

Historical tests of the absolute completeness of the fossil record of tetrapods

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Abstract.—Six compilations of fossil tetrapod families, spanning 100 years, each contain a broadly similar diversity pattern since the Upper Devonian. Comparison of four recent data bases, one of which is derived from a strict cladistic treatment, reveals widespread taxonomic and stratigraphic inaccuracies in three earlier data bases. Improvement of our interpretation of the tetrapod fossil record will come through continued taxonomic and stratigraphic revision as well as discovery of new fossils.

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Introduction

The incomplete nature of the fossil record is well known and has been extensively documented (Newell 1959; Raup 1972, 1976; Sadler 1981; Schindel 1982; Paul 1982; McKinney 1986). The record for terrestrial vertebrates is particularly patchy, and methods have to be established for quantifying that patchiness. How can we recognize those parts of the record that reasonably accurately reflect true taxonomic richness from those that do not? Further, can we quantify the degree of completeness? There are two kinds of completeness: absolute completeness, a measure of the precise proportion of the total true diversity of species, or some other taxon, at some time in the past that is represented by known fossils; and relative completeness, the proportion of species, or other taxa, present at time A compared to those present at time B. Both absolute and relative completeness can also be assessed taxonomically, by comparing major taxa across substantial amounts of geological time.

The question of relative completeness of the fossil record has been addressed by Paul (1982, 1985), Jablonski (1983, 1986), Benton (1985a, 1987, 1989a,b), and others. Measures of absolute completeness of the fossil record would be of more value but are ultimately beyond calculation. One means of obtaining

an estimate of absolute completeness is a historical approach to scientific studies of the fossil record. This is based on the assumption that our knowledge of the fossil record is broadly improving through research time—an improvement that is interrupted by numerous false starts and backward steps, no doubt—and that some day paleontologists will have documented every organism that ever left a fossil in any rock formation anywhere in the world (absolute completeness value = 100%). We stress that we are considering absolute completeness of the fossil record, that is, that part of past life that has been preserved in the rock record; we are not suggesting that a complete knowledge of all past life is ever theoretically attainable. The idea is to compare our knowledge of the fossil record of particular groups at different times over the past 100 years of research time, and to pinpoint areas of change that may indicate future likely progress and our place on the road to a total knowledge of the fossil record.

We used the record of fossil terrestrial tetrapods as a test case in a study of six compilations dating from 1889 to 1987. We asked: how has our view of overall diversity through time changed in 100 years of research time? How have extinction and origination rates calculated from the different data bases changed? How have familial stratigraphic du-

rations changed? How has the intensity of extinction changed at particular postulated mass extinction events? Finally, what are the major contributing factors to the patterns of change noted in the past 100 years of research?

Data Sources

The earliest of the six data bases considered here was compiled from three sources. Data on families of birds were taken from Nicholson and Lydekker (1889) and were used to complement the lists of all other tetrapod families taken from Zittel (1902, 1925). The other data sources were the three editions of *Vertebrate Paleontology* by A. S. Romer (1933, 1945, 1966); Benton (1987); and Carroll (1987). The data bases are designated here as Z 1900 for Zittel; the three editions of *Vertebrate Paleontology* as R 1933, R 1945 and R 1966; and as B 1987 (Benton) and C 1987 (Carroll). These recent data bases are both in need of further revision as a result of changes in mammalian taxonomy in particular (e.g., Prothero and Schoch 1989) and in Tertiary stratigraphy (e.g., Woodburne 1987). However, we preferred to use published data bases, unaltered despite inadequacies, as test cases so that our tests may be repeated readily. Improved data bases in the future will provide further tests of our results.

Means of Comparison.—To compare the data bases, ranges of tetrapod families in geological time were resolved to epoch level, such as Middle Triassic or Late Cretaceous, and wherever possible, sub-epoch level. Ranges in the Mississippian, Pennsylvanian, and Paleogene are given to sub-epoch level in R 1966 and C 1987. Benton's data base is the only one in which tetrapod family ranges are given to stratigraphic stage level and his data were lumped to allow comparison with the others. For example, the range of the Family Teleosauridae is listed in B 1987 as Toarcian to Valanginian, but was taken as Early Jurassic to Early Cretaceous in this comparison.

All the data bases which give ranges to epoch level use middle Permian, middle Cretaceous, middle Paleocene, and middle Oligocene as divisions of the geological timescale, a traditional aspect of vertebrate paleontol-

TABLE 1. Amount of data randomized for each Class in each data base, expressed as a percentage. The figures for R 1933 represent the percentage of families in each Class that were derived from R 1945 using R 1933 genera. Abbreviations given in text.

Data base	Class Amphibia	Class Reptilia	Class Aves	Class Mammalia	All Tetrapods
C 1987	0	4.9	11.3	2.1	4.2
B 1987	0	0	0	0	0
R 1966	6.3	0	33.1	2.6	9.7
R 1945	0	0	0	0	0
R 1933	0	10.5	100	0	10.5
Z 1900	46.2	6.8	4.2	0	6.6

ogy. Although the Palmer (1983) timescale used in this study does not include these divisions, they were retained for the sake of comparison. Lumping Benton's data involved designation of the appropriate stratigraphic stages of Palmer's (1983) timescale into each of the erroneous time periods, for example, the Berriasian, Valanginian, Hauterivian, and Barremian comprise the middle Cretaceous.

The broad stratigraphic ranges employed in these data bases tend to smooth out data representing any periods of rapid extinction, such as a large-scale elimination of families confined to one stratigraphic stage, so the B 1987 data base, with its finer resolution, should provide more precise information regarding the timing of extinction events.

In the older data bases some family ranges were noted simply as Eocene, or Permian—Early Triassic for example. In these cases a randomization of the data was required, as follows. For an Eocene range, for example, the origination was determined by randomly selecting one of three counters, the counters having been marked E, M and L to represent Early, Middle and Late. When the E counter was selected the extinction was determined by the same method using all three counters. When the origination was determined as Middle Eocene, only the M and L counters were employed to determine the time of extinction. When the origination was determined as Late Eocene, the extinction was automatically fixed as Late Eocene. The R 1966 data base required most attention in this respect, with 9.7% of the total number of families having their ranges randomized in this fashion (Table 1).

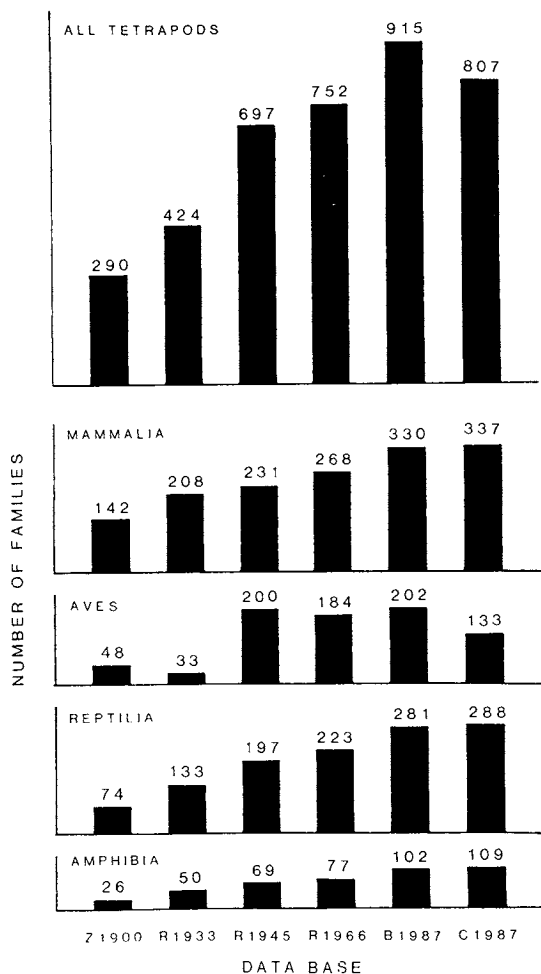


FIGURE 1. Number of tetrapod families arranged by class and as a total number as given by each of six data bases. Abbreviations as in text.

In the most recent data bases, B 1987 and C 1987, randomizing of the data was confined to the Tertiary and therefore has no effect on the interpretation of the Paleozoic and Mesozoic extinction events.

The figures in Table 1 for R 1933 do not represent family ranges that have been randomized as outlined, but families that have been taken from R 1945 of which R 1933 lists only genera; genera attributed to Class Aves are not assigned to families in R 1933, and a small number of reptile genera are similarly listed unattributed to families.

Calculation of Rates

A listing of tetrapod families was compiled from each data base and numbers of origi-

nations and extinctions were calculated epoch by epoch for marine and nonmarine tetrapods together. Total extinction (R_E) and total origination (R_S) rates were calculated as the number of families that disappeared or appeared respectively during an epoch or subepoch divided by the estimated duration of that interval (t):

$$R_E = E/t \quad (1)$$

$$R_S = S/t \quad (2)$$

where E is the number of extinctions and S is the number of originations. Per-taxon extinction (r_e) and origination (r_s) rates were calculated by dividing the total rates by the end-of-interval familial diversity D (Sepkoski 1978):

$$r_e = (1/D)E/t \quad (3)$$

$$r_s = (1/D)S/t \quad (4)$$

The Palmer (1983) geological timescale was used throughout this project for calculating the duration of each time interval, regardless of the data base. The choice of this particular timescale from several current standards is not crucial to our tests: our intention was simply to remove the timescale as a variable or source of error between data bases.

Diversities, Rates, and Major Events

Diversities.—The numbers of families of amphibians, reptiles, birds and mammals in each data base are shown in Fig. 1. This initial comparison of data shows a steady increase in the total number of families recognized during the past 100 years, and the totals in each class, with the exception of Aves. The sparse record of fossil birds and the inaccurate interpretation of specimens has hindered the compilation of a credible data base for Aves throughout the century. In the two most recent data bases, Benton's Aves section is inaccurate (discussed below), and Carroll's is incomplete, thus reducing the number of tetrapod families overall in C 1987 (Fig. 1).

The same general pattern is retained in the plots of marine and nonmarine family diversity against time for the six data bases, despite an increase in the number of families from 290 (Z 1900) to 807 (C 1987) and 915 (B 1987). Diversity declines are consistently recorded

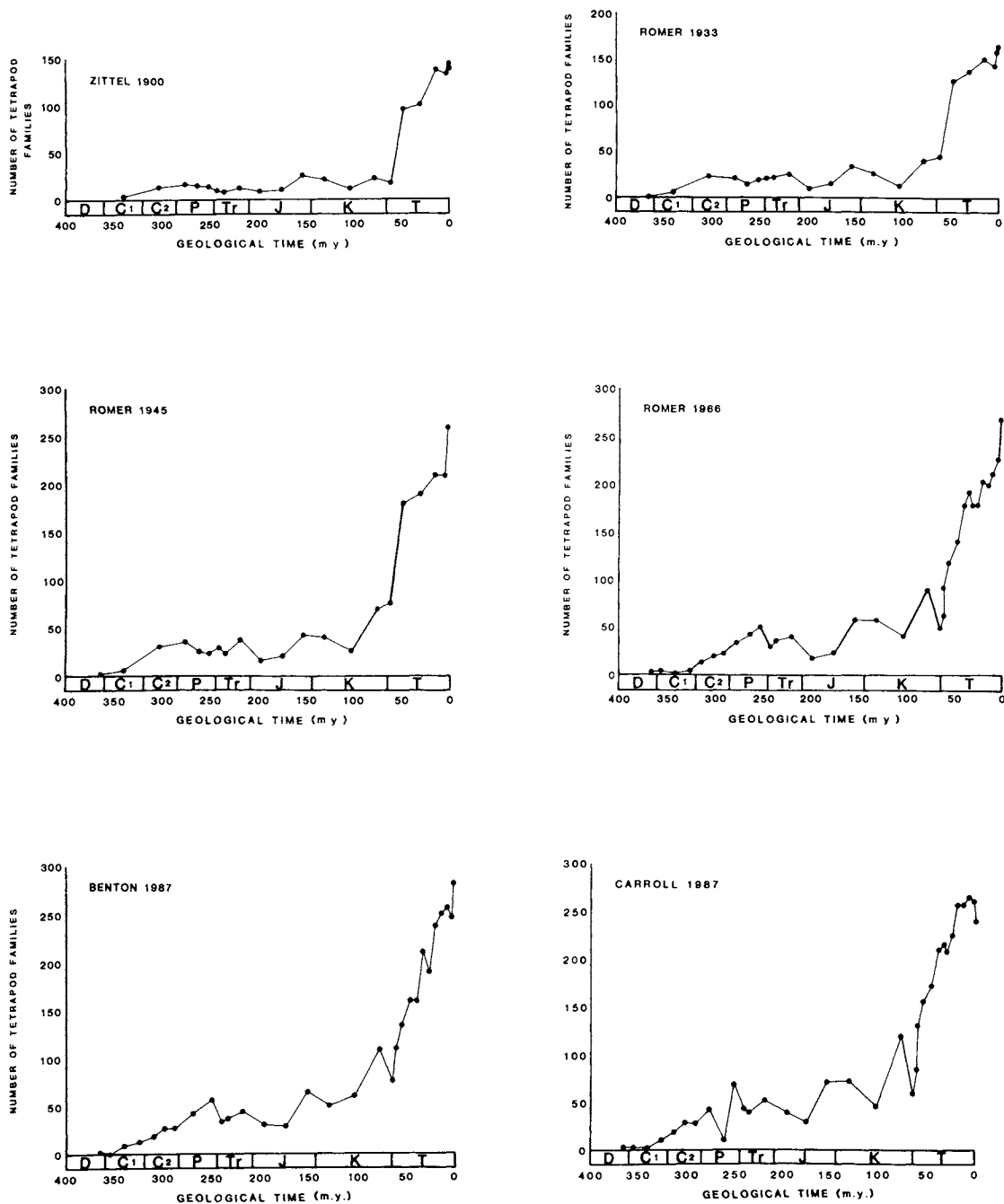


FIGURE 2. Numbers of tetrapod families plotted against geological time for each of six data bases. The diversity patterns are broadly similar showing a gradual increase from Early Devonian to Late Cretaceous followed by a substantial increase in family numbers in the Tertiary. Abbreviations: D = Devonian, C1 = Mississippian, C2 = Pennsylvanian, P = Permian, Tr = Triassic, J = Jurassic, K = Cretaceous, T = Tertiary.

for the Late Permian—Early Triassic, Late Triassic—Early Jurassic, Late Jurassic—Early Cretaceous and Late Cretaceous—Paleocene although the scale of the faunal turnover varies

in magnitude. Sudden fluctuations in familial diversity can be attributed to a variety of causes. Variations in origination and extinction rates may reflect an extinction event,

TABLE 2. Number of extinctions (E), originations (O), and overall decline in diversity (DD), recorded in each data base for specified boundaries. Extinction figures are for the epoch or sub-epoch below the boundary. Origination figures are for the epoch or sub-epoch above the boundary. Abbreviations: Perm., Permian; Trias., Triassic; Jur., Jurassic; Cret., Cretaceous; Pal., Paleocene; Eoc., Eocene; Olig., Oligocene; Mio., Miocene; Plio., Pliocene; E., Early; M., Middle; m., middle; L., Late. Others given in text.

	Z 1900			R 1933			R 1945			R 1966		
	O	E	DD	O	E	DD	O	E	DD	O	E	DD
L. Mio.-Plio.										21	12	9
Mio.-Plio.	18	14	4	14	8	6	21	20	1	26	21	5
Olig.-Mio.	15	52	-37	27	39	-12	32	52	-20	47	65	-18
E. Olig.-m. Olig.										23	9	14
Eoc.-Olig.	30	35	-5	46	54	-8	56	66	-10	56	63	-7
L. Cret.-E. Pal.	10	5	5	18	23	-5	37	43	-6	55	22	33
E. Cret.-m. Cret.	11	1	10	14	1	13	14	0	14	9	19	-10
L. Jur.-E. Cret.	8	3	5	14	6	8	17	15	2	20	7	13
L. Trias.-E. Jur.	10	4	6	19	3	16	32	11	21	25	13	12
E.-M. Trias.	5	3	2	14	15	-1	18	13	5	14	17	-3
L. Perm.-E. Trias.	10	6	4	14	16	-2	15	20	-5	3	21	-18
E. Perm.-m. Perm.	6	4	2	21	14	7	29	19	10	32	45	-13
E. Perm.-L. Perm.												

in which major physical forces cause an elimination of taxa, or they may result from any number of factors inherent in the fossil record.

Origination and Extinction Rates.—The numbers of originations and extinctions, and the calculated total and per-taxon origination and extinction rates, were used in an examination of tetrapod diversity through time as given by each data base.

Plots of familial diversity derived from each data base show the same pattern in the most general sense, with an initial increase in family numbers followed by fluctuations in diversity throughout the late Paleozoic and Mesozoic (Fig. 2). In all but Z 1900, the Late Cretaceous marks a time in which diversity increases markedly above previous levels. There is no hint of the Late Cretaceous—Paleocene extinction in R 1933 and R 1945, while the other data bases show a significant decline in diversity preceding an escalation in numbers throughout the Tertiary. Substantial declines in diversity are evident throughout the series of graphs for the Late Permian, Late Triassic, Early Cretaceous and Late Cretaceous. The declines may reflect extinction events or a much reduced origination rate coupled with a normal extinction rate. Other declines are observed, such as those in the Tertiary, which have come to light in the three most recent compilations (Fig. 2), but the four

mentioned above are the most consistent and of greatest magnitude. To determine whether the declines represent extinction events or decreased rates of origination, the numbers of extinctions and originations were compiled from each data base and examined in this context (Table 2).

In examining a diversity decline for, say, the Late Triassic, the number of Late Triassic extinctions is considered in tandem with the number of Early Jurassic originations to give an overall figure for the change in family numbers across the boundary. This accommodates the underlying assumption that all the extinctions in an epoch occurred as the epoch closed, and all originations in the subsequent epoch occurred as it opened, which is the only workable scenario in this type of analysis. Four major extinction events are analyzed here.

Major Events.—The perceived magnitude of the Late Permian event has increased marginally with research time, beginning at a high level in Z 1900 in which ten of 14 families recorded for the Late Permian (71.4%) become extinct, and ending in C 1987 when 58 of 68 families (85.3%) suffer extinction. The percentage of families present in the Late Permian suffering extinction, and the actual number of families, increases steadily from Z 1900 to C 1987. The greatest decline in overall diversity is shown in B 1987 because of a re-

TABLE 2. Extended.

B 1987			C 1987		
O	E	DD	O	E	DD
18	12	6	20	16	4
43	12	31	62	16	46
40	88	-48	48	98	-50
			24	17	7
63	64	-1	79	82	3
49	21	28	72	11	61
5	14	-9	27	0	27
21	8	13	24	26	-2
21	3	18	35	21	14
14	11	3	25	21	4
45	16	29	58	33	25
			35	3	32
31	46	-15			

duced number of originations (see Table 2). The per-taxon extinction rate for the beginning of the Late Permian and for the end of the Permian is very high (Fig. 3). This is a consistent feature of all the data bases examined here, but the Early Triassic per-taxon origination rate calculated for B 1987 is significantly lower than that calculated for the other data bases (Fig. 3), explaining the greater drop in diversity in B 1987. Synonymous genera of mammal-like reptiles with origins in the Late Permian and Early Triassic were eradicated from B 1987 through taxonomic restructuring, and a large number of the spurious originations recorded in R 1966 and C 1987 were eliminated.

The general perception of the Late Triassic event has differed from that of the Late Permian. The percentage of families which suffer extinction increased initially, and then decreased, while the number of families present has increased steadily during the course of research time. An exception to this pattern is found in B 1987 which shows a reduced number of extinctions relative to R 1966 and C 1987 and a significantly smaller number of Early Jurassic originations (Table 2). This trend is borne out by the per-taxon and total extinction rates for the Late Triassic (Figs. 3, 4) and the per-taxon and total origination rates for the Early Jurassic (Figs. 3, 4). This results in a diversity decline which does not vary

greatly in comparison to the others because the reduction in the number of families suffering extinction in the Late Triassic is countered by a reduction in the number of Early Jurassic originations.

The reason for this reduction may be twofold. Synonymous genera, especially of mammal-like reptiles and thecodontians, bolster the number of apparent originations and extinctions recorded in R 1966, and their subsequent removal by cladistic analysis is reflected in the B 1987 data for the Late Triassic. A second source of error in R 1966 has been largely excluded from B 1987. Revisions of stratigraphy, coupled with taxonomic work, have shown that a number of families, listed in R 1966 as suffering extinction in the Late Triassic, actually extended into the Early Jurassic (Olsen and Galton 1977, 1984). The eradication of this source of error has been assisted by the increasingly successful recovery of tetrapod remains from rocks of the Jurassic period, a hitherto notoriously incomplete section of the tetrapod fossil record (Romer 1966; Benton 1989b).

The number of families in the Early Cretaceous that suffered extinction at the end of that epoch increased steadily from ten in 1900 to 27 in C 1987. When this number is expressed as a percentage of the families present in the Early Cretaceous, however, there is an overall reduction because the number of families recorded for this epoch has increased steadily over the past 100 years, and proportionately faster than the increase in the number of families that suffered extinction. This illustrates the point that any increase in the number of extinctions must be considered, not only in relation to the number of originations, but also to the overall number of families. The exception to the general pattern is B 1987 in which the lowest number of Early Cretaceous extinctions (five) and the highest number of middle Cretaceous originations (14) are found, contrasting with a range of 11 to 27 family extinctions and zero or one family originations as recorded in the other data bases (Table 2). The five extinctions comprise only 10% of the families known for that time, and overall diversity increases. In contrast, C 1987 shows a 37.5% reduction in families with

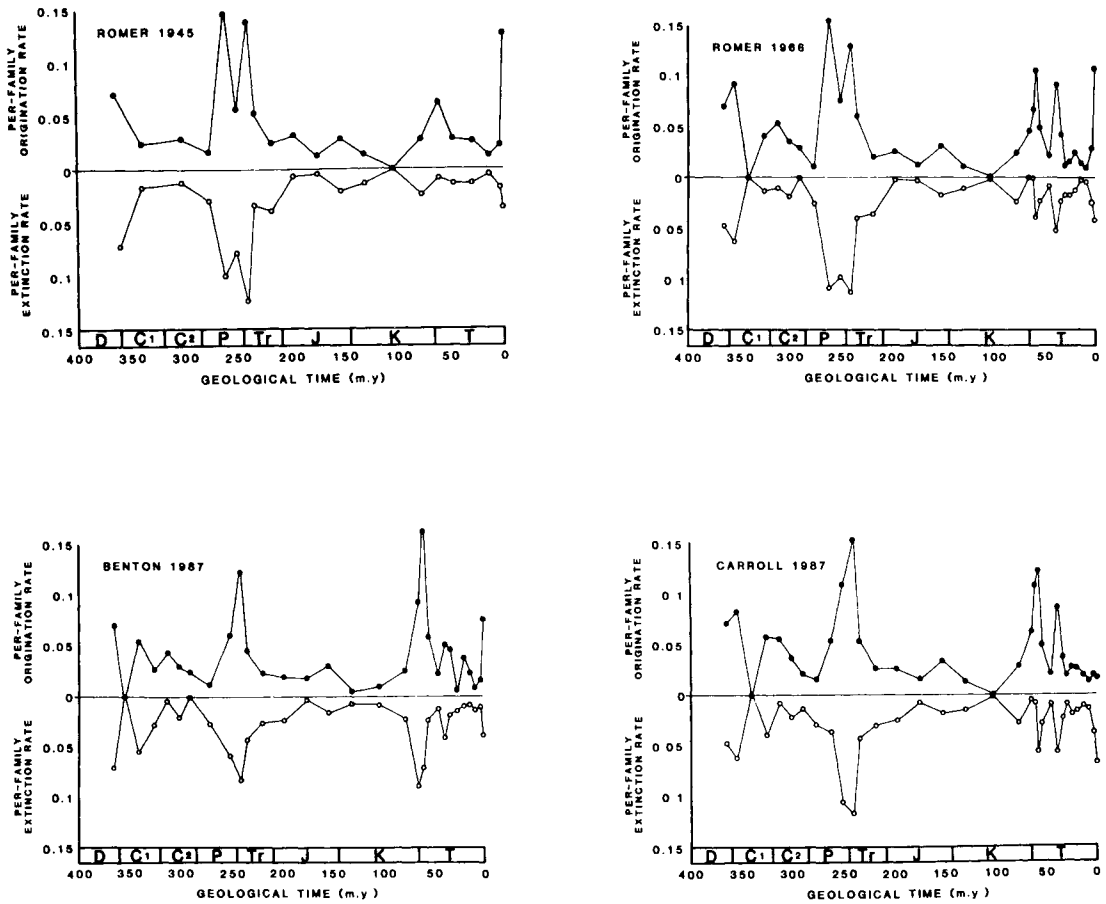


FIGURE 3. Plots of per-family origination and per-family extinction rate through geological time as calculated from four data bases. Abbreviations as in Fig. 2.

27 extinctions and zero middle Cretaceous originations.

A major Late Cretaceous extinction event has been revealed only in the three most recent data bases. Although R 1933 and R 1945 show significant familial extinctions, they also show greater numbers of Early Paleocene originations, resulting in an overall increase in diversity (Table 2). The number of Late Cretaceous extinctions has increased from ten (1900) to 72 (C 1987), but the number of Early Paleocene originations recorded in R 1966, B 1987 and C 1987 fell markedly, revealing a large-scale extinction event and diversity decline. The familial extinctions expressed as numbers of families, and as percentages of the total number of families, are essentially similar for R 1966 (47, 51.7%) and B 1987 (49,

51.9%), but C 1987 differs somewhat. The percentage is slightly increased (60.5%) but the number of families becoming extinct is much greater (72), resulting in a significantly greater decline in overall diversity (Table 3). The per-taxon and total extinction rates for the Late Cretaceous bear out this pattern (Figs. 3, 4) and the per-taxon and total origination rates calculated for B 1987 illustrate why this data base records a much reduced decline in diversity.

Comparison of Two 1987 Data Bases.—The two 1987 data bases, B 1987 and C 1987, were compiled independently, and a comparison offers some valuable insights into how data bases may differ even when they were compiled at the same time. Five separate extinction events were analyzed in detail. All the families that

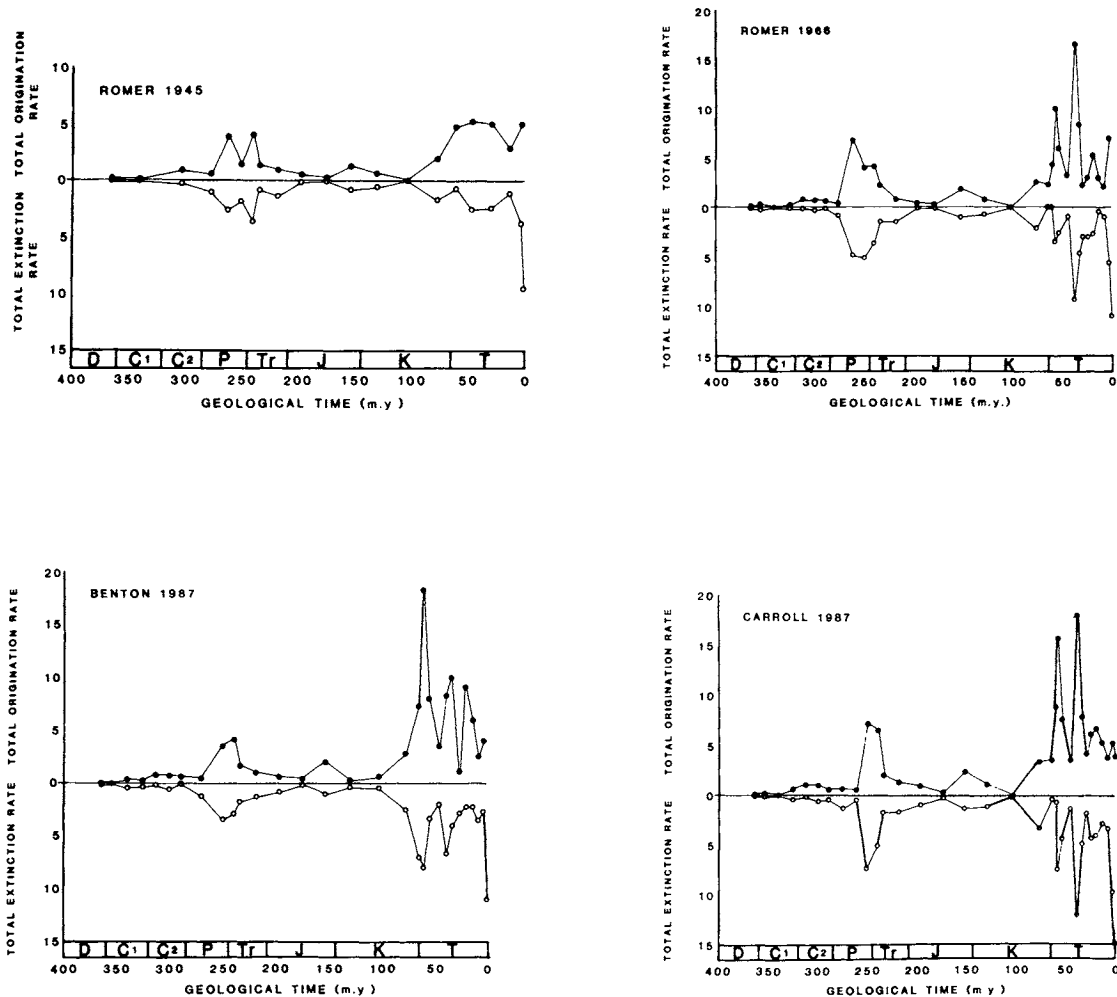


FIGURE 4. Plots of total origination and total extinction rate through geological time as calculated from four data bases. Abbreviations as in Fig. 2.

died out during each extinction event were listed, and their stratigraphic ranges, phylogenetic validity, and constituent genera were checked. The results are presented in Table 3.

A cursory inspection of the data in Table 3 reveals that only four of Carroll's 217 families considered here are invalid, their constituent genera having been reassigned. The four in question are families of mammal-like reptiles, a group which has been extensively revised using cladistic methodology by Kemp (1982) and Hopson and Barghusen (1986). The other categories of inaccuracy represented in Table 3 do not detract from the quality of the C 1987 data base.

A large number of monogeneric or mono-

specific families are present in all major clades, but this is also the case with B 1987. The proportion of families in C 1987 which have been listed as incorrectly dated is not significant either. For the purposes of this exercise, families which suffered extinction in one particular stage were considered. For example when considering the Late Cretaceous event (the mass extinction of those families whose fossil remains are common in Maastrichtian deposits but absent from Danian deposits), two lists were compiled: one from B 1987 containing all families whose last appearance is recorded in the Maastrichtian, and one from C 1987 containing all families whose last appearance is recorded in the Late Cretaceous. As noted

TABLE 3. Number of families suffering extinction, and the errors contained therein, for five extinction events as derived from two data bases, Benton 1987 and Carroll 1987. Abbreviations as in Table 2.

	Number of families suffering extinction	Mono-generic	Reassigned	Incorrectly dated
Benton 1987				
L. Cret.	36	0	0	1
E. Cret.	3	0	0	0
L. Jur.	19	0	0	0
L. Trias.	27	0	0	2
L. Perm.	28	0	0	2
Carroll 1987				
L. Cret.	72	15	0	18
E. Cret.	29	8	0	10
L. Jur.	23	4	0	7
L. Trias.	37	9	1	6
L. Perm.	56	10	4	20

earlier, C 1987 gives family ranges to epoch level only, thus C 1987 details all families which suffered extinction in the "Senonian" (Coniacian, Santonian, Campanian, and Maastrichtian). In this study those terminating in the Coniacian, Santonian, and Campanian are designated as incorrectly dated. This merely indicates that the family ranges given in C 1987, like those of Romer (1933, 1945, 1966), are not to a time scale which is sufficiently fine to reveal patterns of change accurately.

Changes in Familial Durations

Many paleontologists would expect that the stratigraphic range of a family would increase through research time as improved collecting techniques uncover new species or genera in new geological formations outside the former maximum range. This may be designated the conventional view. It would also seem reasonable, however, to assume that in some cases the range would be shortened by the removal of invalid genera or species which had extended a family range beyond its true limits. This idea, that family ranges will tend to reduce through research time, often as a result of strict phylogenetic analysis, may be termed the cladistic view. How have our determinations of family ranges changed in 20 years? Every taxonomic group from subfamily to order given in Harland et al. (1967) (H 1967)

was listed and compared with B 1987. The taxonomic validity of the units and their stratigraphic ranges were examined. The 1967 and 1987 data bases give family ranges to stratigraphic stage level. In H 1967, however, subfamilies, superfamilies, suborders, infraorders, or orders may be listed instead of families. All ranges are recorded to stage level but the non-uniform taxonomic assignments throughout are a hindrance.

Examination of four classes (Amphibia, Reptilia, Aves and Mammalia) in H 1967 revealed the following. Of the 72 taxa (family, suborder, etc.) listed for the Amphibia, 13 (18.1%) are invalid and have subsequently been reassigned. Of the 182 taxa listed for the Reptilia, 32 (17.6%) have been reassigned. H 1967 lists 217 families and subfamilies for the Aves, but since Benton (1987) used H 1967 in compiling the Aves section of B 1987 there is little information to be had from a comparison. This section of Benton's data base will need considerable revision judging by the validity of the rest of H 1967. H 1967 lists 129 taxa for the Mammalia. Of these, 77 are families while the remaining 52 are superfamilies, suborders, or orders. All of the 77 families are valid and are found in B 1987. Of the 52 other taxa two are invalid, while the other 50 are valid groupings into which many of Benton's families can be slotted.

A number of the genera that make up the various taxa employed by H 1967 are invalid and have been rejected or reassigned in the past 20 years. Many of the families which are regarded as valid, and have counterparts in B 1987, may have had a slight rearrangement of genera or species since 1967. These generic changes may affect the stratigraphic range of the families, either shortening or lengthening them.

Determining Family Ranges.—The temporal range of each family given in H 1967 and B 1987 was calculated as follows. For those families whose stratigraphic range lies within one stratigraphic stage, the range in time is taken as half the length of that stage. For example, the Omphalosauridae are recorded in B 1987 as confined to the Anisian. Palmer (1983) shows the Anisian to be of 5 m.y. duration, so that the range of the Omphalosauridae is

TABLE 4. Number of families in Benton (1987) whose range has increased, decreased, or remained static, in terms of duration in millions of years and number of geologic stages spanned, relative to the combined Romer (1966)/Harland et al. (1967) data base. All randomized families excluded.

		Increase	Decrease	Tied	Z	2-Tailed P
Amphibia	m.y.	15	5	13	-1.8666	.062
	stages	15	5	13	-1.9786	.0479
Reptilia	m.y.	40	30	30	-.1463	.8837
	stages	40	26	34	-.0894	.9287
Aves	m.y.	10	1	171	-2.4006	.0164
	stages	10	1	171	-2.445	.0145
Mammalia	m.y.	95	52	53	-3.4071	.0007
	stages	86	48	66	-3.3401	.0008
All tetrapods	m.y.	160	88	267	-3.5075	.0005
	stages	151	80	284	-3.6064	.0003
All tetrapods excluding Aves	m.y.	150	87	96	-3.0588	.0022
	stages	141	79	113	-3.1078	.0019

taken as 2.5 m.y. For those families whose range extends beyond a single stratigraphic stage, the range in time is taken as the interval between the mid-points of the first and last stages. For example, the range of the Scelidosauridae is given in H 1967 as Sinemurian to Oxfordian. The mid-points of these stages, 201 Ma and 159.5 Ma according to Palmer (1983), yield 41.5 m.y. as the range assigned to the Scelidosauridae. The range of every valid family present in both H 1967 and B 1987 was calculated using this method and the ranges compared in order to test whether stratigraphic ranges had generally increased or decreased.

There were some problems in determining comparable families in the H 1967 and B 1987 data bases, since H 1967 does not always give families. Benton's (1987) list of families was taken as a standard because it includes only families. Corresponding groups were established by comparison of R 1966 and H 1967 with B 1987. In many cases, direct comparison of families is possible, but there are instances when broader taxonomic groupings are employed. For example, Benton (1987) lists the Family Taeniolabididae (Santonian to Ypresian). Harland et al. (1967) list the suborder Taeniolabidoidea (Campanian to Early Eocene, taken as Ypresian using the Palmer [1983] timescale) but do not detail constituent families, so in this case we compare family with suborder.

At first, we used H 1967 to find equivalents for the 915 families of marine and nonmarine

tetrapods listed in B 1987 because most family ranges in H 1967 are given to stage level. Not all of the 915 families listed in B 1987 are to be found in H 1967, so R 1966 was used to fill any gaps where possible. Families erected over the past twenty years were omitted from this analysis since they can give no information on changing concepts of stratigraphic durations. 718 families are represented both in B 1987 and in either H 1967 or R 1966. As discussed above, not all of the family ranges in the two earlier publications are given to stage level. Those families which also occur in B 1987 but whose range is not given to single stage level were also omitted from the analysis initially, leaving a total of 515 families for comparison.

Comparing Two "Stage-level" Data Sets.—A valid statistical comparison of the two data sets proved elusive. The simplest approach proved to be the most useful. The non-parametric Wilcoxon matched-pairs signed-rank test was employed (SPSSX.2 statistical package on a VAX mainframe computer) to determine the number of ranges in B 1987 that had increased, decreased, or remained the same relative to those in the R 1966/H 1967 combined data base (Table 4).

Of the 515 families of tetrapods included in the analysis, 52% have equal ranges in both data bases. However, since the Aves section of B 1987 is derived almost exclusively from H 1967, its inclusion skews the results considerably towards a greater proportion of tied ranges simply because there are 182 families

TABLE 5. Number of families in Benton (1987) whose range has increased, decreased, or remained static, in terms of duration in millions of years and number of geologic stages spanned, relative to the combined Romer (1966)/Harland et al. (1967) data base. All randomized families included.

		Increase	Decrease	Tied	Z	2-Tailed P
Amphibia	m.y.	31	24	16	-.7331	.4635
	stages	30	22	19	-.6193	.5357
Reptilia	m.y.	76	71	35	-.556	.5782
	stages	71	61	50	.2669	.7896
Aves	m.y.	10	3	186	-1.9917	.0464
	stages	10	3	186	-2.103	.0355
Mammalia	m.y.	121	80	65	-3.081	.0021
	stages	112	75	79	-3.0162	.0026
All tetrapods	m.y.	238	178	302	-2.3101	.0209
	stages	223	161	334	-2.495	.0126

of birds, 34.6% of the total number of families analyzed, and of these, 171 have ranges of equal value in both data bases. Eliminating the Class Aves from the results reveals a truer pattern of change in family ranges between the two data bases (Table 4).

The numbers of increases, decreases, and ties vary slightly for the two aspects of the data considered; ranges in millions of years and the number of stratigraphical stages spanned. This apparent ambiguity results from those families which span an equal number of stages but not the same stages. For example the amphibian family Dissorophidae is recorded as spanning ten stages in each data base, Moscovian to Tatarian in H 1967, and Bashkirian to Kazanian in B 1987. These ranges, calculated as described above, are 52.5 m.y. and 58.8 m.y., respectively, and are recorded as having increased from H 1967 to B 1987, although the number of stratigraphical stages spanned by the family is recorded as a tie.

Most of the 333 families of amphibians, reptiles and mammals have been updated and their ranges altered in the past 20 years. A total of 236 families (70.9%) show an increased or decreased range, with the remaining 97 families (29.1%) unchanged. Of the 236 families exhibiting change, the ranges of 149 (44.8% of the total) have increased in the past 20 years while 87 (26.1% of the total) have experienced a decrease in their range. This appears to fit what we called the conventional view, that most families whose range has been altered would show an increase. We would suggest, however, that few would expect so

many families (26.1%) to show a decreased range. Such a result suggests that taxonomic revisions are continuing to play a major role in improving our knowledge of the fossil record.

Inclusion of the randomized families returns the data bases to their initial complement of 718 families which are listed in B 1987 and have an equivalent in either H 1967 or R 1966. Analysis of these data sets reveals a greater number of ties and a lesser number of increased ranges (Table 5). Removing the biasing influence of Class Aves reveals a lesser number of ties, as expected, and a greater number of decreased ranges. The inclusion of carefully randomized data supports the supposition that many families have had their ranges shortened with continued taxonomic and stratigraphic revisions.

Discussion

Many possible sources of error affect the fossil record and compromise its usefulness in the studies of macroevolution (Raup 1972, 1976; Sepkoski 1975, 1978; Signor 1978, 1985; Padian and Clemens 1985; Benton 1988, 1989a,b). Well known examples include variation in the area of sediment exposed for each stratigraphic period, in the estimated volume of rock for that period, and in the number of taxonomists working on a given period fauna, termed paleontologist interest units (Sheehan 1977). Most of these factors may be assessed and taken into account when parts of the fossil record are being compared. Lazarus taxa (Jablonski 1983, 1986) also have a dis-

ruptive influence, and the absence of terrestrial deposits for certain time spans hinders accurate assessment of times of origination and extinction. Sampling errors are of less importance at the family level than at the species level (Raup 1979), but serious sources of error at higher taxonomic levels may still arise from inadequate phylogenetic analysis. The essence of this study has been to show that detailed consideration of the phylogeny and taxonomy of the constituent genera and species of any given family is vital in establishing the accuracy of the family range, and hence, of the diversity patterns.

Taxonomic inadequacy is one inevitability of paleontology. In its early stages, vertebrate paleontology was a science restricted to those with the means to obtain specimens. A lack of communication between individuals and between countries, and varying opinions about the features that characterize particular taxa, contributed to a false multiplication of species and higher taxa. The recent application of cladistics has provided a measure of uniformity in vertebrate systematics and removed many of the ill-defined genera and families that were erected by early workers.

A comparison of recent analyses of the vertebrate fossil record shows the need to revise the data bases. Most recent studies have used data bases that do not fully reflect the cladistic analyses. For example, Olson (1982), in a study of vertebrate extinctions at the Permian-Triassic boundary used data derived mostly from Romer (1966) that were "... modified as deemed appropriate to account for changes since his listing was compiled . . ." A similar modification was carried out by Padian and Clemens (1985). In a succinct review of the pitfalls common in analyses of terrestrial vertebrate diversity, they tackled the problems of biases in, and limitations of, stratigraphic and taxonomic data, problems also considered by Benton (1985a, 1989a,b). Although using Romer (1966) and Harland et al. (1967) for compilation of systematic diversity, Padian and Clemens (1985) corrected for systematic revisions made in the previous 15 years. They also used Sepkoski's most recent update of his 1982 list of vertebrate diversity.

Such revisions provide much needed im-

provements but there is always a need for further work. Romer (1966) is no longer suitable as a source of tetrapod taxonomy and diversity data (Maxwell and Benton 1987). This study has shown Harland et al. (1967) to be unreliable, and Sepkoski's (1982) compilation, with revisions, still suffers from taxonomic problems (Benton 1985a,b). A comprehensive breakdown of the inaccuracies in parts of Sepkoski's (1982) data base (Patterson and Smith 1988) shows that the need for taxonomic revisions is continual and overwhelming. Even the most recent works in this field must therefore be regarded as inaccurate to a degree.

The comparison of the data bases of Benton (1987) and Harland et al. (1967) revealed a great many changes in family ranges over the past 20 years. The change is not systematic, but consists of increased ranges in some cases and decreased ranges in others, suggesting the importance of taxonomic and stratigraphic reassessments. It is not enough simply to modify older data bases by the addition of new fossil finds to already existing families.

A similar study of fossil brachiopod genera (Grant 1980) revealed large increases in numbers of genera for certain geological periods. These were linked to the actual number of brachiopod workers, and their proportion to the percentage of outcrop area per geological period. The greater the number of workers per period, the greater the number of genera discovered and described. This simple rule applies to all portions of the fossil record and undoubtedly affects tetrapod data bases.

Despite all the negative aspects outlined, there is real value in the type of analysis presented here. The notoriously patchy tetrapod record is probably better analyzed phylogenetically than many more complete invertebrate fossil records, and it is worthy of study. We have to pinpoint inaccuracies and areas of constant change to facilitate their improvement.

Conclusions

1. The six data bases of fossil tetrapod diversity considered here, taken as snapshots of paleontological knowledge over the past 100 years, all show the same general pattern

of numbers from Late Devonian to Late Cretaceous followed by a rapid increase in the Tertiary.

2. The most recent data bases, Harland et al. (1967), Benton (1987) and Carroll (1987) reveal, in fine detail, the well established declines in tetrapod family diversity throughout the Phanerozoic.

3. Advances in knowledge over the past 20 years have led to increases in the stratigraphic durations of 44.8% of tetrapod families, and decreases in 26.1% of the total. The increases are largely the result of new finds, as might have been expected, but the causes of the reductions in ranges are less obvious. They result from taxonomic reassignment, particularly of early taxa such as amphibians, thecodontians and mammal-like reptiles, but also of archosaurs and mammals.

4. Recent improvements in our knowledge of the tetrapod fossil record have resulted from re-evaluations of taxonomy and stratigraphy, and not just from the discovery of new fossils.

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Literature Cited

- BENTON, M. J. 1985a. Patterns in the diversification of Mesozoic non-marine tetrapods and problems in historical diversity analysis. *Special Papers in Palaeontology* 33:185-202.
- BENTON, M. J. 1985b. Mass extinction among non-marine tetrapods. *Nature* 316:811-814.
- BENTON, M. J. 1987. Mass extinctions among families of non-marine tetrapods: the data. *Mémoires de la Société Géologique de la France* 150:21-32.
- BENTON, M. J. 1988. Mass extinctions in the fossil record of reptiles: paraphyly, patchiness, and periodicity (?). Pp. 269-294. *In* Larwood, G. P. (ed.), *Extinction and Survival in the Fossil Record*. Clarendon Press; Oxford.
- BENTON, M. J. 1989a. Patterns of evolution and extinction in vertebrates. Pp. 218-241. *In* Allen, K. C., and D. E. G. Briggs (eds.), *Evolution and the Fossil Record*. Belhaven Press; London.
- BENTON, M. J. 1989b. Mass extinctions among tetrapods and the quality of the fossil record. *Philosophical Transactions of the Royal Society of London B* 325:369-386.
- CARROLL, R. L. 1987. *Vertebrate Palaeontology and Evolution*, W. H. Freeman; New York.
- GRANT, R. E. 1980. The human face of the brachiopod. *Journal of Paleontology* 54:499-507.
- HARLAND, W. B. ET AL. (EDS.). 1967. *The Fossil Record*. Geological Society; London.
- HOPSON, J. A., AND H. A. BARGHUSEN. 1986. An analysis of therapsid relationships. Pp. 83-106. *In* Hotton, N., III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), *The Ecology and Biology of Mammal-like Reptiles*. Smithsonian Institution Press; Washington and London.
- JABLONSKI, D. 1983. Apparent vs. real extinctions at the end of the Cretaceous period. *Geological Society of America, Abstracts and Programs* 15:602.
- JABLONSKI, D. 1986. Causes and consequences of mass extinctions: a comparative approach. Pp. 183-229. *In* Elliot, D. K. (ed.), *Dynamics of Extinction*. Wiley; New York.
- KEMP, T. S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. Academic Press; London.
- MAXWELL, W. D., AND M. J. BENTON. 1987. Mass extinctions and data bases: changes in the interpretation of tetrapod mass extinction over the past 20 years. *In* Currie, P. J., and E. H. Koster (eds.), *4th Symposium on Mesozoic Terrestrial Ecosystems, Occasional Paper of the Tyrrell Museum of Palaeontology, Alberta* 3:156-160.
- McKINNEY, M. L. 1986. How biostratigraphic gaps form. *Journal of Geology* 94:875-884.
- NEWELL, N. D. 1959. The nature of the fossil record. *Proceedings of the American Philosophical Society* 103:264-285.
- NICHOLSON, H. A., AND R. LYDEKKER. 1889. *A manual of palaeontology for the use of students, with a general introduction to the principles of palaeobiology*. Third Edition. 2 volumes. Blackwood; Edinburgh.
- OLSEN, P. E., AND P. M. GALTON. 1977. Triassic-Jurassic extinctions: are they real? *Science* 197:983-986.
- OLSEN, P. E., AND P. M. GALTON. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia africana* 25:87-110.
- OLSON, E. C. 1982. Extinctions of Permian and Triassic non-marine vertebrates. *Special Paper of the Geological Society of America* 190:501-511.
- PADIAN, K., AND W. A. CLEMENS. 1985. Terrestrial vertebrate diversity: episodes and insights. Pp. 41-96. *In* Valentine, J. W. (ed.), *Phanerozoic Diversity Patterns*. Princeton University Press; Princeton, New Jersey.
- PALMER, A. R. 1983. The decade of North American Geology 1983 time scale. *Geology* 11:503-504.
- PATTERSON, C., AND A. B. SMITH. 1987. Is the periodicity of extinctions a taxonomic artefact? *Nature* 330:248-251.
- PAUL, C. R. C. 1982. The adequacy of the fossil record. Pp. 75-117. *In* Joysey, K. A., and A. E. Friday (eds.), *Problems of Phylogenetic Reconstruction*. Academic Press; London.
- PAUL, C. R. C. 1985. The adequacy of the fossil record reconsidered. *Special Papers in Palaeontology* 33:7-15.
- PROTHERO, D. R., AND R. M. SCHOCH. 1989. *The Evolution of Perissodactyls*. Oxford University Press; New York.
- RAUP, D. M. 1972. Taxonomic diversity during the Phanerozoic. *Science* 215:1065-1071.
- RAUP, D. M. 1976. Species diversity in the Phanerozoic: an interpretation. *Paleobiology* 2:289-297.
- RAUP, D. M. 1979. Biases in the fossil record of species and genera. *Carnegie Museum of Natural History Bulletin* 13:85-91.
- ROMER, A. S. 1933. *Vertebrate Paleontology*. First Edition. University of Chicago Press; Chicago.

- ROMER, A. S. 1945. *Vertebrate Paleontology*. Second Edition. University of Chicago Press; Chicago.
- ROMER, A. S. 1966. *Vertebrate Paleontology*. Third Edition. University of Chicago Press; Chicago.
- SADLER, P. M. 1981. Sediment accumulation rates and the completeness of stratigraphic sections. *Journal of Geology* 89:569-584.
- SCHINDEL, D. E. 1982. Resolution analysis: a new approach to the gaps in the fossil record. *Paleobiology* 8:340-353.
- SEPKOSKI, J. J., JR. 1975. Stratigraphic biases in the analysis of taxonomic survivorship. *Paleobiology* 1:343-355.
- SEPKOSKI, J. J., JR. 1978. A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. *Paleobiology* 4: 223-251.
- SEPKOSKI, J. J., JR. 1982. A compendium of fossil marine families. Milwaukee Public Museum, Contributions in Biology and Geology 51 (and supplements to July, 1986).
- 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. *Paleobiology* 4:394-406.
- SIGNOR, P. W., III. 1985. Real and apparent trends in species richness through time. Pp. 129-150. *In* Valentine, J. W. (ed), *Phanerozoic Diversity Patterns*. Princeton University Press; Princeton, New Jersey.
- WOODBURNE, M. O. (ED.). 1987. *Cenozoic Mammals of North America. Geochronology and Biostratigraphy*. University of California Press; Berkeley.
- ZITTEL, K. A. VON. 1902. *Text-book of Palaeontology: Volume II; Vertebrates; Fishes to Birds*.
- ZITTEL, K. A. VON. 1925. *Text-book of Palaeontology: Volume III; Mammalia*.