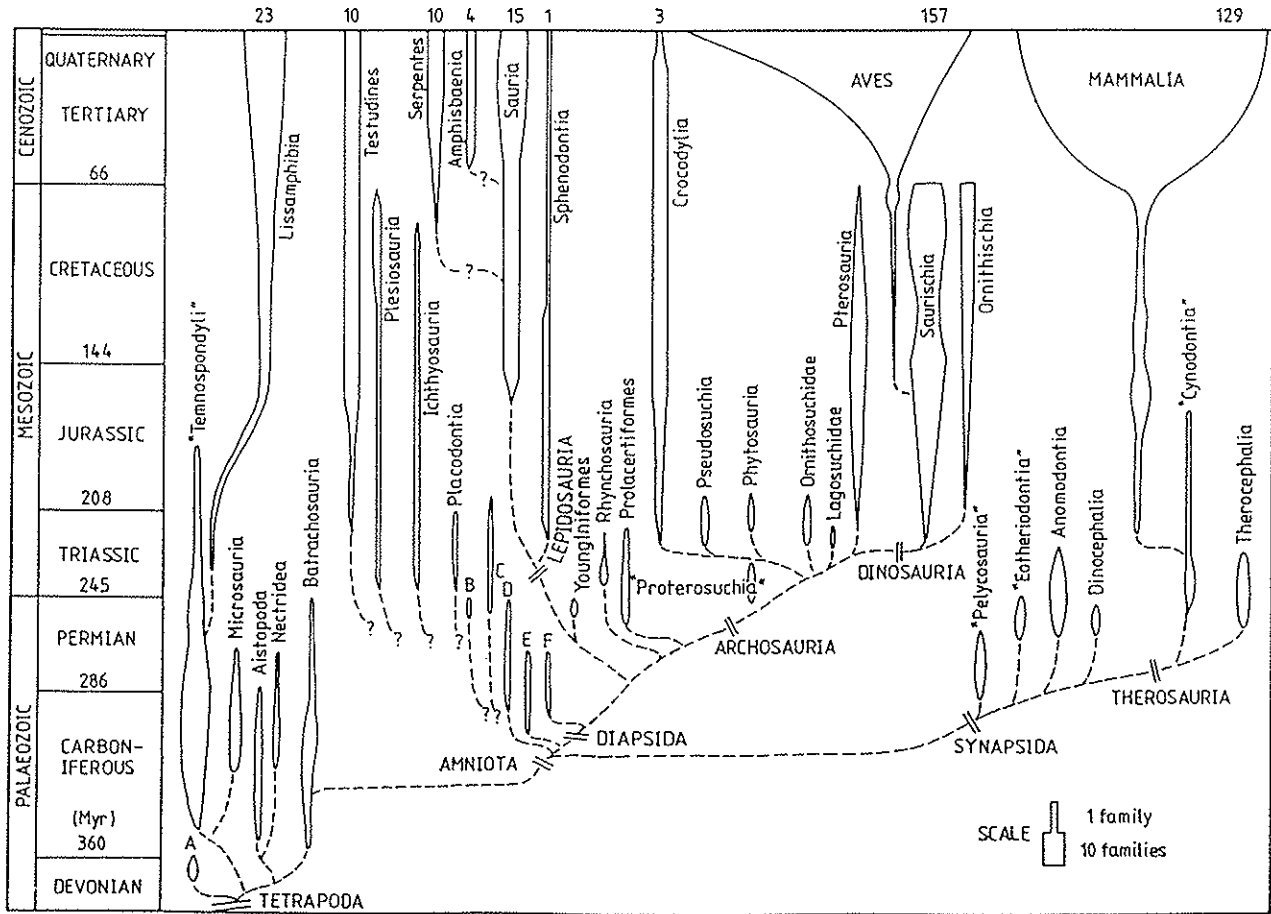


Figure 1 : Phylogenetic tree of the Tetrapoda, showing relationships, stratigraphic duration, and diversity of each group. The major groups are indicated as balloons that show the known stratigraphic range by their height, and the relative numbers of families present by their width (see scale in bottom right-hand corner). Relationships of the groups are indicated by dashed lines on the basis of recent cladistic analyses (e.g. Gaffney, 1980; Kemp, 1982; Benton, 1984, 1985c; Smithson, 1985; Gauthier, 1986; Heaton & Reisz, 1986; Panchen & Smithson, 1988)

Abbreviations: A, Ichthyostegalia; B, Pareiasauria; C, Procolophonia; D, Captorhinidae; E, Protorothyrididae; F, Araeoscelidia.

The incompleteness of the fossil record of terrestrial tetrapods has been characterised in another way by Padian and Clemens (1985, p. 82). Most dinosaur genera are known only from 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 K-T mass extinction event since dinosaur families generally span more than one stage.

It is possible to estimate the 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. Viscaan, 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).

Advantages of the fossil record of tetrapods

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.

(1) There is a high probability of identifying clades. Rates of evolution, extinction, origination, and so on, should apply to monophyletic groups (*sensu* Hennig, 1966; that is, holophyletic groups, *sensu* Ashlock, 1971) only, and not to paraphyletic groups (groups that had a single ancestor, but exclude some of the descendants of that ancestor). This is because monophyletic groups (clades) have a unique history that exists and is to be discovered, whereas paraphyletic groups may start off with a unique history, but their boundaries are adjusted *a posteriori*, and they are in part a human invention (Cracraft, 1981). For example, the well-known "Class Reptilia" is paraphyletic. That is, all reptiles derive from a single common ancestor (or the group could be defined in that way by juggling some early groups between "Amphibia" and "Reptilia"). However, the group "Reptilia" does not include all of the descendants of that ancestor (Aves and Mammalia are excluded). The boundary line between reptiles and birds, or reptiles and mammals is an arbitrary cut-off, and the line could be moved up and down depending on which synapomorphy is regarded as defining. This means that the upper limit of Reptilia is not fixed by any positive attribute, only by the absence of a synapomorphy. The lower limit of "Reptilia", and of clades, is also arbitrary in one sense, in that it can be drawn at many different levels, but it depends on a positive attribute, the acquisition of a synapomorphy, which defines an evolutionary event.

The finding of clades for macroevolutionary studies depends on cladistic analysis. Vertebrates have proved highly amenable to this technique, as have only a few invertebrate groups (e.g. echinoderms, arthropods). This suggests that it may be hard to define cladistic families for the bulk of the record of fossil invertebrates. The significance of this problem has been highlighted by Patterson and Smith (*pers. comm.*, 1987), who find that as much as 76% of the standard data set on fossil echinoderms and fish (Sepkoski, 1982), used in most recent studies of mass extinctions, is invalid because the families are paraphyletic, polyphyletic, monogeneric, or monospecific. A re-analysis of a cladistically-based data set of marine animals would probably yield rather different patterns of extinction. A study of this sort on "pre-cladistic" and cladistic data sets of non-marine tetrapods (Maxwell & Benton, 1987) has shown considerable, but unpredictable, changes in the patterns of extinction. This study suggested that, from 1966 to 1986, the major improvements in our knowledge of the past distribution of tetrapods stemmed more from the rigorous identification of monophyletic groups than from the discovery of new fossils. These improvements may not be possible in most of the fossil records of marine invertebrates because of the problems of cladistic analysis.

(2) Tetrapods offer great 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,

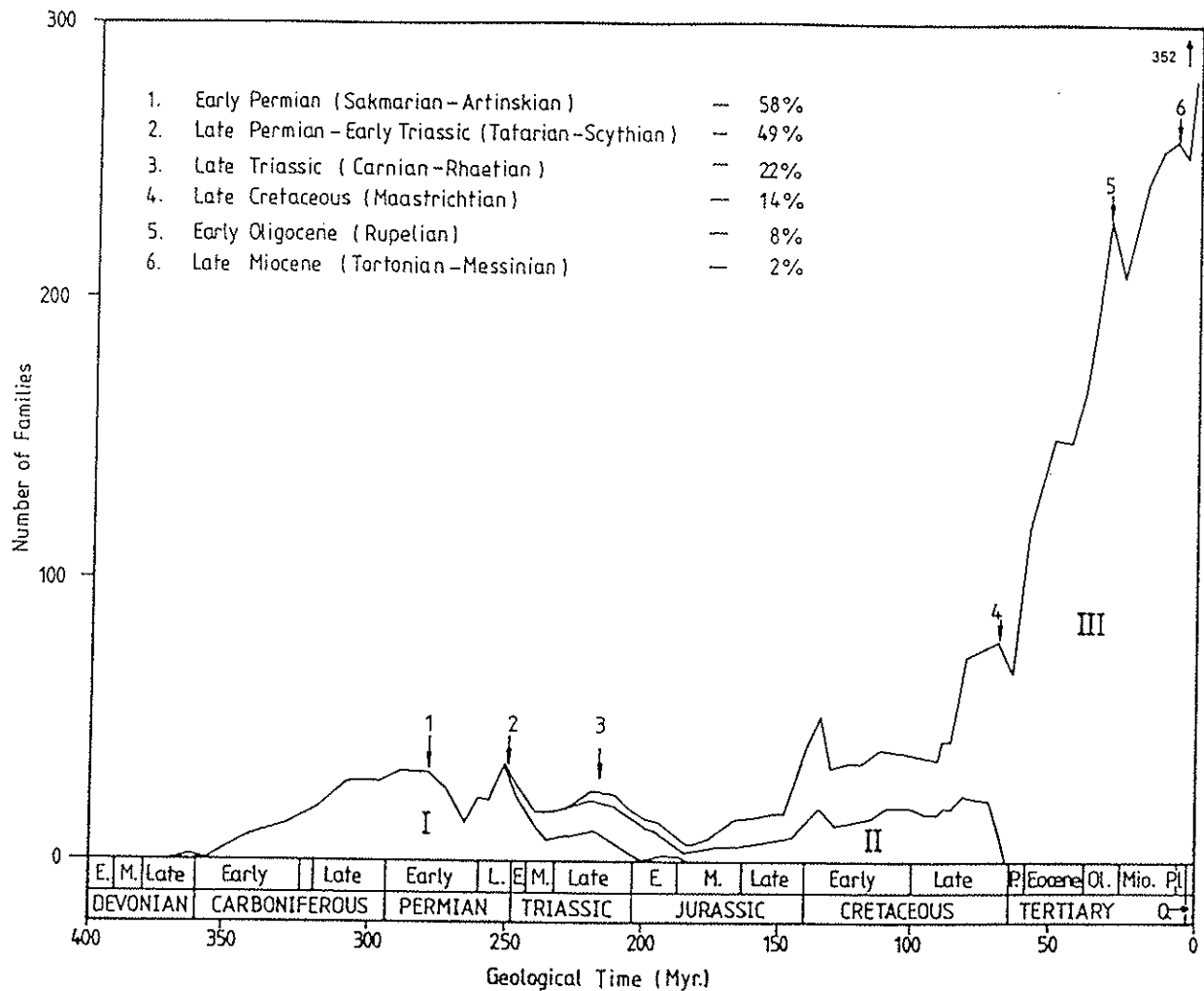


Figure 2: Standing diversity with time for families of tetrapods. The upper curve shows total diversity with time, and six apparent mass extinctions are indicated by drops in diversity, numbered 1-6. The relative magnitude of each drop is given in terms of the percentage of families that disappeared. The time scale is that of Palmer (1983). Three assemblages of families succeeded each other through geological time: I, II, III (see text for details). Abbreviations: Carb., Carboniferous; Dev., Devonian; Trias., Triassic.

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.

(3) The generic- and species-level taxonomy of tetrapods is a mature branch of systematics. Because *Homo sapiens* is a non-marine tetrapod, zoologists have devoted more attention to the 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.

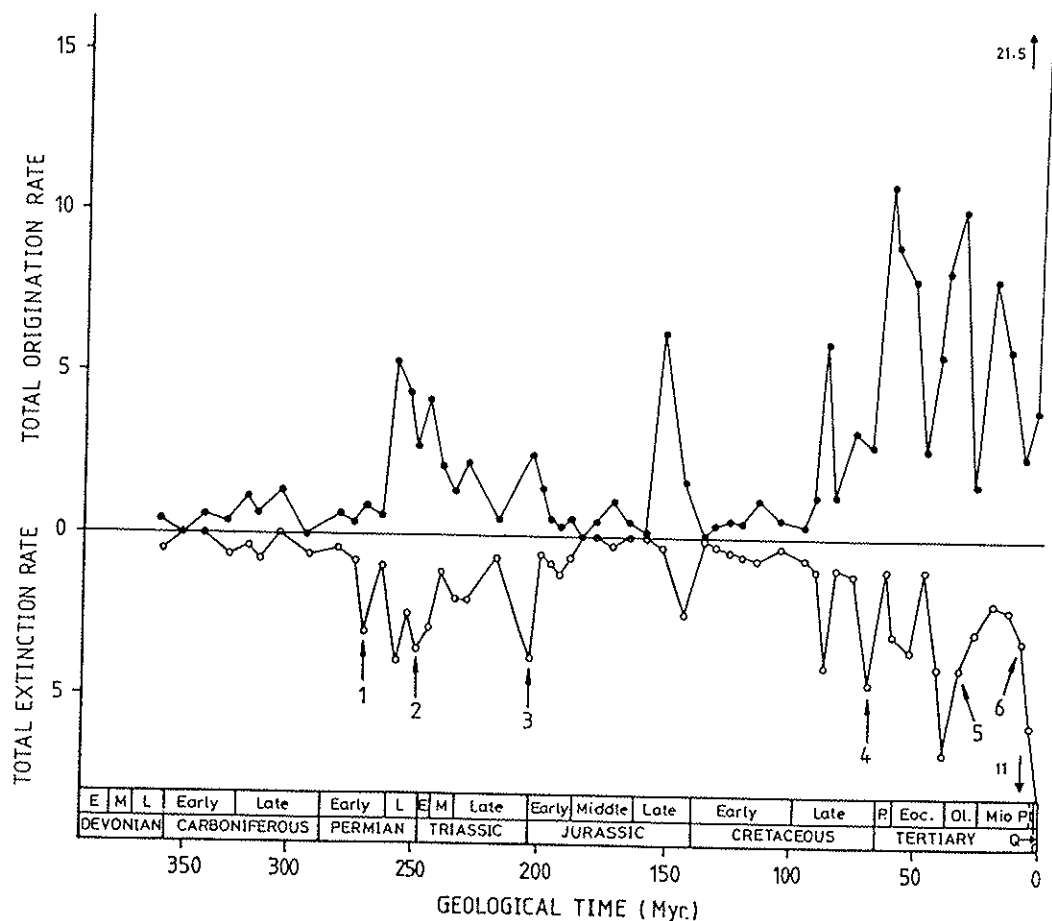


Figure 3: Total rates of origination and extinction for families of amniotes, calculated stage by stage for 56 stages between the Late Devonian and the Pleistocene. The Miocene was divided into Early, Middle and Late units only, and the Pliocene was treated as a single time unit.

TETRAPOD FAMILY DIVERSITY ANALYSIS

Several authors have recently plotted graphs of the diversity of tetrapod families and orders through time (e.g. 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, 1985a, b, 1988) have been based on a new compilation of data on families of non-marine tetrapods (Benton, 1987, 1988). These new compilations differ significantly from those derived from Romer (1966) and Harland et al. (1967) in several ways:

(1) New records up to the end of 1985 are included. This has affected the date of origination or extinction of as many as 50% of families.

(2) 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.

(3) 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 2-19 Myr. in length, with a mean duration of 6 Myr.). This

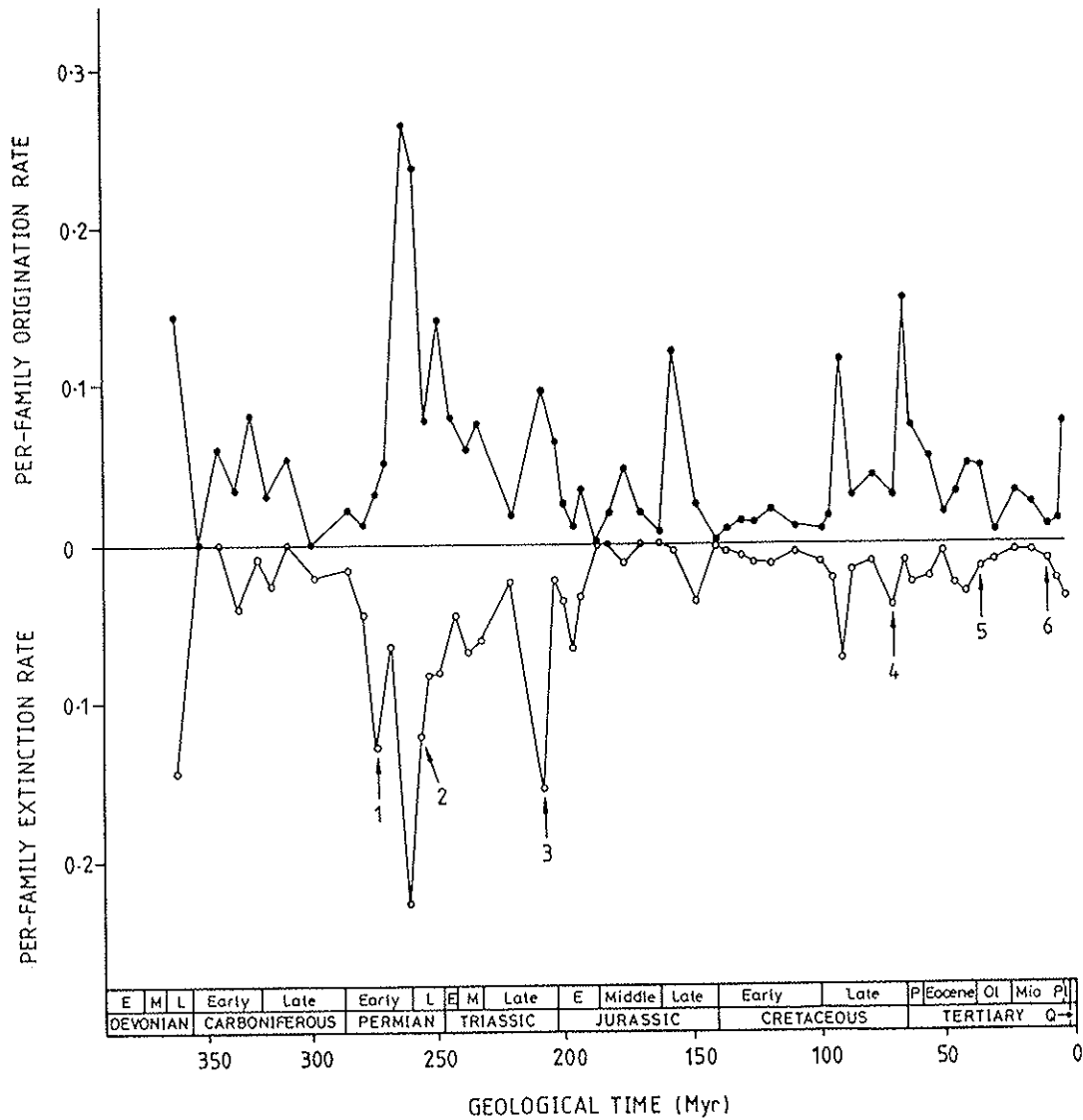


Figure 4: Per-taxon rates of origination and extinction for families of amniotes. Conventions as in Fig. 3.

allows more detailed analysis than simply relying on the Lower, Middle and Upper divisions of geological periods in Romer (1966) and elsewhere.

The new compilations of data on fossil tetrapod family diversities have been used for a variety of graphs and calculations. A small number of families that are based on single species or single genera have been omitted.

The diversity of non-marine tetrapods has increased through time, with a particularly rapid acceleration in the rate of increase from the Late Cretaceous (Campanian) onwards (Fig. 2; Benton, 1985a, b). Three major diversity assemblages have been identified (Benton, 1985b), which appeared to dominate for a time, and then gave way to another: I. labyrinthodont amphibians, "anapsids", and mammal-like reptiles dominated from Late Devonian to Early Triassic times; II. early diapsids, dinosaurs, and pterosaurs

dominated during the Mesozoic; and III. the "modern" groups - frogs, salamanders, lizards, snakes, turtles, crocodiles, birds, mammals - have dominated from Late Cretaceous times to the present day.

There appear to be six declines in diversity (Fig. 2, nos. 1-6) that are attributable to mass extinction events, four of which fall in the late Palaeozoic to Mesozoic interval. The other drops (Early Jurassic, end-Jurassic, mid-Cretaceous) probably indicate mainly a change in the quality of the fossil record (Benton, 1985a, b), and mass extinctions cannot be assumed here. These three episodes correspond to times when the SCM described above gives particularly low values.

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):

$$R_e = \frac{E}{\Delta t} \quad \text{and} \quad R_s = \frac{S}{\Delta t},$$

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):

$$r_e = \frac{1}{D} \cdot \frac{E}{\Delta t} \quad \text{and} \quad r_s = \frac{1}{D} \cdot \frac{S}{\Delta t}$$

The per-taxon rates can be seen as the "probability of origin" or the "risk of extinction". In these calculations, the recent summary geological time scale of Palmer (1983) was used for stage lengths in Myr.

The graphs of total rates (Fig. 3) for amniote 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 (Fig. 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 (Fig. 3) generally track the total extinction rates quite closely. Peaks in both rates may be produced in part by episodes when the fossil record is better than usual, corresponding to particular Fossil-Lagerstaetten, such as the Sakamena Group (Late Permian) and the Solnhofen Limestone (Tithonian). 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. When extinction and origination rates are recalculated relative to the numbers of taxa available (Fig. 4), the rates do not track each other so closely, although "Lagerstaetten 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 (nos. 1, 2, 3: Fig. 2). Per-taxon extinction rates are barely elevated at the times of the Maastrichtian, Rupelian, or Late Miocene mass extinctions (nos. 4, 5, 6: Fig. 2). These mass extinctions correspond to depressed per-taxon origination rates (Fig. 4), as noted by Benton (1985b).

MASS EXTINCTIONS

The history of non-marine tetrapods has apparently been punctuated by at least six mass extinction events (Fig. 2; Benton 1985b), 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, 1987) 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 data from the Triassic record appear to contradict the idea (Benton, 1986a, 1988).

The four extinction events in the late Palaeozoic to Mesozoic interval, together with the other possible events, are summarised briefly below, with notes on the groups that became extinct, and those that survived. More details of reptile extinctions is given in Benton (1988).

Early Carboniferous (Serpukhovian) Extinction: 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 and Raup (1986, p. 23), by Saunders and 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 (Figs. 3, 4). This cannot be regarded as a well-supported tetrapod extinction event.

Late Carboniferous (Kasimovian-Gzelian) Extinction: 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 (Figs. 3, 4).

Early Permian (Artinskian) Extinction: fifteen families died out during this event (no. 1: Fig. 2):

Labyrinthodontia: Saurerpetontidae, Trematopsidae, Archeriidae;

Lepospondyli: Urocordylidae, Hapsidopareiontidae, Ostodolepidae, Lysorophidae;

"Anapsida": Protorothyrididae, Bolosauridae, Mesosauridae;

Diapsida: Araeoscelididae;

Synapsida: Eothyrididae, Edaphosauridae, Ophiacodontidae, Sphenacodontidae.

There were six families of labyrinthodont amphibians that 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.

Late Permian (Tatarian) Extinction: twenty seven families of tetrapods died out at the end of the Permian (event no. 2: Fig. 2):

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

"Anapsida": Captorhinidae, Millerettidae, Parciasauridae;

Diapsida: Weigeltisauridae, Younginidae, Tangasauridae;

Synapsida: Ictidorhinidae, Gorgonopsidae, Dromasauridae, Endothiodontidae, Cryptodontidae, Aulaccephalodontidae, 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, Brachyopidae). It also caused the end of many major reptilian families, and 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 (Figs. 3, 4), but not as high as those in the Ufimian, the first stage in the Late Permian, when there was not a drop in tetrapod family diversity.

Early Triassic (Scythian) Extinction: there was another smaller extinction event about 5 Myr. 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, since reptilian diversity remained roughly constant as a result of a high origination rate at the time. There was a small mass extinction of marine invertebrates at this time also (Raup & Sepkoski, 1984, 1986).

Late Triassic (Carnian - "Rhaetian") Extinction: 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 Myr., depending upon which of the current time scales is employed. Raup and Sepkoski (1984, 1986) have argued that the Late Triassic extinction consisted of a single event, but Benton (1986a, b) has identified at least two phases of extinction in the fossil record of tetrapods (no. 3: Fig. 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 Myr. 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 (Figs. 3, 4), but the peaks are higher for the latter event.

Jurassic - Cretaceous event: Raup and Sepkoski (1984, 1986) and Sepkoski and 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 Myr.)
	Tithonian	(144 Myr.)
Cretaceous:	Cenomanian	(91 Myr.)

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 non-marine tetrapod data (Fig. 2) after the Pliensbachian, Tithonian, and Cenomanian, with the decline after the Tithonian standing out best. There are also slight peaks in total (Fig. 3) and per-taxon (Fig. 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.

Late Cretaceous (Maastrichtian) Extinction: 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 (no. 4: Fig. 2) was less than for the two Permian events and the Late Triassic events already described. The total extinction rate for the Maastrichtian (Fig. 3) is higher than any before it, but the per-taxon rate for tetrapods (Fig. 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 partly by a slightly elevated extinction rate, and partly by a low origination rate (Benton, 1985b).

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, Dryptosarridae, Tyrannosauridae, Camarasauridae, Diplo-docidae, Titanosauridae, Hypsilophodontidae, Hadrosauridae, Pachycephalosauridae, Nodosauridae, Ankylosauridae, Protoceratopsidae, Ceratopsidae

Sauria: Mosasauridae;

Aves: Baptonithidae, "Enantiornithes", Lonchodytidae, Torotigidae;

Mammalia: Marsupialia: PEDIOMYIDAE, Stagodontidae;

"Euryapsida": Plesiosauria: Elasmosauridae, Cryptocleididae, Polycotylidae.

The K-T event was clearly taxonomically selective: certain major groups became completely extinct during Maastrichtian times: the Pterosauria (2 families), the Dinosauria (19 families) and the Plesiosauria (3 families). Other groups were less affected - turtles, crocodylians, 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.

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