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## Chapter 9

# **PATTERNS OF EVOLUTION AND EXTINCTION IN VERTEBRATES**

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## **PATTERNS OF EVOLUTION AND EXTINCTION IN VERTEBRATES**

Vertebrates have not figured as strongly in analyses of patterns of diversity and extinction as have invertebrates. This is probably because of a general perception of their fossil record as less complete, both taxonomically and stratigraphically, than that of marine invertebrates in particular. This is especially the case since much of the vertebrate fossil record is terrestrial, and terrestrial environments are generally poorly represented compared to marine ones. A final problem is the overall size of the data set—there are probably only about 1400 known families of living and extinct fish and tetrapods (the land vertebrates—amphibians, reptiles, birds and mammals). This compares with over 3000 families of marine invertebrates (Sepkoski 1982). However, the vertebrate fossil record has advantages for macroevolutionary study, since the taxonomy is mature enough in many parts for the recognition of monophyletic groups, and there is scope for detailed ecological analysis.

## **THE NATURE OF THE VERTEBRATE FOSSIL RECORD**

Vertebrates have been informally divided into 'fish' and tetrapods. The 'fish' include a variety of swimming forms in the seas and in freshwater, and the term is useful shorthand for these forms, although it is no longer generally used in classifications because it is ill-defined. Carroll (1987) provided a formalised classification of vertebrates (Table 9.1). Their broad temporal distributions and relationships are shown in Figure 9.1.

Table 9.1. Numbers of families of fishes and tetrapods.

Taxon	Living and extinct	Total living	Living only	Singletons*
Class Agnatha	39	2	1	7
Class Placodermi	37	0	0	11
?Class Acanthodii	5	0	0	0
Class Chondrichthyes	76	40	5	5
Class Osteichthyes	618	416	207	18
Chondrostei	52	3	0	5
'Holostei'	10	2	0	1
Teleostei	531	409	206	12
Sarcopterygii	25	3	1	0
All 'fish'	775	459	213	41
Class Amphibia	102	23	1	16
Class 'Reptilia'	233	43	7	49
Class Aves	202	157	48	11
Class Mammalia	379	129	26	0
All tetrapods	916	352	82	76
All vertebrates	1691	811	295	117

\*Singletons are families represented by a single species from a single geologic formation.

### *An outline of vertebrate evolution*

The first vertebrates are known from scrappy fossils of bony plates from the Late Cambrian. These are ascribed to agnathan (literally 'jawless') fishes which flourished in freshwater and marine environments in the Silurian and Devonian as generally heavily armoured forms. They declined thereafter, and are represented today by the eel-like lampreys and hag-fishes.

The only extinct clan of vertebrates, the placoderms ('platy skin'), were also heavily armoured fishes in Devonian seas and freshwaters. These were the first vertebrates with jaws—the agnathans had only suckers and rasping tooth plates. The placoderms were able to adopt fully predatory modes of life, and some became very large. *Dunkleosteus* may have reached a length of 9 m.

The Chondrichthyes ('cartilaginous fish'), including sharks, rays, and chimaeras, arose in the Devonian and went through a major radiation in the Carboniferous and Permian. These early groups largely died out in the

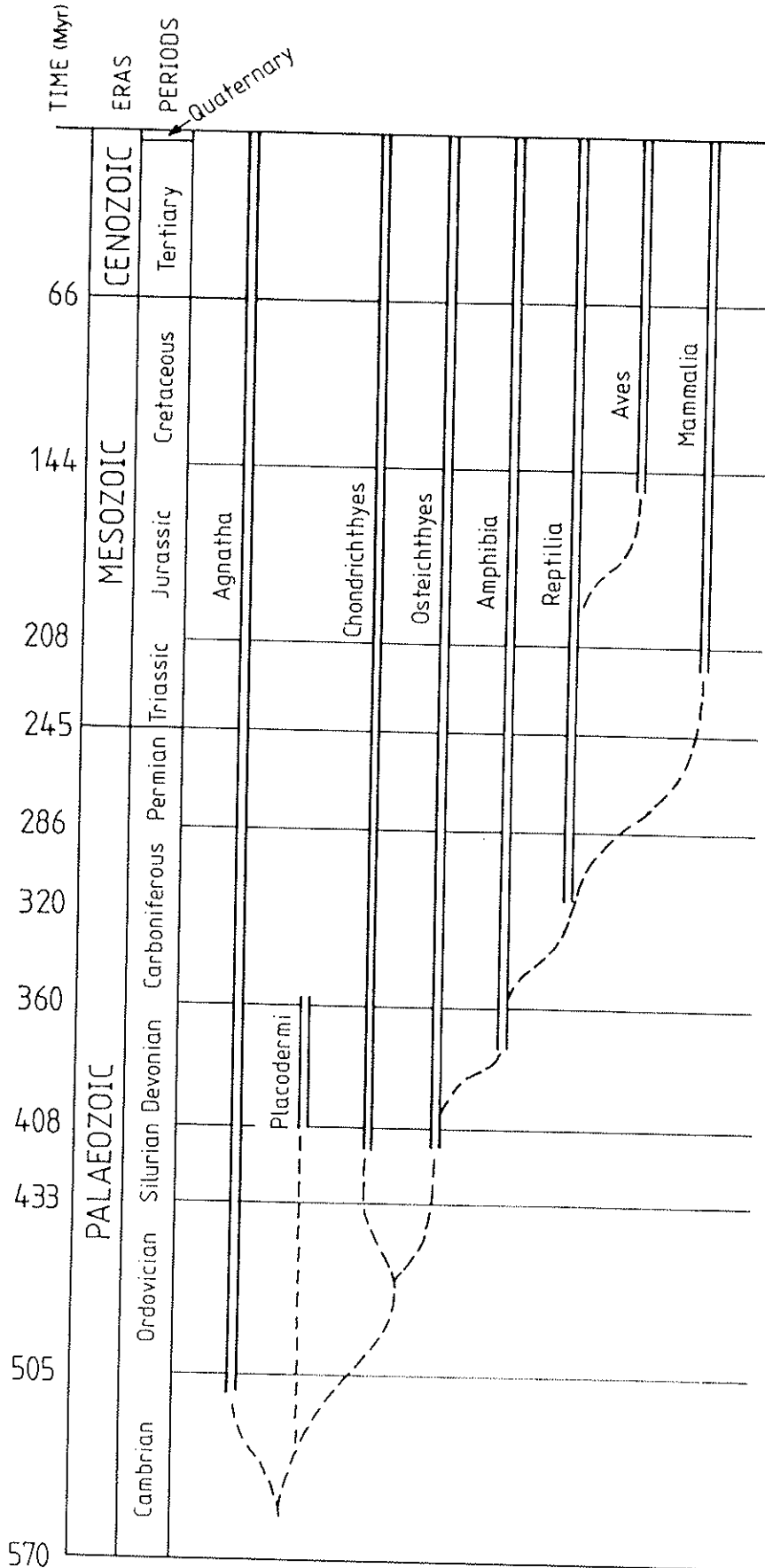


Figure 9.1. Summary of the temporal distribution of vertebrate classes and their probable relationships. (After Carroll 1987.)

Permian and Triassic, and a second radiation, when all the modern groups arose, began in Jurassic times.

The Osteichthyes ('bony fish') also arose in the Devonian, and they have become by far the most diverse and abundant group of fish—there are over 20 000 living species in 409 families. Osteichthyan evolution went through three phases of major radiation. The first, from Devonian to Late Triassic times, consisted mainly of heavily-scaled forms with simple jaws, the 'chondrosteans', of which the sturgeon and paddle fish are living representatives. This radiation also involved a variety of sarcopterygians, or lobe-finned fish, which included the ancestors of tetrapods. Living sarcopterygians include the rare coelacanth, and the lungfishes. The second osteichthyan radiation, which began in the Early Triassic and continued through the Mesozoic, was of 'holostean' forms which still had heavy scales, but whose jaw apparatus was more advanced than in 'chondrosteans'. Living forms include *Amia*. The third, and largest, osteichthyan radiation took place in the Jurassic and Cretaceous and involved the teleosts, which have light scales and very flexible jaws that together allow fast swimming and great adaptability in feeding modes. Modern teleosts include familiar forms such as cod, herring, carp, and perch, as well as more unusual fish such as flatfish, sea horses, and angler fish.

The Amphibia ('both' modes of life—water and land) include frogs and salamanders today, but these modern groups did not appear until the Mesozoic, radiating mainly in the Late Cretaceous and Tertiary. The first amphibians arose in the Late Devonian and radiated in the Carboniferous, Permian and Triassic as the heavily-built semi-aquatic temnospondyls (Carboniferous–Jurassic), the generally more terrestrial anthracosaurs (Carboniferous–Permian), and the small salamander and lizard-like lepospondyls (Carboniferous–Early Permian).

The Reptilia ('crawling' animals) arose from anthracosaurs in the Late Carboniferous. They soon split into three main lineages, the anapsids (including living turtles), the diapsids (including dinosaurs, crocodiles, pterosaurs, lizards and snakes), and the synapsids (the mammal-like reptiles essentially of the Permian and Triassic). These are all basically terrestrial groups, with some secondarily aquatic forms (turtles, crocodiles, sea snakes). The main radiations took place in the Permian (Synapsida), Late Triassic–Cretaceous (Dinosauria), and Late Cretaceous onwards (lizards, snakes).

The Aves (birds) are feathered flying diapsids which arose from smaller bipedal carnivorous dinosaurs in the Late Jurassic, and radiated modestly in the Late Cretaceous and more extensively in the Cenozoic to reach the present total of about 150 families.

The Mammalia arose in the Late Triassic from small carnivorous mammal-like reptiles and radiated only a little in the Jurassic and Cretaceous. The modern groups—Monotremata (echidna, platypus), Marsupialia (pouched forms: kangaroo, wombat, opossum) and Eutheria (placental mammals: bats, humans rabbits, rats, whales, horses, etc.) all arose

around the Early Cretaceous (Late Jurassic–Early Cretaceous for the Monotremata, and mid-Cretaceous for the Marsupialia and Eutheria). The Marsupialia and Eutheria radiated modestly in the Late Cretaceous, and then diversified extensively in the Cenozoic to give the present total of about 130 families.

### Relationships

It is important to establish clades, or monophyletic groups, for use in macroevolutionary studies (Cracraft 1981; Benton 1988a). 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. Such groups should, however, as far as can be determined, include all of the descendants of a single common ancestor (i.e. *monophyletic* is synonymous with *holophyletic* for some authors; Figure 9.2). It would clearly be pointless in most contexts to discuss the evolution of a *poly-*

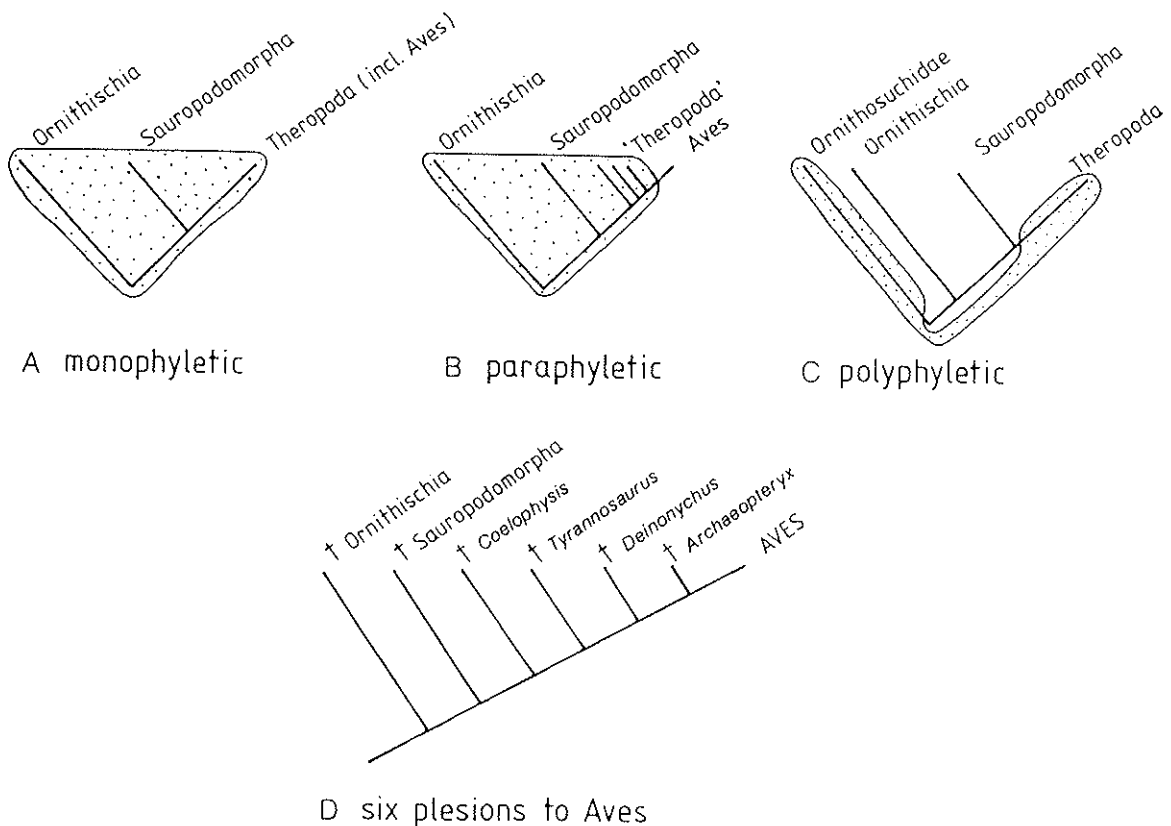


Figure 9.2. Kinds of phylogenetic group, based on a dinosaurian example. A: Dinosauria, a monophyletic group, including all descendants of one ancestor; B: Dinosauria (excluding birds), a paraphyletic group, including some, but not all, descendants of one ancestor; and, C: a polyphyletic group of carnivorous bipeds derived from more than one immediate ancestor. D: The relationships of birds to their closest extinct relatives among the dinosaurs, all of which are plesions of the crown-group Aves.

*phyletic* group (i.e. derived from several ancestors) since these are entirely human inventions. A *paraphyletic* group (Figure 9.2), 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 are artificial. Reptilia, therefore, 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 Vertebrata is cladistic character analysis, in which patterns of relationship are established on the basis of shared derived characters (synapomorphies). Most vertebrate 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 vertebrates 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. Chondrostei, Labyrinthodontia, Cotylosauria, Eosuchia, Thecodontia, Prototheria.

Most studies of vertebrate macroevolution have been based on families, and the new classifications, therefore, have 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 (Figure 9.2D). 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 of origination and extinction rates until a second occurrence is discovered. For example, the Family Archaeopterygidae arose and disappeared instantaneously, being represented only by the species *Archaeopteryx lithographica* (albeit by several specimens) from rocks of a single age.

Figure 9.3 shows the broad patterns of evolution in the 'fishes' and the tetrapods. It would clearly be inappropriate to survey the relationships and

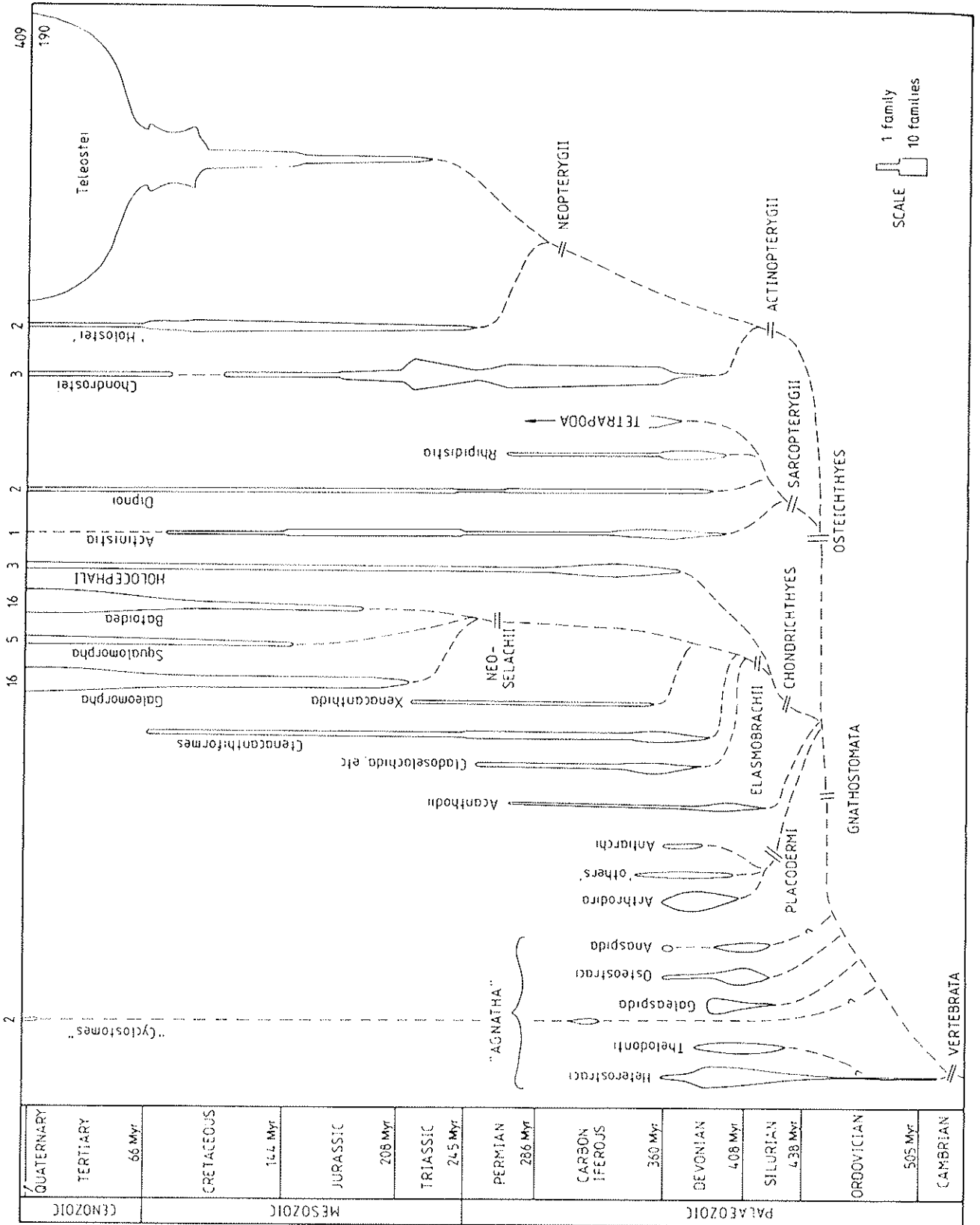
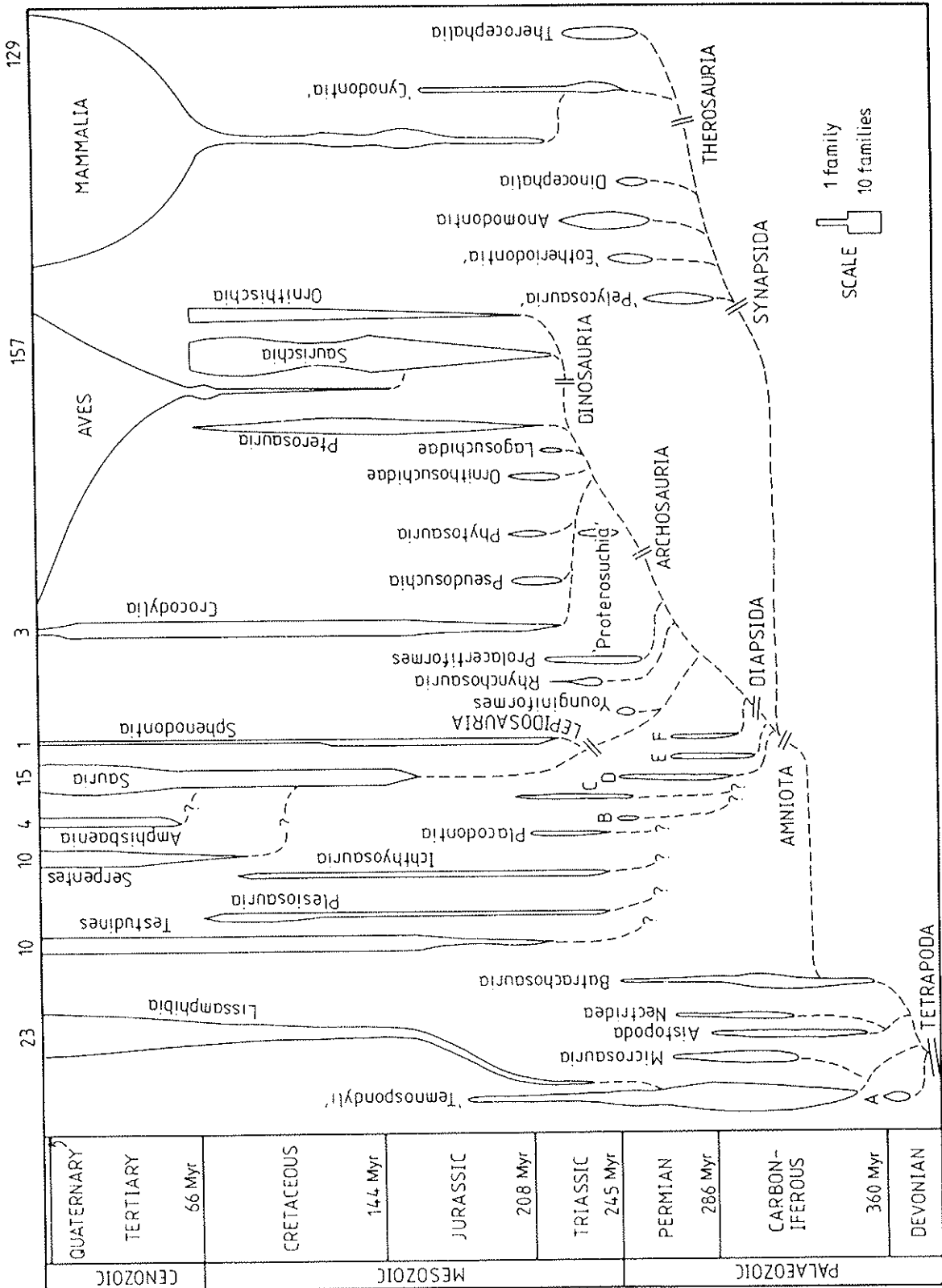


Figure 9.3. Phylogenetic trees of A: fish taxa, and B: the Tetrapoda, showing relationships, stratigraphic duration, and diversity of each group. The major groups are indicated as balloons that show the known stratigraphic range by their height, and the relative numbers of families present by their width (see scales in bottom right-hand corner). Relationships of the groups based on recent cladistic analyses



(e.g. Gaffney 1980; Kemp 1982; Benton 1984; 1985c; Gauthier 1986; Heaton and Reisz 1986; Maisey 1986; Panchen and Smithson 1987; 1988) are indicated by dashed lines. Abbreviations: A, Ichthyostegalia; B, Pareiasauria; C, Procolophonina; D, Captorhinidae; E, Protorothyrididae; F, Araeoscelidia.



evolutionary fate of all vertebrate families here. Reviews that treat major groups cladistically include: Maisey (1986) on early chordate and 'fish' relationships; Forey (1984) on agnathans; Goujet (1984) on placoderms; Maisey (1984) on chondrichthyans; Gardiner (1984) on osteichthyans; Panchen and Smithson (1987) on sacropterygians; and papers in Benton (1988b) on tetrapods.

### *Size of the data set*

There are 459 families of living fishes (including 409 families of teleosts) and 352 families of living tetrapods (including 157 families of birds and 139 families of mammals). The total figures for living and extinct families are 775 for fishes and 916 for tetrapods, or 1691 for all vertebrates. This is smaller than the marine animal data set of 3300 families (Sepkoski 1982) used in most studies of diversification and mass extinction to date. This total of 1691 is reduced to 1396, because 295 families of vertebrates have no known fossil representatives (these are mainly teleosts, birds and mammals). A further culling of the data has been made to exclude the small number of families that have been based on a single species or a single genus found in one geological formation ('singletons', a total of 117 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 sensibly included in calculations of rates of origination or extinction.

### *Incompleteness of the record*

The relative incompleteness of the fossil record of vertebrates has been described by many authors (e.g. Pitrat 1973; Thomson 1977; Padian and Clemens 1985; Benton 1985a; 1985b; 1987; see Chapter 5). The record of fishes is generally assumed to have been better than that of non-marine tetrapods, largely since aquatic environments are assumed to be more frequently preserved than terrestrial environments. However, there is a gap between the Llanvirnian and the Llandoveryan which is presently devoid of fish fossils. Particular groups of fishes are also absent from long stretches of geologic time. For example, the Myxinidae (hagfishes) appear in the Late Carboniferous, but are unknown between that time and the present day. Coelacanth (Actinistia) are unrepresented from the Late Cretaceous to the present, and there is a mid-Cretaceous gap (Barremian–Santonian) in the record of chondrostean bony fish. The record of non-marine tetrapods is demonstrably 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.

It is possible to estimate the completeness of the vertebrate record in a broad way by examining the numbers of families present per stage. The Simple Completeness Metric (SCM, Paul 1982; Benton 1987; 1988a) compares the numbers of families that are known to be present compared to the numbers thought to be present. The SCM is based on the fact that vertebrate 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) 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. 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 using the vertebrate fossil record in evolutionary studies*

#### *High probability of identifying clades*

Rates of evolution, origination, and extinction must be analysed, as noted above, on the basis of monophyletic groups. Vertebrates have proved highly amenable to cladistic analysis, in contrast to fossil invertebrate groups (with the exception of echinoderms and arthropods). The significance of this problem has been highlighted by Patterson and Smith (1987), who discovered 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 study of various data sets of non-marine tetrapods (Maxwell and Benton 1987) suggested that the major improvements in our knowledge of the evolutionary patterns of tetrapods has stemmed more from the rigorous identification of monophyletic groups than from the discovery of new fossils.

#### *Scope for ecological analysis*

Many detailed studies of the functional morphology and palaeoecology (autecology) of single species of fossil vertebrates 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 great potential for detailed palaeobiological interpretations 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 including size, diet, position in food chains, locomotory adaptations, reproductive mode, growth rate, habitat preference and geographic distribution.

#### *Refined generic- and species-level taxonomy*

Because *Homo sapiens* is a non-marine tetrapod, zoologists have devoted more attention to the systematics of vertebrates than they have to the systematics of brachiopods, annelids, pogonophorans or hyolithids. Our understanding of the relationships and the bounds of living vertebrate 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.

## DIVERSIFICATION

### *The data*

Several authors have plotted graphs of the diversity of vertebrate families and orders through time (e.g. Charig 1973; Pitrat 1973; Bakker 1977; Thomson 1977; Olson 1982; Padian and Clemens 1985; Colbert 1986) based largely on data from the classic source works of Romer (1966) and Harland *et al.* (1967). More reliable, however, are studies based on a new compilation of data on families of tetrapods (Benton 1985a; 1985b; 1987; 1988a). The data set on fish families used here is also new, compiled from Sepkoski (1982; revisions 1986) and Carroll (1987), with modifications from other recent sources. These new compilations differ significantly from those derived from Romer (1966) and Harland *et al.* (1967) in several ways. First, 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. Second, the latest cladistic classifications have been incorporated, as far as possible, and attempts have been made to test that all families are clades. Third, 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 practical division of geologic time for this compilation (relevant stages vary from 2 Myr to 19 Myr in length, with a mean duration of 6 Myr). This allows more detailed analysis than simply relying on the Lower, Middle and Upper divisions of geologic periods in Romer (1966), Carroll (1987) and elsewhere.

### *Diversification of fish taxa*

The diversity of fishes has increased markedly through time (Figure 9.4A) from a known level of 0–1 families in the latest Cambrian and Ordovician

to levels of 1–17 in the Silurian (radiations of ostracoderm agnathans and acanthodians (late Silurian only)), and 25–46 in the Devonian (ostracoderms, placoderms, acanthodians, sarcopterygians). These groups declined markedly in the Late Devonian, but diversity levels in the Carboniferous remained at about the same level (31–46 families) because of radiations of chondrichthyans and chondrostean bony fish. Fish diversities overall fell in the Permian to Early Cretaceous interval to levels below 40 families, with mean values of about 28. The Permian decline was caused by the loss of families of acanthodians, chondrosteans, and sarcopterygians, and a major late Permian extinction of chondrichthyans (11 to 3 families). The ‘holostean’ bony fish never achieved great diversity in the Mesozoic, but a progressive diversification of teleosts began in the Late Jurassic, although they had been present at low diversity (2–3 families) since the Middle Triassic, and the neoselachian sharks began to radiate during the Jurassic as well. These two groups, and particularly the teleosts, radiated dramatically in the Late Cretaceous when overall fish diversity leapt to 61–85 families, and again in the Tertiary, when the major jump (from 87 to 186 families) took place during the Early and Middle Eocene. The present total of 459 families was not approached in the Pleistocene (232 families) because of the large number of teleost families with no known fossil record as yet.

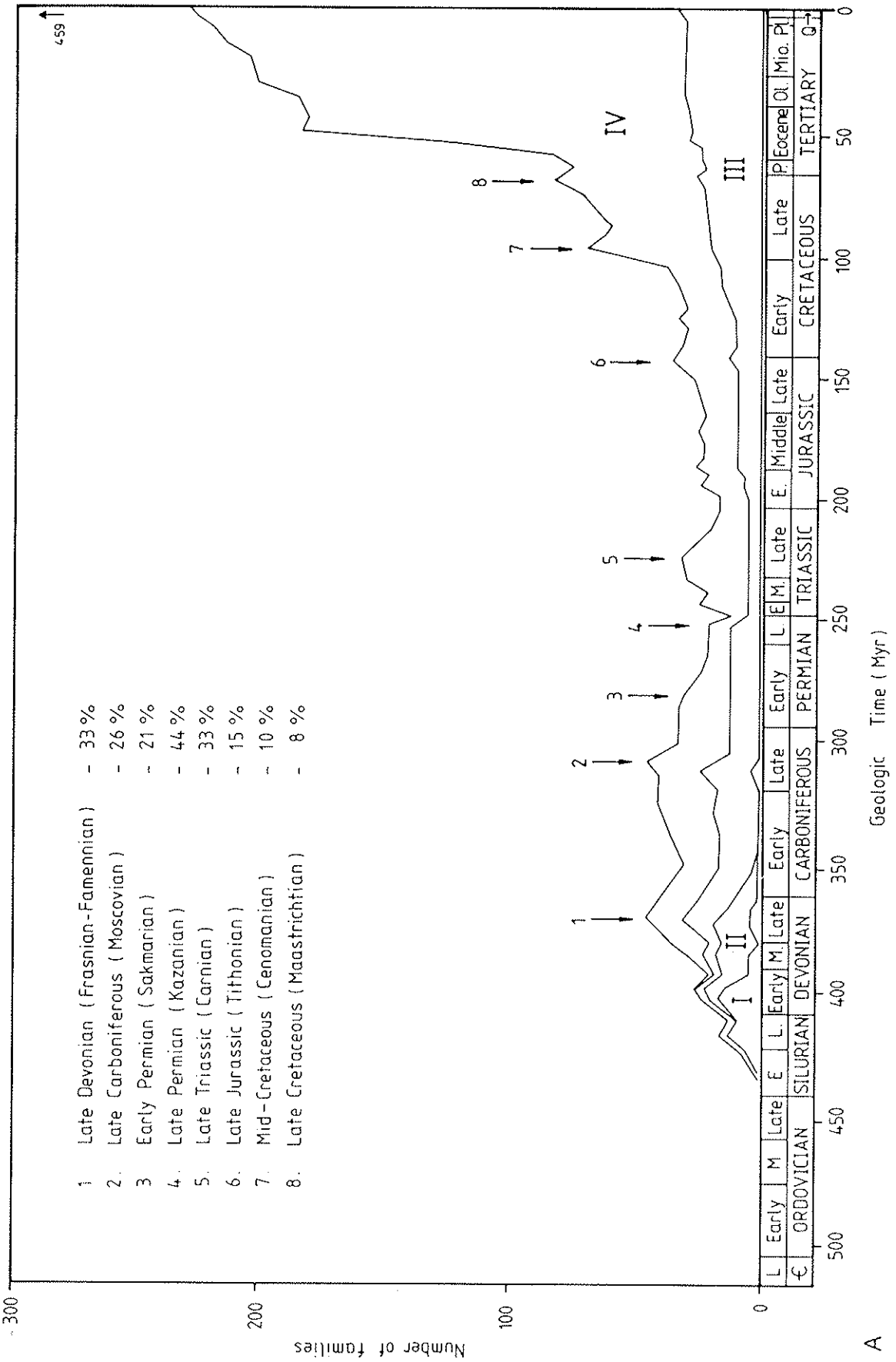
### *Diversification of tetrapods*

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 9.4B; Benton 1985a; 1985b). Three major diversity assemblages have been identified (Benton 1985b), each of which appears to have been dominant for a time, before giving 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) dominated during the Mesozoic at diversity levels of 20–50 families; and III (the ‘modern’ groups—frogs, salamanders, lizards, snakes, turtles, crocodiles, birds, mammals) dominated from Late Cretaceous times to the present day, rising rapidly from overall diversities of 50 to 89 in the Maastrichtian to successive peaks of 158 in the Early Eocene, 234 in the Late Oligocene, and 279 in the Late Miocene.

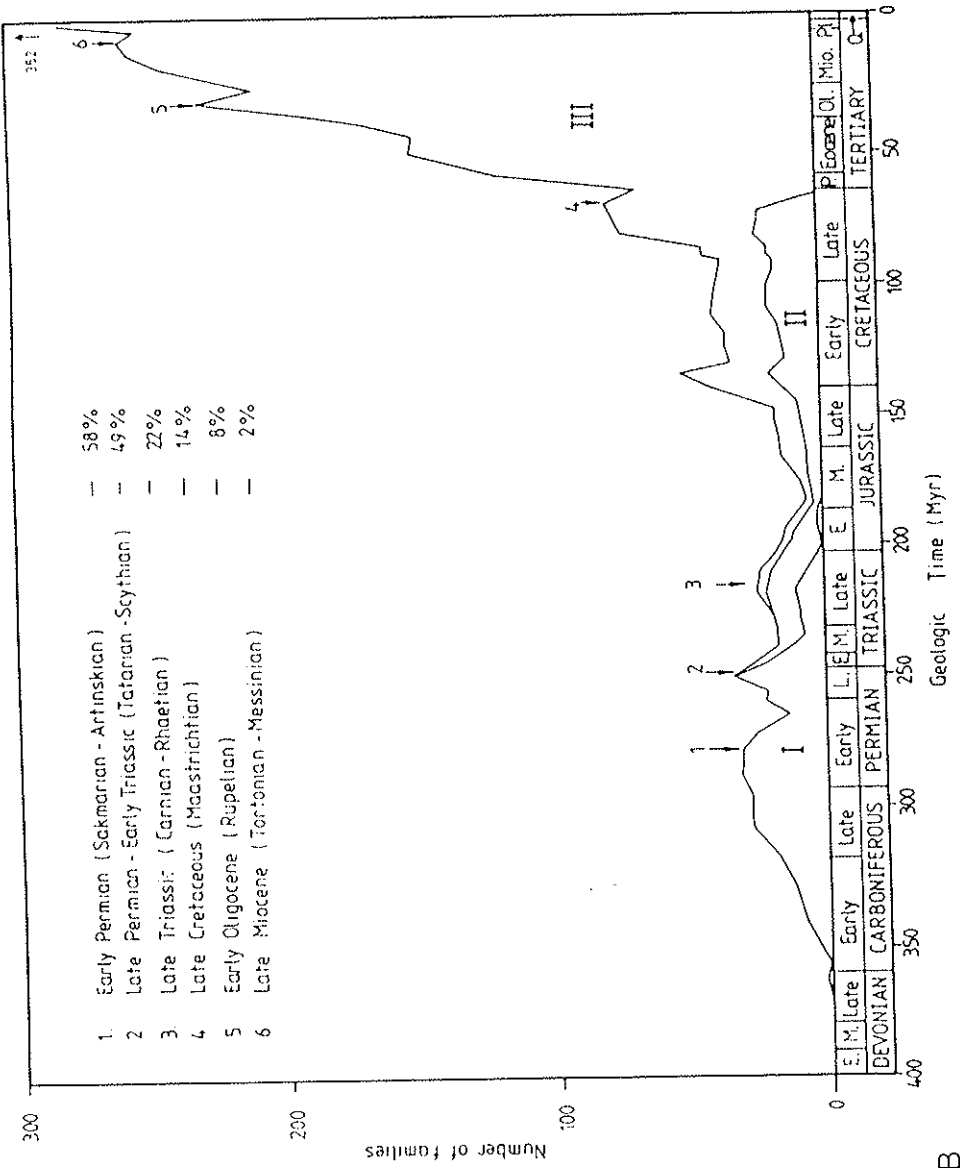
## MASS EXTINCTION

### *Methods*

Extinction and origination rates were calculated stage by stage for fish and for tetrapod families based on the new data sets. Total extinction ( $R_e$ ) and



A



B

Figure 9.4. Standing diversity against time for families of A: fishes and B: tetrapods. The upper curve shows total diversity against time, and apparent mass extinctions are indicated by drops in diversity, their commencements numbered 1-8 and 1-6, respectively. 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). Four fish clades are indicated (Figure 9.4A): I, Agnatha; II, Placodermi; III, Chondrichthyes (+ Acanthodii); IV, Osteichthyes. Three assemblages of families of tetrapods succeeded each other through geologic time (Figure 9.4B): I, II, III (see text for details). Abbreviations: E, Early; L, Late; M, Middle; Mio, Miocene; Ol, Oligocene; P, Palaeocene; Pl, Pliocene; Q, Quaternary.

total origination ( $R_o$ ) 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 ( $\Delta t$ ):

$$R_e = \frac{E}{\Delta t} \quad \text{and} \quad R_o = \frac{O}{\Delta t} ,$$

where  $E$  is the number of extinctions and  $O$  is the number of originations. Per-taxon extinction ( $r_e$ ) and origination ( $r_o$ ) rates were calculated by dividing the total rates by the end-of-stage family diversity  $N$  (see Chapter 2):

$$r_e = \frac{E}{N\Delta t} \quad \text{and} \quad r_o = \frac{O}{N\Delta t} .$$

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

Mass extinction events (see Chapter 2) are times when large numbers of taxa of diverse taxonomic and ecological position appear to die out in a geologic instant (Jablonski 1986). No clear numerical definition of mass extinctions has yet been possible, but indications are provided by major drops in overall diversity, and times of unusually high extinction rates.

### *Diversity drops*

The fish record (Figure 9.4A) shows numerous minor drops in overall diversity, and it is difficult to determine which were mass extinctions and which merely fluctuations of no particular significance. Clearly, not every drop can be a mass extinction. Figure 9.4A indicates those intervals (nos. 1–8) when a decline of about 10% or more in total diversity took place. These drops all correspond to mass extinction intervals that have been identified on the basis of other data sets. They are considered chronologically below.

There appear to be six declines in diversity in the tetrapod record (Figure 9.4B, 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 1985a; 1985b), and mass extinctions cannot be assumed here. These three episodes correspond to times when the SCM described above gives particularly low values. These serious gaps in the fossil record of tetrapods do not appear to be reflected to the same extent in the fish record.

### *Origination and extinction rates*

Figure 9.5 shows total origination and extinction rates (for these graphs for tetrapods alone, see Benton 1985a; 1985b; 1988a). The total rates were

found to be dependent on two non-random sources of error. The first of these is variation in the total numbers of taxa available to give rise to new taxa, or to become 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. The second non-random source of error is 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 and 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 9.5), the rates do not track each other so closely, although 'Lagerstätten peaks' remain in the Ufimian, Tithonian, and Coniacian for tetrapods (Figure 9.5B).

There are particularly high per-taxon extinction rates at times of mass extinctions corresponding to the Famennian, Kazanian, and Carnian events for fish (nos. 1, 4, 5: Figure 9.4A) and the Artinskian, Tatarian, and 'Rhaetian' events for tetrapods (nos. 1, 2, 3: Figure 9.4B). Per-taxon extinction rates are barely elevated at the times of the Moscovian, Sakmarian, Tithonian, Cenomanian and Maastrichtian events for fish (nos. 2, 3, 6, 7, 8: Figure 9.4A), and the Maastrichtian, Rupelian, or Late Miocene mass extinctions for tetrapods (nos. 4, 5, 6: Figure 9.4b). These mass extinctions correspond to depressed per-taxon origination rates in most cases (Figure 9.5; see Benton 1985b).

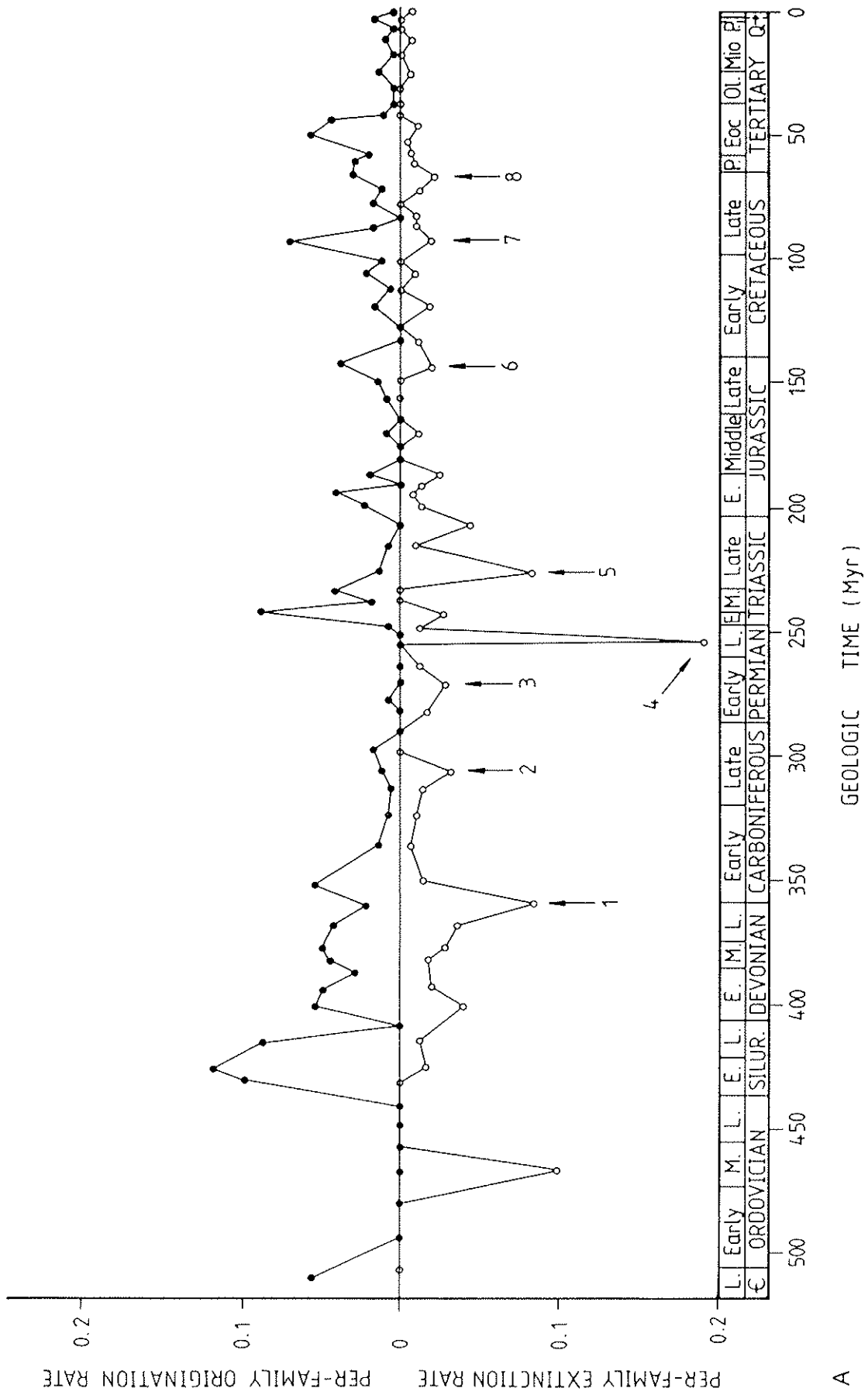
### *Mass extinction events*

The history of fishes and of tetrapods has been punctuated by at least eight and six mass extinction events respectively (nos. 1–8; 1–6: Figure 9.4A and 9.4B, respectively). Some of these overlap with each other, and with extinction events reported for other groups of organisms (see Chapters 2, 5). The fossil record of vertebrates is probably not complete enough to test the hypothesis of periodicity of mass extinctions (Raup and Sepkoski 1984; 1986), but data from the Triassic record appear to contradict the idea (Benton 1986a; 1988a). The vertebrate events are the following.

#### *Late Devonian (Frasnian–Famennian)*

Thirty-five families of fish died out during these two stages, which was a high rate of loss from a starting point of only 46 in the Frasnian. The main extinctions were among agnathans (the last heterostracans and osteostracans), placoderms (loss of 16 families, and virtual annihilation), and sarcopterygians (loss of ten families of rhipidistians and lungfish), with smaller losses among chondrichthyans and chondrosteans. This presumably





A

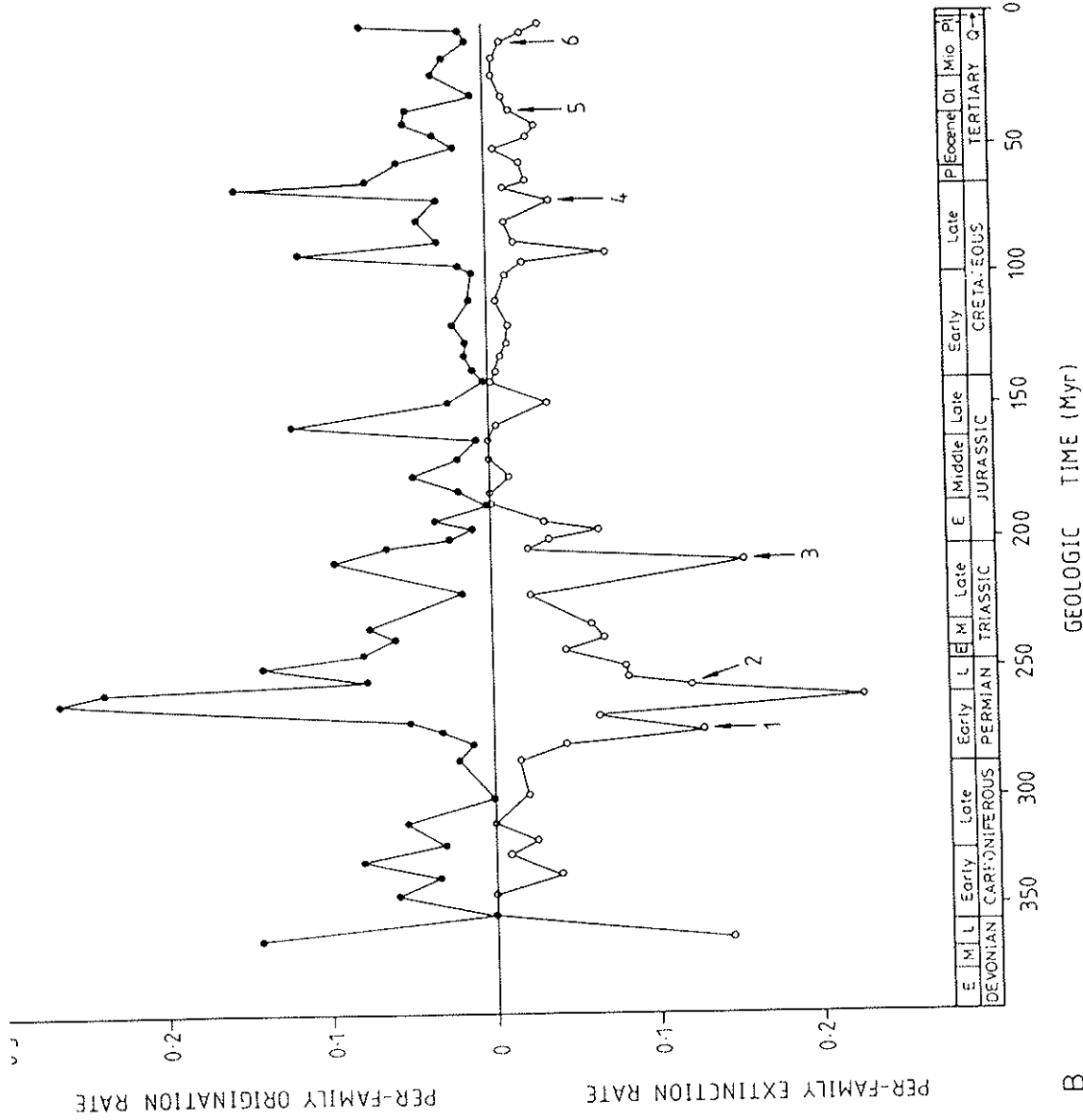


Figure 9.5. Per-taxon rates of origination and extinction for families of A: fishes, and B: tetrapods. Rates were calculated stage by stage for 73 stages between the Late Cambrian and the Pleistocene (fishes), and 56 stages from the Late Devonian (tetrapods). The Miocene was divided into Early, Middle, and Late units only, and the Pliocene was treated as a single time unit. Origination rates are plotted above the zero line (increases), and extinction rates below (declines).

corresponds to the Late Devonian extinction events among marine invertebrates (House 1985; McGhee *et al.* 1986; see Chapter 2).

#### *Late Carboniferous (Moscovian)*

Fifteen families of fish (mainly primitive chondrichthyans, as well as a few acanthodians, chondrosteans and sarcopterygians) disappeared during this stage. Six families of tetrapods (a cross-section of basal amphibians) also disappeared. These drops may correspond to the late Carboniferous events noted tentatively by Sepkoski and Raup (1986, p. 23) among marine animals. The end-Namurian event (in the preceding Bashkirian stage) noted by Saunders and Ramsbottom (1986) is not shown by either the fish or the tetrapod data. McGhee (see Chapter 2) notes two minor extinction events among marine invertebrates, during the Viséan–Serpukhovian interval (early Carboniferous) and in the Stephanian (i.e. Kasimovian or Gzelian, late Carboniferous), but neither of these is indicated in the record of fossil vertebrates.

#### *Early Permian (Sakmarian–Artinskian)*

Seven families of fishes (mainly palaeonisciform chondrosteans) were lost in the Sakmarian stage, with only one further loss in the Artinskian. Among tetrapods, however, 15 families (a variety of amphibians, anapsid reptiles and synapsids) were lost at the same time. This marked a major drop in the diversity of the ‘sail-backed’ pelycosaur synapsids which were replaced as dominant land reptiles by the therapsids in the late Permian. This event is not one of the postulated periodic events of the Palaeozoic (Sepkoski and Raup 1986; see Chapter 2).

#### *Late Permian (Kazanian–Tatarian)*

The fish data show major losses in the Kazanian stage (loss of 12 families of chondrichthyans and chondrosteans), with only one family dying out in the terminal Permian Tatarian stage. However, tetrapod extinctions are focused mainly in the Tatarian, with the loss of 27 families (many lineages of amphibians, anapsid and diapsid reptiles, and especially synapsids). Indeed, this event virtually wiped out the dominant therapsid mammal-like reptiles (loss of 15 out of 19 families), and probably triggered the subsequent rise of the archosaurs. These events correspond to the first of Raup and Sepkoski's (1984; 1986) major periodic extinctions, although it is unclear whether this is supposed to be focused in the Kazanian and/or Tatarian stages (a total time-span of 10–11 Myr). McGhee (see Chapter 2) shows that the end-Permian ‘event’ in the seas extended through most of the last 10 Myr of that period.

#### *Early Triassic (Scythian)*

About 5 Myr later, another smaller extinction event seems to have taken place among tetrapods, with the loss of 13 families of amphibians and mammal-like reptiles. There was a small mass extinction event at this time

also among marine invertebrates (Raup and Sepkoski 1984; 1986), but little effect on the fishes. Sepkoski and Raup (1986) argued that this extinction peak, and the one at the end of the Carnian, were caused by sampling errors, but McGhee (see Chapter 2) suggests that both are probably real extinction events during which ammonoids and other marine invertebrates died out.

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

Sixteen families of fishes died out during the late Triassic, most of these (13) in the Carnian stage (mainly chondrosteans). Among tetrapods, it seems that there were two discernible events, one at the end of the Carnian, and one at the end of the 'Rhaetian' (this latter stage is often now included in the Norian: see Benton 1986a; 1986b; Olsen and Sues 1986; Olsen *et al.* 1987). Ten families of tetrapods (diapsids, therapsids, and marine forms) died out in the Carnian, and eight (mainly amphibians and thecodontians) in the 'Rhaetian'. These extinctions, though few in number, seem to have mediated major faunal changes in the sea and on land. The loss of many chondrosteans was followed by a small increase in holostean diversity, and later of teleosts. The loss of Triassic marine reptiles was followed by great radiations of ichthyosaurs and plesiosaurs in the Early Jurassic. On land, the loss of most therapsids, and all thecodontians and rhyneosaurs, was followed by a two-phase radiation of the dinosaurs in the Late Triassic and the Early Jurassic.

#### *Late Jurassic (Tithonian)*

Fishes declined marginally by six families (mainly chondrichthyans and teleosts) at this time, and tetrapods more markedly (Figure 9.4B). However, in the latter case at least, this may be the effect of a relatively poor early Cretaceous fossil record (see above). This event does not stand out as clearly as it does in Raup and Sepkoski's (1984; 1986) marine data.

#### *Mid-Cretaceous (Cenomanian)*

A slightly larger drop, of ten families of teleosts and 'holosteans', took place during the Cenomanian stage, another of the postulated periodic extinction events (Raup and Sepkoski 1984; 1986). The tetrapod record shows no clear drop at this time.

#### *Late Cretaceous (Maastrichtian)*

The Cretaceous–Tertiary boundary (K–T) event is surely the best known mass extinction (see Chapters 2, 5), and not least for its effects on the reptiles (dinosaurs, pterosaurs and plesiosaurs all died out then). However, in terms of the relative loss of families, this event was smaller than all of those that preceded it. Among fishes, 11 families, mainly of teleosts, died out (out of a total of 85 present). A larger relative drop took place among tetrapods (loss of 36 out of 89 families), but the losses affected only the key groups already noted. As with most of the extinction events, most

major vertebrate taxa were apparently virtually unaffected: chondrichthyans, bony fish (except teleosts), amphibians, turtles, lizards, crocodiles, birds, and placental mammals. For both fishes and tetrapods, the Maastrichtian stage was marked also by high rates of origination (appearance of 18 and 21 new families, respectively) which reduced the overall decline during this stage.

#### *Early Oligocene (Rupelian)*

This relatively minor event affected only the tetrapods, with the 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.

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

This event also affected only the tetrapods, with the loss of 21 families, mainly among mammals. It does not match the periodic marine events.

#### *Periodicity*

In general, the vertebrate fossil record is not adequate to test Raup and Sepkoski's (1984; 1986) theory of extinction periodicity (see Chapters 2 and 5). Most of the extinctions postulated above (the Late Devonian (?), Late Carboniferous (?), Late Permian, Late Triassic, Late Jurassic, Middle and Late Cretaceous) match marine mass extinctions identified by those authors. However, some (the Late Devonian, the Late Carboniferous, Late Permian and Late Triassic) do not match very well, and others (the Early Permian, Early Triassic, Early Oligocene and Late Miocene) do not fit the 26 Myr cycles at all. Further, many of the 26 Myr extinctions (see Chapter 2) seem to be absent from the vertebrate data (viz. Early Jurassic (Pliensbachian), Middle Jurassic (Callovian?), Early Cretaceous (Barremian–Aptian?), Late Eocene (Priabonian), Middle Miocene (Langhian–Serravallian)). Note, however, that Sepkoski and Raup (1986) found only limited evidence for the Middle Jurassic and Early Cretaceous events, which are necessary to fill gaps in the 26 Myr periodicity pattern. Overall, the vertebrate data are suggestive, but by no means conclusive, evidence against periodicity.

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