

Mass extinctions among families of non-marine tetrapods : the data

by MICHAEL J. BENTON*

Abstract — There are 858 families of living and extinct non-marine tetrapods. Of these, 776 have a fossil record. The geological ranges of these families are tabulated, accurate to the level of the stratigraphic stage (mean duration, 6 Ma). These data are used to indicate the occurrence, and the magnitudes, of six mass extinction events. The fossil record of non-marine tetrapods is generally regarded as poor, and this question is explored. The incompleteness of the record varies from 0 % (no fossils) to apparently 100 % for some stages. Lissamphibians have the most incomplete record, and synapsids and the mammals appear to have the most complete record.

Les crises biologiques dans les familles de tétrapodes non-marins : les données

Résumé — Il y a 858 familles de tétrapodes non-marins fossiles et actuelles. 776 sont représentées à l'état fossile. Les distributions stratigraphiques de ces familles sont énumérées jusqu'au niveau de l'étage stratigraphique (durée moyenne, 6 Ma). Ces renseignements sont utilisés pour déiquer l'existence et l'importance de six crises biologiques. Les documents fossiles concernant les tétrapodes non-marins sont considérés généralement comme incomplets et cette question est examinée. L'état des documents varie de 0 % (pas de fossiles) à, apparemment, 100 % pour quelques étages. Les lissamphibiens sont le plus incomplètement représentés tandis que les synapsides et les mammifères semblent être le mieux représentés.

I. — INTRODUCTION.

The fossil record of non-marine tetrapods (amphibians, reptiles, birds, mammals) offers useful information on mass extinctions, adaptative radiations and rates of evolution [e.g. Van Valen, 1973; Bakker, 1977; Martin & Klein, 1984; Russell, 1984; Benton, 1985b, c; Padian & Clemens, 1985]. However, the fossil record of non-marine tetrapods is very poor in parts, and it might be considered too patchy for worthwhile evolutionary studies. In this paper, I tabulate the record of families of terrestrial tetrapods, and attempt to assess the completeness of that record for different time intervals and for different taxonomic groups. The listing may be used as a supplement to the compendium of families of marine invertebrates and vertebrates by Sepkoski [1982].

II. — THE DATA SET.

A compilation of the fossil and living families of non-marine amphibians, reptiles, birds and mammals was made (see Appendix). Fully marine groups were excluded

(i.e. mesosaurs, ichthyosaurs, placodonts, nothosaurs, plesiosaurs, marine lizards (mosasaurs, aigialosaurids, dolichosaurids), marine turtles (carettochelyids, protostegids, toxochelyids, dermochelyids, cheloniids), and marine mammals (cetaceans, sirenians, desmostylians, pinnipeds). A number of remaining families are partially marine in habits, but they were retained in the list.

The list of families was compiled from the latest general taxonomic reviews, where possible, and supplemented by more recent papers, up to 1985. The main sources of data are noted at the beginning of each major group, and subsidiary references are indicated for some families. The total number of living and extinct families of non-marine tetrapods is 858. Of these, 82 families have no fossil representatives, leaving a total of 776. Further, 77 families of extinct tetrapods are represented by only one species (often based on a single specimen from a single locality). These families are listed in the Appendix, but calculations were based on the remaining 699 families alone.

The total range in geological age for each family was determined from the most recent literature, and this was resolved to the level of the stratigraphic stage. The Miocene and Pliocene were not divided into stages, and ages were determined as Lower Miocene, Middle Miocene, Upper Miocene, or Pliocene. The duration of the stratigraphic stages during which tetrapods lived varies from 2-19 Ma (mean duration, 6 Ma).

This compilation of data is a slightly revised version of the data set used in a number of other publications [Benton, 1985b, c, 1986].

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III. — MASS EXTINCTIONS.

Mass extinctions of non-marine tetrapods may be detected in a broad way by examining a plot of total family diversity through time (fig. 1). There is a general rising trend in total family diversity from the Famennian to the present-day, and this trend is particularly marked in the late Cretaceous and Cenozoic parts of the diagram. The number of families present remained below about 50 until the late Cretaceous (Campanian), when it rose to 70-80, and it increased thereafter to the present total of 337. These results are discussed in more detail in Benton [1985b].

Declines in diversity occurred several times. These declines could be interpreted as extinction events, or as

the result of a particularly poor fossil record. Benton [1985b] argued that there were probably six mass extinctions in the record of non-marine tetrapods (fig. 1), and that the declines in the mid-Permian, the early to mid Jurassic, and the mid-Cretaceous were caused by a particularly poor fossil record. This topic deserves further study.

IV. — COMPLETENESS OF THE RECORD.

The fossil record of non-marine tetrapods is very patchy, and palaeontologists rely heavily on a relatively small number of fossil Lagerstätten for their information in much of the pre-Cenozoic. In some cases, the record is

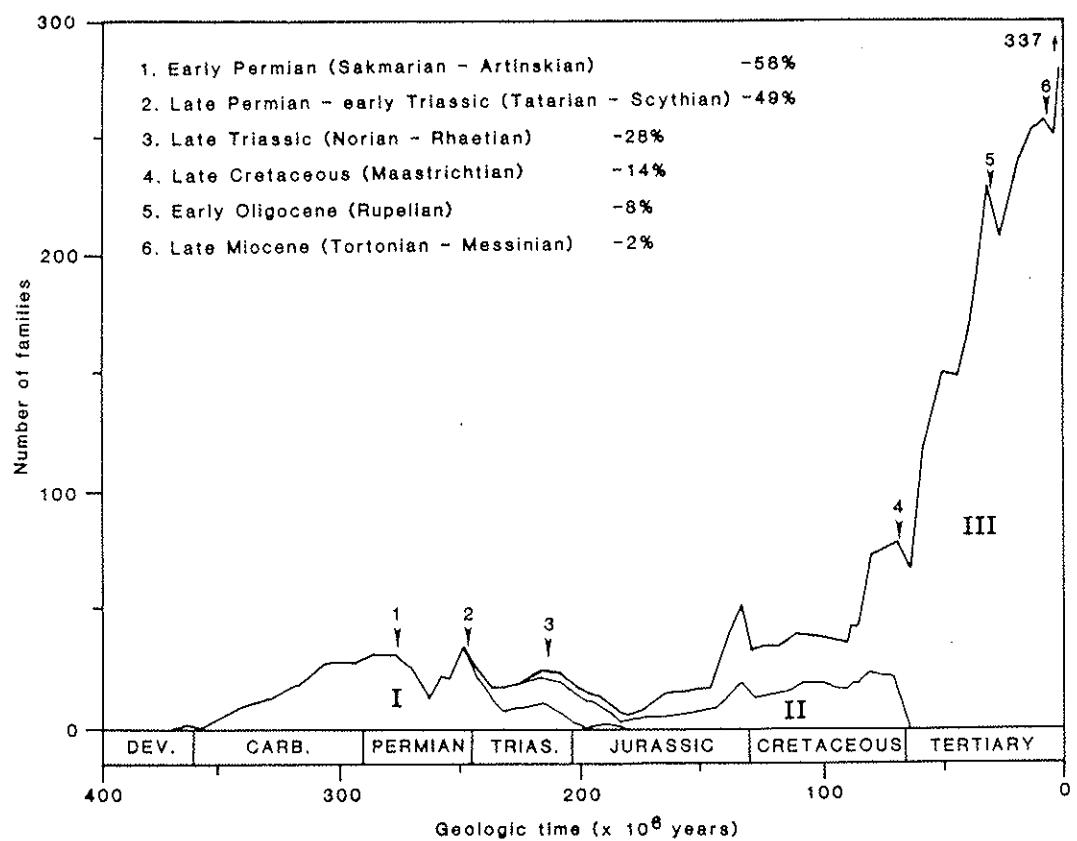


FIG. 1. — Standing diversity with time for families of terrestrial tetrapods. The upper curve shows total diversity with time, and six apparent mass extinctions (numbered 1-6) are indicated by drops in diversity. The relative magnitude of each drop is given in terms of the percentage of families that disappeared. Three assemblages of families succeeded each other through geological time : I, labyrinthodont amphibians, anapsids, mammal-like reptiles; II, early diapsids, dinosaurs, pterosaurs; III, the "modern" groups : frogs, salamanders, lizards, snakes, turtles, crocodiles, birds, mammals. (Further details are given in Benton [1985b]). Carb. = Carboniferous; Dev. = Devonian; Trias = Triassic.

FIG. 1. — Diversité des tétrapodes non-marins en fonction des temps géologiques. La courbe supérieure montre la diversité totale, et six crises biologiques possibles (numérotées 1-6) sont indiquées par des réductions de la diversité. L'importance relative de chaque réduction est donnée en pourcentage de familles qui disparaissent. Trois groupes de familles se sont succédées au cours des temps géologiques : I, labyrinthodontes, anapsides, synapsides; II, diapsides primitifs, dinosaures, ptérosaures; III, les groupes "modernes" : grenouilles, salamandres, lézards, serpents, tortues, crocodiles, oiseaux, mammifères. (Pour en savoir plus, voir Benton [1985b]). Carb. = Carbonifère; Dev. = Dévonien; Trias = Trias.

so poor that there are only one or two specimens known from a stratigraphic stage, and in the Aalenian (middle Jurassic), there are no records at all.

There are various ways of assessing the completeness of a fossil record [Paul, 1982]. The simplest is to compare the number of taxa that have been recorded with the number that are known to have occurred in each stratigraphic stage. If a family is known from below and above a stage, it must have occurred during the intervening interval, even if specimens have not been found (this phenomenon has been termed the Lazarus effect by Jablonski [1983, 1986]). "Then said Jesus unto them plainly, Lazarus is dead... And he that was dead came forth, bound, hand and foot with grave-clothes..." : John, xi, 1-44]. The more "Lazarus" taxa there are in a stratigraphic stage, the more incomplete that part of the fossil record is.

In order to calculate the completeness metrics, the full ranges of all 699 families of non-marine tetrapods that are known as fossils were plotted. A survey was made of the records for each family, and fossils were noted as "present" or "absent" for each stage during which the family is known to have existed. A matrix of 3 861 records was generated, of which 2 628 were known occurrences. The remaining 1 233 records then represent "Lazarus" taxa. A simple completeness metric for the entire record of non-marine tetrapods is $2\,628/3\,861 = 68.07\%$. This value is a measure of the several factors that contribute to "completeness": volume of sediment deposited during a stage, area of exposure, intensity of palaeontological study, and so on.

The summary data for completeness are listed by stratigraphic stage in table I. Completeness metrics range from 0 % (Aalenian) to 100 % (Famennian, Serpukhovian, Ufimian, Tatarian, Scythian). There are particularly poor fossil records (completeness metric < 50 %) in the late Carboniferous (Gzelian), the early to middle Jurassic (Toarcian-Bajocian), the middle to late Jurassic (Callovian-Oxfordian), the early Cretaceous (Berriasian-Aptian), and the late Cretaceous (Cenomanian-Santonian). Even in the Tertiary, there are a number of rather poor fossil records (completeness metric, 50-75 %) in the early Palaeocene (Danian), the middle to late Eocene (Lutetian-Priabonian), the late Oligocene (Chattian), and the middle to late Miocene (see fig. 2).

These simple completeness metrics do not give a perfect measure of the relative incompleteness of the fossil record. When a stage with a poor record occurs between two stages with good records, then there will be many "Lazarus" taxa, and the metric will be fairly accurate. However, if there is a succession of poor records, we will detect relatively fewer "Lazarus" taxa because fewer families can span a wide time interval, and the metric becomes less reliable (this is illustrated in simple terms in fig. 3). For example, the fossil record in the Sinemurian and Pliensbachian (early Jurassic) is probably much worse than the metrics of 88.2 % and 76.9 % would seem to suggest. The only way to improve the accuracy of the

TABLE I. — Completeness of the fossil record of non-marine tetrapods, measured by stratigraphic stage, and by taxonomic class. The total numbers of families present in each stage are given (column 1), followed by the numbers known as fossils (column 2). The difference between these two figures corresponds to the "Lazarus" taxa. The completeness metrics are plotted in figure 2.

TABLE I. — Perfection des documents fossiles des tétrapodes non-marins, indiquée par étage stratigraphique, et par classe taxonomique. Les nombres totaux de familles dans chaque étage (colonne 1) sont suivis par les nombres connus à l'état fossile (colonne 2).

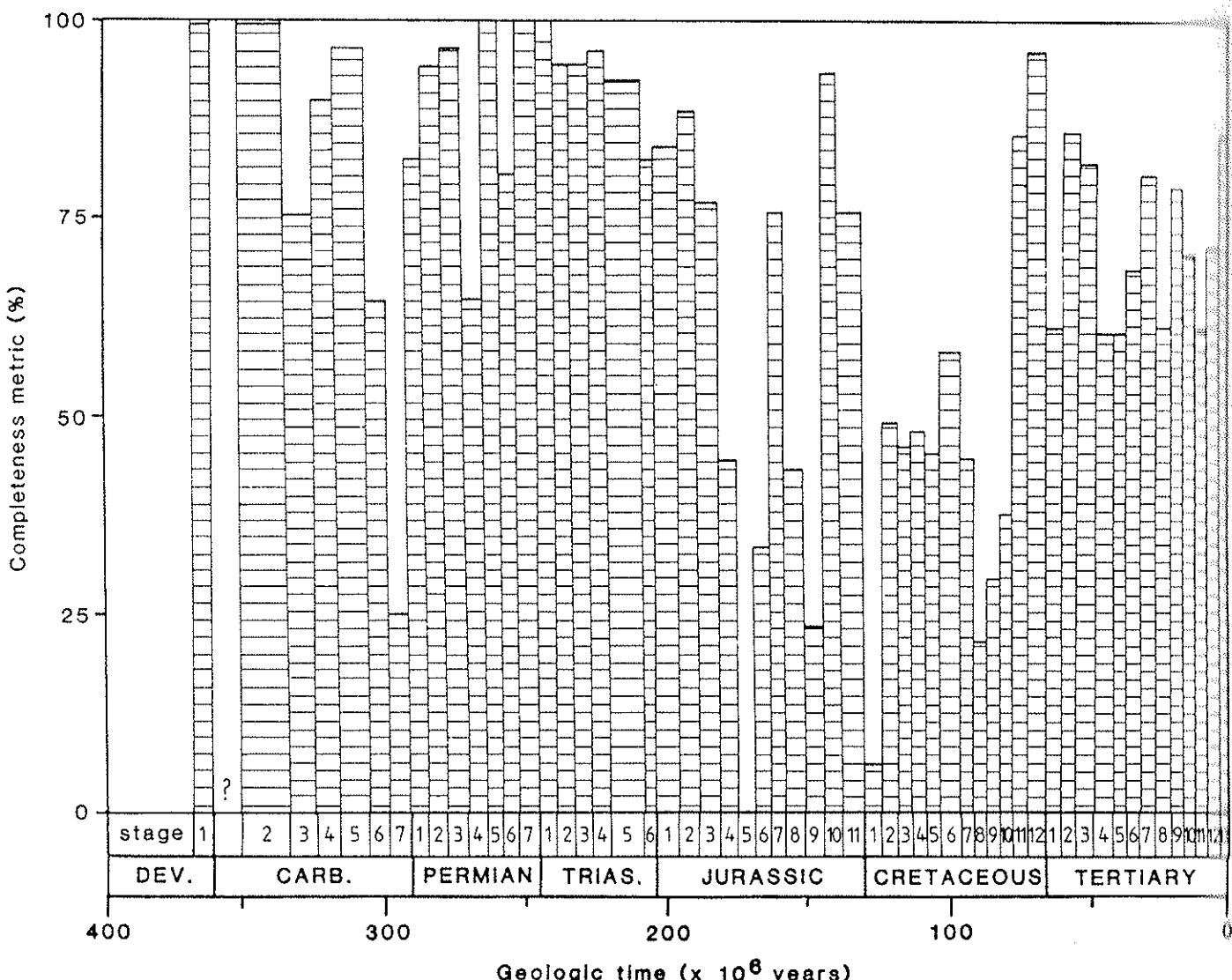
	AMPHIBIA		'REPTILIA'		AVES		MAMMALIA		TOTAL		Completeness metric (%)
	1	2	1	2	1	2	1	2	1	2	
DEVONIAN											
1. Famennian	2	2							2	2	100
CARBONIFEROUS											
1. Tournaisian	0	0							0	0	-
2. Visean	7	7							7	7	100
3. Serpukhovian	12	9							12	9	75
4. Bashkirian	19	17							19	17	89.5
5. Moscovian	25	24	2	2					27	26	96.3
6. Kasimovian	22	12	6	6					28	18	64.3
7. Gzelian	22	5	6	2					28	7	25.0
PERMIAN											
1. Asselian	23	18	8	7					31	25	80.6
2. Sakmarian	22	20	9	9					31	29	93.5
3. Artinskian	15	14	10	10					25	24	96.0
4. Kungurian	8	3	6	6					14	9	64.3
5. Ufimian	11	11	11	11					22	22	100
6. Kazanian	6	2	14	14					20	16	80.0
7. Tatarian	9	9	27	27					36	36	100
TRIASSIC											
1. Scythian	11	11	17	17					28	28	100
2. Anisian	4	3	13	13					17	16	94.1
3. Ladinian	4	4	13	12					17	16	94.1
4. Carnian	4	4	18	17					22	21	95.5
5. Norian	4	3	19	18					3	3	91.7
6. "Rhaetian"	3	2	16	13					3	3	81.8
JURASSIC											
1. Hettangian	1	0	14	12					3	3	18.15
2. Sinemurian	1	0	14	13					2	2	15.15
3. Pliensbachian	2	1	10	9					1	0	13.10
4. Toarcian	2	1	6	3					1	0	9.4
5. Aalenian	1	0	5	0					1	0	0.0
6. Bajocian	2	1	6	2					1	0	33.3
7. Bathonian	2	0	8	6					6	6	12.12
8. Callovian	2	0	10	7					4	0	16.7
9. Oxfordian	2	0	11	4					4	0	17.4
10. Kimmeridgian	3	2	30	28					9	9	32.39
11. Tithonian	4	2	37	26	1	1	10	10	52	39	75.0
CRETACEOUS											
1. Berriasian	4	0	24	2	0	0	6	0	34	2	5.9
2. Valanginian	4	0	24	13	1	1	6	3	35	17	48.6
3. Hauterivian	4	1	25	13	1	0	7	3	37	17	45.9
4. Barremian	4	1	27	15	1	0	6	2	38	18	47.4
5. Aptian	5	1	30	13	1	0	4	4	40	18	45.0
6. Albian	5	1	30	18	2	1	3	3	40	23	57.5
7. Cenomanian	5	0	28	16	1	0	2	0	36	16	44.4
8. Turonian	5	0	28	7	2	1	2	0	37	8	21.6
9. Coniacian	5	0	30	8	5	4	2	0	42	12	28.6
10. Santonian	5	0	31	13	3	0	5	3	43	16	37.2
11. Campanian	8	4	44	38	3	2	17	17	72	61	84.7
12. Maastrichtian	10	9	48	45	8	8	15	15	81	77	95.1
CENOZOIC											
1. Danian	9	5	25	8	4	0	32	30	70	43	61.4
2. Thanetian	19	15	32	24	6	2	68	66	125	107	85.6
3. Ypresian	19	7	34	22	22	19	78	75	153	123	80.4
4. Lutetian	18	7	35	23	27	11	74	51	154	92	59.7
5. Bartonian	18	2	32	19	26	10	93	70	163	101	59.8
6. Priabonian	18	2	32	21	42	30	95	73	187	126	67.4
7. Rupelian	19	9	36	24	51	30	121	117	227	180	79.3
8. Chattian	20	7	37	18	50	10	100	83	207	118	57.0
9. Lower Miocene	22	11	38	25	69	45	115	109	244	190	77.9
10. Middle Miocene	24	14	39	25	73	32	121	103	257	174	67.7
11. Upper Miocene	24	11	40	24	73	22	122	99	259	156	60.2
12. Pliocene	23	14	40	24	78	41	113	99	254	178	70.1
13. Pleistocene	23	16	38	29	113	107	107	87	281	239	85.0
TOTALS	575	324	1173	781	663	377	1360	1146	3861	2628	
Completeness metric (%)	56.3	78.2	56.9	84.3	68.1						

completeness metrics would be to try to estimate the numbers of absent "non-Lazarus" taxa, those that died out or arose at some unknown time during the gap in the record. Such an estimate, or measure of probability, would depend on several factors : (1) the numbers of families known at each end of the interval, (2) the mean family duration of the relevant taxa, and (3) the potential numbers of taxa that arose and died out during the gap. This has not been attempted here.

It is commonly asserted that the fossil record of, say, birds is relatively very poor, compared to that of mammals

because flying animals are only rarely preserved [e.g. Fisher, 1967]. This kind of opinion can now be tested. Simple completeness metrics were calculated for the fossil records of various groups of non-marine tetrapods, and these are listed in table II.

In fact, the lissamphibians (frogs, salamanders, etc.) have the worst fossil record (42.0 % complete), probably because of their small size and the extreme delicateness of their bones. The fossil record of lepidosaurs (lizards, snakes, *Sphenodon*) is also poor (48.6 % complete), probably for the same reasons. The birds as a whole have



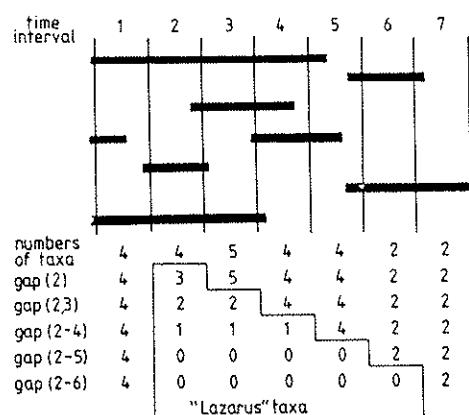


FIG. 3. — Estimates of the completeness of the fossil record become relatively worse as the gap increases. In many cases, it is known that families not found as fossils within a particular stage must have been present because they are known from both sides of the gap. These "Lazarus" taxa can only be predicted from such gap-spanning distributions, and the larger the gap, the less taxa span it. This can have the effect of making simple completeness metrics higher than they should be.

FIG. 3. — Les estimations de la perfection des documents fossiles deviennent proportionnellement moins exactes en fonction des lacunes. Souvent, nous savons que des familles qui ne sont pas connues à l'état fossile dans un étage donné, étaient en fait présentes parce qu'elles sont connues de part et d'autre de la lacune. Ces taxons "Lazare" ne peuvent être reconnus que par de telles distributions qui traversent la lacune. Plus grande est la lacune, moins nombreux sont les taxons qui la traversent. Il en résulte que les mesures de perfection peuvent être surestimées.

TABLE II. — Completeness metrics for particular taxonomic groups, extracted from the data in table I.

TABLE II. — Mesures de perfection pour quelques groupes taxonomiques, dérivées des données du tableau I.

	Total assumed	Total fossils	Completeness metric (%)
AMPHIBIA	575	324	56.3
Labyrinthodontia	165	126	76.4
Lepospondyli	68	51	75.0
Liassamphibia	350	147	42.0
"REPTILIA"	1173	781	78.2
Testudines	154	107	69.5
Diapsida	813	485	59.7
Lepidosauria	259	126	48.6
Archosauria	520	328	63.1
Synapsida	110	104	94.5
AVBS	663	377	56.9
Passeriformes	75	47	62.7
MAMMALIA	1360	1146	84.3
Marsupilia	107	79	73.8
Eutheria	1130	983	87.0
Rdentalata	55	47	85.5
Carnivora	63	62	97.1
Insectivora	33	27	81.8
Chiroptera	65	50	75.7
Primates	85	59	70.3
Artiodactyla	155	149	96.6
Perissodactyla	78	75	96.2
Rodentia	225	199	88.4

a rather better fossil record than might have been expected (56.9 % complete), about the same as the amphibians as a whole (56.3 % complete), and not much worse than the Diapsida as a whole (59.7 % complete). The best fossil records are those of mammal-like reptiles (synapsids : 94.5 % complete), placental mammals (87.0 % complete), and mammals as a whole (84.3 % complete). Amongst placental mammals, the main orders have generally good fossil records, the best being those of the carnivores (97.1 % complete), the artiodactyls (96.6 %), and the perissodactyls (96.2 %). As might be expected, the primates (70.3 %) and bats (75.7 %) have rather poorer fossil records.

References

(References for the paper and the appendix. Many of the papers cited in the appendix are not listed here, in order to save space. They may be found in Benton [1985c].)

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APPENDIX

Listing of families of non-marine tetrapods.

* families that contain one species from one locality (often a single specimen); omitted from calculations.
 + living families with no fossil representatives.
 Families that are still living are designated "REC". Those that survived until historic times, but are now extinct, are termed "HOL". Stratigraphic abbreviations: ALB, Albian; ANI, Anisian; APT, Aptian; ART, Artinskian; ASS, Asselian; BAJ, Bajocian; BAR, Barremian; BAS, Bashkirian; BER, Berryasian; BRT, Bartonian; BTH, Bathonian; CAL, Callovian; CEN, Cenomanian; CHT, Chattian; CMP, Campanian; CON, Coniacian; CRN, Carnian; DAN, Danian; FAM, Famennian; GZE, Gzelian; HAU, Hauterivian; HET, Hettangian; KAS, Kasimovian; KAZ, Kazanian; KIM, Kimmeridgian; KUN, Kungurian; LAD, Ladinian; LMI, Lower Miocene; LUT, Lutetian; MAA, Maastrichtian; MMI, Middle Miocene; MOS, Moscovian; NOR, Norian; OXF, Oxfordian; PLB, Pliensbachian; PLE, Pleistocene; PLI, Pliocene; PRB, Priabonian; RHT, Rhaetian; RUP, Rupelian; SAK, Sakmarian; SAN, Santonian; SCY, Scythian; SER, Serpukhovian; SIN, Sinemurian; TAT, Tatarian; THA, Thanetian; TOA, Tourcian; TTH, Tithonian; TUR, Turonian; UFI, Ufimian; UMI, Upper Miocene; VAL, Valanginian; VIS, Visean; YPR, Ypresian.

AMPHIBIA (Carroll and Winer 1978; Anderson and Cruickshank 1978)

ICHTHYOSTEGALIA**Ichthyostegidae*****Acanthostegidae**

FAM

FAM

LOXOMMATOIDEA**Loxomatidae**

VIS - MOS

TRIMERORACHOIDEA**Colosteidae**

VIS - MOS

Saurerpetontidae

BAS - ART

Trimerorachidae

KAS - UFI

Dvinosauridae

UFI - TAT

EROPHOIDEA**Dendrerpetontidae**

SER - BAS

Cochleosauridae

BAS - ASS

Edopidae

MOS - ASS (A. R. Milner 1980)

ERYOPOIDEA**Eryopidae**

?KAS - UFI (Gubin 1983)

Dissorophidae

?BAS - KAZ (Gubin 1980)

Intasuchidae

UFI

Branchiosauridae

MOS - SAK

Micromelerpetontidae

MOS - SAK

***Doloserpentidae**

ART

Trematopsidae

KAS - ART

Parioxyidae

SAK

Zatracheidae

MOS - SAK

Archegosauridae

ASS - UFI (A. R. Milner 1980)

Melanosauroidea

UFI - TAT

RHINESUCHOIDEA**Rhinesuchidae**

KAZ - TAT

Lydekkerinidae

SCY

***Sclerothoracidae**

SCY

***Peltobatrachidae**

TAT

Uranocentrodontidae

TAT - SCY

CAPITOSAUROIDEA***Latiscopidae**

NOR

Benthosuchidae

TAT - SCY

Capitosauridae

SCY - RHT

Mastodonosauridae

SCY - LAD

RHYTIDOSTOIDEA**Rhytidosteidae**

SCY

***Laidleriidae**

SCY

TREMATOSAUROIDEA**Trematosauridae**

SCY

Indobrachyopidae

(Cosgriff and Zawiskie 1979)

BRACHYPOIDEA***Kourerpetontidae**

?Perm

Brachyopidae

TAT - LAD

Chigutisauridae

CRN - TOA (Warren and Hutchinson 1983)

METOPOSAUROIDEA**Metoposauridae**

CRN - NOR

***Almasauridae**

NOR

PLAGIOSAUROIDEA**Flagiosauridae**

SCY - RHT

AMPHIBIA: BATRACHOSAURIA ***PALAEOSTEGALIA*****Crassigyrinidae**

(Pancken 1980)

HERPETOSPONDYLI**Proterogyrinidae**

VIS - SER

EMBOLOMERI**Eogyrinidae**

SER - ASS

Archeriidae

MOS - ART

Anthracosauridae

BAS - MOS

GEPHYROSTEGIDA**Gephyrostegidae**

SER - MOS

Roherpetontidae

VIS - SER

SEYMOURIAMORPHA**Seymouriiidae**

SAK - UFI

Discosauroidae

ASS - SAK

Kollaspididae

UFI - TAT

Lanthanosuchidae

UFI - TAT (Ivakhnenko 1980)

Chroniosuchidae

TAT

INCERTAE SEDIS**Limnoscelidae**

BAS - SAK

***Solenodonsauridae**

MOS

***Tsejawaiidae**

ASS

***Nyctoleteridae**

UFI

Diadectidae

?ASS - UFI

AMPHIBIA: LEPOSPONDYLI**AISTOPODA****Ophiderpetontidae**

VIS - GZE

Phlegetontidae

BAS - MOS

***Lethiscidae**

VIS

NECTRIDEA (A. C. Milner 1980)**Keralerpetontidae**

SER - KUN

Scincosauridae

MOS - SAK

Urocordylidae

SER - ART

MICROSAURIA**Tuditanidae**

BAS - GZE

Hapsidopareiontidae

BAS - ART

Pantylidae

BAS - SAK

Gymnarthridae

BAS - KUN

Ostodolepididae

ART

***Trihacacetontidae**

KAS - GZE

Microbrachidae

BAS - MOS

INCERTAE SEDIS**Adelogyrinidae**

VIS - SER (Smithson 1980)

Lysorophidae

MOS - ART

Acherontiscidae

VIS - SER?

AMPHIBIA: LISSAMPHIBIA (Carroll and Winer 1978)**ANURA (Estes and Reig 1973)*****Triadobatrachidae**

SCY

Ascapidae

PLB - REC

Discoglossidae

KIM - REC

Pipidae

?APT - REC

Palaeobatrachidae

TTH - PLE

Rhinophrynidae

THA - REC

Pelobatidae

MAA - REC

Pelodytiidae

MMI - REC

Leptodactylidae

THA - REC

Bufoinae

THA - REC

Ceratophrynidiae

?MMI - REC

Hylidae

THA - REC

Microhylidae

LMI - REC

Hippophoridae

PLE - REC

Ranidae

CHT - REC

GYMNOPHIONA (Estes 1981)**Caecliliidae**

THA - REC

CAUDATA (Estes 1981; Milner 1983)***Karauridae**

?U. Jur.

Cryptobranchidae

THA - REC

+Hynobiidae

REC

Prosirenidae

BAJ - LMI

Proteidae

THA - REC

Batrachosauroididae

CMP - PLI

Amphiumidae

MAA - REC

Dicamptodontidae

THA - REC

Scapherpetontidae

CMP - YPR

Ambystomatidae

RUP - REC

Plethodontidae

LMI - REC

Salamandridae

THA - REC

Sireniidae

CMP - REC

REPTILIA: EARLY ANAPSID FORMS (Anderson and Cruickshank 1978)**Romeriidae**

MOS - ART (Reisz 1979)

Captorhinidae

SAK - TAT (Ricqles and Taquet 1982)

Bolosauridae

ASS - ART

***Acleistorhinidae**

ART

***Eunotosauridae**

KAZ

***Nyctiphuretidae**

UFI

Procolophonidae

TAT - RHT? (Olsen 1980)

Millettidae

KAZ - TAT

Rhiphaeosauridae

UFI

Pareiasauridae

KAZ - TAT

REPTILIA: TESTUDINES (Gaffney 1975, 1979; Mlynarski 1976)			Alligatoridae	CMP - REC
PROGANOCHELYDIA			Nettosuchidae	UMI - PLI
Proganochelyidae		NOR - PLB (Olsen and Galton 1984)	Crocodylidae	CMP - REC
PLEURODIRA			Pristichampsidae	THA - PLE
Pelomedusidae		TUR - REC	Gavialidae	?LUT - REC
Chelidae		?CHT - REC	Thoracosauridae	CMP - THA?
BAENOIDEA			*Dolichochoampsidae	?U. Cret.
Glyptopsidae		KIM - TTH	Euthecodontidae	YPR - PLE
Baenidae		TTH - BRT	PTEROSAURIA (Wellnhofer 1978; Benton and Norman 1986)	Benton and Norman 1986)
TRIONYCHOIDEA			Dimorphodontidae	NOR - SIN
Kinosternidae		RUP - REC	*Sudimorphodontidae	NOR
Dermatemyidae		TTH - REC	*Anurognathidae	TTH
Trionychidae		?CMP - REC	Rhamphorhynchidae	TOA - TTH
CHELONIOIDEA			Pterodactylidae	KIM - TTH
Plesiochelyidae		KIM - TTH	Germanodactylidae	TTH
TESTUDINOIDEA			Ctenochasmatidae	TTH - SAN
Chelydridae		MAA - REC (Whetstone 1978)	*Pterodaustriidae	?L. Cret.
Emydidae		?YPR - REC	*Ornithodesmidae	BAR
Testudinidae		LUT - REC	Ornithocheiridae	?TTH - CMP
INCERTAE SEDIS			Dsungaripteridae	KIM - APT
Pleurosternidae		TTH - APT	Pteranodontidae	ALB - MAA
Meiolaniidae		?MAA - PLE	*Criorhynchidae	VAL/ HAU
REPTILIA: DIAPSIDA: EARLY FORMS (Benton 1985a)			Azhdarchidae	TUR - MAA
*Petrolosauridae		?KAS	DINOSAURIA: EARLY FORMS (Benton and Norman 1986)	Benton and Norman 1986)
Araeoscelidae		ASS - ART	*Staurikosauridae	CRN
*Galesphyridae		TAT	*Herrerasauridae	CRN
Weigeltisauridae		KAZ - TAT	DINOSAURIA: THEROPODA (Benton and Norman 1986)	Benton and Norman 1986)
*Claudiosauridae		TAT	*Procompsognathidae	NOR
*Heleosauridae		TAT	Podokesauridae	CRN - PLB?
Kuehneosauridae		ORN - NOR	Cœluridae	KIM - MAA
*Monjurosuchidae		?JUR.	*Noasauridae	MAA
Thalattosauroidae		LAD - CRN	*Shanshanosauroidae	U. Cret.?
Claraziidae		LAD	Compsognathidae	TTH
Champsosauridae		ALB - YPR? (Sigogneau-Russell and Efimov 1984)	*Segisauridae	HWT
Trilophosauridae		CRN	*Avimimidae	?U. Cret.
RHYNCHOSAURIA			Ornithomimididae	KIM - MAA
*Mesosuchidae		SCY	*Garudimimidae	?U. Cret.
*Howesiidae		SCY	*Deinocheiridae	MAA
Rhynchosauridae		ANS - CRN	Dromaeosauridae	APT - MAA
PROLACERTIFORMES			Saurornithoididae	CMP - MAA
Protorosauridae		KAZ	Oviraptoridae	CMP - MAA
Prolacertidae		SCY - LAD	*Caenagnathidae	CMP
Tanytropheididae		ANS - NOR	Elmisauridae	CMP - MAA
YOUNGINIFORMES			Megalosauroidea	HET - MAA
Younginidae		TAT	Allosauridae	OXF - SAN
Tangasauridae		TAT	Ceratosauridae	KIM - TTH
*Saurosternidae		TAT	Dryptosauridae	CMP - MAA
LEPIDOSAUROMORPHA INC. SED.			Spinosauridae	VAL - SAN
*Paliguinidae		SCY	Tyrannosauridae	ALB - MAA
*Palaeegamidae		TAT	*Itemiridae	?U. Cret.
REPTILIA: DIAPSIDA: ARCHOSAURIA (Benton and Norman 1986)			Segnosauridae	SAN - CMP
"THECODONTIA"			Therizinosauridae	CEN - TUR (MAA?)
Proterosuchidae		TAT - SCY	DINOSAURIA: SAUROPODOMORPHA (Benton and Norman 1986)	Benton and Norman 1986)
Erythrosuchidae		SCY - ANS?	Anchisauridae	NOR - TOA
Proterochampsidae		LAD - CRN	Plateosauridae	NOR - PLB
Euparkeridae		SCY	Melanorosauridae	?RHT - SIN
Phytosauridae		CRN - RHT	*Barapasauridae	TOA
Aetosauridae		CRN - RHT	*Vulcanodontidae	PLB/ TOA?
Rauisuchidae		SCY - RHT	Cetiosauridae	BAJ - ALB
Poposauridae		LAD - NOR	Camarasauridae	KIM - MAA
Ornithosuchidae		CRN - NOR	Brachiosauridae	KIM - BAR?
Lagosuchidae		LAD	Diplodocidae	KIM - MAA
*Scleromochlidae		CRN	Titanosauridae	BAR - MAA
*Eretosuchidae		CRN	DINOSAURIA: ORNITHISCHIA (Benton and Norman 1986)	Benton and Norman 1986)
CROCODYLOMORPHA (Buffetaut 1982; Benton and Norman 1986)			Fabrosauridae	SIN - TTH
*Trialestidae		CRN	Heterodontosauridae	HET - PLB
Saltoposuchidae		NOR	Hypsilophodontidae	CAL - MAA
Sphenosuchidae		CRN - SIN	Iguanodontidae	CAL - ALB
Protosuchidae		RHT - SIN	Hadrosauridae	APT - MAA
*Orthosuchidae		HET/ SIN	Pachycephalosauridae	BAR - MAA
Libycosuchidae		BAR - CEN	*Scelidosauridae	SIN
Uruguaysuchidae		APT - MAA	Stegosauridae	BTH - CON
Notosuchidae		MAA	Nodosauridae	CAL - MAA
Hsisosuchidae		?KIM - CMP	Ankylosauridae	CON - MAA
Baurusuchidae		CON - LUT	Psittacosauridae	APT?
Sebecidae		THA - PLI	Protoceratopidae	SAN - MAA
*Crocodyleimidae		KIM	Ceratopsidae	CMP - MAA
Trematochampsidae		?CON - CMP	REPTILIA: DIAPSIDA: LEPTOSAURIA	Benton and Norman 1986)
Goniopholididae		KIM - MAA	PRIMITIVE FORMS	(Benton 1986a)
Pholidosauridae		BTH - CEN	Sphenodontidae	CRN - REC
Bernissartidae		KIM - HAU?	Sapheosauridae	TTH
Paralligatoridae		CMP	Pleurosauridae	KIM - BER
Atoposauridae		KIM - APT	*Gephyrosauridae	HET/ SIN

MASS EXTINCTIONS AMONG FAMILIES OF NON-MARINE TETRAPODS

SAURIA (Estes 1983)	HET/ SIN	THEROCEPHALIA	KAZ
*Fulengidae	MAA - REC	*Crapartinellidae	UFI - KAZ
Iguanidae	KIM	Pristoognathidae	TAT
Euposauridae	PRB	Moschorhinidae	TAT
*Arretosauridae	CMP - REC	Whaitsiidae	KAZ - SCY
Agamidae	THA - REC	Ictidosuchidae	TAT - SCY
Chamaeleonidae	TTH	Scaloposauridae	SCY
Ardeosauridae	TTH	*Ericiolacertidae	SCY - ANS
Bavarisauridae	THA - REC	Bauriidae	SCY - ANS
Gekkonidae	CMP - REC	"CYNODONTIA" (Battail 1982)	TAT
Teiidae	REC	Silphestidae	TAT
+Gymnophthalmidae	THA - REC	Procynosuchidae	TAT
Lacertidae	MAA - REC	Dvinidae	TAT - SCY
Scincidae	REC	Galesauridae	SCY - ANS
*Dibamidae	KIM - TTH	Cynognathidae	SCY - ANS
Paramacellodidae	THA - REC	Diademodontidae	SCY - ANS
Xantusiidae	?PRB - REC	Trirachodontidae	SCY - HET
Cordylidae	MAA - REC	Traversodontidae	ANS - NOR?
Xenosauridae	KIM - TTH	Chiniquodontidae	RHT - CAL
Dorsetisauridae	CMP - REC	Tritylodontidae	?NOR - PRB (Chatterjee 1983)
Anguidae	MAA - RUP	Tritheledontidae	
Necrosauridae	MAA - REC		
Helodermatidae	CMP - REC		
Varanidae			
AMPHIBIAENIA (Estes 1983)			
*Oligodontosauridae	THA	AVES (Fisher 1967; Feduccia 1980)	
Amphisbaenidae	?RUP - REC	ARCHAEOPTERYGIFORMES	
Rhineuridae	THA - REC	Archaeopterygidae	TTH
Hypothyrididae	RUP - CHT	HESPERORNITHIFORMES	
+Bipedidae	REC	Enaliornithidae	ALB
+Troganophidae	REC	Baptornithidae	CON - MAA
SERPENTES (Rage 1984)		Hesperornithidae	CON - CMP
Typhlopidae	?YPR - REC	ICHTHYORNITHIFORMES	
+Leptotyphlopidae	REC	Ichthyornithidae	TUR - CON (Fox 1984)
+Lapparantopheidiae	?L. Cret.	Apatornithidae	CON
Simoleopheidiae	CEN	?Enantiornithes	MAA (Witmer 1981)
Aniliidae	CMP - REC	SPHENISCIFORMES	
+Uropeltidae	REC	Spheniscidae	YPR - REC
#Dinilysidae	CMP	RATITAE	
+Xenopeltidae	REC	*Eleutherornithidae	YPR
Boidae	CMP - REC	Struthionidae	PLI - REC
Palaeophiidae	MAA - LUT	Aepyornithidae	YPR - HOL
Acrochordidae	MMI - REC	Bromiceiidae	PLI - REC
Nigeropheidiae	DAN - LUT	Dromornithidae	PLE
*Anomalopheidiae	YPR	Casuaridae	PLE - REC
*Russelopheidiae	YPR	Emeidae	UMI - HOL
Colubridae	RUP - REC	Dinornithidae	PLI - HOL
Elapidae	IMI - HRC	Apterygidae	?PLE - REC
Viperidae	IMI - REC	Rheidae	YPR - REC
REPTILIA: SYNAPSIDA (Anderson and Cruikshank 1978; Kemp 1982)		*Gobipterygidae	CMP
"PELYCOSAURIA"		Tinamidae	PLI - REC
Eothyrididae	?KAS - ART	GAVIIFORMES	
Caseidae	ART - KUN	Lonchodytidae	MAA
Edaphosauridae	KAS - ART (Reisz et al. 1982)	Gaviidae	THA - REC
Ophiacodontidae	MOS - ART	PODICIPITIFORMES?	
Varanopidae	?KAS - KUN	Podicipitidae	IMI - REC
Sphenacodontidae	KAS - ART (Reisz et al. 1982)	PROCELLARIIFORMES	
DINOCEPHALIA		Diomedidae	?LUT - REC
Estemmenosuchidae	UPI	Procellariidae	RUP - REC
Brithopodidae	KUN - UPI	Oceanitidae	UMI - PLE
Anteosauridae	UPI - KAZ	Pelecanoididae	?PLE - REC
Titanosuchidae	KAZ	PELECANIFORMES	
Tapinocephalidae	UPI - KAZ	Phaethontidae	YPR - REC
ROTHEROSUCHIA		Pelecanidae	IMI - REC
Phthinosuchidae	KUN - UPI	Cyphornithidae	IMI
*Eotitanosuchidae	UPI	Pelagornithidae	IMI - MM
Ictidornithidae	KAZ - TAT	Sulidae	RUP - REC
Gorgonopsidae	KAZ - TAT	Elopterygidae	MAA - BRT
ANOMODONTIA (Cluver and King 1983)		Phalacrocercidae	MAA - REC
*Otsheridae	UPI	Anhingidae	?BRT - REC
Venjukoviidae	KUN - UPI	Fregatidae	YPR - REC
Dromasauridae	KAZ - TAT	*Cladornithidae	RUP
Eodicyodontidae	?UPI	ODONTOPTERYGIFORMES	
Endothiodontidae	TAT	*Odontopterygidae	YPR? UMI
Cryptodontidae	TAT	Pseudeodontornithidae	IMI UMI
Aulacocephalodontidae	TAT	CICONIFORMES	
Dicynodontidae	TAT	Ardeidae	YPR - REC
Kannemeyeriidae	SCY - CRN	+Scopidae	REC
Pristerodontidae	TAT	Ciconiidae	?PRB - REC
Emydopidae	TAT - SCY	+Balaenicipitidae	REC
Cistecephalidae	TAT	*Plegadornithidae	SAN
Roberttiidae	UPI	Plataleidae	PRB - REC
Diictodontidae	KAZ - TAT	PHOENICOPTERYGIFORMES	
Kingoriidae	TAT - SCY	Torotigidae	?VAL - MAA
		*Scaniornithidae	DAN
		*Telmabatidae	YPR
		Agnopteridae	PRB - CHT
		Palaeodiidae	IMI - PLI

Presbyornithidae	YPR	APODIFORMES	
Phoenicopteridae	PRB - REC	Aegialornithidae	?PRB
ANSERIFORMES		+Hemiprocridae	REC
Anhimidae	PLE - REC	Apodidae	?PRB - REC
Anatidae	PRB - REC	Trochilidae	* PLE - REC
FALCONIFORMES		COLIIFORMES	
*Neocalthartidae	PRR	+Coliidae	REC
Cathartidae	YPR - REC	TROGONIFORMES	
Teratornithidae	PLE - HOL	Trogonidae	?PRB - REC
Sagittariidae	PRB - REC	CORACIFORMES	
Accipitridae	PRB - REC	Alcedinidae	PRB - REC
Pandionidae	PLE - REC	Todidae	RUP - REC
Falconidae	MMI - REC	Momotidae	LUT - REC
GALLIFORMES		Meropidae	PLE - REC
Gallinuloididae	LUT - MMI	Coraciidae	PRB - REC
Opisthoicomidae	MMI - REC	+Brachypteraciidae	REC
Cracidae	YPR - REC	+Leptosomatidae	REC
Megapodiidae	PLE - REC	Upupidae	PLE - REC
Tetraonidae	IMI - REC	Phoeniculidae	LMI - REC
Phasianidae	RUP - REC	Bucerotidae	LUT - REC
Numididae	HOL - REC	PICIFORMES	
Meleagrididae	PLE - REC	Primobucconidae	YPR - LUT?
GRUIFORMES		+Galbulidae	REC
*Mesitornithidae	REC	Bucconidae	PLE - REC
Turnicidae	PLE - REC	Capitonidae	PLE - REC
*Geranoididae	YPR	+Indicatoridae	REC
Eogruidae	PRB - UMI	Rhamphastidae	PLE - REC
Gruidae	YPR - REC	Picidae	LMI - REC
Aramidae	RUP - REC	PASSERIFORMES	
*Psophiidae	REC	+Eurylaimidae	REC
Ergilornithidae	RUP	Furnariidae	PLE - REC
Orthocremnidae	?PRB	Formicariidae	PLE - REC
Rallidae	MAA - REC	+Conopophagidae	REC
*Heliornithidae	REC	Rhinocryptidae	?LMI / MMI - REC
*Rhynochetidae	REC	+Pittidae	REC
*Eurypygidae	REC	?+Philepittidae	REC
Bathornithidae	RUP - CHT	+Acanthisittidae	REC
Cariamidae	RUP - REC	Tyrannidae	PLE - REC
Psilopteraidae	LMI - PLE	+Pipridae	REC
Phororhacidae	RUP - PLE	+Cotingidae	REC
Brontornithidae	RUP - MMI	+Phytotomidae	REC
*Cunampaiidae	RUP	+Menuridae	REC
Otididae	LUT - REC	+Atrichornithidae	REC
DIATRYMIFORMES		*Palaeospizidae	CHT
Gastornithidae	YPR - PRB	Alaudidae	PLI - REC
Diatrymidae	YPR - LUT	Hirundinidae	PLE - REC
CHARADRIIFORMES		Motacillidae	LMI - REC
Jacanidae	PLE - REC	+Campephagidae	REC
Rhegminornithidae	LMI - REC	Pycnonotidae	PLE - REC
Rostratulidae	LUT - REC	+Irenidae	REC
Haematopodidae	LMI - REC	Laniidae	LMI - REC
Charadriidae	HOL - REC	+Vangidae	REC
Scolopacidae	MAA - REC	Bombycillidae	PLE - REC
Recurvirostridae	YPR - REC	+Dulidae	REC
?Phalaropodidae	PLE - REC	Cinclidae	PLE - REC
+Dromadidae	REC	Palaeoscincidae	MMI - REC
Burhinidae	LMI - REC	Troglodytidae	PLE - REC
+Glareolidae	REC	Mimidae	PLE - REC
+Thinocoridae	REC	Prunellidae	PLE - REC
+Chionidiidae	REC	Muscicapidae	LMI - REC
Stercorariidae	PLE - REC	Paridae	PRB - REC
Laridae	YPR - REC	Sittidae	PLI - REC
+Rhynchospidae	REC	Certhiidae	PLE - REC
Alcidae	YPR - REC	+Dicaeidae	REC
COLUMBIIFORMES		+Nectariniidae	RRC
Pteroclidae	?PRB - REC	+Zosteropidae	REC
Columbidae	LMI - REC	Meliphagidae	HOL - REC
Raphidae	HOL	Emberizidae	PLI - REC
PSITTACIFORMES		Parulidae	PLE - REC
Psittacidae	IMI - REC	+Drepanidae	REC
MUSOPHAGIFORMES		Vireonidae	PLE - REC
+Musophagidae	REC	Icteridae	PLE - REC
CUCULIFORMES		Fringillidae	?MMI - REC
Cuculidae	?PRB - REC	+Estrildidae	REC
STRIGIFORMES		+Viduidae	REC
Tytonidae	IMI - REC	Ploceidae	?IMI - REC
Protostrigidae	?THA - BRT	Sturnidae	PRB - REC
Strigidae	?PRB - REC	Oriolidae	PLE - REC
CAPRIMULGIFORMES		Dicruridae	PLE - REC
+Steatornithidae	REC	Calleidae	HOL - REC
+Aegothelidae	REC	+Grallinidae	REC
+Podargidae	REC	?Artamidae	REC
Caprimulgidae	PLE - REC	+Cracticidae	REC
Nyctibiidae	PLK - REC	+Ptilonorhynchidae	REC
		+Paradiseidae	REC
		Corvidae	MMI - REC

MAMMALIA (Lillegraven et al. 1979; Savage and Russell 1983)	
MULTITUBERCULATA	
Paulchoffattiidae	KIM - BAR?
Plagiaulacidae	KIM - BAR?
Neoplagiaulacidae	CMP - RUP
Ptilodontidae	CMP - THA
Cimolodontidae	CMP - THA
Taeniolabididae	SAN - YPR
Eucosmodontidae	SAN - YPR
Chulsanbaataridae	CMP
Sloobantaaridae	CMP
Cimolomyidae	CMP - THA
?Haramiyidae	NOR - BTH
TRICONODONTA	
Morganucodontidae	RHT - SIN
Amphilestidae	BTH - TTH
Triconodontidae	KIM - CMP
DOCODONTA	
Docodontidae	BTH - TTH
SYMMETRODONTA	
Kuehneotheriidae	RHT - HST
Amphidontidae	KIM - TTH?
Spalacotheriidae	TTH - CMP
"EUPANTOTHERIA"	
Amphitheriidae	RHT
Peramuridae	BTH - APT?
Paurodontidae	KIM - TTH
Dryolestidae	BTH - VAL
MONOTREMATA	
Ornithorhynchidae	MMI - REC
Tachyglossidae	PLE - REC
MARSUPIALIA	
Didelphidae	CMP - REC
Pediomyidae	CMP - MAA
Stagodontidae	CMP - MAA
Borhyaenidae	THA - PLI
Polydolopidae	THA - YPR
Caroloameghinidae	YPR
Bonaparthieriidae	YPR
Groeberidae	PRB
Microbathyriidae	RUP - REC
Caenolestidae	RUP - REC
Dasyuridae	MMI - REC
Peramelidae	?MMI - REC
Thylacoleonidae	?MMI - PLE
Phalangeridae	MMI - REC
Burramyidae	MMI - REC
Petauridae	MMI - REC
Wynyardiidae	MMI
Ektopodontidae	MMI - PLI
Macropodidae	MMI - REC
Vombatidae	MMI - REC
Potoroidae	MMI - PLI
Diprotodontidae	MMI - PLE/ HOL?
Sparassocynidae	UMI - PLI
Thylacosmilidae	UMI - PLI
Argyrolagidae	UMI - PLI
Thylacinidae	UMI - REC
Palorchestidae	PLI
+Myrmecobiidae	REC
+Notoryctidae	REC
+Thylacomyidae	REC
+Tarsipedidae	REC
EUTHERIA INCERTAE SEDIS	
*Endotheriidae	APT/ ALB
Aegialodontidae	VAL - ALB
Peppotheriidae	CMP
Deltatheriidae	SAN - MAA
EDENTATA	
Ernanodontidae	THA
Dasyopidae	THA - REC
Glyptodontidae	THA - PLE
Megalonychidae	?BRT - PLE/ HOL?
Palaeopeltidae	RUP
Mylodontidae	RUP - PLE
Megatheriidae	RUP - PLE
Entelopsidae	IMI
Myrmecophagidae	IMI - REC
Peltaphilidae	IMI - UMI
+Bradypodidae	REC
+Choloepidae	REC
ANAGALIDA	
Zalambdalestidae	CMP - TBA
Eurymyliidae	THA - PRB

Pseudictiopidae	THA	YPR
Anagalidae	THA	ROP
LEPTICTIDIA		
Leptictioidea n. fam.	CMP	MAA
Leptictidae	DAN	RUP
MACROSCELIDEA		
Macroscelididae	RUP	REC
LAGOMORPHA		
Leporidae	BRT	REC
Ochotonidae	RUP	REC
CIMOESTA		
Palaearctiidae	CMP	BRT
TAENIODONTA		
Stylinodontidae	DAN	PRB
PANTODONTA		
Pantolambdidae	DAN	THA
Titanoididae	DAN	THA
Pantolambdodontidae	THA	PRB
?Bemalambdidae	THA	
Pastoralodontidae	THA	YPR
Phenacolophidae	THA	
Harpyodidae	THA	
Barylambdidae	THA	
Cyriacotheriidae	THA	
Coryphodontidae	THA	RUP
PANTOLESTA		
Pentacodontidae	DAN	
Pantolestidae	DAN	RUP
Ptolemaiididae	RUP	
APATOTHERIA		
Apatemyidae	DAN	RUP
CREODONTA		
Oxyaenidae	THA	PRB
Hyaenodontidae	DAN	UMI
CARNIVORA		
Miacidae	DAN	PRB
Amphicyonidae	PRB	OMI
Canidae	PRB	REC
Ursidae	PRB	REC
Viverridae	PRB	REC
Felidae	PRB	REC
Procyonidae	RUP	REC
Mustelidae	RUP	REC
Hyaenidae	IMI	REC
+Ailuropodidae	REC	
INSECTIVORA		
Mixodectidae	DAN	THA
Erinaceidae	?DAN	REC
Soricidae	?DAN	REC
Talpidae	?BRT	REC
Geolabidae	RUP	CNT
Chrysocloridae	IMI	REC
Tenrecidae	?IMI	REC
+Solenodontidae	REC	
+Nesophontidae	REC	
DERMOPTERA		
Plagiomenidae	DAN	BRT?
Placentidae	YPR	
Mixodectidae	YPR	
+Cynocephalidae	REC	
CHIROPTERA		
Icaronycteridae	YPR	
Palaeochiropterygidae	YPR	BRT
Emballonuridae	BRT	REC
Rhinolophidae	BRT	REC
Vespertilionidae	BRT	REC
Hipposideridae	PRB	REC
Megadermatidae	RUP	REC
Phyllostomatidae	?REC	REC
Molossidae	?CHT	REC
Pteropodidae	LMI	REC
Myzopodidae	PLI	REC
+Rhinopomatidae	REC	
+Craseonycteridae	REC	
+Nycteridae	REC	
+Noctilionidae	REC	
+Mormoopidae	REC	
+Desmodontidae	REC	
+Natalidae	REC	
+Furipteridae	REC	
+Thyropteridae	REC	
+Mystacinidae	REC	
SCANDENTIA		
Tupaillidae	PLE	REC

PRIMATES			
Paromomyidae	?MAA - BRT	Lophiodontidae	YPR - BRT
Plesiadapidae	DAN - YPR	Brontotheriidae	YPR - RUP
Carpolestidae	DAN - YPR	Isectolophidae	YPR - BRT?
Picroidontidae	DAN - THA	Helaletidae	YPR - CHT
?Uintasoricidae	THA - BRT	Lophialepididae	YPR - PRB
Adapidae	YPR - UMI	Hyracodontidae	YPR - CHT
Omomyidae	YPR - CHT	Palaeotheriidae	LUT - RUP
?Microsyopidae	YPR - BRT	Deperetellidae	LUT - RUP
?Amphilemuridae	LUT - PRB	Amynodontidae	LUT - UMI
Tarsiidae	RUP - REC	Tapiridae	RUP - REC
Parapithecidiae	RUP	Rhinocerotidae	RUP - REC
Pliopithecidiae	RUP - UMI		
Cebidae	CHT - REC	NOTOUNGULATA	(Marshall et al. 1983)
Lorisidae	LMI - REC	Perutheriidae	MAA
Cercopithecidae	LMI - REC	Arctostylopidae	THA - YPR
Hominidae	LMI - REC	Henricosborniidae	THA - YPR
Oreopithecidae	UMI	Notostylopidae	THA - BRT?
Lemuridae	PLE - REC	Oldfieldthomasiidae	THA - PRB
+Cheirogaleidae	REC	Isotemnidae	THA - MMI
+Indriidae	REC	Archaeohyracidae	THA - RUP
+Daubentonidae	REC	Interatheriidae	THA - UMI
+Callitrichidae	REC	Archaeopithecidae	YPR
ARCTOCYONIA		Notohippidae	?BRT - UMI
Arctocyonidae	MAA - PRB	Mesotheriidae	PRB - PLE
Paroxylaenidae	LUT - CHT	Hegetotheriidae	PRB - PLI
TILLODONTIA		Homalodotheriidae	RUP - UMI
Esthonychidae	THA - PRB	Leontiniidae	RUP - MMI
TUBULIDENTATA		Toxodontidae	RUP - PLE
Orycteropidae	IMI - REC	TRIGONOSTYLOPOIDEA	THA - BRT?
DINOCERATA		Trigonostylopidae	
Uinlatheriidae	THA - BRT	XENUNGULATA	
Gobiatheriidae	YPR - PRB	Carodniidae	THA
ARTIODACTYLA		EMBRITHOPODA	
Dichobunidae	YPR - CHT	Arsinoitheriidae	RUP
Cebochoeridae	YPR - RUP	PROBOSCIDEA	
Amphimerycidiae	YPR - RUP	Moeritheriidae	LUT - RUP
Mixtotheriidae	LUT - RUP	Mammutidae	RUP - PLE
Anoplotheriidae	LUT - CHT	Gomphotheriidae	LMI - PLE
Dacrytheriidae	LUT - RUP	Deinotheriidae	LMI - PLE
Haplوبوندنتidae	LUT - PRB	Stegodontidae	PLI - REC
Helohyidae	LUT - PRB	Elephantidae	
Anthracotheriidae	LUT - PLI	HYRACOIDEA	
Choeropotamidae	BRT - RUP	Pliohyracidae	RUP - LMI
Xiphodontidae	BRT - PRB	Procaividae	IMI - REC
Leptomerycidiae	BRT - UMI	Myohyracidae	LMI
Leptochoeridae	BRT - CHT	PHOLIDOTA	
Agrichoeridae	BRT - IMI	Epoicotheriidae	THA - RUP
Protoceratidae	BRT - UMI	Metacheiromyidae	THA - LUT
Camelidae	BRT - REC	Manidae	LUT - REC
Hypertragulidae	BRT - MMI	RODENTIA	
Gelocidae	PRB - UMI	Ischyromyidae	?THA - IMI
Cainotheriidae	PRB - LMI	Theridomyidae	YPR - MMI
Entelodontidae	PRB - LMI	Gliridae	YPR - REC
Tayassuidae	PRB - REC	Ctenodactylidae	?YPR - REC
Suidae	?RUP - REC	Chapattemyidae	LUT
Tragulidae	RUP - RBC	Aplodontidae	BRT - REC
Cervidae	RUP - REC	Geomyidae	BRT - REC
Bovidae	RUP - REC	Zapodidae	BRT - REC
Merycoidodontidae	RUP - UMI	Cylindrodontidae	BRT - CHT
Giraffidae	IMI - RBC	Prototypychidae	BRT
Antilocapridae	IMI - REC	Eomyidae	BRT - PLI
Hippopotamidae	MMI - RBC	Cricetidae	PRB - REC
+Moschidae	REC	Eutypomyidae	RUP - CHT
ACREODI		Eocardiidae	RUP - MMI
Mesonychidae	DAN - RUP	Phiomydne	RUP - MMI
ASTRAPOTHERIA		Sciuridae	RUP - REC
Astrapotheriidae	YPR - MMI	Heteromyidae	RUP - REC
PYROTHERIA		Castoridae	RUP - REC
Pyrotheriidae	YPR - RUP	Erethizodontidae	RUP - REC
Columbitheriidae	YPR	Dasyproctidae	RUP - REC
CONDYLARTHRA		Chinchillidae	RUP - REC
Peritychidae	DAN - THA	Octodontidae	RUP - REC
Hyopsodontidae	DAN - BRT	Echimiyidae	RUP - REC
Mioclaenidae	DAN	Thryonomyidae	RUP - REC
Phenacodontidae	DAN - PRB	Rhizomyidae	RUP - REC
Tricuspidontidae	THA	Cephalomyidae	CHT
Meniscotheriidae	THA - YPR	Mylagaulidae	CHT - UMI
Didolodontidae	THA - RUP	Diamantomyidae	IMI
LITOPTERNA		Miophiomyidae	IMI
Proterotheriidae	THA - PLI	Bathyergoididae	IMI
Macrauchenidae	THA - PLE	Kenyamyidae	IMI
Adianthidae	PRB - IMI	Anomaluridae	IMI - REC
PERISSODACTYLA		Pedetidae	IMI - REC
Equidae	THA - REC	Bathyergidae	IMI - REC
Chalicotheriidae	YPR - PLE	Muridae	MMI - REC
		Dipodidae	MMI - REC
		Hystricidae	MMI - REC
			+Petromyidae
			REC