Mammalian and avian survival across the Cretaceous–Tertiary boundary

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The Cretaceous–Palaeogene (K/Pg) or, popularly, Cretaceous–Tertiary (K/T) boundary has long been recognised to mark the end of the Mesozoic Era and the final extinction of non-avian dinosaurs, pterosaurs, the great marine reptiles and many less ostentatious, though formerly abundant taxa, such as ammonite molluscs. The primary mechanisms suggested to have facilitated this 'mass extinction' event initially included disease, competition with newly evolving mammals and birds, climate changes and mass volcanism associated with the Deccan traps in India (see Archibald & Clemens 1982). However, these putative causes lacked explanatory power in the specificity of extinctions or in their timescale of action. It was the discovery of a world-wide spike in iridium concentrations (Alvarez 1980) and then a contemporaneous impact crater off the Yucatan Peninsula (see Sharpton & Marin 1997) that provided the smoking gun of global scale and antibiotic potential appropriate to the apparent scope of the extinction. Henceforth, the events around the K/T boundary have primarily been viewed through the lens of a bolide (asteroid/comet) impact.

With a few notable exceptions (e.g. Archibald 1996a) the prominence of the impact theory and its undoubted immediate biological influence may have encouraged two assumptions that need to be examined independently of the biotic implications of the bolide impact. One of these is that terrestrial vertebrate ecology had reached some kind of steady state by the Cretaceous and that, if a catastrophic abiotic factor explained the final extinction of the great reptiles, there is little role for biotic interactions (e.g. competition) in explaining extinction and survival during the Late Cretaceous. Changes in evolutionary thinking also provided an ideal landscape upon which such notions could flourish. Punctuated equilibrium theory (Eldredge & Gould 1972) in particular often viewed abiotic shifts as essential for breaking down evolutionary deadlocks and jump-starting evolution (e.g. Sepkoski 1987). Thus follows the second assumption, that mammals and, to a lesser extent, birds could only have diversified substantially after the extinction of the dinosaurs.

Penny & Phillips (2004) emphasised the importance of testing hypotheses associated with the diversification of the lineages that evolved into modern mammals and birds independently of hypotheses regarding the extinction of the dinosaurs and pterosaurs. Similarly, neither a bolide-inflicted extinction of dinosaurs and pterosaurs nor post-K/T diversification of modern mammal and bird groups is evidence for competition among vertebrate groups and innovation within them having ground to a halt during the Late Cretaceous. Indeed, there was considerable phylogenetic and ecological turnover among avian and mammalian faunas throughout the Mesozoic Era (Kielan-Jaworowska *et al.* 2004; Padian & Chiappe 1998). Even among dinosaurs the familiar ceratopsid (horned), hadrosaurid (duck-bill) and tyrannosaurid dinosaur families were evolutionary newcomers of the Late Cretaceous.

Regardless of the evolutionary and extinction mechanisms at play in the Late Cretaceous, battle lines may have already been drawn between paleontologists and molecular phylogeneticists. Sudden extinctions and subsequent radiations fitted comfortably with the late 20th century evolutionary zeitgeist of many paleontologists, whose thinking had strayed considerably from more explicitly Darwinian, adaptationist roots. Molecular sequence data on the other hand and especially molecular clocks are models of neo-Darwinian gradualism. By the late 1990s these two schools were at loggerheads. Molecular clocks predicted that dozens of modern lineages of birds and mammals coexisted with dinosaurs, while the fossil record confined almost all of these to post K/T appearances (see Bromham *et al.* 1999).

The fossil record by the mid 1990s and the challenge from molecular dating

By the end of the last millennium the story from the fossil record was simple. It was well documented that dinosaurs were still flourishing at the time of the last Cretaceous deposits in which they were found across each of the better sampled continents

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(Europe, Asia, North and South America). Even their absence from the latest Cretaceous 'ten foot gap' at Hell Creek was convincingly explained as a combination of sampling artefact and sedimentation/erosion anomaly (Pearson *et al.* 2001). Only non-articulated, older reworked dinosaur and pterosaur fossils were found in post-K/T sediments. In contrast, no pre-K/T fossil could unambiguously be attributed to any extant mammalian or avian order. Indeed, no firm evidence could place any modern (crown) member from among monotremes, marsupials, placentals or birds in any Cretaceous fauna. It is in this clean temporal disjuncture between the fossil records of the great reptiles and the modern birds and mammals that conflict with molecular studies is found.

One after another, molecular dating studies utilising various fossil calibrations indicated that the majority of interordinal avian divergences examined and almost all interordinal placental mammal divergences occurred before the K/T extinction event (e.g. Cooper & Penny 1997; Kumar & Hedges 1998; Penny *et al.* 1999). Some paleontologists speculated that unknown genetic mechanisms may have accelerated and then decelerated molecular evolution in parallel among what were really post-K/T lineages, in such a way as to be hidden from dating analyses (e.g. Foote *et al.* 1999). Nevertheless, substantive evidence was mounting for modern mammal and bird groups having diversified extensively, well before the extinction of dinosaurs and pterosaurs. Notably, more recent analyses of rate evolution across the K/T boundary have dismissed the rate acceleration/deceleration speculations (Slack *et al.* 2006; Springer *et al*. 2003).

Bromham *et al,*. (1999) may have signalled a turning point in the fossils versus molecules debate. They sought instead to reconcile the alternative perspectives while exploring various shortcomings of both. Literal readings of the fossil record had often failed to acknowledge biogeographic and ecological considerations and the difficulty of assigning taxa to stem lineages of modern groups. Equally, more appropriate methodologies for molecular dating were required to overcome the influence of stochastic error and violations of the often presumed clocklikeness of molecular sequence evolution.

Bridging the divide

Late Cretaceous fossils have now been linked with at least three modern placental mammal groupings: *Batadon* and *Paranyctoides* with lipotyphlan insectivores (see McKenna & Bell 1997), 'zhelestids' with Ungulatomorpha (Archibald 1996b), and zalambdalestids with Glires (Archibald *et al*. 2001). If these phylogenetic statements are correct, much of the difference between the molecular dates and the fossil record would effectively be bridged. However, each of the proposed relationships requires further testing. The molecular evidence clearly shows that Lipotyphla (Eulipotyphla and Afroinsectivora) and Ungulatomorpha (Fereuungulata, Paenungulata and Tubulidentata) are polyphyletic and contain taxa that may have arisen from different sides of the placental root. Thus sister relationships with Lipotyphla and Ungulatomorpha do not clearly discriminate between their respective (proposed) fossil sister-taxa being within, or outside the placental crown group. Zalambdalestids on the other hand possess some very 'primitive' characters for placental mammals, such as epipubic (marsupial) bones. Whether the characters that link this taxon with Glires are in fact convergent and simply associated with similar functional/ecological constraints requires further study.

Despite uncertainty in the affinities of fossils that are putative close relatives of superordinal clades of modern placentals, their publication is symbolic of a gradual whittling down of differences between paleontological and molecular interpretations of the early diversification of modern mammal groups. The current situation for Cretaceous birds is similar. *Vegavis* is an undoubted Anseriform (Clarke *et al.* 2005) from the very latest Cretaceous (≈66 Ma), while several other admittedly fragmentary remains have been assigned to modern avian orders (e.g. Stidham 1998; Hope 2002).

Some early molecular dating estimates for the basal divergences among placental mammals and among modern birds (e.g. Cooper & Penny 1997; Kumar & Hedges 1998) were very old, at more than 125 Ma. Improvements in taxon sampling, substitution modelling and "relaxation" of the molecular clock constraint have resulted in slightly younger dates, typically 90–115 Ma (e.g. Springer *et al.* 2003; Harrison *et al.* 2004). By modelling sampling and uncertainty in the fossil record (Tavare *et al.* 2002) has further closed the gap between fossil and molecular expectations. A salient notification that there has been a shift towards agreement between recent interpretations of the fossil record and the molecular dates is that prominent sceptics of pre-K/T radiations of placental and modern avian orders (e.g. Benton 1999) are now advocating their Cretaceous origins (Benton & Donghue 2007).

K/T boundary: business as usual for the ancestors of modern bird and mammal lineages?

Bininda-Emonds *et al.*, (2007) presented a comprehensive species-level molecular dating analysis of mammalian diversification through time. They found no evidence for a diversification spike close to the K/T boundary, while Penny & Phillips (2007) used their data to argue that the initial mammalian radiation occurred some 20 Ma prior to the K/T; this is roughly in line with the inferred timing for initial diversifications among each of the three oldest avian superordinal groupings, Palaeognathae, Galloanserae and Neoaves (Slack *et al.* 2006).

One question that arises from the ≈80 Ma diversifications of 'modern' mammalian and avian lineages is whether their adaptive radiation involved competitive (or other) displacement of some dinosaurs and pterosaurs, or only of earlier mammalian and avian groups? Certainly large declines in the relative richness of small dinosaurs (< 10 kg) and small pterosaurs (< 2 m wingspan) that were documented in Penny & Phillips (2004) and Slack *et al.* (2006) are suggestive, although more detailed paleontological analysis is required.

A second question is whether there is any signal for the influence of the K/T boundary event around 65Ma on the evolution of modern mammals and birds. In addition to taxonomic diversity, considerable ecological diversity had also evolved among various mammal and bird groups during the Cretaceous. Whether or not from modern lineages, among the mammals there were carnivores, omnivores, herbivores, and specialist anteaters and mollusc-eaters, to name just a few dietary types. Functional analyses show these mammals were variously terrestrial, scansorial/arboreal, aquatic, and even gliding in their habits (e.g. Kielan-Jaworowska *et al.* 2004; Meng *et al.* 2008). It is now emerging that Cretaceous birds were also far more ecologically diverse than had been thought (Zhou 2006). One obvious candidate however, for a definitive signal across the K/T boundary is a shift in size. This is the one important aspect of the 'mammals and birds inherit the Earth from the ruling reptiles' paradigm that remains standing.

The same explanations for the phylogenetic diversity predicted in molecular dating studies being absent from the fossil record could also be levelled at the apparent absence of large terrestrial mammals and birds from the Late Cretaceous. Namely, they might well be hidden by the gaping geographic holes and taphonomic biases that exist in the Late Cretaceous record (Cracraft 2001). In order to further examine this possibility, I used phylogenetic inference from modern taxa to predict whether large terrestrial mammals coexisted with dinosaurs, or did not evolve until after the K/T extinction event.

Evolution of large terrestrial mammals and birds

In this study I set out to infer the size of ancestral mammals at each node that represents a pre-K/T divergence on the modern mammalian tree. Modern taxa were represented in the study as tips from either side of the deepest divergence for each mammalian order. Point estimates for each of these nodes were taken from three molecular dating studies – Phillips *et al.* (in prep. a), Springer *et al.* (2003), and Bininda-Emonds *et al.* (2007), in that order of preference – with a less preferred study being used only when that node was not included in a more preferred study. In this way a phylogenetic timeline was constructed and size classes were allocated at the tips, given the median adult mass (averaged over males and females) for the modern taxa that each tip and its associated lineage represent. Size classes were small (<1 kg), medium (1–20 kg) and large (>20 kg). Most 'generalist' insectivorous/omnivorous Mesozoic mammals known from fossils fit into the small class (Kielan-Jaworowska *et al.* 2004), while the medium size class includes numerous more specialised Mesozoic mammals and contains the upper size limit of known Mesozoic mammals. Large mammals are only known from post-K/T fossil records.

Most likely ancestral size classes were inferred using multistate maximum-likelihood within BayesTraits* (Pagel & Meade 2006). Likelihood ratio testing suggested that the additional parameterisation cost of unlinking the directional reversibility for state changes was not warranted. In order to enhance precision, the mammalian root node was fixed at the small size class, in agreement with earlier workers and the fossil record (e.g. Luo *et al.* 2002; Kielan-Jaworowska *et al.* 2004). Notably, the maximum-likelihood (ML) estimates for state changes were zero for shifts from small to large and *vice versa*, such that the characters are effectively ordered (small, medium, large), although were not constrained to be.

Figure 1 shows that all ML reconstructed ancestors at pre-K/T nodes were of either small or medium size. This result is congruent with the fossil record and does not require that large Mesozoic mammals have been hidden by biases in the fossil record. The apparent lack of large mammals during the 125 Ma or more of Mesozoic history contrasts sharply with at least 14 independent derivations of large size among the lineages leading to modern mammals (see Figure 1) and many more among extinct Cainozoic mammals.

The present results for mammals are consistent with an investigation (Phillips *et al.*, in prep. b) into the evolution of flightlessness among ratite birds (e.g. ostrich, rheas, emu, moa, kiwi). Among these birds, loss of flight appears to have evolved at least four times independently on different land masses, in concert with increases in size and in each case along lineages that cross, or diverged after the K/T boundary. No equivalents of these predominantly large, cursorial omnivores/herbivores existed among the known Cretaceous avifauna and as such, the ratites might more appropriately be considered as ecological replacements for the aptly named ostrich dinosaurs (ornithomimids). It may be inferred from analysis of the dated molecular phylogenies that much of the taxonomic diversity of ratites originated in the Cretaceous, as essentially did their terrestriality and their dietary habits. In these respects the evolution of large birds mirrors the evolution of large mammals. Taxonomic and ecological diversity appears to have evolved over tens of millions of years during the Late Cretaceous and provided a launching pad for later diversification of often more sizable descendents.

The K/T boundary and the associated final extinction of the dinosaurs and pterosaurs does appear to provide a signal for phylogenetic inference of mammalian and avian evolution in the form of the removal of a size constraint. Size can be a highly labile character among vertebrates. Bunce *et al.* (2005) and Clauset & Erwin (2008) have shown for birds and mammals respectively that 10-fold mass differences occur between modern lineages within less than one million years. Given that it took the first ten million years of the Tertiary before cow-sized mammals appeared, special forces outside of the realm of currently studied developmental-genetic mechanisms do not seem to be required to explain mammal and bird evolution in the aftermath of the extinction of 'the great reptiles'. On the other hand, apparent ecological release at the K/T boundary for birds and mammals (in relation to size) redirects the emphasis of further investigation. Much recent attention has been paid to differential effects of abiotic killing mechanisms among taxa at the K/T boundary (e.g. Robertson *et al.* 2004). It is now pertinent to ask to what extent and by which biological mechanisms was competitive exclusion between dinosaurs, pterosaurs, birds and mammals maintained and/or broken down before the end of the Cretaceous.

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* BayesTraits is a computer package for performing analyses of trait evolution among groups of species for which a phylogeny or sample of phylogenies is available.

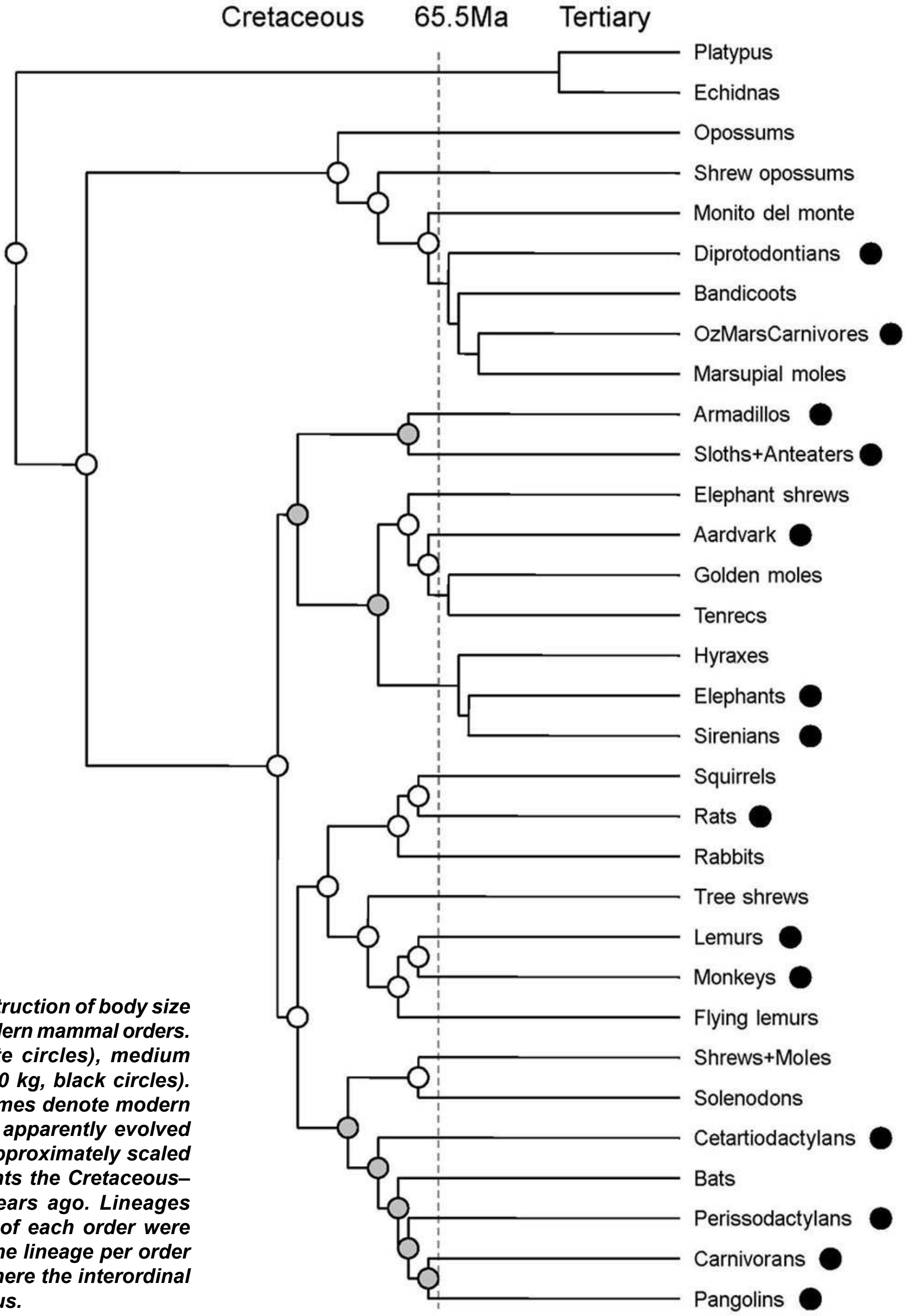

Figure 1. Maximum-likelihood reconstruction of body size at pre-Tertiary ancestral nodes for modern mammal orders. Size classes are small (<1 kg, white circles), medium (1–20 kg, grey circles) and large (>20 kg, black circles). Black circles to the right of taxon names denote modern lineages along which large size has apparently evolved independently. Branch lengths are approximately scaled to time and the dashed line represents the Cretaceous–Tertiary boundary at 65.5 million years ago. Lineages representing both sides of the root of each order were employed in the analysis, but only one lineage per order is included here for clarity, except where the interordinal divergence occurred in the Cretaceous.

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