

# 13. Mass extinctions in the fossil record of reptiles: paraphyly, patchiness, and periodicity (?)

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## Abstract

The fossil record of reptiles has been cited frequently in discussions of mass extinction events and, in particular, the event at the end of the Cretaceous when the dinosaurs, pterosaurs, and marine reptiles died out. There are a number of problems in analysing the fossil record of reptiles, not least the fact that 'Reptilia' is a paraphyletic group; that is, it is partially a human invention. One solution to that problem is to expand the study to include all Amniota (i.e. reptiles, birds, and mammals). The fossil record of reptiles spans 300 Ma and includes 233 families, of which 200 are non-marine and only 43 are still living. The fossil record of reptiles is no poorer than that of other tetrapod groups, according to a Simple Completeness Metric (SCM), but the completeness varies greatly from stage to stage.

The diversity of families of fossil amniotes remained relatively low until the late Cretaceous, when levels rose rapidly from a total of about 50 families world-wide to the present figure of 329. There is evidence for at least six, and possibly as many as thirteen, mass extinctions in the fossil record of amniotes, and the intensity of these events varies greatly. Taken at face value, the amniote fossil record does not support a model of periodic mass extinctions.

## Introduction

In considering mass extinctions, the fossil record of reptiles is often cited. The disappearance of the dinosaurs, as well as the flying reptiles, the pterosaurs, and the marine reptiles, the ichthyosaurs, plesiosaurs, and mosasaurs, at the end of the Cretaceous period comes to most people's minds as the best known example of a mass extinction. However, on closer analysis, it turns out that less is known about this event than is commonly assumed. Recent papers offer diametrically opposed views of how the dinosaurs disappeared—suddenly and catastrophically (Russell 1984), or gradually, over many millions of years (Schopf 1982; Carpenter 1984; Sloan *et al.* 1986). The Cretaceous–Tertiary boundary mass extinction event (the 'K–T event') is only one of several mass extinctions that have affected the history of reptiles, but data are just as confused for most of these as well.

In this paper, some aspects of the quality of the fossil record of reptiles will be considered—how incomplete is it and is it uniformly incomplete? Then, the patterns of diversification and mass extinction for the amniotes in general, and the various reptile groups in particular, will be outlined with comments on the extinct forms and the survivors. The nature of each event will be considered in turn, and the suggestion of a large-scale pattern, such as regular cyclicity, of mass extinction events will be discussed. However, first of all, we must consider whether there is any meaning in the phrase 'rates of evolution or extinction of the reptiles'. Is this a biologically meaningful concept?

### Rates of evolution of paraphyletic groups

The 'Reptilia', as understood by most biologists and palaeontologists (see e.g. Romer 1966) is a paraphyletic group. 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'—the relationships of the earliest reptiles, and of the 'reptile-like amphibians', are controversial, and it is still not clear where the boundary should be drawn: Carroll 1969, 1970, 1982; Heaton 1980; Heaton and Reisz 1986). However, the group 'Reptilia' does not include all of the descendants of that ancestor (Aves and Mammalia are excluded).

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. 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).

In the case of the reptiles, the Carboniferous, Permian, or early to middle Triassic systematist of reptiles would be observing a monophyletic group, whether he were a cladist or not. He could measure the rate of evolution of Reptilia with impunity since it is a monophyletic group in all senses. However, by the end of the Triassic period and in the Jurassic a contemporary taxonomist would have had a problem—should he recognize the two or three families of small hairy reptiles with their advanced jaws and inner ears as the new Class Mammalia, or not? Probably not, since their future key role in the history of life could not have been predicted. Likewise, the end-Jurassic or early Cretaceous taxonomist would have had to decide where to assign the first few feathered reptiles—whether to a new Class Aves, or whether to leave them alone.

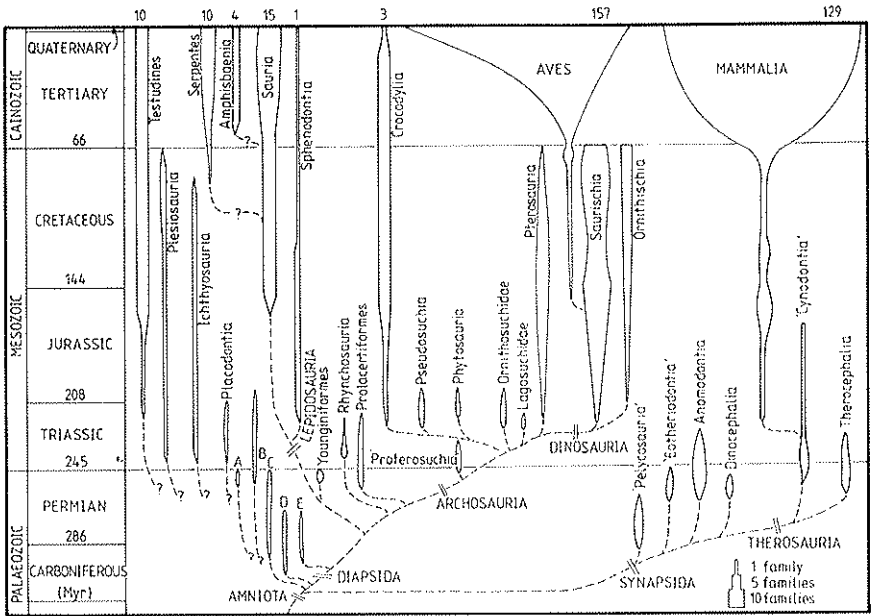
The decision to extract Mammalia and Aves from 'Reptilia' is clearly an *a posteriori* decision. In a study of the rates of evolution and extinction of reptiles, these two groups should be included in order to make the clade Amniota complete. Their exclusion artificially dents the diversity of the clade, and would clearly lower the values of any calculated measures of rates of origination or diversification. Until the origin of the Mammalia (generally reckoned to have occurred in the latest Triassic), of course, 'Reptilia' = Amniota, but after that, 'Reptilia' ceases to be a monophyletic group, and thus it cannot be used as a meaningful entity in macroevolutionary analysis. Nevertheless, several authors (e.g. Simpson 1952; Cutbill and Funnell 1967; Charig 1973; Pitrat 1973; Thomson 1977; Olson 1982) have done so.

No doubt, many other paraphyletic, and even polyphyletic, groups have been included in recent macroevolutionary analyses (see also Cracraft 1981). It is to be hoped that serious attempts will be made to use only clades in future studies—monophyletic groups that include all the descendants of a single common ancestor. The best way to identify clades is, of course, by means of cladistic analysis.

## The fossil record of reptiles

### 1. Scope

The first reptiles, and thus the first amniotes, according to most recent classifications (e.g. Romer 1966; Anderson and Cruickshank 1978; Carroll 1982; Heaton and Reisz 1986) are the Protorothyrididae (= Romeriidae), known first from the Moscovian Stage (*c.* 300 Ma) 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 Aracoscelidia (Reisz *et al.* 1984) and the 'Pelycosauria' (Kemp 1982), the most primitive groups of the Diapsida and Synapsida, respectively. These



**Fig. 13.1.** Phylogenetic tree of the Amniota, 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). Abbreviations: A, Parciaisauria; B, Procolophonina; C, Captorhinidae; D, Protorothyrididae; E, Araeoscelidia. Relationships of the groups are indicated by dashed lines on the basis of recent cladistic analyses (e.g. Gaffney 1980; Kemp 1982; Benton 1984, 1985a; Gauthier and Padian 1985; Heaton and Reisz 1986).

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, crocodiles, 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 diversity and importance of the Diapsida and Synapsida are indicated in the phylogenetic tree in Fig. 13.1. On the left-hand side are a number of lineages whose relationships are uncertain—the Permo-Triassic procolophonians and parciaisauroids, the Testudines (turtles), and the marine plesiosaurs, ichthyosaurs, and placodonts.

In all, there are 233 families of fossil and living reptiles, at a conservative estimate (Benton 1987), of which 200 are non-marine and 33 are exclusively marine. These figures exclude monospecific, monogeneric, and other doubtful or paraphyletic families. Of these, only 43 families still survive. There are 702 families of fossil and living amniotes, of which 644

are non-marine, 58 are exclusively marine (see Appendix), and 329 are still living.

## 2. *Quality of the fossil record*

The relative incompleteness of the fossil record of tetrapods has been described by many authors (e.g. Pirat 1973; Bakker 1977; Carroll 1977; Olson 1982; Padian and Clemens 1985; Benton 1985*b,c*, 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 characterized 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.

The completeness of a fossil record can be estimated according to a Simple Completeness Metric (SCM), by assessing the relative numbers of taxa that are known to be present compared to the numbers that ought to be present (Paul 1982). In the present study, families are the taxa of interest, and each tetrapod family generally spans 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. If a stratigraphic stage is entirely devoid of fossils, the SCM (numbers of Lazarus taxa/numbers of taxa represented by fossils) will equal 0 per cent. If every taxon is represented by fossils, the SCM will equal 100 per cent.

Benton (1987) has assessed the completeness of the fossil record of non-marine tetrapods, stage by stage, and by taxonomic classes. According to the SCM, the Aalenian (Jurassic) had a value of 0 per cent, while the Viséan (Carboniferous), Ufimian (Permian), and Scythian (Triassic) had values of 100 per cent. These values are only estimates of course, and the 100 per cent values are probably spurious since both the numbers of Lazarus taxa *and* the numbers of taxa represented by fossils are very small, and they are likely to be equally underestimated. For 'Reptilia' alone, the

completeness of the fossil record matches that for tetrapods as a whole, with particularly weak areas (SCM < 50 per cent) in the early—middle Jurassic (Toarcian–Bajocian), the late Jurassic (Oxfordian), the late Cretaceous (Turonian – Santonian), and the early Palaeocene (Danian).

Overall, the fossil record of reptiles compares well with that of other tetrapods. For all stratigraphic stages, the SCM is 78.2 per cent, compared to 84.3 per cent for mammals, 56.9 per cent for birds, and 56.3 per cent for amphibians. For the major reptile groups, the values are: Testudines, 69.5 per cent; Diapsida, 59.7 per cent (Lepidosauria, 48.6 per cent, Archosauria, 63.1 per cent); and Synapsida, 94.5 per cent (Benton 1987).

### 3. Family diversity data

Several authors have recently plotted graphs of the diversity of reptile families and orders through time (e.g. Charig 1973; Pitrat 1973; Bakker 1977; Thomson 1977; Olson 1982; Padian and 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*b,c*, 1986*a,b*) have been based on a new compilation of data on families of non-marine tetrapods (Benton 1987). This is supplemented by a compilation of data on the marine families given here in the Appendix. These new compilations differ significantly from those derived from Romer (1966) and Harland *et al.* (1967) in several ways:

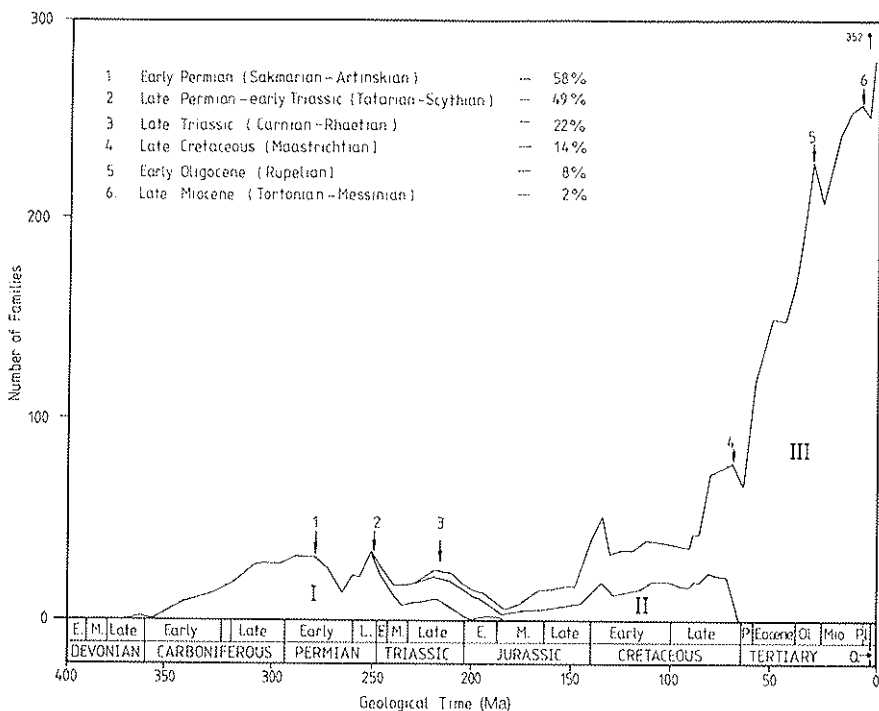
(1) New records up to the end of 1985 are included. This has affected the date of origination or extinction of as many as 50 per cent of families.

(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. Analyses of the diversity of orders and other higher taxa have not been carried out on the basis of the new compilation, but these would probably produce very different results from those in Olson (1982), Padian and Clemens (1985), and Colbert (1986).

(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 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) and elsewhere.

### 4. Family diversity analysis

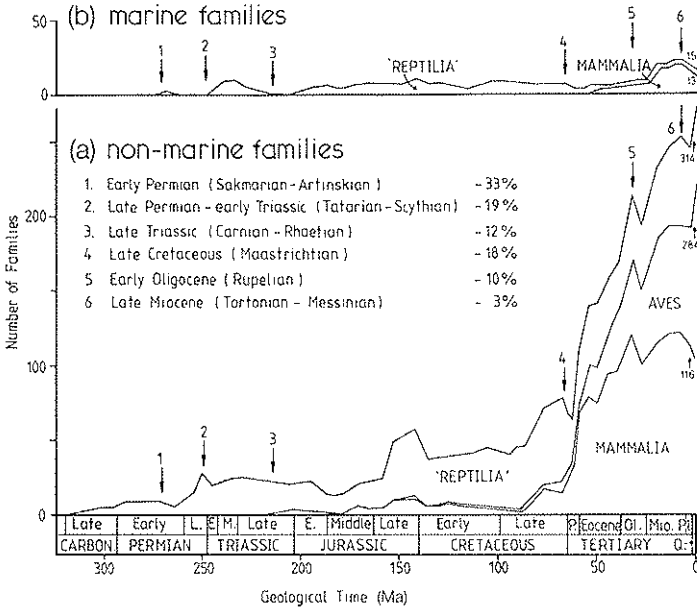
The new compilations of data on fossil tetrapod family diversities have been used for a variety of graphs and calculations. A small number of



**Fig. 13.2:** Standing diversity with time for families of non-marine terrestrial 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; Mio., Miocene; Ol., Oligocene; P., Palaeocene; Pl., Pliocene.

families that are based on single species or single genera have been omitted. This adjustment to the data set does not materially affect the results, and it excludes a number of problematic specimens, as well as plesion 'families' that lack autapomorphies (full details in Benton 1985c, 1987).

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. 13.2; Benton 1985b,c). Three major diversity assemblages have been identified (Benton 1985c), 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; II (early diapsids, dinosaurs, 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.



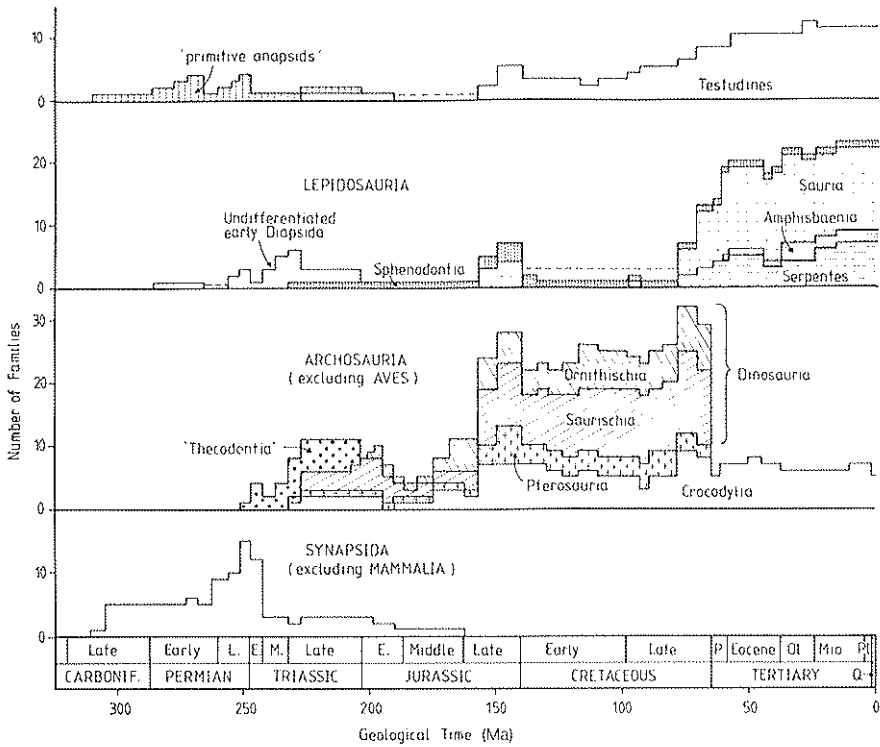
**Fig. 13.3.** Standing diversity with time for families of (a) non-marine and (b) marine amniotes. The curves for 'Reptilia', Mammalia, and Aves are shown separately. The relative magnitudes of the six drops in diversity that were probably caused by mass extinctions are shown for all amniotes together. Other conventions and abbreviations as in Fig. 13.2.

There appear to be six declines in diversity (Fig. 13.2, nos 1-6) that are attributable to mass extinction events. The other drops (early Jurassic, end-Jurassic, mid-Cretaceous) probably indicate mainly a change in the quality of the fossil record (Benton 1985*b,c*), and mass extinctions cannot be assumed here. These three episodes correspond to times when the SCM described above gives particularly low values.

The diversity of amniotes (i.e. tetrapods minus the amphibians) through time is plotted in Fig. 13.3, with data for non-marine and marine families separated. The six mass extinction events are indicated, although their effects are rather different from those for tetrapods as a whole (Fig. 13.2). The early Jurassic, end-Jurassic, and mid-Cretaceous falls in the non-marine record (Fig. 13.3a) are not matched by obvious declines in the marine record (Fig. 13.3b). This confirms, to some extent, the suggestion that these declines represent gaps in the fossil record of terrestrial amniotes since the marine record is largely independent. The problem with pressing this point too far is that the total diversity of families of marine amniotes is so low at all times that fluctuations probably mean very little.

The patterns of family diversity of the major reptilian groups are very different (Fig. 13.4). Most of the major groups shown here are assumed to





**Fig. 13.4.** Patterns of family diversity of the major reptilian groups. Diversity is plotted stage by stage, and each group is indicated by a different pattern of shading.

be monophyletic (Testudines, Lepidosauria, Sphenodontia, Sauria (?), Amphisbaenia, Serpentes, Ornithischia, Pterosauria, Crocodylia), but others are paraphyletic ('primitive anapsids', early Diapsida', Archosauria, 'Thecodontia', Saurischia, Synapsida). these graphs confirm the diversification of 'modern' groups from late Cretaceous times onwards, although the crocodiles have retained roughly constant diversity since the late Jurassic. Of the extinct groups, the dinosaurs (Saurischia + Ornithischia) and the pterosaurs maintained roughly level diversities from the late Jurassic until their extinction at the end of the Cretaceous. The Synapsida (mammal-like reptiles) clearly peaked in the late Permian, and their diversity crashed at the end of the Permian, and after the early Triassic, although they continued at low diversity until the end of the middle Jurassic.

Extinction and origination rates were calculated stage by stage for amniote families (marine and non-marine together), 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 ( $\Delta t$ ):

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

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):

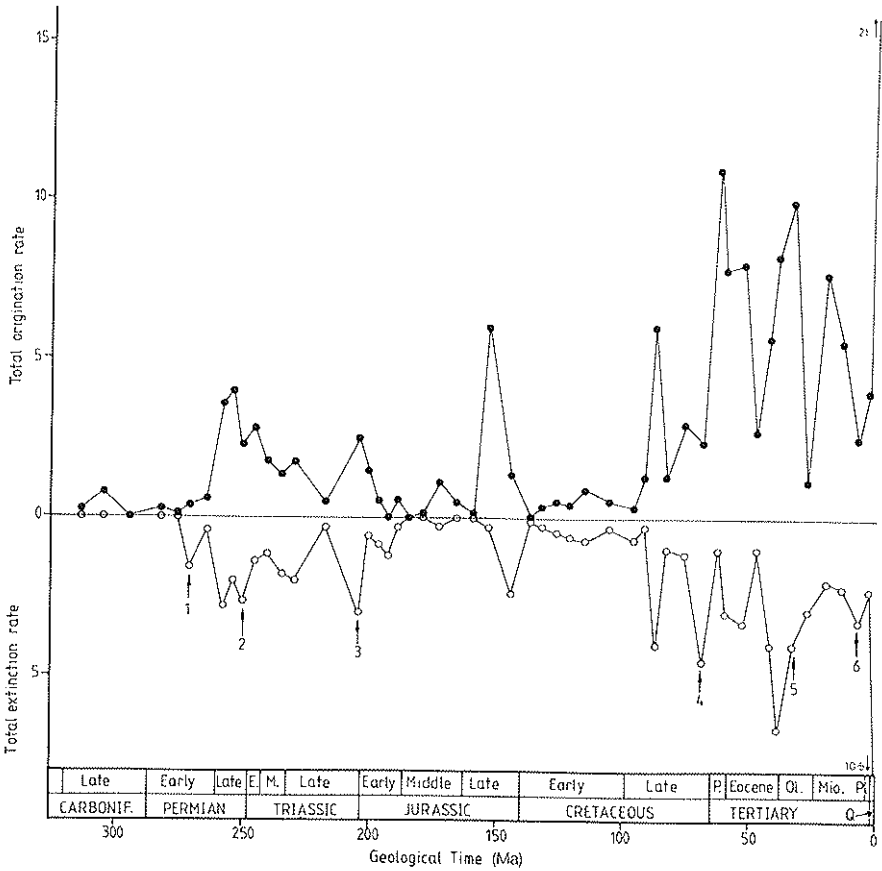
$$r_e = \frac{1}{D} \cdot \frac{E}{\Delta t} \quad \text{and} \quad r_s = \frac{1}{D} \cdot \frac{S}{\Delta t}.$$

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 Ma.

The graphs of total rates 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 Tatarian, 'Rhaetian', Maastrichtian, Rupelian, and late Miocene correspond to mass extinctions 2, 3, 4, 5, and 6 (Fig. 13.3), 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), Chattian (late Oligocene), and Pleistocene do not match any of the drops in amniote diversity that have been ascribed to mass extinctions. Conversely, the total extinction rate in the Artinskian (no. 1, Fig. 13.3) is not very high.

The total origination rates (Fig. 13.5) 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-Lagerstätten, such as the Sakamena Group (late Permian), the Solnhofen Limestone (Tithonian), the Messel deposits (Lutetian), Quercy Phosphorites (Bartonian-Rupelian); or the Oeningen Molasse (middle Miocene). The improvement in the record boosts the apparent number of family originations and extinctions (Hoffman and Ghiold 1985).

origination rates are re-calculated relative to the numbers of taxa available (Fig. 13.6), 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 (nos 1, 2, 3: Fig. 13.3). Per-taxon extinction rates are barely elevated at the times of the Maastrichtian, Rupelian, or late Miocene mass extinctions (nos 4, 5, 6: Fig. 13.3). These mass extinctions correspond to



**Fig. 13.5.** Total rates of origination and extinction for families of amniotes, calculated stage by stage for 51 stages between the late Carboniferous and the Pleistocene. The Miocene was divided into early, middle, and late units only, and the Pliocene was treated as a single time unit.

depressed per-taxon origination rates (Fig. 13.6), a phenomenon noted also for non-marine tetrapods as a whole (Benton 1985c).

The graphs of total rates and of per-taxon rates show broad trends. The total rates (Fig. 13.5) apparently *increase* on average towards the present day, while the per-taxon rates (Fig. 13.6) tend to *decrease*. Benton (1985c) found the same phenomenon for non-marine tetrapods. Raup and Sepkoski (1982) found, on the other hand, that total extinction rates for marine animals declined markedly through time, while Van Valen (1984), Van Valen and Maiorana (1985), and Kitchell and Pena (1985) found the same for per-taxon rates. In all these cases, the rates of decline were very

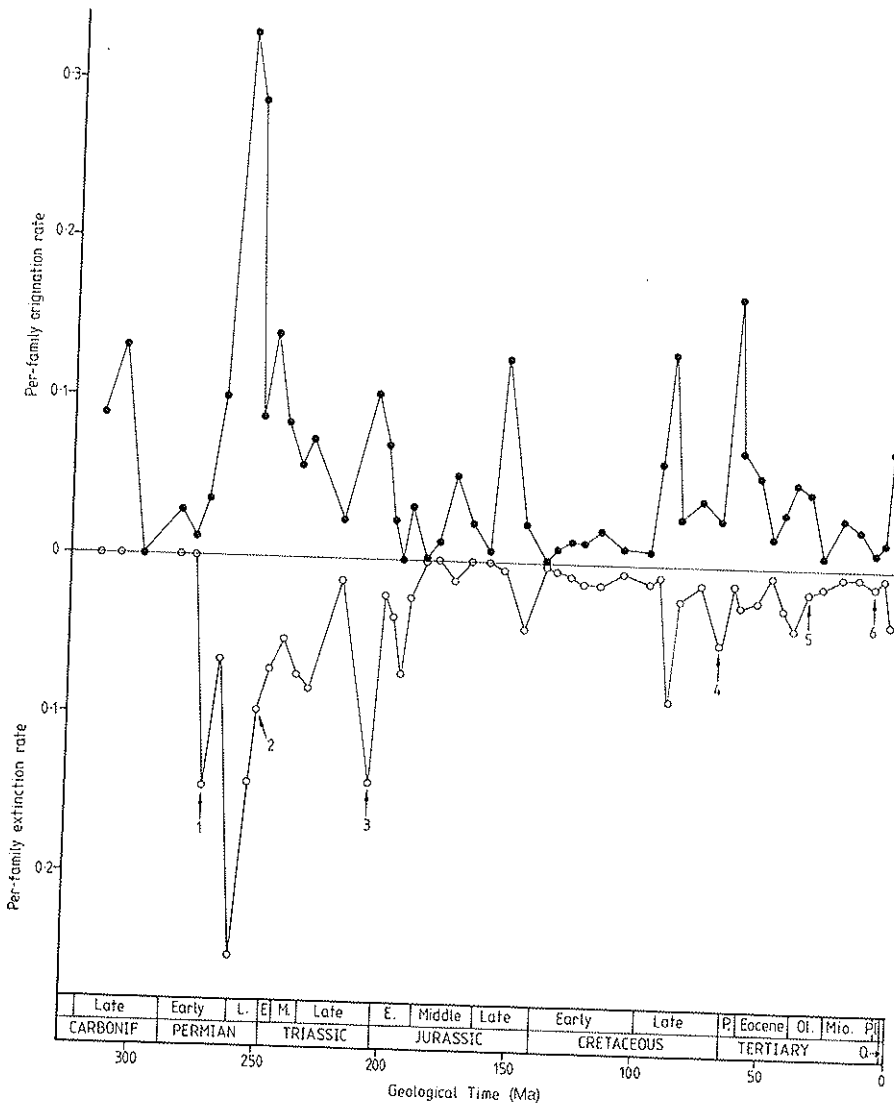


Fig. 13.6. Per-taxon rates of origination and extinction for families of amniotes. Conventions as in Fig. 13.5.

marked, while for non-marine tetrapods and for amniotes the declines in per-taxon rates are small.

The present data do not lend strong support to the idea that family extinction and origination rates indicate optimization of fitness through evolutionary time (Raup and Sepkoski 1982) or to relative decreases in diffuse competition between taxa within communities (Van Valen 1984).

Indeed the declines in extinction and origination rates in the marine record may be largely accounted for by the increase in the mean number of species per family through time (Flessa and Jablonski 1985). The fact that the per-taxon rates for families of amniotes or tetrapods do not decline so rapidly through time as those for marine animals in general may imply that the species:family ratio has not altered so much in these groups.

### 5. *Mass extinctions*

The history of non-marine tetrapods has apparently been punctuated by at least six mass extinction events (Fig. 13.2; Benton 1985c), together with up to seven other possible extinction events. These had widely differing effects, ranging from a 58 per cent drop in family diversity for the early Permian event to a 2 per cent drop for the late Miocene event.

These events also affected the amniotes, but to different extents after the removal of the amphibian data (Fig. 13.3). The late Triassic event hardly shows up at all in the non-marine amniote data (Fig. 13.3a, '3'), and the marine graph (Fig. 13.3b) is unconvincing for all six extinction events, except possibly the K-T ('4'), and the late Miocene ('6'). The relative declines in family numbers are summed for marine and non-marine amniotes together (Fig. 13.3), and the values range from 33 per cent (early Permian) to 3 per cent (late Miocene). The first three extinction events apparently had less marked effects on amniote family diversity as a whole (Fig. 13.3) than on non-marine tetrapods (Fig. 13.2), probably since the excluded amphibian families were heavily affected each time.

The six extinction events mentioned here, as well as other possible events, will be briefly described with notes on the groups that became extinct, and those that survived.

#### *Early Permian (Artinskian)*

Eight families died out during this event (no. 1: Figs 13.2 and 13.3):

'Anapsida': Protorothyrididae, Bolosauridae, Mesosauridae;

Diapsida: Aracoscelididae;

Synapsida: Eothyrididae, Edaphosauridae, Ophiacodontidae,  
Sphenacodontidae.

There were only three families that are known to have survived into the succeeding Kungurian Stage—the Captorhinidae ('Anapsida'), and the Caseidae and Varanopidae (Synapsida). The bulk of this mass extinction event affected the early synapsids, the pelycosaurs (loss of four families), and the two families of pelycosaurs that survived became extinct during the Kungurian Stage. The total extinction rate for amniote families in the Artinskian is not particularly high (Fig. 13.5), although the per-taxon

extinction rate (Fig. 13.6) is higher than most others. The total diversity of early Permian amniotes is too low ( $n = 6-11$ ) to read a great deal into these data.

#### *Late Permian (Tatarian)*

Twenty-one families of amniotes died out at the end of the Permian (event no. 2: Figs 13.2 and 13.3):

'Anapsida': Captorhinidae, Millerettidae, Parciasauridae;  
 Diapsida: Weigeltisauridae, Younginidae, Tangasauridae;  
 Synapsida: Ictidorhinidae, Gorgonopsidae, Dromasauridae,  
 Endothiodontidae, Cryptodontidae, Aulacocephalodontidae,  
 Dicynodontidae, Pristerodontidae, Cistecephalidae, Diictodontidae,  
 Moschorhinidae, Whaitsiidae, Silphestidae, Procyonosuchidae, Dviniidae.

The 'anapsids' and diapsids that died out range in size from 'small lizard' (Millerettidae) to massive herbivore (Parciasauridae), and they include the first gliding reptiles (Weigeltisauridae). These families occurred world-wide. None of the other 'anapsid' families actually spans the Permian-Triassic boundary, although the Procolophonidae might. Likewise, there may have been a slight hiatus in the evolution of the diapsids — the Proterosuchidae, the earliest archosaurs, is the only diapsid family known to have survived the end-Permian extinction event. However, several other larger diapsid lineages are known to have crossed the Permo-Triassic boundary (Fig. 13.1). The three diapsid families that died out were not restricted geographically, occurring as far apart as England and Madagascar.

The end-Permian extinction event decimated the mammal-like reptiles. Fifteen families out of the 20 that existed at the start of the Tatarian Stage died out (75 per cent decline). The groups going extinct range in size from the small dromasaurids to the hefty aulacocephalodontids. The extinctions span all groups of synapsids (Eotheriodontia, Anomodontia, Therocephalia, 'Cynodontia'), although the majority of families going extinct (eight) belong to the Anomodontia (eight out of ten extinct: 80 per cent decline). There seems to be no geographic control on extinction and survival.

Several families of mammal-like reptiles survived across the Permo-Triassic boundary (Emydopidae, Kingoriidae, Ictidosuchidae, Scaloposauridae, Galesauridae). However, the widespread '*Lystrosaurus* faunas' of South Africa, India, China, Russia, Antarctica, and Australia, which are generally dated as lowermost Triassic in age (Anderson and Cruickshank 1978; Tucker and Benton 1982), are apparently depleted. The best known examples of this fauna, in South Africa and Antarctica, are heavily dominated by one dicynodont genus, *Lystrosaurus* (c. 90 per cent of all individual tetrapod specimens collected; Benton 1983). There seems to be little doubt that these are 'post-extinction faunas' in which diversity is low

and a great deal of ecospace has been emptied by a major event. Four or five million years later, apparently more balanced faunas are found in which no single genus is so dominant, and in which other lineages have diversified.

The total (Fig. 13.5) and per-taxon (Fig. 13.6) extinction rates for the Tatarian are fairly high, but not as high as those in the Ufimian, the first stage in the late Permian, when there was not a drop in amniote family diversity.

#### *Early Triassic (Scythian)*

There was another smaller extinction event about 5 Ma later, at the end of the Scythian Stage, when seven reptile families died out:

Diapsida: Proterosuchidae, Euparkeriidae;

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

These extinctions did not cause an overall decline in amniote diversity (Fig. 13.3) because of the matching rate of origination of new families in the Scythian. This event had a greater effect on the amphibians (Fig. 13.2). Several authors have suggested that there was a mass extinction event amongst tetrapods at this time (Olson 1982; Benton 1985*b,c*, 1986*a,b*; 1987, Bray 1985), while others have pointed to a small mass extinction of marine invertebrates (Raup and Sepkoski 1984, 1986; Hoffman 1985; Hoffman and Ghiold 1985; Benton 1986*a*).

#### *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 time scales is employed. Raup and 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 (no. 3: Figs 13.2 and 13.3), 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 amniotes died out:

Diapsida: Thalattosauridae, Trilophosauridae, Rhynchosauridae, Proterochampsidae;

Synapsida: Kannemeyeriidae, Chiniquodontidae;

'Euryapsida': Nothosauridae, Simosauridae, Cymatosauridae,

Henodontidae.

These families include a broad range in ecological and taxonomic terms. Two of the families (Rhynchosauridae, Kannemeyeriidae) were important

herbivores with nearly global distributions, but other similarly widespread herbivores (Actosauridae) survived. Most other thecodontian groups, as well as the earliest dinosaurs and a few mammal-like reptiles, survived as well.

The marine reptiles were heavily affected, with four out of six families going extinct. The last of the nothosaurs disappeared (Nothosauridae, Simosauridae), as well as one plesiosaur family (Cymatosauridae), and one placodont family (Henodontidae). The Placochelyiidae (placodonts) and the Shastasauridae (ichthyosaurs) survived the event.

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

'Anapsida': Procolophonidae;

Diapsida: Phytosauridae, Actosauridae, Rauisuchidae, Ornithosuchidae;

'Euryapsida': Placochelyiidae.

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 amniote families (Figs 13.5 and 13.6), but the peaks are higher for the latter event.

#### *Jurassic–Cretaceous events*

Raup and Sepkoski (1984, 1986) and Sepkoski and Raup (1986) have identified a number of 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
	Bajocian	176 Ma
	Callovian	163 Ma
	Tithonian	144 Ma
Cretaceous:	Hauterivian	124 Ma
	Aptian	113 Ma
	Cenomanian	91 Ma

Raup and Sepkoski (1986), and Sepkoski and Raup (1986) express some



doubt about the Bajocian, Callovian, Hauterivian, and Aptian peaks, but regard the Pliensbachian, Tithonian, and Cenomanian events as 'significant'.

The data on amniote families, and on reptiles in particular, are particularly weak during parts of this time interval (see above). There are indeed declines in family diversity in the non-marine tetrapod (Fig. 13.2) and the amniote (Fig. 13.3) data after the Pliensbachian, Tithonian, and Cenomanian, with the decline after the Tithonian standing out best. There are also slight peaks in total (Fig. 13.5) and per-taxon (Fig. 13.6) extinction rates in the Pliensbachian and Cenomanian, with a more marked peak in the Tithonian. However, the extinction rate peaks in the Coniacian are even larger, but this could be an artefact of the short estimated duration (1 Ma) of that stage (Sepkoski and Raup 1986).

There could be mass extinction events amongst amniotes at the times found by Raup and Sepkoski (1984) in the record of marine animals, but the present data are not good enough to decide either way.

#### *Late Cretaceous (Maastrichtian)*

The Cretaceous-Tertiary boundary (K-T) event is surely the best known mass extinction, and not least for its effect on the reptiles (dinosaurs, pterosaurs and plesiosaurs all died out then). However, in relative terms at least, the percentage loss of families of amniotes as a whole (no. 4: Fig. 13.3) was less than for the two Permian events already described, and for non-marine tetrapods (no. 4: Fig. 13.2), the K-T event was apparently less significant than the late Triassic events as well. The total extinction rate for the Maastrichtian (Fig. 13.5) is higher than any before it, but the per-taxon rate for amniotes (Fig. 13.6) is not so impressive, being lower than the 'Rhactian', Pliensbachian, and Coniacian rates, for example. The decline in amniote family diversity at the K-T boundary is caused partly by a slightly elevated extinction rate, and partly by a low origination rate (Benton 1985c).

Thirty-six families of amniotes 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: Baptornithidae, 'Enantiornithes', Lonchodytidae, Torotigidae;

## Mammalia

Marsupialia: Pediomyidae, Stagodontidae;  
Eutheria: Lepticoidea n. fam., Perutheriidae;

## 'Euryapsida'

Plesiosauria: Elasmosauridae, Cryptocleididae, Polycotylidae.

The K–T event was clearly taxonomically selective and 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, crocodiles, 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.

There has been much debate about whether the K–T event was sudden or not. Many of the reptile groups that had been dominant in the Mesozoic were declining well before the end of the Cretaceous. The ichthyosaurs died out in the Cenomanian, 30 Ma earlier (Baird 1984), and the pterosaurs were reduced from five or six families to only two in the Maastrichtian. Nevertheless, 19 families of dinosaurs existed at the start of Maastrichtian times and died out before the K–T boundary. Russell (1984) argued that they nearly all died out catastrophically right at the K–T boundary, while Schopf (1982), Carpenter (1984), and Sloan *et al.* (1986) suggested that the dinosaurs declined in diversity and abundance during the 8–9 Ma of the Maastrichtian, and that only a few genera remained by the time of the K–T boundary. More palaeontological and stratigraphic work is required on this important aspect of the K–T event.

*Late Eocene (Priabonian)*

Raup and Sepkoski (1984, 1986), and others, identify a mass extinction amongst marine animals at the Eocene–Oligocene boundary, but this does not appear in the summary tetrapod or amniote data (Figs 13.2 and 13.3). This corresponds to the 'Grande Coupure' of French vertebrate palaeontologists, a marked extinction event amongst amphibians, reptiles, birds, and mammals in Europe. A detailed analysis of amphibians and reptiles at this time (Rage 1984) shows extensive extinctions amongst species and genera. However, the event seems to have had less effect at the family level, and it was apparently largely restricted to Europe. On a global scale, there were slight declines in the diversity of non-marine tetrapod (Fig. 13.2) and amniote (Fig. 13.3) families, and extinction rates were high (Figs 13.5 and 13.6). However, there were no extinctions of families of amphibians or reptiles.

*Early Oligocene (Rupelian)*

Tetrapod, and amniote, diversity declined markedly in the mid-Oligocene (no. 5: Figs 13.2 and 13.3), after the extinction of 28 families during the early Oligocene. The main losses occurred amongst the Mammalia (26 families of non-marine and marine mammals), with only one bird family and one reptile family (the lizards *Necrosauridae*) becoming extinct at that time. Extinction rates of amniote families were not particularly high (Figs 13.5 and 13.6), but they were matched by low origination rates. This event has been recognized also by Prothero (1985) for North American land mammals, but it does not appear to correspond to events that affected marine invertebrates.

*Late Miocene (Tortonian–Messinian)*

The late Miocene extinction event amongst tetrapods and amniotes is marked by a decline in family diversity (no. 6: Figs 13.2 and 13.3). Twenty families of amniotes died out, but no reptiles were amongst them. The majority of extinctions affected the mammals, with particular losses amongst primates, artiodactyls, notoungulates, and cetaceans. Extinction rates (Figs 13.5 and 13.6) were not particularly elevated. This event follows the Middle Miocene mass extinction identified by Raup and Sepkoski (1984, 1986) for marine animals.

*Pleistocene*

The Pleistocene extinctions do not show up on the graphs of non-marine tetrapod and amniote family diversity (Figs 13.2 and 13.3), because of the matching rise in numbers of Pleistocene and Holocene families. Twenty-one families of amniotes died out in the Pleistocene, but amongst reptiles these include only the giant Australian turtles, the *Meiolaniidae*, and the *Euthecodontidae*, crocodiles known from Africa and Australasia at that time.

*6. Periodicity of amniote mass extinctions?*

Raup and Sepkoski (1984, 1986), and Sepkoski and Raup (1986) have presented evidence for periodicity in the occurrence of mass extinctions on the basis of several analyses of the fossil record of families and genera of marine animals. In the mid-Permian to Pleistocene span of time, they found a mean spacing of 26 Ma between events, and a considerable literature has already grown up to do with the nature of the periodicity, and the possible extraterrestrial causes (Sepkoski and Raup 1986).

The record of fossil reptiles, and of amniotes as a whole, spans the same time interval and, for the non-marine portion of the data set at least (which represents 90.1 per cent of the numbers of families — 644 non-marine: 58

marine), it provides a partially independent test of the periodicity hypotheses. The main problem, as has been outlined above, is the fact that the fossil record of non-marine amniotes is probably more patchy than that of marine invertebrates.

The mass extinctions identified by Raup and Sepkoski (1984, 1986) on the basis of their analysis of marine animals are listed in Table 13.1, with age dates from Palmer (1983). The mass extinctions amongst amniote

**Table 13.1.** The extinction events determined in the marine animal fossil record by Raup and Sepkoski (1984, 1986), with age dates from Palmer (1983). Events regarded as 'doubtful' or 'possible' by Raup and Sepkoski (1986) are shown with a question mark. The extinction events that affected non-marine tetrapods, and amniotes in general, are indicated, also with a question mark for the uncertain events. The spacings between the latter events are indicated

Marine events (system and stage)	End of interval (Ma)	Tetrapod and amniote events	Spacing (Ma)
Tertiary, Pliocene?	1.6		
	5.3	Tertiary, late Miocene	
			24.7
Tertiary, Middle Miocene	11.2		
	30.0	Tertiary, early Oligocene	
			6.6
Tertiary, late Eocene	36.6	Tertiary, late Eocene?	
			29.8
Cretaceous, Maastrichtian	66.4	Cretaceous, Maastrichtian	
	87.5	Cretaceous, Coniacian?	
			21.1
Cretaceous, Cenomanian	91	Cretaceous, Cenomanian?	
Cretaceous, Aptian	113		
			53
Cretaceous, Hauterivian?	124		
Jurassic, Tithonian	144	Jurassic, Tithonian	
Jurassic, Callovian?	163		
			49
Jurassic, Bajocian?	176		
Jurassic, Pliensbachian	193	Jurassic, Pliensbachian?	
			15
Triassic, 'Rhaetian'	208	Triassic, 'Rhaetian'	
Triassic, Norian	216		
Triassic, Carnian?	225	Triassic, Carnian	
			17
Triassic, Scythian?	240	Triassic, Scythian?	
			15
Permian, Tatarian	245	Permian, Tatarian	
			5
	263	Permian, Artinskian	
			18

families are listed for comparison. Many of the amniote events correspond to the marine events, but there are large gaps, particularly in the Jurassic and Cretaceous, where there is no clear evidence for mass extinctions. There are also three extinctions amongst amniotes ((?) Coniacian, early Oligocene, late Miocene) that are not matched by marine events, one (Artinskian) that lies outside the time interval studied by Raup and Sepkoski (1984, 1986), and one (Carnian) that seems more certain for amniotes than for marine animals.

In view of the uncertainties involved, it is probably pointless to try to calculate periodicities from the amniote mass extinctions. Nevertheless, the spacings between all probable and possible events are indicated in Table 13.1. Some of the spacings approximate to the 26 Ma period suggested by Raup and Sepkoski (1984, 1986) or to multiples thereof, but the majority do not, particularly those in the Permian and Triassic. If taken at face value, the non-marine tetrapod family data and the amniote family data do not support a model of periodic extinction events.

### Acknowledgement

I thank Ms Libby Lawson for drafting the diagrams.

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## Appendix

The distributions in geological time of families of marine amniotes. Supplement to the listing of non-marine amniotes in Benton (1987), based largely on Sepkoski (1982; and revisions dated August 1985), with additional sources of information indicated in the relevant places. Families that contain marine and non-marine members have been listed in Benton (1987), and they are not repeated here. Stratigraphic abbreviations are the standard stage abbreviations given in Harland *et al.* (1982).

'Reptilia': *Incertae sedis* (Anderson and Cruickshank 1978)

Mesosauridae ART

'Reptilia': *Testudines*

Chelonioidae	
Protostegidae	CEN-CHT
Toxochelyidae	ALB-YPR
Dermochelyidae	YPR-REC
Cheloniidae	ALB-REC

'Reptilia': *Diapsida: Archosauria*

Crocodylomorpha (Buffetaut 1982)

Teleosauridae	TOA-VAL
Metriorhynchidae	BTH-HAU
Dyrosauridae	MAA-PRB



'Reptilia': *Diapsida: Lepidosauria*

## Sauria

Aigialosauridae	TTH-ALB?
Dolichosauridae	?ALB-CMP?
Mososauridae	CEN-MAA

'Reptilia': *Euryapsida*

## Nothosauria

Nothosauridae	SCY-CRN
Pachypleurosauridae	ANS-LAD (Carroll 1985)
Simosauridae	?ANS-CRN

## Plesiosauria (Brown 1981)

Pistosauridae	LAD
Cymatosauridae	?LAD-CRN
Plesiosauridae	IJET-TOA
Leptocleididae	HET-HAU
Pliosauridae	HET-CON?
Elasmosauridae	TOA-MAA
Cryptocleididae	CAL-MAA
Polycotylidae	APT-MAA

## Placodontia

Placodontidae	SCY-LAD
Helveticosauridae	ANS-LAD
Placochelyiidae	ANS-RITT
Henodontidae	CRN

## Ichthyosauria (Mazin 1982, 1984)

Unnamed family	SCY-LAD
Omphalosauridae	ANS
Mixosauridae	ANS-LAD
Shastasauridae	LAD-NOR
Ichthyosauridae	HET-TTH
Stenopterygiidae	SIN-PLB
Leptopterygiidae	SIN-CEN

## Mammalia (Savage and Russell 1983)

## Cetacea (Fordyce 1982)

Protocetidae	LUT
Basilosauridae	BRT-RUP
Dorudontidae	PRB-RUP
Squalodontidae	RUP-UMI
Cetotheriidae	RUP-PLI
Patriocetidae	CHT
Agorophiidae	CHT
Eurhinodelphidae	LMI-UMI
Kentriodontidae	LMI-UMI

Acrodelphidae	LMI-PLI
Platanistidae	LMI-REC
Ziphiidae	LMI-REC
Physeteridae	LMI-REC
Phocaenidae	LMI-REC
Delphinidae	LMI-REC
Balaenopteridae	LMI-REC
Balaenidae	MMI-REC
Monodontidae	UMI-REC
Sirenia	
Dugongidae	YPR-REC
Manatidae	LMI-REC
Carnivora: Pinnipedia	
Enaliarctidae	LMI
Desmatophocidae	?LMI-UMI
Odobenidae	LMI-REC
Phocidae	MMI-REC
Otaridae	UMI-REC