The Fossil Record of Cretaceous Tetrapods

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The fossil record of the Cretaceous is critical for understanding the evolution of modern tetrapods. Using a measure of relative completeness of the fossil record—the Simple Completeness Metric (SCM)—quality of the fossil record and diversity during the Cretaceous appear to be closely related, suggesting an artifactual component. The SCM calculations also show that knowledge of the fossil record has improved in the last ten years. Recent proposals that modern orders of birds and mammals originated early in the Cretaceous are rendered unlikely by four arguments: (1) the SCM calculations indicate that the fossil record of Cretaceous birds and mammals is relatively good; (2) it is unlikely that all modern orders, independently, would have remained cryptic throughout the Cretaceous; (3) control samples of exquisitely preserved tiny Cretaceous tetrapods lack any specimens of modern groups of birds and mammals; and (4) the suggestion that the undiscovered ancestors of modern groups are to be found in unsampled parts of the Earth is not supported by cladistic evidence.

INTRODUCTION

One of the most profound challenges to the integrity of the paleontological enterprise has been made recently. Phylogenetic studies based on molecular data have suggested major gaps in the Cretaceous fossil record of birds and mammals (Hedges et al., 1996; Cooper and Penny, 1997; Cooper and Fortey, 1998; Kumar and Hedges, 1998). These claims have important implications for our understanding of evolution in terms of the origination and rate of evolution of modern birds and mammals, the impact of the KT event upon the diversity of higher taxa, and the quality of the fossil record. If the molecular results are correct, paleontologists have to accept that more than half the fossil record of birds and mammals is missing, pulling a major plank from beneath the whole profession. Does the disagreement between fossils and molecules really imply that half the fossil record of the past 130 million years is entirely undetectable?

There are two aspects to this question. First, is the fossil record well understood? Geological approaches confirm that the fossil record is adequate (Donovan and Paul, 1998), for example by comparison of uncertainties in stratigraphic ranges (Strauss and Sadler, 1989; Marshall, 1990; Bleiweiss, 1998). In particular, a study of the fossil record of modern bird groups (Bleiweiss, 1998) suggests that there were no long gaps before the first-known fossils assignable to extant taxa. Further if the fossil record were really poor, new discoveries should dramatically change the main outlines of tetrapod diversity; this is not the case (Maxwell and Benton, 1990).

The second question, whether the fossil record is a good indicator of the history of life, is harder to answer. However, new techniques that assess the congruence between stratigraphic and phylogenetic data (Gauthier et al., 1988; Norell and Novacek, 1992; Huelsenbeck, 1994; Benton, 1995; Benton and Storrs, 1996; Benton and Hitchin, 1997; Benton et al., 2000) show a good agreement, even for continental tetrapods (Benton and Simms, 1995; Benton, 1998). The demonstration of congruence between stratigraphic and phylogenetic data is crucial; because both give the same story, it can be assumed that it is the true story. Biases affecting stratigraphic data are different from those that affect phylogenetic (often molecular) data. Congruence between the two probably indicates convergence on the truth.

The aim of this article is to present data on the relative completeness of the fossil record of tetrapod families through the Cretaceous, to compare these results with those from a decade ago (Benton, 1987), to study the link between the quality of the fossil record and diversity patterns, and to consider the question of early origins of modern bird and mammal groups.

METHOD

The stratigraphic occurrences of 345 tetrapod families (20 amphibian, 138 reptile, 42 bird, and 145 mammal) that existed between the Callovian (Middle Jurassic) and the Ypresian (early Eocene) have been extracted from *The Fossil Record 2* (Benton, 1993). This compilation includes families that are almost exclusively monophyletic. Families known from a single specimen from a single locality ('singletons') have been removed from the dataset because they artificially inflate measures of diversity and fossil-record quality. Of importance are the numbers of originations and extinctions, as well as the intervening stratigraphic stages where the taxa are known from fossils (see Appendix 1). In addition, each tetrapod family has been assigned to a category of size, based on consideration of all species in the family and taking growth into account (see Benton, 1996). The categories are: Small (snout-vent length $L < 15cm$); Medium ($15cm < L < 150cm$); and Large ($L > 150cm$). The level of stratigraphic resolution used in the analyses is the stage, and the timescale is based on Harland et al. (1990).

One of the easiest ways to assess the quality of the fossil record consists in looking at gaps within the stratigraphic ranges of taxa. A measure of the relative completeness of the fossil record, the simple completeness metric (SCM; Benton, 1987), was calculated. This is the ratio of observed fossil occurrences to total inferred fossil occurrences. For each family, known fossil occurrences were recorded stage by stage. Gaps within ranges indicate the Lazarus effect (Jablonski, 1986). Total fossil occurrences are calculated as observed fossils plus Lazarus taxa. Consequently, low SCM values show when Lazarus taxa were most numerous, indicating poorly documented intervals. The SCM is calculated for both stratigraphic intervals and taxonomic groups (Fig. 1). The SCM, however, may result in overestimated measures of completeness for two reasons. First, this is because the Lazarus effect can only be identified within the known range of taxa, but can not account for taxa that become extinct or originate during the gaps. Sec-
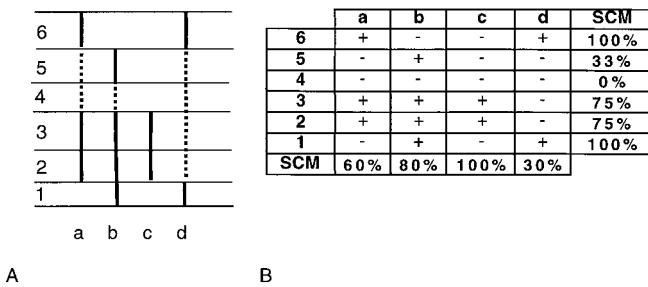
FIGURE 1—Lazarus taxa and the Simple Completeness Metric (SCM). (A) Theoretical example of the stratigraphic ranges of four taxa (a-d) within six stratigraphic units (1–6). Solid lines indicate the presence (+) of the taxa in the fossil record and dotted lines represent their absence (−), illustrating the Lazarus effect. (B) Calculation of the SCM, the ratio between the number of Lazarus units and the total number of units. The units can be both stratigraphic intervals (rows) or taxonomic groups (columns; after Benton and Storrs, 1996).

FIGURE 2—Quality of the fossil record of tetrapod families estimated by the Simple Completeness Metric (SCM). Total numbers of originations and extinctions reveal strong similarities of pattern to each other, and to the SCM values. Abbreviations of stages are from Harland et al. (1990).

ond, as pointed out by Benton (1987), the SCM becomes less reliable when there is a long succession of poor records because fewer families can span wide time intervals. Despite these problems, the SCM is a straightforward measure that becomes more robust when large datasets of fossil occurrences are used.

In this study, the potential correlations among SCM, extinctions, originations, and stage durations were investigated statistically. Among the nonparametric measures of association, we preferred the Kendall rank-order correlation coefficient T (tau) because it can be extended to the partial correlation statistics $T_{xy.z}$. The latter permits the removal of the influence of a third variable upon the measured relation between two variables, and it acts as a useful statistical control (Siegel and Castellan, 1988).

RECORD QUALITY, EXTINCTIONS, AND ORIGINATIONS

The SCM of all tetrapod families has been calculated for all stages from the Callovian to the Ypresian (Fig. 2). The quality of the fossil record is good (SCM > 75%) for the Kimmeridgian, Tithonian, Albian, and from Campanian to Ypresian. On the other hand, paleontological information is poor for the Berriasian-Aptian and Cenomanian-Santonian intervals, as noted in previous works (Benton, 1987; Bardet, 1995). Almost all major variations of SCM values for tetrapods stem from the record of 'reptile' (Amniota, excluding Mammalia and Aves) families, mainly because they dominate the totals numerically.

The curves for total numbers of originations and extinctions of tetrapod families closely match variations in the SCM through the time interval considered here (Fig. 2). The stages with low SCM also exhibit the lowest numbers of originations and extinctions; the links are statistically significant (Kendall rank-order correlation, T = 0.692 and T = 0.564 respectively, p < 0.005, one-tailed tests). Further statistical investigations show that the numbers of extinctions and originations are strongly correlated (Kendall rank-order correlation, T = 0.541, p < 0.005), but not when the potential effect of the SCM is removed (Kendall partial rank-order correlation, $T_{xy.z}$ = 0.254). This suggests a strong influence of the fossil record (as estimated by the SCM) upon patterns of extinction and origination.
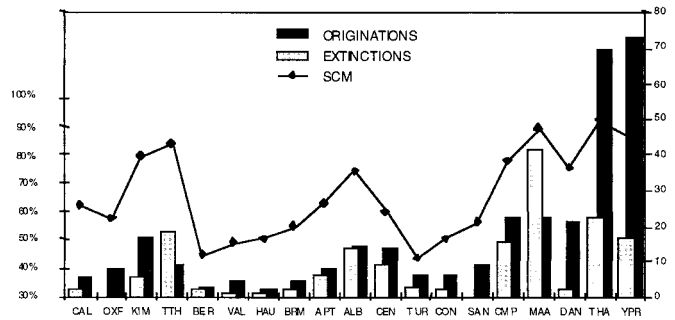
In addition, the correlation between extinctions and originations through the Cretaceous is not an artifact of stage durations (Kendall partial rank-order correlation, $T_{xy.z}$ = 0.510, p < 0.001), nor is the SCM linked to this parameter (Kendall rank-order correlation, T = 0.259)

Is the SCM related to the mean size of the animals? It might be expected that small tetrapods would be less adequately represented in the fossil record than large ones. In order to test this hypothesis, the SCM has been calculated for the three categories of size defined earlier. Note that these categories include similar numbers of taxa throughout the Cretaceous. Figure 3 shows that small-sized tetrapods do not have more gaps in their fossil record than medium- and large-sized ones, but even fewer on average. Hence, small size is not a significant factor in fossil recovery potential.

IMPROVEMENT IN KNOWLEDGE SINCE 1987

It is also of interest to study the evolution of SCM values for tetrapods in the last decade. Has our knowledge of the Cretaceous fossil record improved since 1987 and, if so, by how much, in which stages, and for which groups? Benton (1987) presented the diversity of continental tetrapods and estimated the quality of their fossil record through the
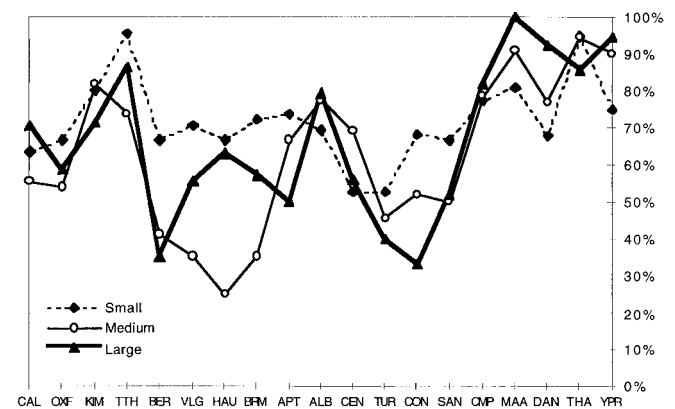
FIGURE 3—Comparison of the SCM of tetrapods for three categories of body size (see text for details). Small-sized tetrapods have similar, if not better, values of SCM than bigger tetrapods through the Cretaceous.
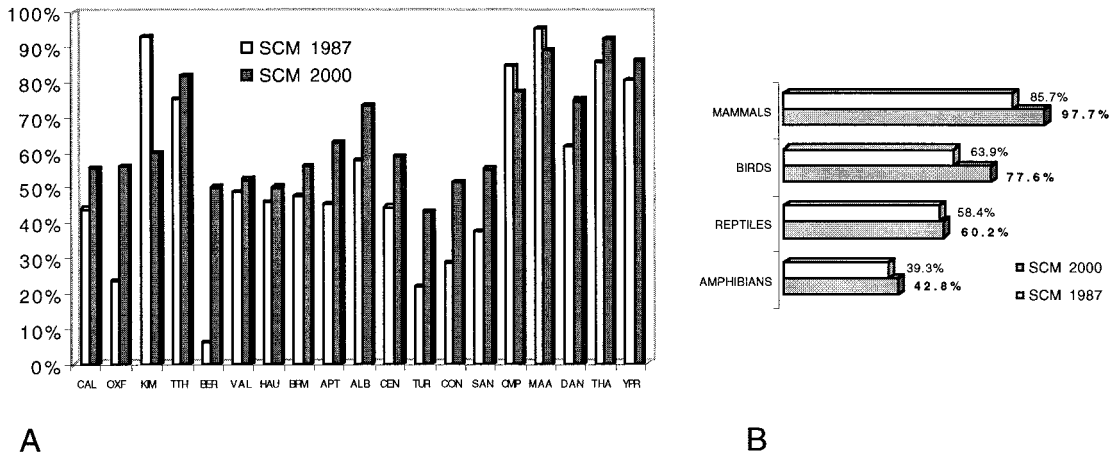
FIGURE 4—Comparison of the SCM of continental tetrapods from the database of Benton (1987) and from this work, by stages (A) and by major groups (B). In most cases, collection of new fossils, and revisions of taxonomy and stratigraphy during the past decade have improved the SCM values (i.e., fewer Lazarus taxa as gaps are filled).

Phanerozoic with the SCM index. After removing the marine families from our database, the SCM has been computed for both stages and classes. The results are compared with those of Benton in the Callovian-Ypresian interval (Fig. 4A).

The most striking fact is the improvement of the SCM, especially in the previously poorly documented stages (Oxfordian, Berriasian, Aptian-Santonian). This suggests that new discoveries, coupled with stratigraphic and taxonomic revisions in the past decade, have improved the quality of documentation of Cretaceous tetrapods.

The SCM of all the classes has improved (Fig. 4B), especially birds and mammals. Of the 19 stages studied here, mammals exhibit SCM values of 100% for 14, and never get lower than 80%. The total SCM of reptiles has barely been modified in the past decade despite the large number of additional families considered in the calculations (669 families in this study, against 548 in 1987). The amphibians have the worst fossil record within tetrapods, and their SCM values exhibit no significant shifts in the last decade. The global SCM of all continental tetrapods for the interval considered here (70.4%) is higher than in 1987 (64%), and very similar to the value previously found by Benton (1987) for the entire Phanerozoic (68.1%)

DISCUSSION AND CONCLUSIONS

The influence of the fossil record upon variations in observed diversity is a central issue. Biases inherent in the fossil record and its study include sampling strategy (methodology, volume of rock studied, accessibility of deposits), paleontological interest (Sheehan, 1977), monographic effects (Raup, 1972), the Lagerstätten effect (Hoffman and Fenster, 1986), and the Signor-Lipps effect (Signor and Lipps, 1982). The lowest (LO) and highest occurrence (HO) of a taxon only rarely, if ever, correspond to the actual dates of origination and extinction of that taxon. However, failing anything better, diversity studies consider the LO and HO as the points of origination and extinction. Thus, the quality of the fossil record may influence strongly observed diversity patterns and our ideas about evolution. In order to deal with these problems, studies of

global diversity are usually made at least at familial level, for which sampling biases are less substantial (Raup, 1972, 1986; Benton, 1996, 1999). However, it is shown here that, even at family and stage levels, the fossil record firmly shapes apparent origination and extinction patterns, especially in time intervals between the major bioevents. Conversely, Lazarus taxa may also be more numerous just after major biotic crises, reflecting the extreme rarity of organisms that fail to enter the fossil record at that time (Wignall and Benton, 1999). Therefore, Lazarus taxa do not have the same meaning through the Phanerozoic.

Nevertheless, SCM calculations show that the quality of the fossil record is globally good for tetrapods in the Callovian-Ypresian interval and is quite similar to the whole-Phanerozoic value. Birds and mammals have high SCM values (77.6% and 97.7%, respectively). For birds, however, the figures must be an overestimation because of the small number of families. The highly mineralized teeth of mammals and their fundamental importance for systematics undoubtedly are responsible for the extreme SCM values calculated for mammals.

The Cretaceous fossil record looks complete enough to dispute the claims of some molecular biologists (Cooper and Penny, 1997; Kumar and Hedges, 1998), who give Early Cretaceous dates for the radiations of modern bird and mammal orders. To accept their claims implies a long, unknown Cretaceous fossil record, which is not indicated by the SCM calculations. This is a probabilistic argument, but it is equivalent to assessing the probability or improbability that, at some time in the future, paleontologists ought to find Early Cretaceous parrots, penguins, elephants, and guinea pigs. Even if it were argued that these modern groups were represented by cryptic ancestors (Cooper and Fortey, 1998), that does not resolve a second problem. Why should some 20–30 lineages, the modern bird and mammal orders reputed to have existed undetected through most of the Cretaceous, *all* uniformly remain cryptic until they blossomed forth in abundance and with autapomorphies in place and fully displayed between 70 and 55 million years ago? A third argument, that the Cretaceous representatives of the modern bird and mam-

mal orders were small and fragile and, hence, unlikely to be preserved as fossils, is denied by the simplest observation of all: there is a control sample for the Cretaceous, in the form of dozens of sites that now yield exquisite specimens of tiny and delicate birds, basal mammals, lizards, and salamanders from many parts of the world. In none, to date, is there a hint of an ancient representative of a modern bird or mammal group. Furthermore, the analyses presented herein show that the absence of tetrapods from the fossil record is independent of their size. The fourth argument is the proposal that paleontologists have not found the fossils yet because the modern avian and mammalian orders originated in relatively unsampled areas, such as Australia or New Zealand (Cooper and Penny, 1997). However, this idea is not supported by cladistic paleobiogeographic evidence. Relationships and known geographic distributions of the modern bird and mammal orders indicate origins for most of them in the well-sampled northern hemisphere continents (Sibley and Ahlquist, 1990; Szalay et al.,1993; Benton, 1997). In any case, the appeal to unexplored regions is exactly the argument used in the 1750s to deny the possibility of extinction. Some day, so it was said, living mammoths and mastodons would be found in the unexplored reaches of the savage western parts of North America. Perhaps!

ACKNOWLEDGMENTS

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APPENDIX 1

Numbers of originations, extinctions, and values of SCM (Simple Completeness Metric, see method) for tetrapod families in the Callovian-Ypresian interval. The stage durations are based on Harland et al. (1990).

Stages	Durations	Origi-nations	Extinc-tions	SCM %
Ypresian	6.5	73	16	86.1
Thanetian	4	69	22	91.3
Danian	4.5	21	2	74.7
Maastrichtian	9	22	41	89.3
Campanian	9	22	15	78.1
Santonian	3.6	9	0	56.8
Coniacian	1.9	6	2	50.7
Turonian	1.9	6	3	43.8
Cenomanian	6.6	13	9	59.7
Albian	15	14	13	73.1
Aptian	12.5	8	6	62.7
Barremian	7.3	4	2	54.7
Hauterivian	3.2	2	1	50.0
Valanginian	5.7	4	1	49.0
Berriasian	4.9	3	2	44.7
Tithonian	6.5	9	18	83.9
Kimmeridgian	2.6	16	5	79.3
Oxfordian	2.4	8	0	57.1
Callovian	4.2	5	2	63.9

APPENDIX 2

Measures of correlation for originations (O), extinctions (E), Simple Completeness Metric (SCM), and stage durations (D). The Kendall rank-order correlation coefficient T and the Kendall partial rank-order correlation coefficient $T_{xy.z}$ are provided with their associated probabilities (one-tailed tests).

Variables	Measures of association T	$T_{xy.z}$	Probabilities
E and O	0.541		p<0.005
E and SCM	0.564		p<0.005
O and SCM	0.692		p<0.005
E and D	0.343		p<0.025
O and D	0.215		No correlation
SCM and D	0.259		No correlation
E and O, with SCM held constant		0.254	No correlation
E and O, with D held constant		0.510	p<0.001
E and SCM, with O held constant		0.312	p<0.05
O and SCM, with E held constant		0.557	p<0.001