

PATTERNS IN THE DIVERSIFICATION OF MESOZOIC NON-MARINE TETRAPODS AND PROBLEMS IN HISTORICAL DIVERSITY ANALYSIS

by MICHAEL J. BENTON

ABSTRACT. The history of the world-wide diversity of terrestrial tetrapods between the late Permian and the early Eocene divides into three main phases: late Permian to late Triassic (labyrinthodonts, synapsids), late Triassic to late Cretaceous (early diapsids, dinosaurs, pterosaurs), late Cretaceous onwards (lissamphibians, turtles, squamates, crocodiles, birds, mammals). During each phase, higher levels of family diversity were achieved than before. The great increase in family diversity from the Cretaceous onwards was largely caused by increasing provinciality as Pangaea broke up.

Historical diversity analysis suffers from the typical problems of the incompleteness of the fossil record, and varying palaeontological interest devoted to particular groups. Taxonomic problems are just as important. Historical diversity is a measure of the number of dichotomies within a monophyletic clade, and the number of apomorphies arising, in a particular time. The groups to be analysed must be monophyletic, and the study should preferably be based on a uniform cladistic classification. 'Ancestor hunting' seriously hinders such studies since it blurs the true picture of adaptive radiations.

ONE of the most important times in the history of terrestrial vertebrate life was the Mesozoic and early Tertiary. This episode, from 250 to 50 million years ago, saw the land dominated successively by mammal-like reptiles, dinosaurs, and then by mammals. There were major extinction events at the Permian-Triassic boundary, towards the end of the Triassic, and at the Cretaceous-Tertiary boundary. These events have received extensive scientific and popular attention, but only a few palaeontologists have explored the exact patterns from the vertebrate fossil record (e.g. Bakker 1977; Russell 1979, 1982; Benton 1983*a*).

The aims of this paper are to explore the pattern of family diversity through time for all terrestrial tetrapods from the beginning of the late Permian (258 Ma) to the end of the early Eocene (45 Ma). Marine groups are excluded here because they radiated under different conditions, and there is no reason to suppose that their evolution followed the same broad pattern as that of the terrestrial groups. Several questions are tackled here. Did the extinction events affect some groups more than others, and in particular how did the diversity, and origination and extinction rates, of the 'losers' and the 'winners' change before and after the events? Are there any discernible trends through time in the diversity of all, or of some, terrestrial tetrapods? This kind of analysis offers useful insights into what happened in the past—and it is an advance over the standard kinds of stories about 'life in the age of the dinosaurs'—but there are many associated problems, and these are explored.

THE DATA

A list was made of all families of terrestrial and freshwater amphibians, reptiles, birds, and mammals that lived from the late Permian to the early Eocene (a total of about 500). The omitted marine groups are Ichthyosauria, Placodontia, Nothosauria, Plesiosauria, marine lizards and snakes (Aigialosauridae, Dolichosauridae, Mosasauridae, Palaeophidae, Simoliophidae), marine crocodiles (Metriorhynchidae, Teleosauridae), marine turtles (Cheloniidae, Dermochelyidae, Protostegidae, Toxochelyidae), and marine mammals (Cetacea, Pinnipedia, Sirenia). Families based on single specimens were excluded from the analysis. The exact ranges by stratigraphic stage were

noted for each terrestrial family from the most recent available literature (Appendix). Then, for each higher taxonomic category, the numbers of families present, and the numbers originating and becoming extinct were totalled for each stage.

Calculations were made of the total rates of origination (R_s) and extinction (R_e) for each group in each stage, as follows (Sepkoski 1978):

$$R_s = S/dt \text{ and } R_e = E/dt \quad (1)$$

where S is the number of originations, and E is the number of extinctions, observed during the time-interval dt . The time-intervals for the stages were taken from Odin (1982*a, b*). These total rates of origination and extinction depend on the total number of families already present. Measures of the per-taxon rates (or probabilities) of origination (r_s) and extinction (r_e) are, then:

$$r_s = S/Ddt \text{ and } r_e = E/Ddt \quad (2)$$

where D is the diversity or number of taxa present. The rate of diversification of a clade, r_d , is simply the difference between r_s and r_e .

THE DIVERSIFICATION OF TETRAPODS IN THE MESOZOIC

The first impression given by the graph (text-fig. 1) of tetrapod diversity from the late Permian to the early Eocene is of a decline in the early Jurassic, and a rapid increase in the late Cretaceous and Palaeocene. These themes will be explored in more detail.

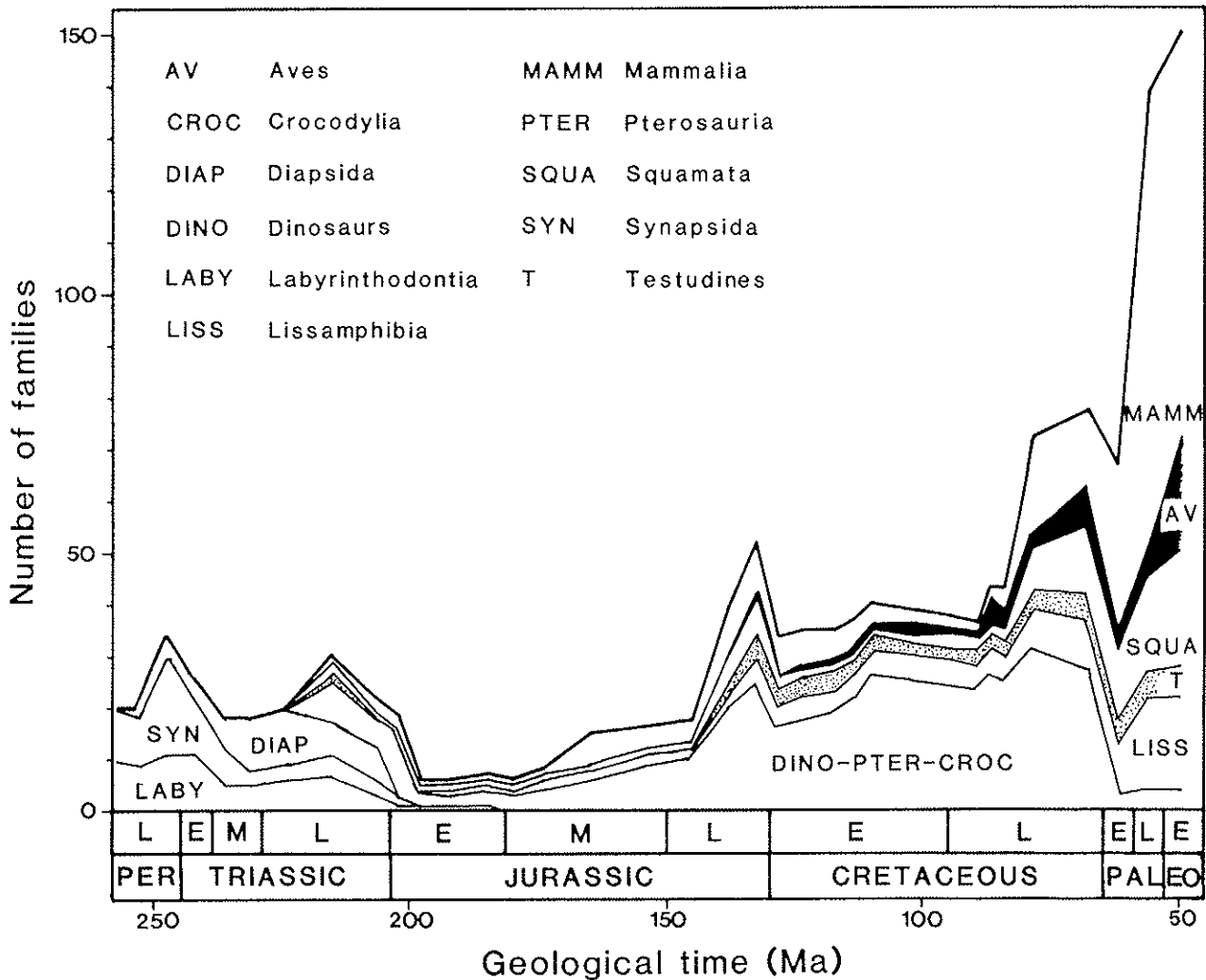
In the late Permian, labyrinthodont amphibian and synapsid (mammal-like reptile) families were most abundant, with small numbers of anapsids (captorhinomorphs, procolophonids, pareiasaurs) and early diapsid reptiles. The early amphibians and synapsids declined in diversity during the Triassic, and became extinct in the early Jurassic. During the Triassic, various diapsid groups radiated to maintain the overall tetrapod diversity at a level similar to that in the Permian. Many new groups of tetrapods arose first in the late Triassic (Norian and Rhaetian): dinosaurs, crocodiles, pterosaurs, sphenodontids, lizards (?), turtles, and mammals.

The graph shows a sudden decline in the diversity of all groups during the early and middle Jurassic. This is probably the result of a long gap in the fossil record—there are only sporadic and rather poor fossil beds with terrestrial vertebrates during this time. Further evidence that this decline was not a real biological event is provided by the sudden jump in diversity at the end of the Jurassic, when extensive finds are known from the Kimmeridgian and Portlandian.

Total tetrapod diversity levels appear to remain constant in the early Cretaceous and then start to increase in the late Cretaceous. However, it is possible that the poor record of smaller terrestrial vertebrates (e.g. frogs, salamanders, lizards, snakes, birds, mammals) during this time may have kept the total diversity levels artificially low. There is a sudden increase in the diversity of all of these forms—but little change in the diversity of larger tetrapods such as crocodiles and dinosaurs—in the late Cretaceous (Santonian, Campanian), where there are several deposits with small vertebrates.

As is well known, the dinosaurs and pterosaurs became extinct at the end of the Cretaceous, but the other groups under consideration here carried on into the Palaeocene with little noticeable change in diversity. The numbers of families of crocodiles and birds declined, those of amphibians, turtles, and squamates remained constant and the mammals increased slightly in diversity. The diversity of all surviving groups increased dramatically during the Palaeocene and Eocene to reach the highest levels yet seen. This increase occurred mainly among the mammals and birds, with smaller contributions from the lissamphibians and squamates.

The overall pattern shows three phases of tetrapod diversification during which different groups achieved equilibrium levels, and were then replaced by others which achieved new equilibrium levels. This kind of kinetic model for diversification through time has been made familiar by Sepkoski (1978, 1979, 1981) for the marine fossil record, and Niklas *et al.* (1983) for the record of vascular land plants. The suggestions given here regarding the record of terrestrial tetrapods are



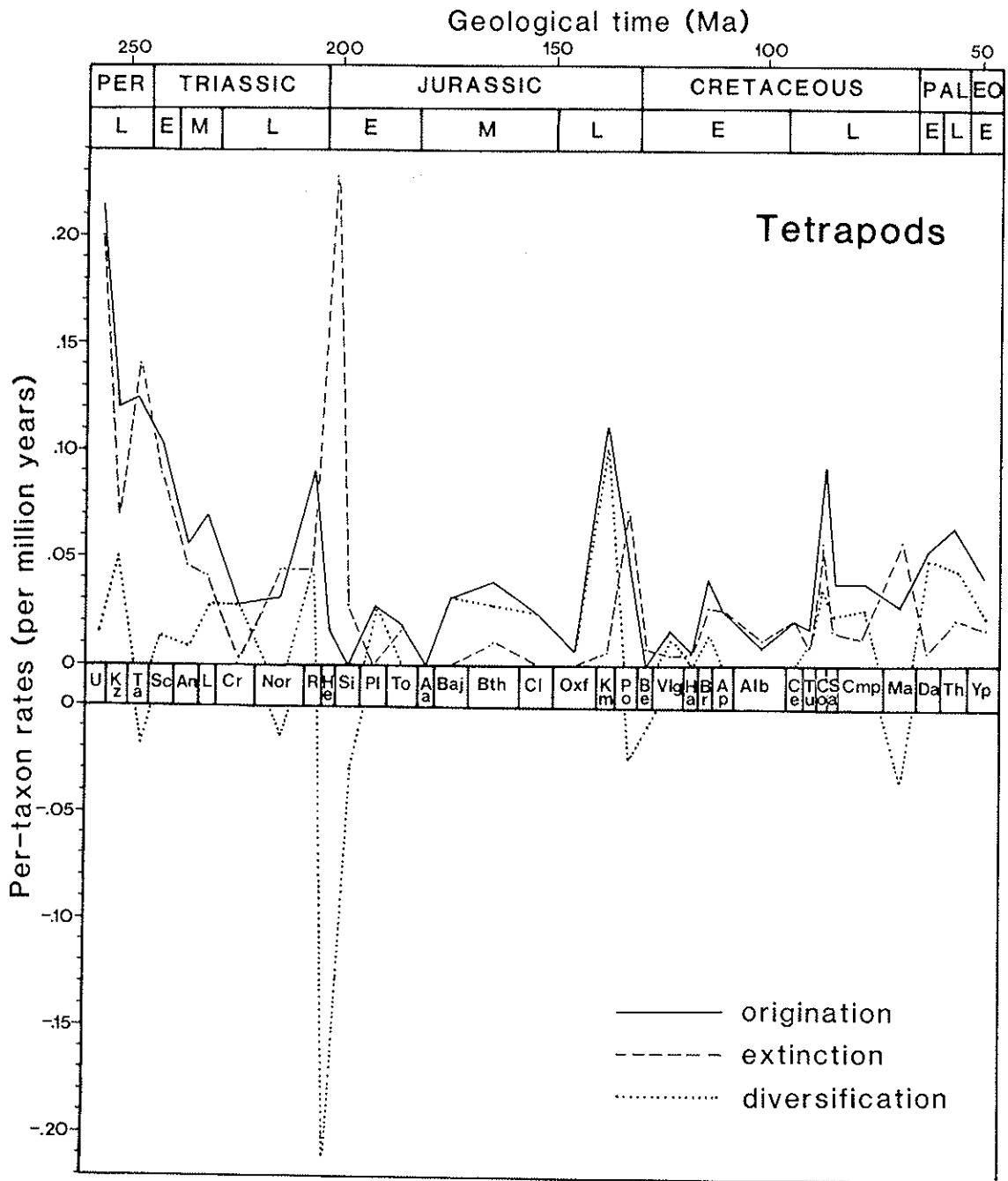
TEXT-FIG. 1. The pattern of world-wide diversity of terrestrial tetrapods between the late Permian and the early Eocene. Family diversity is plotted on the vertical axis, and time (in millions of years) on the horizontal axis. The main groups within the Tetrapoda are distinguished. Note the overall rise in diversity, especially from the late Cretaceous onwards, and the two gaps in the record (early-middle Jurassic and early Cretaceous). Abbreviations: E, early; EO, Eocene; L, late; M, middle; PAL, Palaeocene; PER, Permian.

preliminary, prior to a full study of the entire record from the late Devonian to the present day. The data presented here (text-fig. 1) suggest three assemblages of families that dominated in succession:

- (i) (-late Triassic): Labyrinthodont amphibians, synapsids.
- (ii) (late Triassic-late Cretaceous): early diapsids, dinosaurs, pterosaurs.
- (iii) (late Cretaceous-): Lissamphibians, turtles, crocodiles, squamates, birds, mammals.

Taxa in group (i) reached an equilibrium level of twenty-five to thirty families in the Permian and Triassic, taxa of group (ii) reached a level of twenty to twenty-five families in the late Jurassic and Cretaceous, and taxa in group (iii) reached a diversity of twenty-five to thirty families in the late Cretaceous and continued diversifying towards a much higher level during the Tertiary.

The two gaps in the record of terrestrial vertebrates (early to middle Jurassic and early Cretaceous) are highlighted by an examination of the overall per-taxon rates of origination and extinction of all families (text-fig. 2). Origination rates are high at the beginning of the late Permian and they fall



TEXT-FIG. 2. The patterns of origination, extinction, and diversification of terrestrial tetrapod families between the late Permian and the early Eocene. Per-taxon rates are plotted on the vertical axis, and time (in millions of years, and by stratigraphic stage) on the horizontal axis. The time-scale is from Odin (1982a, b). The high extinction rate in the early Jurassic is probably the result of the poor fossil record of the early and middle Jurassic, rather than being a true rate. The overall rates show no particularly large disturbance at the Cretaceous-Tertiary boundary. Abbreviations of stratigraphic stages are: Aa, Aalenian; Alb, Albian; An, Anisian; Ap, Aptian; Baj, Bajocian; Be, Berriasian; Br, Barremian; Bth, Bathonian; Ce, Cenomanian; Cl, Callovian; Cmp, Campanian; Co, Coniacian; Cr, Carnian; Da, Danian; Ha, Hauterivian; He, Hettangian; Km, Kimmeridgian; Kz, Kazanian; L, Ladinian; Ma, Maastrichtian; Nor, Norian; Oxf, Oxfordian; Pl, Pliensbachian; Po, Portlandian; R, Rhaetian; Sa, Santonian; Sc, Scythian; Si, Sinemurian; Ta, Tatarian; Th, Thanetian; To, Toarcian; Tu, Turonian; U, Ufimian; Vlg, Valanginian; Yp, Ypresian.

throughout the Triassic. There is a high origination rate in the late Triassic (Norian) when many new families appear in the record, as noted above. Origination rates are high again in the late Jurassic (Kimmeridgian) and in the late Cretaceous (Coniacian). These two highs occur after several stages with low origination rates which are probably caused by the poor fossil record for those times. Thus, many of the families that we find first in the record in the Kimmeridgian and Coniacian probably arose somewhat earlier in the missing parts of the record.

The record of extinction rates also confirms that the gaps in the record have had a significant effect on the diversity pattern that we see. Extinction rates are high at the beginning of both gaps—in the early Jurassic (Hettangian) and at the end of the Jurassic (Portlandian). Many of the families that appear to have become extinct in these stages may have survived longer into the early and middle Jurassic and the early Cretaceous vacuums. Thus any new fossil deposit discovered in either of these poorly represented intervals is liable to extend the ranges of families at either end. This point has been noted already with regard to the early Jurassic vacuum by Milner (1977).

Overall per-taxon family extinction rates are very high at the beginning of the late Permian, and again at the end of the Permian (Tatarian). The latter high rate corresponds with the end-Permian extinction event recorded amongst other groups of organisms (Schopf 1974). The overall extinction rate also remains high during the late Cretaceous and early Tertiary, and it is slightly higher at the end of the Cretaceous.

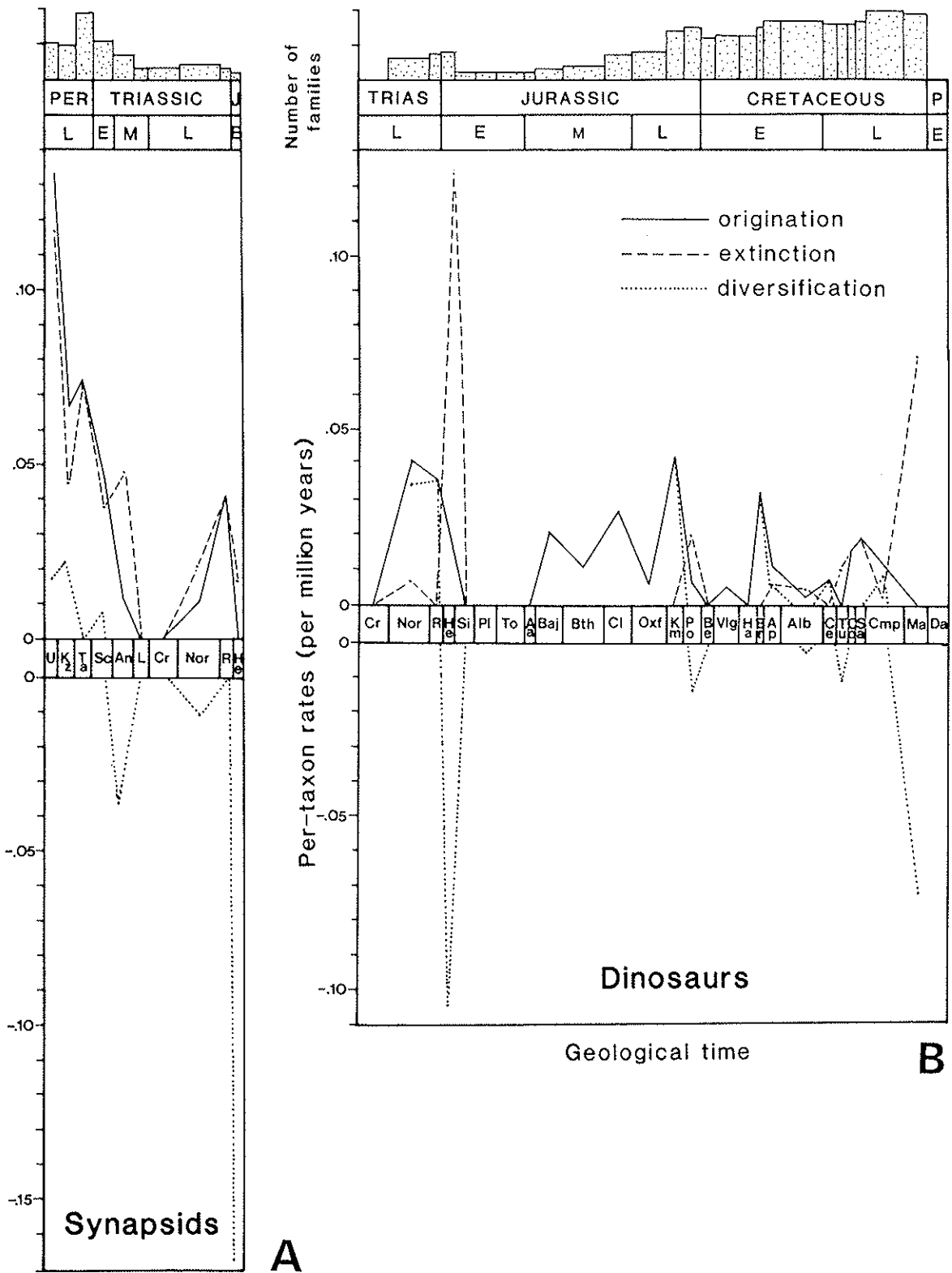
The overall per-taxon diversification rates for terrestrial tetrapods (text-fig. 2) show times of rapid increases and decreases in diversity. Diversification rates were high in the late Permian (Kazanian), late Triassic (Rhaetian), late Jurassic (Kimmeridgian), late Cretaceous (Coniacian), and Palaeocene. Diversification rates were negative in the latest Permian (Tatarian), late Triassic (Norian), early Jurassic (Hettangian, Sinemurian), latest Jurassic–early Cretaceous (Portlandian, Berriasian), mid-Cretaceous (Albian), and latest Cretaceous (Maastrichtian). The Kimmeridgian and Coniacian highs, and the Hettangian–Sinemurian, Portlandian–Berriasian, and Albian lows are probably artefacts of the two long gaps in the record, as discussed above. The Tatarian, Norian, and Maastrichtian lows correspond with proposed major extinction events. The latter two are followed by the Rhaetian and Palaeocene highs respectively, evidence of some kind of recovery.

The late Permian pattern is interesting in that it shows a high rate of turnover of families throughout, and the terminal Permian extinction event appears to have left impoverished early Triassic faunas which only 'recovered' over several stratigraphic stages.

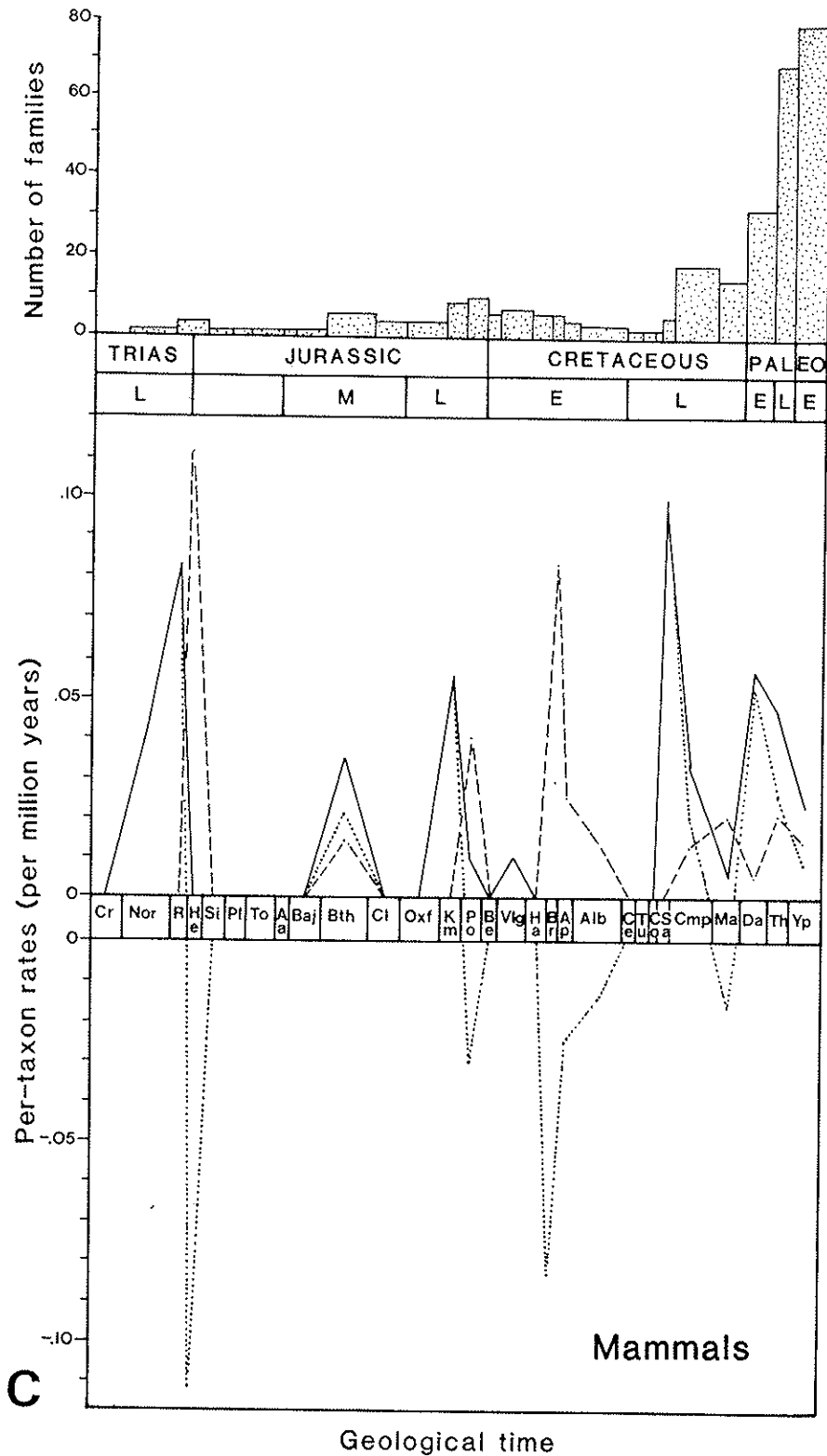
We must look a little closer at the main groups that were involved in the changes in diversity through the Mesozoic: the synapsids, the dinosaurs, and the mammals.

The synapsid record (text-fig. 3A) shows high diversity and high per-taxon origination and extinction rates in the late Permian. These fall steadily through the Permo-Triassic boundary and rise only in the late Triassic at the time when one group achieved mammal grade. The diversification rate is high in the Kazanian, and negative in the Anisian, Norian, and Hettangian. The rates in the Triassic are subject to great error because of the statistically low numbers of families present (n ranges from two to eleven).

The dinosaur record (text-fig. 3B) shows a moderate number of families during their initial radiation (six to eight). Some of these families only contained one or two genera, and they soon died out. This is the kind of high turnover one expects early in an adaptive radiation. The number of families is low in the early and middle Jurassic (largely the effect of the poor record), but rises to a level of fourteen to fifteen at the end of the Jurassic. This approximate level is maintained through the early Cretaceous, although it rises to sixteen to seventeen in the late Cretaceous, and nineteen to twenty at the end. There was also a high initial per-taxon origination rate in the late Triassic which fluctuates through the Jurassic to reach a high in the Kimmeridgian. The rate is high again in the early Cretaceous (Hauterivian) and in the late Cretaceous (Coniacian, Santonian). The per-taxon extinction rate peaks in the latest Jurassic (Portlandian), late Cretaceous (Turonian–Santonian) and, of course, at the end of the Cretaceous (Maastrichtian). The diversification rate for dinosaurs shows highs in the late Triassic (Norian, Rhaetian), the middle and late Jurassic (Callovian, Kimmeridgian), and early Cretaceous (Barremian). There were negative values in the



TEXT-FIG. 3. The patterns of diversity, origination, extinction, and diversification of three main groups of terrestrial tetrapods between the late Permian and the early Eocene: the synapsids (mammal-like reptiles; A), the dinosaurs (B), and the mammals (C). Numbers of families are shown as simple histograms at the top. Per-taxon rates are plotted on the vertical axis, and time (in millions of years, and by stratigraphic stage) on the horizontal axis. A, the synapsids show high diversity and high origination and extinction rates initially, declining through the Triassic. B, the dinosaurs show slowly increasing diversity through the Mesozoic. There



was a high origination rate in the late Triassic and during the late Jurassic. The high extinction rate in the early Jurassic is probably produced by the subsequent gap in the record. There is no evidence for a gradual decline in diversity or origination rates of dinosaur families during the late Cretaceous. c, the Mesozoic record of mammal families fluctuates wildly in most of the Mesozoic, probably because of the statistically low number of families. The number of families rose from the late Cretaceous onwards, but there was considerable turnover during this early radiation. Abbreviations for stage names are given with text-fig. 2.

early Jurassic (Hettangian), latest Jurassic (Portlandian), mid-late Cretaceous (Albian, Turonian), and, of course, at the end of the Cretaceous (Maastrichtian).

It is important to note the constant turnover of dinosaur families throughout the late Cretaceous. Families were appearing and disappearing at similar rates, and the diversification rates fluctuate less wildly about zero than earlier in the dinosaur record. They may have reached a situation of dynamic equilibrium in terms of family diversity. Many new families of dinosaurs arose in the late Cretaceous, with particularly high origination rates of 0.4–0.7 families per million years in the Coniacian–Campanian. No new families are noted in the Maastrichtian, but it would be unwise to read too much into that fact, since there were seven other Jurassic and Cretaceous stages during which no new families are recorded. This analysis is on too coarse a scale to answer questions about the question of changes in the diversity of dinosaurs in the last million years or so of the Cretaceous.

The pattern of diversity through time of mammals (text-fig. 3c) shows low numbers of families through the Jurassic, rising to nine to ten at the end of the Jurassic, where there are several well-known productive horizons. Early Cretaceous levels are low, probably owing to the poor record. A maximum Mesozoic level of eighteen families was achieved in the Campanian. The number of families rises in the Palaeocene and, of course, continues to rise irregularly through the Tertiary. The origination and extinction rates, and the stage-by-stage diversification rates are given (text-fig. 3c), but these must be treated with extreme caution owing to the small numbers of families in most stages (*n* ranges from one to ten), except in the late Triassic (?), late Jurassic, and late Cretaceous.

The extinction of the dinosaurs at the end of the Cretaceous may have acted as a 'release' that permitted the mammals to radiate in the Palaeocene much more rapidly than they had done before. However, note that mammals were already diversifying to a significant extent during the late Cretaceous. The per-taxon origination rate for mammals did increase in the early Palaeocene, but it decreased again in the late Palaeocene and early Eocene. This study must be extended to the whole Tertiary record of mammals, but preliminary results suggest that the family diversification rate continued to rise and fall dramatically, with highs in the middle Eocene (Bartonian) and early Oligocene (Rupelian), and lows in the latest Eocene (Priabonian) and late Oligocene (Chattian).

INCREASE IN DIVERSITY AND PROVINCIALITY

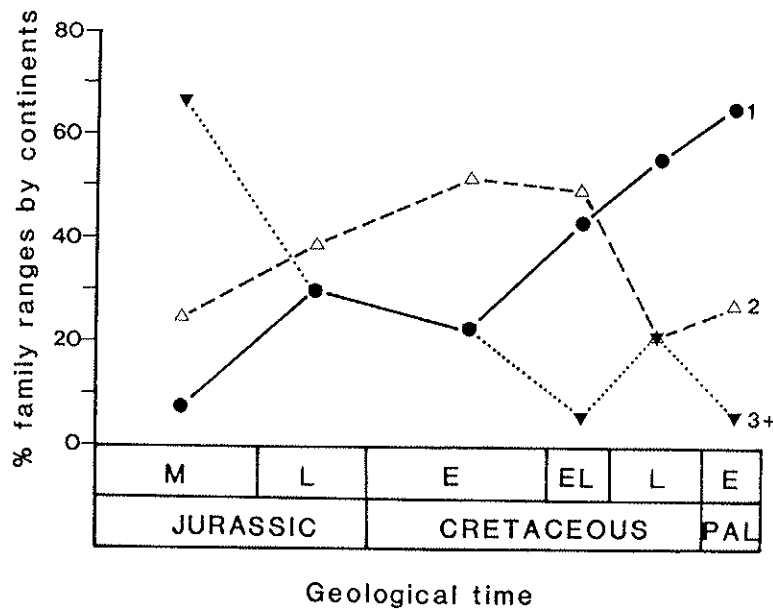
There was apparently a large overall increase in the diversity of terrestrial tetrapods from the late Permian to the early Tertiary, and especially from the late Cretaceous onwards (text-fig. 1). Part of this increase may depend on the quality of the data, but I believe that a large part of it is real. The quality of the data will be considered below. I suggest here that the increase in tetrapod diversity in the late Cretaceous and early Tertiary is directly connected with the breakup of Pangaea and increasing provinciality of faunas.

It is well known that in the Triassic and Jurassic periods numerous tetrapod families achieved virtually world-wide distribution (e.g. Charig 1971; Cox 1974). One would expect the number of such families to decrease through the Cretaceous and Tertiary, and the number of families restricted to single continents to increase. In order to test this hypothesis, I took the family lists that I had compiled and listed the families that arose during each stage of the Jurassic, Cretaceous, and early Tertiary. I noted only the families that were based on more than one species or one specimen. I then listed from the literature the distribution by modern continents of each of these families during their entire temporal range up to, and including, the Ypresian. Then, in order to have statistically useful samples, I grouped the stages and calculated the percentages of families restricted to the area of one present-day continent, to two continents, or to three or more (Table 1).

The proportion of families restricted to one continent rises fairly steadily through the Jurassic, Cretaceous, and Palaeocene from 8 to 66% (text-fig. 4). Those restricted to two continents are commonest in the early and early late Cretaceous. Those that are found on three or more continents

TABLE 1. Geographic distribution of terrestrial tetrapod families by age of origin (Jurassic-Palaeocene). Totals of families first appearing in each time division, and proportions of families whose ultimate total range (up to and including the Ypresian) extended to one present-day continent, to two continents, and to three or more continents.

	First	1 (%)	2 (%)	3 (%)
Early Jurassic (Hettangian-Toarcian)				
Total first appearances: three (sample too small)				
Middle Jurassic (Aalenian-Callovian)	12	1 (8)	3 (25)	8 (67)
Late Jurassic (Oxfordian-Portlandian)	36	11 (30.5)	14 (39)	11 (30.5)
Early Cretaceous (Berriasian-Albian)	17	4 (23.5)	9 (53)	4 (23.5)
Early late Cretaceous (Cenomanian-Santonian)	18	8 (44)	9 (50)	1 (6)
Latest Cretaceous (Campanian-Maastrichtian)	46	26 (56)	10 (22)	10 (22)
Palaeocene (Danian-Thauetian)	74	49 (66)	21 (28)	4 (6)



TEXT-FIG. 4. Increasing provinciality of terrestrial tetrapod faunas during the Jurassic and Cretaceous may explain the overall rise in diversity. The proportion of all tetrapod families that occupied ranges of 1, 2, or 3+ continents at particular times is plotted on the vertical axis, and geological time is shown on the horizontal axis. Families restricted to one continent rose through this time, while cosmopolitan families (3+ continents) fell. Families present on two continents rose in the early Cretaceous. Pangaea split into numerous separate continents in the late Jurassic and Cretaceous, and provinciality of terrestrial tetrapod families became the rule rather than the exception. This graph does not simply show the amount of time allowed for dispersal, so that the more ancient families are the most widely distributed: Jurassic families achieved their cosmopolitan distributions within a span of one or two stratigraphic stages, and I examined the record for four or five stages into the Eocene and Oligocene in order to obtain full ultimate ranges for families arising in the late Cretaceous and Palaeocene. Abbreviations: E, early; L, late; M, middle; PAL, Palaeocene.

(i.e. cosmopolitan) fall from 67% in the middle Jurassic to 6% in the Palaeocene. These data are not simply an expression of the progressively reduced amount of time allotted for the groups to disperse, if that is one's view of biogeography, since the cosmopolitan families of the Jurassic and Cretaceous achieved their full ranges within a stage or two.

In general terms, these figures match our expectations from current models of continental drift in the Mesozoic and the breakup of Pangaea (Hallam 1981; Smith *et al.* 1981). During the middle and late Jurassic the North Atlantic began to open, thus breaking the link between North America and Africa, and North America and South America. The South Atlantic opened during the Cretaceous, and Antarctica and Australia moved away from Africa and South America. The exact pattern of former land and sea is clearly important if we are to interpret the distributions of particular families. For our present purposes, it is appropriate to consider only the broad features. There was a single land mass in the Triassic-early Jurassic. An Asian area became cut off from North America-Europe in the middle and late Jurassic, and there was probably a bridge between Europe or North America and Africa-South America. There may have been many separate major island continents in the late Cretaceous over southern Europe, and seven other main land masses: eastern North America-north-west Europe, western North America-Asia, South America, north-west Africa, eastern Africa, Madagascar-India, Australia-Antarctica. The two parts of North America joined up in the Palaeocene, but India and Madagascar separated. There may have been narrow links from Asia to North America and to Europe. The relatively large numbers of two-continent distributions of terrestrial tetrapods in the early and early late Cretaceous were mainly between North America and Asia.

In conclusion, the split up of Pangaea into seven or more separate continental masses during the late Jurassic and the Cretaceous led to increased provinciality of terrestrial tetrapod families, and cosmopolitanism became the exception rather than the rule. Families that had arisen in Pangaea before late Jurassic times could maintain a cosmopolitan distribution. Families that arose after that were restricted in their potential distribution by oceanic barriers. Thus, to an increasing extent, each continent acquired an endemic fauna as the old cosmopolitan families were replaced. The total world-wide diversity of tetrapod families rose dramatically through the late Cretaceous and early Tertiary.

This simple model could be refined by a detailed study of the vicariant and dispersal history of particular groups through the period during which Pangaea broke up. Sea-level and climatic changes also probably affected the overall diversity of terrestrial tetrapods but, I would suggest, to a lesser extent than continental plate movements. Finally, the causes of the Cretaceous-Tertiary extinction event, whether ultimately extraterrestrial or terrestrial, should be considered. It has already been shown that this seemed to have a limited affect on overall terrestrial tetrapod diversity since it affected only certain groups (text-fig. 1).

PROBLEMS AND IMPLICATIONS OF STUDYING DIVERSITY THROUGH TIME

The analysis of diversity through time is essential to our understanding of large-scale evolutionary patterns. However, the subject is clearly beset by numerous problems, and the limitations of the stratigraphic and taxonomic data must be clearly appreciated. The inadequacy of the fossil record in this respect has been discussed by several authors, and methods of correcting the raw data have been proposed that take account of different areas of rock exposure, varying sediment volumes, varying palaeontological interest in different groups, and so on (e.g. Raup 1972, 1976; Sepkoski 1975, 1978; Sheehan 1977; Signor 1978, 1982). The major gaps in the terrestrial vertebrate record have been considered in the data description above, but there is no space to propose, and to justify, particular corrections here. From the experience of workers on the marine fossil record, it seems that much of the recorded variation in diversity through time is dependent on the patchiness of the fossil record, and of work done on different parts of it, but that the majority is real (Sepkoski *et al.* 1981; Signor 1982). Some other fundamental issues are considered here.

Ranges and dating

It is not possible to know the *exact* stratigraphic range of a particular group of organisms, so we have to use the latest published information, and hope that it approaches the truth. In some cases, the oldest record has not been seriously upset for a long time (e.g. 'the oldest bird'), but in others, new finds keep moving the ranges back in ever-decreasing increments (e.g. 'the oldest vertebrate'). We can only assume that the recorded ranges approach the true ranges asymptotically over (research) time (Raup 1972). The constant palaeontological pressure to find 'the oldest X' or 'the youngest Y' should see to that.

Palaeontologists must rely on others to give them absolute dates for their fossils. One has to have information, as accurate as possible, on the exact lengths of the smallest time segments under investigation in order to calculate origination and extinction rates. Two recently published time-scales (Odin 1982*a, b*; Harland *et al.* 1983) do not offer any final solution. These two collaborative time-scales differ to a significant extent in many important dates. For example, Odin places the Triassic–Jurassic boundary at 204 Ma and the Jurassic–Cretaceous boundary at 130 Ma, while Harland *et al.* place these two at 213 and 144 Ma respectively. Individual stage lengths differ greatly according to the two estimates—thus, Odin sets the Bathonian at twelve million years, while Harland *et al.* set it at six million years. I have chosen to use the time-scale of Odin (1982*a, b*) because he uses more tie-points than Harland *et al.* (1983). The latter have estimated most of the Mesozoic dates on the basis of seven tie-points in the late Cretaceous and one in the middle Triassic. Odin and his collaborators used a far larger sample of tie-points and many less certain dates spanning the whole of the Mesozoic (Kennedy and Odin 1982; Odin and Létolle 1982). Their most important conclusion has been that the stages of the Triassic, Jurassic, and Cretaceous vary greatly in individual length (from 2 to 12 Ma). We can hope for improvements in the precision of these dates in the future.

Are all families equal?

The present study of patterns of diversity through time has had to be based on the best available classifications. Some groups of tetrapods have been revised in a uniform way (whether cladistically or otherwise) in recent years, and I have tried to use the most comprehensive and 'ancestor-free' classifications. It is a well-known fact, however, that all families are not equal, and that one taxonomist may use different criteria to judge the range of morphologies permissible within one family. I can see no way to standardize our view of the scope of higher taxonomic categories. A cladistic analysis can tighten up this aspect of a classification, but the assignment of rank to clades is still arbitrary.

I wanted to test if estimates of family numbers within a larger group at a particular time depended more upon taxonomic whim, or upon the completeness of the record. The only time-plane for which the exact diversity at any categorical level is potentially knowable is the present day. I compared several available classifications of living mammals in order to see if different authors had arrived at markedly different numbers of families (Table 2).

TABLE 2. The numbers of families of living mammals according to some recent classifications. Different classifications give rise to rather different estimates of total world-wide diversity at any particular time.

Romer (1945)	109
Simpson (1945)	118
Walker (1964)	123
Romer (1966)	116
Corbet and Hill (1980)	129
Honacki <i>et al.</i> (1982)	139
Nowak and Paradiso (1983)	129

It is clear that estimates of family numbers of living mammals do vary to some extent (124 ± 15) according to the judgement of individual taxonomists. When we assess the diversity of a particular group in the past, we have the added problem of the selectiveness of the fossil record.

What does diversity mean?

In studying the diversity of fossil organisms we must consider exactly what we are trying to measure. Commonly, palaeontologists select some taxonomic category that is manageable with regard to the size of their analysis, such as orders or families. It is implied that a measure of ordinal or family diversity gives a view of the evolutionary status of a particular larger group throughout its career, and it is assumed that changes in the diversity of one taxonomic category are broadly reflected by changes in the diversity of others.

In basic evolutionary terms, a measure of diversity should reflect the state of 'evolutionary exuberance' of a branching clade. It is evident that one can only talk about the diversity of a monophyletic (i.e. holophyletic) group within a particular broad range of habitats—thus terrestrial Tetrapoda, Mammalia, or Aves, as above. It is probably reasonable to exclude side-branches from a clade that conquer entirely new habitats and radiate there independently of the main clade—e.g. Cetacea, Sirenia. It is meaningless to calculate origination or extinction rates for a polyphyletic group or for a paraphyletic group that has descendants in the same habitats (e.g. Reptilia, Thecodontia). In the analyses above I have lumped all dinosaurs together, and this is usually thought to be a polyphyletic group. They may not form a monophyletic group in the sense of Bakker and Galton (1974), but almost certainly they would by the addition of a few late Triassic thecodontians. The question of whether birds are dinosaur descendants or not is not considered important, since birds have radiated generally into different habitats from those occupied by the dinosaurs.

The 'evolutionary exuberance' of a clade is some measure of its rate of branching (cladogenesis) and its rate of morphological change (anagenesis). One could think of this in cladistic terms as:

Rate of historical diversity change = number of dichotomies \times number of apomorphies per unit time.

The study of the history of diversity changes must then be based on a best-attempt cladogram of all known taxa within the particular monophyletic clade of interest. There is no available cladogram of all tetrapod genera, families or orders yet, but the way ahead for improvements to the analyses given in the present paper is clear.

Ancestor hunting masks adaptive radiations

In the study of fossil vertebrates, as with many other groups, there has been a tradition of 'ancestor hunting'. For example, the oldest known lizard will not be expected to have the diagnostic characters of lizards, but only some vague tendencies in that direction. So, a whole array of Permo-Triassic reptiles has been assigned to the Lepidosauria on the basis of characters supposed to be intermediate between the captorhinomorph condition and that of living lizards. In the process, we have lost all trace of the broad and varied radiation of early diapsids that was going on in the Permo-Triassic. New cladistic classifications of the early diapsids (Benton 1983*b*, 1984; Evans 1984) show some of the diversity of families that evolved, survived for a short period, and then died out without leaving any issue. They were all previously subsumed into the Eolacertilia or Eosuchia as 'almost-but-not-quite-lizards'. We must beware of assigning ancient genera to living or well-known families whose diagnostic characters they lack.

In a large-scale adaptive radiation, where a clade radiates into a new set of adaptive zones, we would expect an early period of extensive branching. Many new species would arise in a burst of evolutionary experimentation. Many would die out after a relatively short time, and this would continue until the ecological space was filled and some kind of equilibrium was reached. We might expect large morphological changes to arise relatively rapidly, and the record of the radiation would be expected to contain many short-lived monospecific families. If all these taxa are assigned to large

undefined 'ancestral' families we lose important evolutionary information about the true number of families present during a period of rapid diversification. Many palaeontologists are reticent about naming new high category taxa for single species or genera. There is no reason, however, to assume that there is a characteristic family longevity within each large clade. The average longevity of families might increase through time, for example, as the larger clade became established.

Is the geological perspective blurred?

It is a well-known problem in evolutionary studies that geological time ($> 10^5$ years) is separated from ecological time ($< 10^2$ years) by a large and important gap. We must not assume, however, that palaeontologists can shed no light on evolution. The kind of study presented here, and those by Raup (1972), Sepkoski (1978, 1979, 1981), Raup and Sepkoski (1982), and others, show significant long-term features of evolution. We can identify large clade radiations and mass extinctions. These studies are at too coarse a time-scale to give detailed information on the nature of a mass extinction, because all data are lumped into approximately 5 Ma time-spans. We can look more closely at successions of particular faunas and make estimates of the relative abundances of different groups during periods of major transition, such as the Permo-Triassic (Benton 1983a), or the late Cretaceous and early Tertiary (Van Valen and Sloan 1977; Archibald 1982; Archibald and Clemens 1982). A combination of studies of taxonomic diversity on a coarse time-scale, and studies of faunal composition on a finer time-scale, can offer a great deal of information on specific events and about mass extinctions and adaptive radiations as general features of evolution.

CONCLUSIONS

1. The study of world-wide diversity of terrestrial tetrapods from the late Permian to the early Eocene shows three broad groups that dominated in succession: the labyrinthodonts and synapsids (late Permian to late Triassic), the early diapsids, dinosaurs, and pterosaurs (late Triassic to late Cretaceous), the lissamphibians, turtles, squamates, crocodiles, birds, and mammals (late Cretaceous onwards). The extinction events at the end of the Permian, in the late Triassic, and at the end of the Cretaceous affected some groups severely, but the replacing forms continued relatively unaffected.
2. The overall increase in total world-wide diversity of terrestrial tetrapods during the Cretaceous and early Tertiary appears to have been connected with increasing provinciality as Pangaea broke up.
3. We have to assume that the relative stratigraphic ranges used in a diversity analysis approach the true ranges. We also have to use absolute age data for the geological periods concerned, and the variety of current, but rather inconsistent, time-scales does not help.
4. The particular classification used in a diversity analysis can affect the results. A cladistic overview helps, but higher taxonomic categories are still assigned according to individual taste.
5. Historical diversity is a measure of the 'evolutionary exuberance' of a monophyletic clade at a particular time. This could be seen as a product of the number of dichotomies and the number of apomorphies arising in a clade during a particular time-interval.
6. 'Ancestor hunting' in taxonomy has blurred the true picture of adaptive radiations because evolutionary novelties are assigned to larger living families or to 'ancestral' groups.
7. Studies of diversity through time can offer important information on major events in evolution that cannot be studied in any other way.

Acknowledgements. I thank G. R. Chancellor and T. S. Kemp for commenting on the manuscript. I thank the President and Fellows of Trinity College, Oxford, for financial support during this work.

REFERENCES

- ARCHIBALD, J. D. 1982. A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. *Univ. California Publ. geol. Sci.* **122**, 1-288.
- and CLEMENS, W. A. 1982. Late Cretaceous extinctions. *Am. Scient.* **70**, 377-385.
- BAKKER, R. T. 1977. Tetrapod mass extinctions—A model of the regulation of speciation rates and immigration by cycles of topographic diversity. In HALLAM, A. (ed.). *Patterns of evolution as illustrated by the fossil record*, 439-468. Elsevier, Amsterdam.
- and GALTON, P. M. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature*, Lond. **248**, 168-172.
- BENTON, M. J. 1983a. Dinosaur success in the Triassic: a noncompetitive ecological model. *Q. Rev. Biol.* **58**, 29-55.
- 1983b. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Phil. Trans. R. Soc. Lond. B*, **302**, 605-717.
- 1984. The relationships and early evolution of the Diapsida. In FERGUSON, M. J. W. (ed.). *The structure, development, and evolution of reptiles*, 575-596. Academic Press, London.
- CHARIG, A. J. 1971. Faunal provinces on land: evidence based on the distribution of fossil tetrapods, with especial reference to the reptiles of the Permian and Mesozoic. In MIDDLEMISS, F. A., RAWSON, P. F. and NEWALL, G. (eds.). *Faunal provinces in space and time. Geol. Jl. Spec. Iss.* **4**, 111-128.
- CORBET, G. B. and HILL, J. E. 1980. *A world list of mammalian species*. British Museum (Nat. Hist.)/Comstock, London.
- COX, C. B. 1974. Vertebrate palaeodistributional patterns and continental drift. *J. Biogeog.* **1**, 75-94.
- EVANS, S. E. 1984. The classification of the Lepidosauria. *Zool. Jl Linn. Soc.* **82**, 87-100.
- HALLAM, A. 1981. Relative importance of plate movements, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic. In NELSON, G. and ROSEN, D. E. (eds.). *Vicariance biogeography, a critique*, 303-330. Columbia University Press, New York.
- HARLAND, W. B., COX, A. V., LLEWELLYN, P. G., PICKTON, C. A. G., SMITH, A. G. and WALTERS, R. 1983. *A geologic time scale*. University Press, Cambridge.
- HONACKI, J. H., KINMAN, K. E. and KOEPLI, J. W. (eds.), 1982. *Mammal species of the world*. Allen Press, Lawrence.
- KENNEDY, W. J. and ODIN, G. S. 1982. The Jurassic and Cretaceous time scale in 1981. In ODIN, G. S. (ed.). *Numerical dating in stratigraphy*, 557-592. John Wiley, Chichester.
- MILNER, A. R. 1977. Triassic extinction or Jurassic vacuum? *Nature*, Lond. **265**, 402.
- NIKLAS, K. J., TIFFNEY, B. H. and KNOLL, A. H. 1983. Patterns in vascular land plant diversification. *Ibid.* **303**, 614-616.
- NOWAK, R. M. and PARADISO, J. L. 1983. *Walker's mammals of the world*. Johns Hopkins University Press, Baltimore.
- ODIN, G. S. 1982a. *Numerical dating in stratigraphy*. xxvii + 1040 pp. John Wiley, Chichester.
- 1982b. The Phanerozoic time scale revisited. *Episodes*, **1982** (3), 3-9.
- and LÉTOLLE, R. 1982. The Triassic time scale in 1981. In ODIN, G. S. (ed.). *Numerical dating in stratigraphy*, 523-533. John Wiley, Chichester.
- RAUP, D. M. 1972. Taxonomic diversity during the Phanerozoic. *Science, NY*, **177**, 1065-1071.
- 1976. Species diversity in the Phanerozoic: an interpretation. *Paleobiology*, **2**, 289-297.
- and SEPKOSKI, J. J. JR. 1982. Mass extinctions in the marine fossil record. *Science, NY*, **215**, 1501-1503.
- ROMER, A. S. 1945. *Vertebrate paleontology*, 2nd edn., University of Chicago Press.
- 1966. *Ibid.* 3rd edn., University of Chicago Press.
- RUSSELL, D. A. 1979. The enigma of the extinction of the dinosaurs. *Ann. Rev. Earth planet. Sci.* **7**, 163-182.
- 1982. The mass extinctions of the late Mesozoic. *Scient. Am.* **246** (1), 58-65.
- SCHOPF, T. J. M. 1974. Permo-Triassic extinctions: relation to sea-floor spreading. *J. Geol.* **82**, 129-143.
- SEPKOSKI, J. J. JR. 1975. Stratigraphic biases in the analysis of taxonomic survivorship. *Paleobiology*, **1**, 343-355.
- 1978. A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. *Ibid.* **4**, 223-251.
- 1979. A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria. *Ibid.* **5**, 222-251.

- SEPKOSKI, J. J. JR. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Ibid.* **7**, 36-53.
- BAMBACH, R. K., RAUP, D. M. and VALENTINE, J. W. 1981. Phanerozoic marine diversity and the fossil record. *Nature*, Lond. **293**, 435-437.
- SHEEHAN, P. M. 1977. Species diversity in the Phanerozoic: a reflection of labor by systematists? *Paleobiology*, **3**, 325-328.
- SIGNOR, P. W. III. 1978. Species richness in the Phanerozoic: an investigation of sampling effects. *Ibid.* **4**, 394-406.
- 1982. Species richness in the Phanerozoic: compensating for sampling bias. *Geology*, **10**, 625-628.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.* **85**, 1-350.
- SMITH, A. G., HURLEY, A. M. and BRIDEN, J. C. 1981. *Phanerozoic palaeocontinental world maps*. University Press, Cambridge.
- VAN VALEN, L. and SLOAN, R. E. 1977. Ecology and the extinction of the dinosaurs. *Evolut. Theory*, **2**, 37-64.
- WALKER, E. P. 1964. *Mammals of the world*. Johns Hopkins University Press, Baltimore.

APPENDIX

SOURCES OF DATA ON FAMILIES OF TERRESTRIAL TETRAPODS FROM THE LATE PERMIAN TO THE EARLY EOCENE

There is no space here to list the 500 or so families of non-marine tetrapods, and their stratigraphic ranges, that formed the data base for this study. The main sources of information are given here in an outline listing of the main higher taxa.

AMPHIBIA: LABYRINTHODONTIA

Order Temnospondyli (Anderson and Cruickshank 1978; Carroll and Winer *in* Carroll 1977; Cosgriff and Zawiskie 1979; Gubin 1980; Warren and Hutchinson 1983)

Order Anthracosauria (Carroll and Winer *in* Carroll 1977)

AMPHIBIA: LISSAMPHIBIA

Order Anura (Carroll and Winer *in* Carroll 1977; Estes and Reig 1973)

Order Urodela (Estes 1981; Milner 1983)

Order Apoda (Estes 1981)

REPTILIA: ANAPSIDA (Anderson and Cruickshank 1978; Keyser and Gow 1981; Ricqlès and Taquet 1982; Thommasen and Carroll 1981)

REPTILIA: TESTUDINES (Gaffney 1979; Młynarski 1976)

REPTILIA: DIAPSIDA

Various (Anderson and Cruickshank 1978; Benton 1984, 1985; Fabre 1980; Sigogneau-Russell 1981)

Order Pterosauria (Buissonjé 1980; Currie and Russell 1982; Wellnhofer 1978; Wild 1978)

Order Rhynchosauria (Benton 1983)

Order Prolacertiformes (Wild 1980)

Order 'Thecodontia' (Anderson and Cruickshank 1978; Charig *et al.* 1976; Galton 1977)

Order Crocodylia (Buffetaut 1982; Steel 1973)

Order Saurischia (Barsbold and Perle 1980; Bonaparte and Powell 1980; Chatterjee 1978; Galton 1977; Kurzanov 1981; Lambert 1983; Langston 1974; Osmólska 1976, 1981; Ostrom 1981; Rozhdestvensky 1970; Steel 1969; Sues 1977)

Order Ornithischia (Coombs 1978; Galton 1980*a, b*; Galton and Powell 1983; Lambert 1983; Maryańska 1977; Steel 1970; Wall and Galton 1979; Weishampel and Weishampel 1983)

Order Younginiformes (Currie 1982)

Order Sphenodontia (Benton 1984, 1985)

Order Squamata (Estes 1983; Fox 1975; Rage 1975*a, b*, 1978)

REPTILIA: SYNAPSIDA (Anderson and Cruickshank 1978; Brinkman 1981; Chatterjee 1983; Cluver and King 1983; Kemp 1982)

AVES (Feduccia 1981; Feduccia and Martin 1976; Fisher 1967; Olson 1977; Walker 1981)

MAMMALIA (Lillegraven *et al.* 1979; Savage and Russell 1983)

REFERENCES FOR APPENDIX

- ANDERSON, J. M. and CRUICKSHANK, A. R. I. 1978. The biostratigraphy of the Permian and Triassic: Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontol. Afr.* **21**, 15-44.
- BARSBOLD, R. and PERLE, A. 1980. Segnosauria, a new infraorder of carnivorous dinosaurs. *Acta palaeontol. Polonica*, **25**, 187-195.
- BENTON, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Phil. Trans. R. Soc. Lond. B*, **302**, 605-717.
- 1984. The relationships and early evolution of the Diapsida. In FERGUSON, M. J. W. (ed.). *The structure, development, and evolution of reptiles*, 575-596. Academic Press, London.
- 1985. Classification and phylogeny of the diapsid reptiles. *Zool. J. Linn. Soc.* **84**.
- BONAPARTE, J. F. and POWELL, J. E. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). *Mém. Soc. géol. Fr.* **139**, 19-28.
- BRINKMAN, D. 1981. The structure and relationships of the dromasaur (Reptilia: Therapsida). *Breviora*, **465**, 1-34.
- BUFFETAUT, E. 1982. Radiation évolutive, paléocécologie et biogéographie des crocodiliens mésosuchiens. *Mém. Soc. géol. Fr.* **142**, 1-88.
- BUISONJÉ, P. H. DE 1980. *Santanadactylus brasiliensis* nov. gen., nov. sp., a long-necked, large pterosaur from the Aptian of Brasil. *Proc. K. Ned. Akad. Wet.* **83**, 145-172.
- CARROLL, R. L. 1977. Patterns of amphibian evolution: an extended example of the incompleteness of the fossil record. In HALLAM, A. (ed.). *Patterns of evolution as illustrated by the fossil record*, 405-437. Elsevier, Amsterdam. Appendix by CARROLL, R. L. and WINER, L. issued separately (1978).
- CHARIG, A. J., KREBS, B., SUES, H.-D. and WESTPHAL, F. 1976. Thecodontia. *Handbuch der Paläoherpetologie*, **13**, 1-137. Gustav Fischer, Stuttgart.
- CHATTERJEE, S. K. 1978. *Indosuchus* and *Indosaurus*, Cretaceous carnosaur from India. *J. Paleont.* **52**, 570-580.
- 1983. An ictidosaur fossil from North America. *Science, NY*, **220**, 1151-1153.
- CLUVER, M. A. and KING, G. M. 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. *Ann. S. Afr. Mus.* **91**, 195-273.
- COOMBS, W. P. 1978. The families of the ornithischian dinosaur order Ankylosauria. *Palaeontology*, **21**, 143-170.
- COSGRIFF, J. W. and ZAWISKIE, J. M. 1979. A new species of the Rhytidosteidae from the *Lystrosaurus* Zone and a review of the Rhytidosteidae. *Palaeontol. Afr.* **22**, 1-27.
- CURRIE, P. J. 1982. The osteology and relationships of *Tangasaurus mennelli* Haughton (Reptilia, Eosuchia). *Ann. S. Afr. Mus.* **86**, 247-265.
- and RUSSELL, D. A. 1982. A giant pterosaur (Reptilia: Archosauria) from the Judith River (Oldman) Formation of Alberta. *Can. J. Earth Sci.* **19**, 894-897.
- ESTES, R. 1981. Gymnophiona, Caudata. *Handbuch der Paläoherpetologie*, **2**, 1-115. Gustav Fischer, Stuttgart.
- 1983. Sauria terrestria, Amphisbaenia. *Ibid.* **10A**, 1-249.
- and REIG, O. A. 1973. The early fossil record of frogs: a review of the evidence. In VIAL, J. L. (ed.). *Evolutionary biology of the Amurans*, 11-63. University of Missouri Press, Columbia.
- FABRE, J. 1980. La famille des Pleurosauridae (Rhynchocephalia). Exemple remarquable d'évolution par néoténie squelettique. *C.r. Acad. Sci. Paris, Sér. D*, **291**, 929-932.
- FEDUCCIA, A. 1981. *The age of birds*. Harvard University Press, Cambridge.
- and MARTIN, L. D. 1976. The Eocene zygodactyl birds of North America (Aves: Piciformes). *Smithsonian Contr. Paleobiol.* **27**, 101-110.
- FISHER, J. 1967. Aves. In HARLAND, W. B. et al. (eds.). *The fossil record*, 733-762. Geological Society London.
- FOX, R. C. 1975. Fossil snakes from the Upper Milk River Formation (Upper Cretaceous), Alberta. *Can. J. Earth Sci.* **12**, 1557-1563.
- GAFFNEY, E. S. 1979. Comparative cranial morphology of recent and fossil turtles. *Bull. Am. Mus. nat. Hist.* **164**, 65-376.
- GALTON, P. M. 1977. On *Staurikosaurus pricei*, an early saurischian dinosaur from the Triassic of Brazil, with notes on the Herrerasauridae and Poposauridae. *Paläontol. Z.* **51**, 234-245.

- GALTON, P. M. 1980a. European Jurassic ornithopod dinosaurs of the families Hypsilophodontidae and Camptosauridae. *Neues Jb. Geol. Paläontol. Abh.* **160**, 73-95.
- 1980b. Armored dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of England. *Géobios*, **13**, 825-837.
- and POWELL, H. P. 1983. Stegosaurian dinosaurs from the Bathonian (Middle Jurassic) of England, the earliest record of the Family Stegosauridae. *Ibid.* **16**, 219-229.
- GUBIN, YU. M. 1980. New Permian Dissorophids of the Ural Forelands. *Paleont. JI*, **14** (3), 88-96. [Translated from Russian.]
- KEMP, T. S. 1982. *Mammal-like reptiles and the origin of mammals*. Academic, London.
- KEYSER, A. W. and GOW, C. E. 1981. First complete skull of the Permian reptile *Eunotosaurus africanus* Seeley. *S. Afr. JI Sci.* **77**, 417-420.
- KURZANOV, S. M. 1981. [On some unusual theropods from the Upper Cretaceous in Mongolia.] *Trudy Sovmestn. Sov.-Mongol. Paleont. Eksped.* **9**, 45-57. [In Russian.]
- LAMBERT, D. 1983. *Collins guide to dinosaurs*. Collins, London.
- LANGSTON, W. JR. 1974. Nonmammalian Comanchean tetrapods. *Geosci. Man*, **8**, 77-102.
- LILLEGRAVEN, J. A., KIELAN-JAWOROWSKA, Z. and CLEMENS, W. A. 1979. *Mesozoic mammals, the first two-thirds of mammalian history*. University of California Press, Berkeley.
- MARYAŃSKA, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontol. Pol.* **37**, 85-151.
- MILNER, A. R. 1983. The biogeography of salamanders in the Mesozoic and early Caenozoic: a cladistic vicariance model. In SIMS, R. W., PRICE, J. H. and WHALLEY, P. E. S. (eds.). *Evolution, time and space: the emergence of the biosphere*, 431-468. Academic Press, London.
- MLYNARSKI, M. 1976. Testudines. *Handbuch der Paläoherpetologie*, **7**, 1-129. Gustav Fischer, Stuttgart.
- OLSON, S. L. 1977. A Lower Eocene Frigatebird from the Green River Formation of Wyoming (Pelecaniformes, Fregatidae). *Smithsonian Contr. Biol.* **35**, 1-33.
- OSMÓLSKA, H. 1976. New light on the skull anatomy and systematic position of *Oviraptor*. *Nature*, Lond. **262**, 683-684.
- 1981. Coossified tarsometatarsi in theropod dinosaurs and their bearing on the problem of bird origins. *Palaeontol. Pol.* **42**, 79-95.
- OSTROM, J. H. 1981. *Procompsognathus*—theropod or thecodont? *Palaeontographica*, Abt. A, **175**, 179-195.
- RAGE, J.-C. 1975a. Un serpent du Paléocène du Niger. Étude préliminaire sur l'origine des Caenophidiens (Reptilia, Serpentes). *C.r. Acad. Sci. Paris, Sér. D*, **281**, 515-518.
- 1975b. Un caenophidien primitif (Reptilia, Serpentes) dans l'Eocène inférieure. *C.r. somm. Soc. géol. Fr.* **1975**, 46-47.
- 1978. L'origine des colubroïdes et des acrochordoïdes (Reptilia, Serpentes). *C.r. Acad. Sci. Paris, Sér. D*, **286**, 595-597.
- RICQLÈS, A. DE and TAQUET, P. 1982. La faune des vertébrés du Permien supérieure du Niger. I. Le captorhinomorphe *Moradisaurus grandis* (Reptilia, Cotylosauria). *Ann. Paléontol.* **68**, 33-106.
- ROZHDESTVENSKY, A. K. 1970. Giant claws of enigmatic Mesozoic reptiles. *Paleontol. JI*, **4**, 117-125. [Translated from Russian.]
- SAVAGE, D. E. and RUSSELL, D. E. 1983. *Mammalian paleofaunas of the world*. Addison-Wesley, Reading, Mass.
- SIGOGNEAU-RUSSELL, D. 1981. Présence d'un nouveau champsosauride dans le Crétacé supérieur de Chine. *C.r. Acad. Sci. Paris, Sér. II*, **292**, 541-544.
- STEEL, R. 1969. Ornithischia. *Handbuch der Paläoherpetologie*, **15**, 1-84. Gustav Fischer, Stuttgart.
- 1970. Saurischia. *Ibid.* **14**, 1-87. Gustav Fischer, Stuttgart.
- 1973. Crocodylia. *Ibid.* **16**, 1-116. Gustav Fischer, Stuttgart.
- SUES, H.-D. 1977. The skull of *Velociraptor mongoliensis*, a small Cretaceous theropod dinosaur from Mongolia. *Paläontol. Z.* **51**, 173-184.
- THOMMASEN, H. and CARROLL, R. L. 1981. *Broomia*, the oldest known millerettid reptile. *Palaeontology*, **24**, 379-390.
- WALKER, C. A. 1981. New subclass of birds from the Cretaceous of South America. *Nature*, Lond. **292**, 51-53.
- WALL, W. P. and GALTON, P. M. 1979. Notes on pachycephalosaurid dinosaurs (Reptilia: Ornithischia) from North America, with comments on their status as ornithopods. *Can. JI Earth Sci.* **16**, 1176-1186.
- WARREN, A. A. and HUTCHINSON, M. N. 1983. The last labyrinthodont? A new brachyopid (Amphibia, Temnospondyli) from the early Jurassic Evergreen Formation of Queensland, Australia. *Phil. Trans. R. Soc. Lond. B*, **303**, 1-62.

- WEISHAMPEL, D. B. and WEISHAMPEL, J. B. 1983. Annotated localities of ornithopod dinosaurs: implications to Mesozoic paleobiogeography. *The Mosasaur*, **1**, 43-87.
- WELLNHOFER, P. 1978. Pterosauria. *Handbuch der Paläoherpetologie*, **19**, 1-82. Gustav Fischer, Stuttgart.
- WILD, R. 1978. Die Flugsaurier (Reptilia, Pterosauria) aus der oberen Trias von Cene bei Bergamo, Italien. *Boll. Soc. Palaeontol. Ital.* **17**, 176-256.
- 1980. Die Triasfauna der Tessiner Kalkalpen. XXIV. Neue Funde von *Tanystropheus* (Reptilia, Squamata). *Schweiz. Paläontol. Abh.* **102**, 1-43.

MICHAEL J. BENTON
Department of Geology
The Queen's University
Belfast BT7 1NN
Northern Ireland