



Pruning and grafting on the mammalian phylogenetic tree

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If results of recent molecular studies are to be believed, many extant placental orders appeared deep in the Cretaceous (Springer 1997; Cooper & Fortey 1998; Kumar & Hedges 1998), some near the time of the first record of eutherians 105 million years ago (Kielan-Jaworowska & Dashzeveg 1989). This is in sharp contrast to the paleontological paradigm that argues most if not all 18 extant orders appeared after the Cretaceous/Tertiary boundary (Carroll 1997). The discrepancy is dismissed in molecular studies as a problem of incompleteness of the fossil record.

Paleontologists have responded to these claims with various statistical analyses. Gingerich & Uhen (1998) examined the artiodactyl-cetacean (or cetartiodactyl) split. They argued that a likelihood analysis shows a maximum age for this split near the Cretaceous/Tertiary boundary, some 65 million years ago. At a conference in Japan on placental ordinal origination J.D. Archibald & D.H. Deutschman (Quantitative analysis of the timing of the origination and diversification of extant placental orders – paper submitted to *Systematic Biology* and presented at the International Symposium on the Origin of Mammalian Orders, Hayama Japan 21–25 October 1998; see also Normile 1998) used Monte Carlo simulations to argue that the apparent early Tertiary ordinal radiation is real. The most comprehensive analysis published to date that examines the timing of extant placental clades (Foote *et al.* 1999) used a mathematical model of branching evolution. Results from use of this model suggest that extant orders did not arise much earlier than when the fossil record shows, mostly in the early Tertiary.

So why the discrepancy in the timing of origin of extant placental clades between molecular and paleontological studies? Possibly the assumption of a 'clock-like accumulation of sequence differences in some genes' (Kumar & Hedges 1998) is incorrect. In many cases it might be correct, but there is relatively little research on whether it is valid for all times during the history of life. In fact, recent work suggests far more variation in at least mitochondrial 'clocks' than has been realized (Strauss 1999). Possibly during tremendous episodes of biotic reorganization, such as at the end of the Cretaceous, both molecular and morphologic evolution might be expected to increase somewhat in concert. That this might be possible is suggested by a recent study (Omland 1997) that showed a correlation in rates of molecular and morphologic evolution across eight very diverse taxa (beetles, dabbling ducks, dwarf dandelions, the plant *Sedum*, the birch family, caniform carnivores, salamanders, and echinoids). Although a mechanism was not clearly identified, it was suggested that bottlenecks might serve to accelerate evolution at both the molecular and morphologic levels. There seems little doubt that such bottleneck effects would be inordinately high as a result of the massive biotic reorganization across the Cretaceous/Tertiary boundary.

Debate has not been isolated to the timing of ordinal appearances, but has also included how fossil Cretaceous eutherians may be related to the origin of extant clades. Are these mostly Late Cretaceous eutherians members of extant orders, ancestral or stem taxa to extant orders, or dead ends having nothing to do with extant orders? Sister taxa, ancestors, or even members have been suggested for the orders Insectivora (e.g., Fox 1979), Primates and Carnivora (e.g., Lillegraven 1969), and the superordinal clades Anagalida (Rodentia, Lagomorpha, Macroscelidea) (McKenna & Bell 1997) and Ungulatomorpha (Artiodactyla, Cetacea, Perissodactyla, Proboscidea, Hyracoidea, Sirenia, and possibly Tubulidentata) (Nessov *et al.* 1998).

Recently all these stem relationships to extant placentals, except 'zhelestids' (the earliest members of Ungulatomorpha) have been called into question (Novacek *et al.* 1998). 'Zhelestids' are best known from exquisitely preserved teeth and jaws first found by the late Lev A. Nessov in the Late Cretaceous of Uzbekistan (e.g., Nessov 1985). Recent monographic studies and phylogenetic analyses clearly show that the most robust hypothesis is that 'zhelestids' form a series of stem taxa relative to early Tertiary archaic ungulates (so-called condylarths) that in turn are ancestral to a number of extinct and extant placental orders (Archibald 1996; Nessov *et al.* 1998).

For reasons not explained and without any new phylogenetic insight, Foote *et al.* (1999) essentially dismissed 'zhelestids' as being 'archaic eutherians allied with either *Prokennalestes* or *zalambdalestids*', thus placing them outside the clade leading to extant placentals. These assertions are not based on the most recent, extensive phylogenetic studies cited above, but rather come from English language publications that cite older, preliminary Russian descriptions of 'zhelestids' by Nessov. Unfortunately, even the supposedly most current classification of mammals (McKenna & Bell 1997) makes the same curious mistake in ignoring a recent analysis of 'zhelestids' published well before their book appeared (Archibald 1996). Also, possible question as to the age of the Uzbekistan 'zhelestids' has been almost completely resolved. Fieldwork has continued at the now famous Dzharakuduk section in the Kyzylkum Desert of Uzbekistan. This work has produced extensive marine invertebrate faunas overlying the 'zhelestid' sites, thus demonstrating a minimum age of 80–85 Ma for these sites (Archibald *et al.* 1998). The confusion is not limited to paleontological studies. A recent molecular study (Cooper & Fortey 1998) used 'zhelestids' and molecular data to argue that some extant placental orders or superorders extended into the Cretaceous. The ungulatomorph study they cite (Archibald 1996) made no such claim. The true phylogenetic position of 'zhelestids' and other Cretaceous eutherians may never be known with the certainty of Tertiary mammals, but this does not mean they can be carelessly grafted to or pruned from any part of the phylogenetic tree.

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