

Mammal Diversification

ABSTRACT:

The advent of molecular clocks has created a rift in the understanding of mammalian emergence and diversification. The fossil record, previously the sole authority on the subject, has long suggested a fairly dormant mammalian lineage all through the Cretaceous period, followed by intense, rapid diversification in the wake of the K/T mass extinction. The use of DNA sequence data to create a molecular clock, however, has initiated a different historical perspective, in which mammal diversification had been ongoing long before the Cenozoic. This clash has paved the way for the emergence of three distinct models of mammalian diversification: the short fuse, the long fuse, and the explosive model. While the short fuse model, which purely reflects the molecular approach, and the explosive model, which purely reflects the fossil record, seem to be mutually exclusive, the long fuse model, which employs both techniques, may hold the key to an acceptable middle ground.

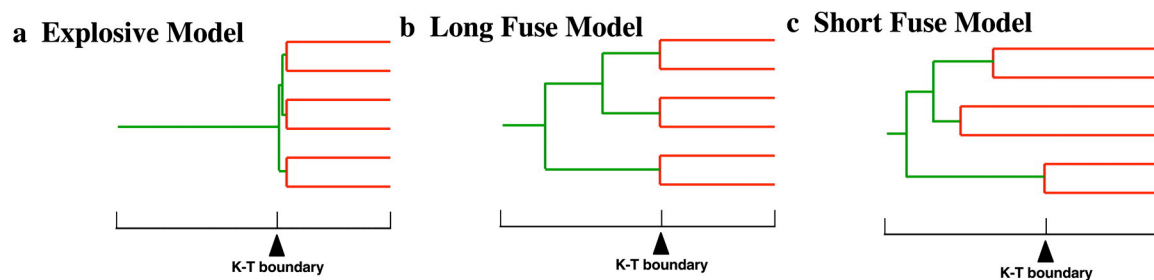
INTRODUCTION:

The transition from reptile to mammal reaches all the way back to the Carboniferous period, over 250 million years ago, with the development of Synapsids. The earliest Synapsids, Pelycosaurs, survived into the Permian period before going extinct. A more mammal-like offshoot of Pelycosaurs, Therapsids, took hold approximately around the time of this extinction. Kemp (2006) argues that the subsequent diversification of Therapsids may have arisen through the disappearance of their relatives, the Pelycosaurs, via the mechanism of incumbent replacement. As Kemp notes, the replacement of Pelycosaurs by Therapsids was a milestone in mammalian evolution because it marked the first metabolic progression from ectotherm toward endotherm: “It was the ancestral Therapsid that had crossed the biological threshold on the road that led ultimately to the metabolically more active, versatile and potentially much more adaptable kind of terrestrial organisms represented by the mammals.” The Therapsids, however, suffered a severe reduction during the end-Permian extinction. Cynodonts, considered the final link between reptiles and “true” mammals, were one of the few Therapsid taxa that survived.

The presence of these distinct mammalian predecessors, tracing all the way back to the end of the Paleozoic period, provides firm evidence that mammalian development was well underway prior to the K/T extinction. However, it must be noted that while the early divergence of this Synapsid lineage certainly lends insight into mammalian evolution, these ancestors were not mammals themselves. Whether or not true mammals actually originated and diversified long before the K/T boundary is a much stickier matter, and touches on the heart of the controversy currently surrounding mammal diversification.

Classical thought had long held that mammalian diversification, by and large, did not occur until directly after the K/T extinction. This theory largely reflected the fossil record, which until recently, was the only available means for assessing phylogenetic timeframes. Recently, however, the advent of the molecular clock has provided a new method for piecing together the timeframe for mammalian diversification. These two approaches, however, do not always yield the same view of history. The resulting discrepancy has produced three distinct models of mammalian diversification: the short fuse, the long fuse, and the explosive models. The explosive model largely reflects paleontological evidence, whereas the short fuse model mainly considers molecular data. The long fuse model, in contrast, attempts to reconcile these two extremes.

Figure 1: Simplified representations of mammal diversification in each of the three models (Springer, 2003)



DISCUSSION:

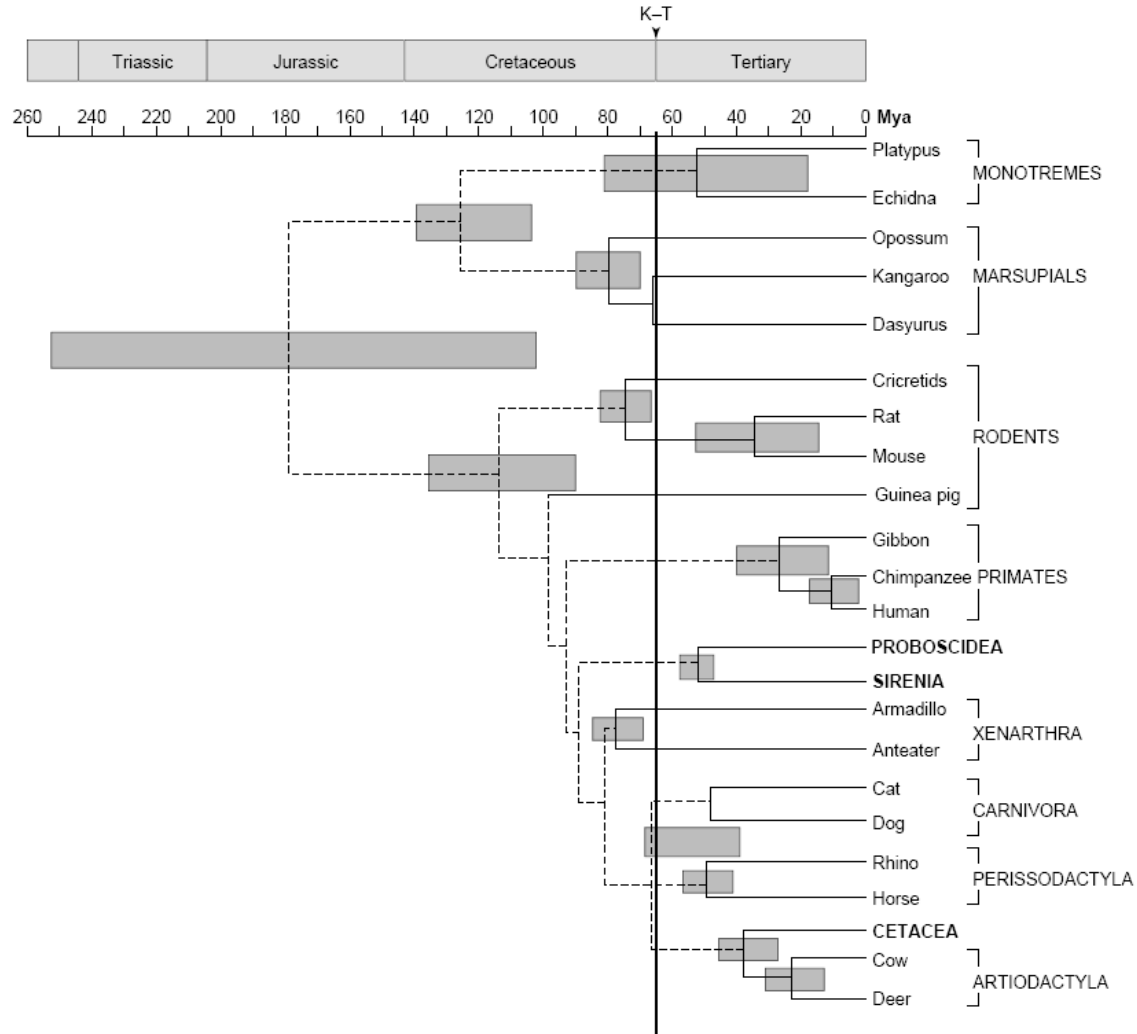
Short Fuse Model: The short fuse model, which is characterized by extensive interordinal and intraordinal diversification prior to the K/T extinction, challenges the previously held belief that mammal diversification did not take off until the extinction of the dinosaurs, when adaptive radiation allowed the mammalian lineages to fill into the newly-opened niches. The evidence for this new interpretation comes from a modern innovation: the molecular clock. By comparing the DNA sequences of different taxa, and plugging in a given mutation (calibration) rate, it can be estimated how long ago the taxa split. Under this molecular assessment, mammals arose surprisingly early in the Mesozoic period, perhaps

even 150 million years ago, as described by Bromham et al (1999). This early origin has surprised many researchers because there is a lack of evidence in the fossil record to support it. However, Bromham notes that this may simply be a result of the biogeography of mammalian origin: it is hypothesized that mammals first evolved in what is currently Africa, a region with a particularly poor fossil record during the late Cretaceous period.

The credibility of the short fuse model, which relies almost entirely on DNA sequence data, is often called into question, even by its proponents (Bromham 1999), because of certain assumptions inherent in the molecular clock. Most notably, the molecular clock assumes that mutation rates remain constant, both through time and among different taxa. However, this assumption is contradicted by evidence that rate variability does occur. Studies of hominid and rodent mutation rates demonstrate that mutation rates among different taxa may be profoundly different: Li et al (1996) report that “the rate of nucleotide substitution is at least two times higher in rodents than in higher primates.” This finding is particularly relevant since both of the taxa examined in this experiment, rodents and hominids, are mammals.

The acknowledgement of this rate variation prevents the molecular clock from generating phylogenies with any great degree of precision. The short fuse model, through association, is ultimately tied to this shortcoming in the molecular clock. As a result, the historical view of mammalian diversification presented by the short fuse model often contains broad confidence intervals. Nonetheless, even at the most recent possible predicted divergences, the short fuse model supports several mammalian diversifications well before the K/T boundary.

Figure 2: Estimation of mammal diversification according to molecular data. The confidence bars are represented as grey rectangles. (Bromham, 1999)



Explosive Model: The explosive model, consistent with the classical understanding of mammal diversification, predicts only limited diversification prior to the K/T boundary. As its name implies, the dormant mammal lineage would have then experienced an explosion of diversification directly following the mass extinctions, presumably due to release from predators and competitors. This notion is consistent with the historically widespread pattern of extinction followed by diversification. The model is founded on the fossil record, which, as Futuyma (2005) observes, is thin up until the Cenozoic. “Almost all

mammalian fossils that can be assigned to modern orders,” he explains, “occur after the K/T boundary.”

In the wake of DNA sequence data, some previous advocates of the explosive model have been led to reconsider their stance, while others have simply made adjustments. In one such example, John Alroy (1999), while admitting that molecular analyses give evidence of interordinal mammalian divergences before the K/T boundary, maintains that these rare occurrences do not deconstruct the argument that there was an explosion of diversification directly afterwards. To defend this point, he cites the increase in mammal body size that occurred in conjunction with the diversification directly after the extinctions. This “rapid and permanent shift” in body size, he holds, can only be explained by the adaptive radiation of mammals into the niches for large body size that had previously been the domain of dinosaurs. The explosive model has come under fire for its sole adherence to and dependence on the fossil record, but Alroy’s argument is one which proponents of the molecular clock cannot ignore.

Long Fuse Model: In response to the mutual exclusiveness of the short fuse and explosive models, the long fuse model attempts to integrate the two extremes. Under the long fuse model, substantial interordinal splitting occurred in the Cretaceous period, before the K/T boundary, but much of the finer, intraordinal diversification occurred later, in the midst of the K/T boundary and the mass extinctions that it marks. Likewise, the long fuse model attempts to reconcile and utilize data from both the fossil record and DNA sequencing.

A prime example of this integrative approach is documented in a recent article by Springer et al (2003). Focusing on placental mammals, they conducted a molecular analysis on twenty-two gene sequences. Wary of the pitfalls of the molecular clock, their

analysis used the Thorne/Kishino method, which improves the molecular analysis in two important ways. First, it takes into account the constraints of the fossil record, and second, it removes the demand for equal mutation rates among each phylogenetic branch. The study also incorporated a Bayesian component (Kelly). Upon completing this integrated analysis, Springer's results express the very definition of the long fuse model: "Analyses...all support interordinal divergences in the Cretaceous followed by intraordinal diversification mostly after the K/T boundary."

The hope that the long fuse model will be able to reconcile the molecular clock and the fossil record is quite promising. Preliminary studies, such as the one conducted by Springer et al, have yielded results that are fairly consistent with both seemingly opposed views of history. However, the long fuse model cannot suffice alone. Equally important, dialogue between paleontologists and molecular biologists must be encouraged. Efforts to promote this interaction, such as the conference arranged by Christopher Brochu (2004), have already begun, and must continue. Only this dialogue can allow the two schools of thought to take steps in unison toward the common goal, a mutually documented and accepted view on mammal diversification.

CITATIONS:

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