

Quantitative Analysis of the Timing of the Origin and Diversification of Extant Placental Orders

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Fossil evidence is consistent with origination and diversification of extant placental orders in the early Tertiary (Explosive Model), and with the possibility of some orders having stem taxa extending into the Cretaceous (Long Fuse Model). Fossil evidence that 15 of 18 extant placental orders appeared and began diversification in the first 16 m.y. of the Cenozoic is, however, at odds with molecular studies arguing some orders diversified up to 40 m.y. earlier in the Early Cretaceous (Short Fuse Model). The quality of the fossil record was assessed by tabulating localities of all mammals in the last 105 m.y. Global locality data (except Africa) for 105 m.y. of eutherian evolution indicate discernible biogeographic patterns by the last 15 m.y. of the Cretaceous. Eutherian genera increase from 11 in latest Cretaceous to 139 in earliest Tertiary, although both are represented by about 50 localities. Yet even in the Late Cretaceous of North America and Asia where eutherians are abundant, none of the 18 extant orders are definitely known. A series of Monte Carlo simulations test whether the rapid appearance of most mammalian orders is statistically significant, and if so, whether it is a radiation event or an artifact of a limited fossil record. Monte Carlo tests affirm that the clustering of appearances in the early Cenozoic is statistically significant. Quantitative analysis of the locality data suggests that the number of genera described is a function of the number of localities sampled. In contrast, the number of orders is not a simple function of localities and thus does not appear to be limited by localities. A second set of Monte Carlo simulations confirms that the increase in orders cannot be explained by the limited number of localities sampled. Even for best-fit simulations, the observed pattern of ordinal appearances is steeper than expected under a variety of null models. These quantitative analyses of the fossil record demonstrate that the rapid ordinal appearances cannot be ascribed to limited Late Cretaceous sample sizes; thus, early Tertiary ordinal diversification is real. Although the fossil record is incomplete, it appears adequate to reject the hypothesis that orders of placentals began to diversify before the K/T boundary.

KEY WORDS: Eutheria; placental ordinal radiation; evolutionary rates.

INTRODUCTION

Recent molecular studies have argued that major clades of organisms such as orders of birds (Cooper and Penny, 1997), orders of mammals (Kumar and Hedges, 1998), and phyla of metazoans (Wray *et al.*, 1996) originated far earlier in time than usually shown by the fossil record. A number of studies utilizing the fossil record (e.g., Bleiweiss, 1998;

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Alroy, 1999; Foote *et al.* 1999) have countered that the fossil record is basically correct in its estimation of the timing of origin of such major clades. Further, Benton *et al.* (2000) found that for a sample of 1,000 published phylogenies there was good congruence between stratigraphy and phylogeny with no evidence of diminution in quality as one moves backwards in time. They noted that one must distinguish between the ‘completeness’ and the ‘adequacy’ of the fossil record. They admit earlier portions of the fossil record are certainly incomplete but adequate for examining broad patterns of the history of life. We agree with this assessment and here present a novel quantitative analysis of the fossil record in order to examine the timing of origination and diversification of orders of extant placentals.

RECOGNIZING AND DEFINING CLADES OF EXTANT PLACENTAL MAMMALS

Placentalia and Eutheria

In order to avoid semantic complications we must address three definitional issues. First, we must distinguish between the taxa Placentalia and Eutheria. We follow Rougier *et al.* (1998) in recognizing Placentalia as the crown group that includes all extant and extinct placental mammals and their most recent common ancestor. Eutheria is then defined to include Placentalia and all (stem) taxa that share a more recent common ancestry with Placentalia than they do with Metatheria (including the crown group Marsupialia). A discussion concerning character-based, stem-based, and node-based taxa (including crown groups) can be found in de Queiroz and Gauthier (1994).

Within Placentalia 18 major extant clades (Fig. 1) are usually recognized (e.g., Wilson and Reeder, 1993) as orders using the Linnean hierarchy. We accept the view that Linnean categories such as orders serve only as placeholders in a classification and thus have no biological meaning as such. For the sake of brevity in the discussion, however, we use ‘order’ to collectively refer to these 18 major clades. Based upon molecular studies, some of these 18 placental orders are now thought not to be monophyletic, but as discussed later, this has little bearing on our analysis of the timing of origin of extant placental orders.

Defining and Recognizing Extant Orders

The second potential complication is how to define each of the 18 extant orders. Because we are interested in examining the earliest possible diversifications within each order we cannot be limited to crown taxa but must also include stem taxa with these crown groups. Such stem taxa are those that bear apomorphies of the order (e.g., P4/m1 carnassial in Carnivora, astragalus with double ginglymi in Artiodactyla, etc.) but not of extant intraordinal clades. Two examples should suffice to demonstrate this point. As a crown group, Proboscidea includes only two species, *Loxodonta africana* and *Elephas maximus*. If we were to use only the crown group, Proboscidea would be recognized as having originated with the split of these two taxa some time in the late Miocene (Fig. 1) (Todd and Roth, 1996; McKenna and Bell, 1997). Yet, we know that numerous taxa share a more recent common ancestry (based on synapomorphies) with these two extant taxa than they

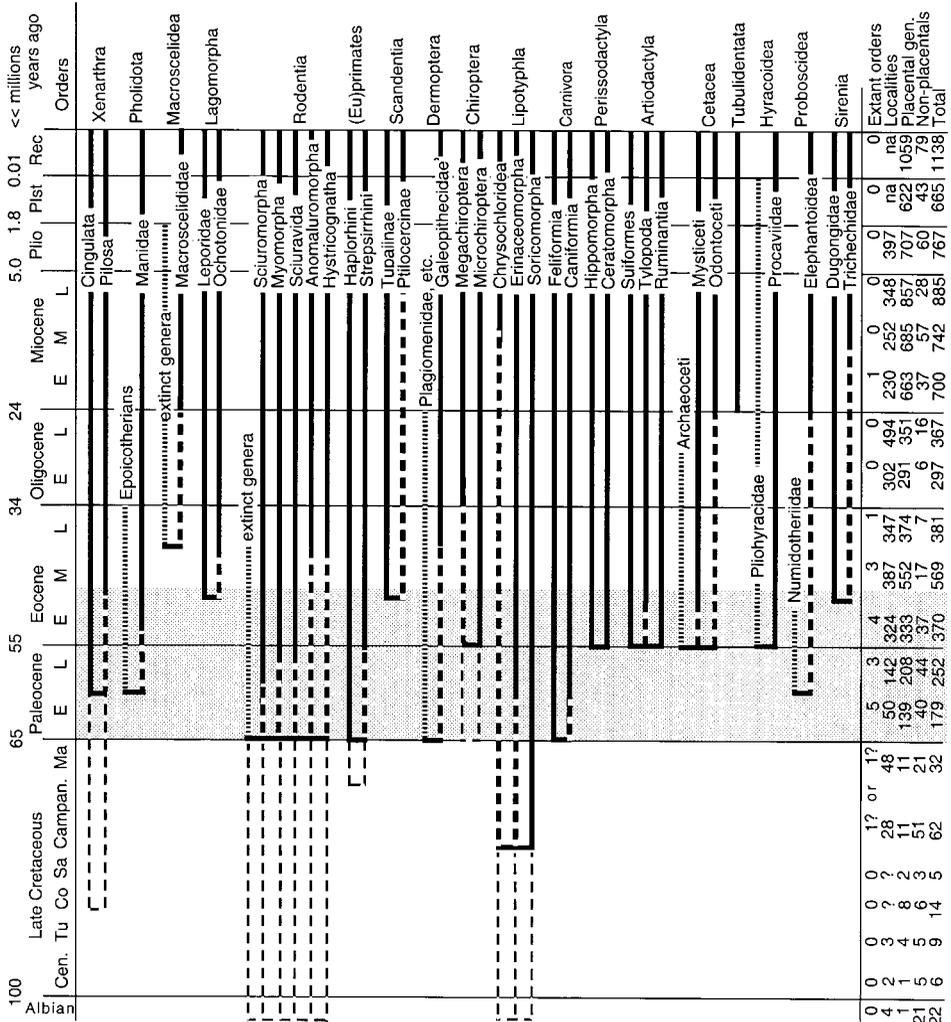


Fig. 1. Ranges of extant placental orders and global mammal locality data. Black bars are major intraordinal clades. Dashed portions are possible extensions only, based on maximum intraordinal range. Closer-spaced, dashed bars are extinct intraordinal clades. Thin, dashed lines delimit Cretaceous extensions of orders advocated in some molecular studies. The Late Cretaceous Lipotyphla record is suspect. Lighter gray shaded area delimits 16 million-year time interval for appearances of 15 of 18 placental orders. Three placental orders in the middle Eocene appear near the beginning of this interval and are thus included in the 16 million-year window. Widths of stage/ages are not proportional to their duration. No interordinal relationships are shown.

do with other extant placental orders. The earliest known of these is *Phosphatherium* (within Numidotheriidae in Fig. 1) at around 60 Ma from Morocco (Gheerbrant *et al.*, 1996). Accordingly, we include within a particular extant placental order extinct taxa that share a more recent common ancestry (based on synapomorphies) with extant members of that order than they do with other extant placental orders.

Another less dramatic example is Carnivora. The two commonly accepted major

extant clades within Carnivora are Feliformia and Caniformia (Fig. 1). Some authors include the extinct early Tertiary Viverravidae and Miacidae as the earliest occurring taxa in Feliformia and Caniformia, respectively (McKenna and Bell, 1997). Other authors recognize Viverravidae and Miacidae as stem taxa to a monophyletic taxon including Feliformia and Caniformia (Wyss and Flynn, 1993). We chose to use the former interpretation, although either interpretation still places the earliest taxon within this major clade in the early Paleocene (Fig. 1).

Stem Taxa Versus Crown Group Diversification

Third and finally, further comments are warranted regarding ordinal stem taxa and ordinal crown groups. As noted in the previous section, for our purposes in this paper we include stem taxa within the order with which they share a more recent common ancestor. In practice, such stem taxa may be very hard to recognize. In the previous examples, stem taxa were recognized as sister to a particular ordinal crown group because they possessed synapomorphies. This may not always be the case. Stem taxa of a particular ordinal crown group may lack or not preserve morphologic characters that indicate their phylogenetic position.

For example, suppose that fossil evidence suggests that two placental ordinal crown groups (X and Y) originated and began to diversify shortly after the K/T (Cretaceous/Tertiary) boundary at about 65 Ma (Fig. 2A). Later, new molecular or pale-

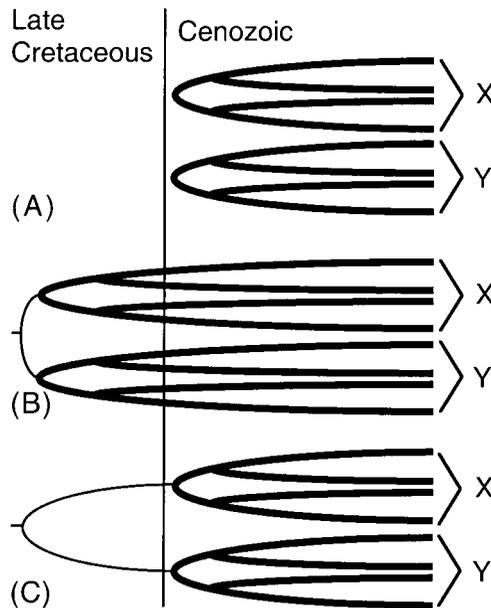


Fig. 2. (A) Fossil evidence suggesting two placental orders (x and y) originating and beginning to diversify shortly after the K/T boundary, some 65 mya. New molecular or paleontologic data indicate an earlier divergence in the Late Cretaceous, but it must be made explicit whether (B) the orders actually extend into the Cretaceous, or (C) the orders share stem taxa indicating a interordinal split within the Late Cretaceous.

ontologic data might indicate these orders split from one another earlier within the Late Cretaceous. An important distinction that must be made is whether these new data indicate that the crown group of the orders extends earlier into the Cretaceous (Fig. 2B) or whether the stem taxa of the order extend earlier into the Cretaceous. (Fig. 2C). This distinction is too often blurred.

Beyond such cases that can be easily solved once semantic issues are resolved, a more scientifically interesting schism has developed between what paleontologic and molecular data say concerning the timing of ordinal origination/diversification of extant placentals. If it is assumed that one can approximate times of divergence using molecular data, then two major kinds of taxonomic splits can be recognized using such data. One such split is between orders. The thin lines in Figs. 2B and 2C represent the intervals of time for which we may not be able to recognize stem taxa belonging to a particular extant order based upon fossils, but which might be recognizable using molecular data. The second split is between clades within the ordinal crown group of orders as represented by the thick lines connected in Figs. 2B and 2C. Specifically, molecular data have extended further backwards in time the origin of as many as five of 18 ordinal crown groups compared to what fossils can demonstrate. Before examining whether molecules or fossils appear to better answer the question of the timing of origin of placental ordinal crown groups, we first explore three models of ordinal origination and diversification. These models form a continuum, but as presented by various authors they can be recognized as more or less distinct.

MODELS OF INTERORDINAL, ORDINAL & INTRAORDINAL ORIGINATION

Explosive Model

The first model (Fig. 3A) argues that most if not all interordinal origination and diversification as well as ordinal origination of extant placentals occurred within a very short interval of about 10 million years, mainly following the K/T boundary 65 Ma. Because of this short 10 m.y. interval given the minimum 100 m.y. existence of eutherians, we call this the Explosive Model. In this model, most of the known species of Late Cretaceous eutherian mammals ('e' in Fig. 3A) had little to do with the appearance and radiation of placental orders. Gingerich (1977, Fig. 1; see also Carroll, 1997, Fig. 2) has advocated this Explosive Model. More recently Gingerich and Uhen (1998, Fig. 8) invoked what we term the Explosive Model when they argued that the Cetacea-Artiodactyla split occurred in the earliest Paleocene or latest Cretaceous. They recognized pre-cetacean and pre-artiodactyl ancestral clades among mesonychian and arctocyonian archaic ungulates, respectively. These mesonychian and arctocyonian archaic ungulates, however, also do not extend much before the K/T boundary if at all (Archibald, 1998).

Long Fuse Model

The second model (Fig. 3B) basically agrees with the Explosive Model in placing intraordinal diversifications mostly following the K/T boundary. Unlike the Explosive Model, however, this second model argues that species or larger clades, which are stem to

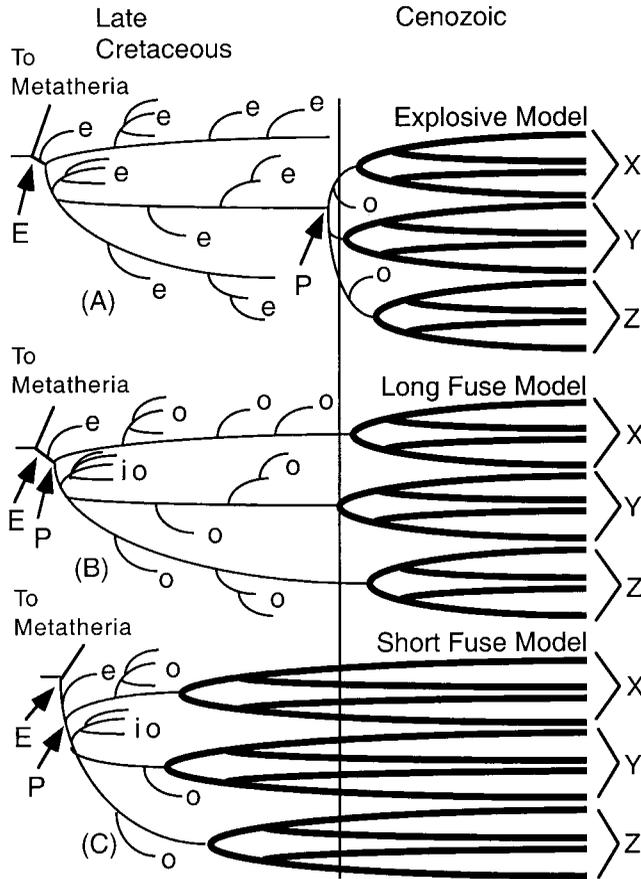


Fig. 3. Alternative views of placental ordinal diversification. Thick lines are orders x, y, and z showing intra-ordinal diversification within ordinal crown groups. (a) Explosive Model with early Tertiary origin and diversification of placental ordinal stem and crown groups, (b) Long Fuse Model with early Tertiary origin and diversification of placental crown groups and Late Cretaceous extension of ordinal stem groups, and (c) Short Fuse Model with Late Cretaceous origin and diversification of placental ordinal stem and crown groups. Abbreviations: E, Eutheria; P, Placentalia; e, eutherian stem taxa; o, ordinal stem taxa; io, stem taxa to more than one ordinal crown group. See text for discussion.

a particular order ('o' in Fig. 3) or are interordinal clades ('io' in Fig. 3), can be found well back in the Late Cretaceous. In reference to this extended interval of evolution for ordinal stem taxa, we call this the Long Fuse Model, somewhat analogous to the terminology of Cooper and Fortey (1998a). In an earlier example of the Long Fuse Model, Lillegraven (1969, Fig. 40) showed clades ancestral to Carnivora, Primates, various ungulate orders, and two other extinct orders extending into the Late Cretaceous to about 70 Ma. A paper by Novacek (1992, Fig. 1) appeared to show another example of the Long Fuse Model in recognizing splits between extant placental orders extending as far back as 115mya. He indicated, much like Gingerich (1997), that the oldest definitive records of extant orders of placentals extend backwards only to about the K/T boundary. More recently, Novacek et al. (2000) seem to doubt a significant extension of placental orders into the Cretaceous.

A series of species (the “zhelestids” at about 85mya), however, were shown as sister taxa to later ungulatomorphs, including extant orders (‘io’ in Fig. 3). Thus, Archibald (1996) clearly indicated a clade belonging to the crown group Placentalia that extended well back into the Late Cretaceous.

Short Fuse Model

A number of molecular studies have suggested the extension of intraordinal clades into the Late Cretaceous. Some of these studies have also explicitly argued that ordinal crown groups originated well back into the Late Cretaceous (Fig. 3C). These results are based on intraordinal comparisons. Springer (1997) reported rate-adjusted intraordinal divergence times of from 81.7 to 107.2 Ma within Lipotyphla, 70.7 Ma within Chiroptera, 85.9 to 108.8 Ma within Rodentia, 69.6 within Primates, and 85.0 within Xenarthra. Kumar and Hedges (1998) found intraordinal divergence times of up to 66.2 Ma within Rodentia and 64.7 for Artiodactyla. In addition, Kumar and Hedges (1998) and Cooper and Fortey (1998a,b) suggested the origin of some extant placental orders, or at least interordinal diversification within Placentalia, occurred near or before the earliest known fossils of eutherians at about 105 Ma. Thus, Kumar and Hedges (1998) placed the origin of Xenarthra at 129 Ma and Rodentia at between 109 and 112 Ma, while Cooper and Fortey (1998a,b) indicated Rodentia and Lipotyphla appeared well before 100 Ma. We call this the Short Fuse Model because of the argument (at least in its extreme) that some placental ordinal crown groups originated and began to diversify well back into the Cretaceous, before or shortly after the appearance of eutherians in the fossil record.

Current Support for the Three Models

The current dogma is that extant orders of placental mammals appeared and began an intraordinal diversification at 65 Ma, following the extinction of non-avian dinosaurs (e.g., Carroll, 1997). The general belief, although based upon few data, is that the interordinal radiation of extant placentals may have begun earlier within the Late Cretaceous (Novacek, 1992; Archibald, 1996; McKenna and Bell, 1997; Nessov *et al.*, 1998). Thus, either the Explosive or Long Fuse models (Figs. 3A and B) might explain the pattern of diversification seen in the fossil record.

Recently, the fossil support for the Long Fuse Model has been challenged. Based on geochronologic ranges and cladistic patterns, Novacek *et al.* (1998) argued that there is no evidence of any extant clades of placentals (or marsupials) in the Cretaceous, with one possible exception. These were the “zhelestids,” a paraphyletic assemblage of taxa best known from middle Asia (Uzbekistan and Kazakhstan), but also recognized from North America and Europe. More recently, Foote *et al.* (1999) echoed the theme that reports of Cretaceous extant ordinal and superordinal placental taxa are now questioned. These authors extended this claim to the “zhelestids,” suggesting that they are “archaic eutherians allied with either *Prokennalestes* or zalambdalestids,” thus placing them outside the clade leading to extant placentals. The basis for this argument was English language publications (Butler, 1990; McKenna and Bell, 1997) that relied on older, preliminary Russian descriptions of “zhelestids.” Recent monographic studies and phylogenetic anal-

yses (Archibald, 1996; Nesso *et al.*, 1998) show that the most robust hypothesis is that “zhelestids” form a series of stem taxa relative to early Tertiary archaic ungulates (so-called condylarths), which in turn are ancestral to a number of extinct and extant placental orders.

If these latter studies are corroborated, it suggests that the Long Fuse Model may be correct for some clades (ungulates and their relatives), but beyond this, the fossil record cannot distinguish between the Explosive and Long Fuse models. Further, this means that, for the most part, the fossil record cannot be used to support or argue against molecular studies that extend superordinal clades of placentals back into the Cretaceous. This is not the case for assessing the origin and diversification of placental ordinal crown groups. As we discuss in the remainder of this paper, quantitative evaluation of the fossil record coupled with several Monte Carlo tests very strongly argue that ordinal crown groups of placentals originated and diversified following the K/T boundary 65 mya.

EVALUATION OF THE FOSSIL RECORD

Ordinal Recognition and Ordinal Range Data

We compiled a new global tabulation of the geochronologic ranges of all 18 extant orders of placental mammals that are traditionally recognized (Fig. 1). This included 4672 placental genera recognized in the most recently published classification of mammals (McKenna and Bell, 1997). The 18 orders shown in Figure 1 are those that are traditionally recognized.

Recent molecular studies suggest Cetacea is not only the sister taxon of Artiodactyla, but also may reside within Artiodactyla with closest relations to Hippopotamidae (Gates *et al.*, 1996). Recognition of this new order, Cetartiodactyla, would result in the reduction by one of the number of extant placental orders but would not change the timing of the origin of the taxon, as both Cetacea and Artiodactyla are first recorded from the early Eocene (Fig. 1). Another molecular study (Stanhope *et al.*, 1998) argued that chrysochlorid and tenrecid insectivores do not form a clade with other lipotyphlans, but rather with a superordinal clade including Proboscidea, Sirenia, Hyracoidea, Macroscelidea, and Tubulidentata that they named Afrotheria. Because of their largely African biogeographic pattern Stanhope *et al.* (1998) coined the ordinal level name Afrosoricida for Chrysochloridae and Tenrecidae. The recognition of Afrosoricida would once again return to 18 the total number of extant placental orders. Neither Chrysochloridae nor Tenrecidae are known before the early Miocene (McKenna and Bell, 1997); thus afrosoricidans (if recognized) are first known well after the early Tertiary radiation of most other orders. This is probably owing to the poor fossil record from the early Tertiary of sub-Saharan Africa.

Possible superordinal clades are not shown in Fig. 1, because as discussed earlier, except for “zhelestids” the evidence for such clades is not strong. Further, such clades are not germane to our analysis of the timing of extant ordinal origination. Unsurprisingly, our results conform to the accepted pattern of an early Tertiary appearance and radiation of extant placental orders. Although eutherians are demonstrated to have been present for at least 105 million years (Kielan-Jaworowska and Dashzeveg, 1989; Cifelli, 1999), 15 of 18 extant placental orders appear in the fossil record in the early Tertiary (Fig. 1). If the newly argued order Cetartiodactyla and Afrosoricida are included, the number of

orders still remains 18. With the latter not known until the early Miocene, however, the number of orders appearing between the early Paleocene and early middle Eocene would be 14 of 18. This is not enough difference to affect any of our results, so we chose to utilize the traditionally recognized 18 ordinal appearances.

McKenna and Bell (1997) report the oldest lipotyphlan as *Otlestes* from the Cenomanian of Uzbekistan. This taxon, currently under study by D. Archibald and A. Averianov, is not a lipotyphlan but an early eutherian lacking apomorphies of any extant or extinct placental order. Lipotyphlans are also reported from the Campanian (*Paranyctoides*) and Maastrichtian (*Batodon*) of North America. Whether these are correct assignments remains in doubt, because there are no recent phylogenetic studies including these taxa. In order not to bias our analysis, we retain the latest Cretaceous origin of this order indicated by McKenna and Bell (1997).

Finally, one of the orders reported by McKenna and Bell (1997) as having a late Eocene appearance, Macroscelidea, has been reported by others as having an early Eocene origin. This pertains to *Chambius* from the early Eocene of Tunisia (Hartenberger, 1986; Butler, 1995). If accepted, this would extend Macroscelidea to the early Eocene, which is commensurate with the time of origin of most other placental orders. As with the case for possible Late Cretaceous lipotyphlans, however, we feel it is best to follow one source (e.g., McKenna and Bell, 1997) so as not to bias our analysis.

Locality and Range Data, and Possible Biogeographic Biases

To examine the question of sampling biases, we combined the global record for the 4672 placental genera and the 18 extant placental orders (McKenna and Bell, 1997) with a worldwide tabulation of fossil mammal localities for the stage/ages of the Late Cretaceous and Cenozoic (Savage and Russell, 1983) (bottom Fig. 1). More recent regional tabulations have appeared, but the older treatment by Savage and Russell (1983) provides a more uniform coverage on a global scale not available in newer regional treatments. Thus our tabulations (3358 localities) slightly underestimate the number of localities per interval, but the more important consistency of coverage is maintained. Age estimates of localities in this earlier tabulation were updated using the more recent age assessments in McKenna and Bell (1997).

Although eutherians are demonstrated to have been present for at least 105 million years (if not earlier) in both North America (Cifelli, 1999) and Asia (Kielan-Jaworowska and Dashzeveg, 1989), the number of eutherian-producing localities before the Campanian is extremely low (Fig. 1). When the Campanian and Maastrichtian are reached, however, the number of localities dramatically increases. In fact, the Maastrichtian (latest Cretaceous) and early Paleocene are similar in duration and in the number of localities (48 and 50, respectively). The best-sampled regions for this latest Cretaceous through early Tertiary interval are North America and Asia. Thus, continued claims for a bias against latest Cretaceous sites (e.g., Kumar and Hedges, 1998) in at least North America and Asia are simply unfounded. If most of the extant orders of placental mammals had begun to diversify in the Late Cretaceous of either Asia or North America they would have almost certainly been recognized by the Maastrichtian, if not by the Campanian (Fig. 1).

The fossil records for other regions of the world are not as good as for Asia or North

America, but there are other lines of evidence that show that Europe, South America, and Australia did not harbor latest Cretaceous members of extant placental orders. What is known of the emerging European record (Gheerbrant and Astibia, 1994) echoes what is seen in Asia, notably the presence of “zhelestids,” but no members of any extant order.

In South America during the Late Cretaceous, there were mammals of pre-therian grade (Bonaparte, 1990; Bonaparte *et al.*, 1993; Krause *et al.*, 1997) and a report of tribosphenic mammals (R. Cifelli, pers. comm., 2000). Eutherians (and metatherians), however, did not reach South America until the Maastrichtian at the earliest, but more likely the earliest Paleocene [see Flynn and Wyss (1998) for a review]. None of the earliest eutherians are referable to modern orders, but *Xenarthra* (edentates) does appear by the late Paleocene (McKenna and Bell, 1997).

Australian metatherians are known by at least the early Eocene (Godthelp *et al.*, 1992). Very likely, earlier Australian metatherians will be found. A single tooth from the same early Eocene locality that was thought to be a terrestrial eutherian is now identified as a metatherian (Woodburne and Case, 1996). Also, an Early Cretaceous dentary was suggested to be a eutherian (Rich *et al.*, 1997), but is more likely a symmetrodont (Kielan-Jaworowska *et al.*, 1998). The first extant terrestrial placental orders do not arrive in Australia until the Pliocene, although bats are known from the early Eocene (McKenna and Bell, 1997).

Thus, there is good evidence of mammals in the Late Cretaceous of South America and early Tertiary of Australia, but in neither are there members of extant placental orders except for Paleocene xenarthrans in South America and early Eocene bats in Australia. This leaves only Africa, where the latest Cretaceous and earliest Tertiary mammal sites are sparse. The intriguing, but as yet not well tested claim of a superordinal clade in Africa (Afrotheria) presents an interesting possible origin of six extant orders of placentals on that continent (Stanhope *et al.*, 1998). The hint of such an origin is suggested by the presence of early Eocene (Gheerbrant, pers. comm., 2000) proboscideans in Africa (Gheerbrant *et al.*, 1996) and middle Eocene sirenians in Africa (McKenna and Bell, 1997). Unless one is prepared, however, to make the unusual and indefensible argument that all 18 extant orders of placentals arose in the Late Cretaceous of Africa, the biogeographic (along with the biostratigraphic) record for placentals is more than sufficient to demonstrate the clustering of appearances of extant placental orders in the early Tertiary.

The reality of this early Tertiary clustering is further bolstered by the observation (Fig. 1) that the number of eutherian genera (11) does not change through the Campanian and Maastrichtian, even though the number of localities increases from 28 to 48. From the Maastrichtian into the early Paleocene the number of localities remains similar (about 50 each), yet there is a dramatic 12-fold increase (11 to 139) in the number of genera. This is almost certainly driven by the biotic upheaval occurring during the same time.

QUANTITATIVE ANALYSIS OF THE FOSSIL RECORD

Monte Carlo Tests for the Clustering of Ordinal Appearances

The clustering of the first appearance of 15 of 18 traditionally recognized extant placental orders in the fossil record within the space of about 16 million years from early Paleocene into early middle Eocene (Fig. 1) is unmistakable. The question arises whether

this clustering of appearances of extant placental orders is beyond what one would expect by chance alone. A recent study (Foote *et al.* 1999) chose a complex, hypothesis-driven approach to examine the question of the timing of origin of extant placental orders. We use a more empirically defined approach using fairly simple Monte Carlo tests based on the fossil record. These Monte Carlo tests examine both the clustering of appearances and whether such clustering is an artifact of the incomplete fossil record. This approach, long applied to other questions in evolution and paleobiology (e.g. Gould *et al.*, 1977), allows us to gain insight into a problem for which no classical statistics exist.

We define Monte Carlo Test as testing the significance of an observed statistic by comparing it with a sample of test statistics based on a particular null model (Manly, 1997). We define null model as a pattern-generating model based on random sampling of an imagined distribution (Gotelli and Graves, 1996). In all of our tests, we use a variety of null models because there is no obvious best model.

In order to examine whether the clustering of ordinal appearances is other than by chance alone, we developed two Monte Carlo tests using the tabulations shown in Fig. 1. The first set of simulations assumes a constant rate of ordinal appearances. This makes the explicit simplifying assumptions that orders appear at a constant rate (i.e., random in time) and that preservation and sampling effort are roughly equal through time. A second null model was explored in which evolution of the orders is described as a random branching process. In this approach, the rate of branching is constant leading to an acceleration of ordinal appearances through time.

For each null model, two sets of data were simulated. In the former, orders could appear anywhere in the 105 million-year record (the time range in millions of years for all known eutherians). In the latter, ordinal appearances were restricted to a 60 million year span (the approximate time range between when the first and last of the 18 extant orders appear). The test statistic was defined as the maximum number of orders that appeared in any 16 million-year window (Figs. 4A and 4C). A cluster of 15 orders in a 16 million-year window was never observed (Figs. 4B, 4D, $p < .001$). These results, however, cannot distinguish between clustering caused by sampling biases or an actual radiation. Further, sampling biases have been claimed by molecular studies to argue for a Cretaceous origin and diversification of extant placental orders (Kumar and Hedges, 1998). As we next show statistically, however, this is an actual radiation that cannot be explained away by a poor fossil record.

Monte Carlo Tests Assessing Ordinal Radiation versus Limited Sampling

We test whether the fossil record is adequate to address the origination of orders by incorporating locality data into several hypothesis tests. The first approach is to develop quantile-quantile plots (see Cleveland, 1993) relating the cumulative numbers of taxa described to the cumulative number of localities (Fig. 5). Quantiles are essential to visualizing distributions as in our study. The f quantile, $q(f)$, of a set of data is a value in the original scale of data with the property that approximately a fraction f of the data is less than or equal to $q(f)$ (Cleveland, 1993). Quantile-quantile plots provide a powerful method for comparing two distributions because they provide a standard for comparison (Wilk and Gnanadesikan, 1968; Gnanadesikan, 1977). If two distributions have the same shape, then their quantile-quantile plot will be linear (Wilkinson, 1999).

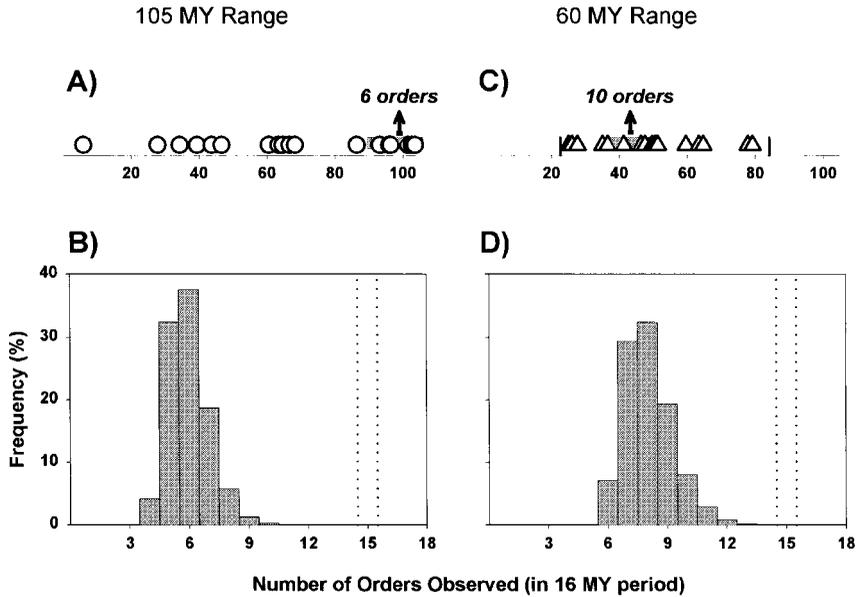


Fig. 4. (A) Single realization (randomly chosen) from the Monte Carlo simulations. The origin of each order is chosen as a random point within the 105 million-year span (open circles). Gray bar represents the 16 million-year window with the maximum clustering of orders. The statistic recorded was the number of orders in this window (= 6). (B) Distribution of the maximum number of orders from 10,000 simulations. A cluster of 15 orders was never observed suggesting $p < .0001$. (C) depicts a single simulation and (D) all 10,000 simulations whereby the origin of each order was restricted to a 60 million year span (open triangles). Again, a cluster of 15 orders was never observed.

In our study, linear q-q plots would argue that the two distributions are similar in shape. In this application, this would suggest that the increased numbers of taxa could be explained by increased sampling effort. In the observed fossil record, the number of described genera rises linearly as a function of the number of localities sampled. In striking contrast, the number of orders shows a pronounced jump at the K/T boundary. These plots suggest that the rapid appearance of the orders is not a simple function of the limited number of early localities.

This observation was tested with another set of Monte Carlo simulations. These simulations combine the theoretical distributions of ordinal appearances (mentioned above) with the empirical data on sampling effort (i.e., number of localities). The simulations assume that the discovery of a new order is rare and thus the chance of discovery increases with the number of localities. By making a distinction between an order's origination and its discovery, these models allow for the discovery of an order to lag behind its origination because of the limited number of localities.

To simulate this process, the assignment of orders to each locality was probabilistic. Each locality (from the observed fossil record) was tested for the presence of any of the extant orders from the null model. The probability that an order was present in any given locality was defined as π . Low values of π permit a significant lag between the origination of an order and its first documentation in the fossil record.

Values of π (0.001 to 0.2) were chosen based on two independent lines of evidence.

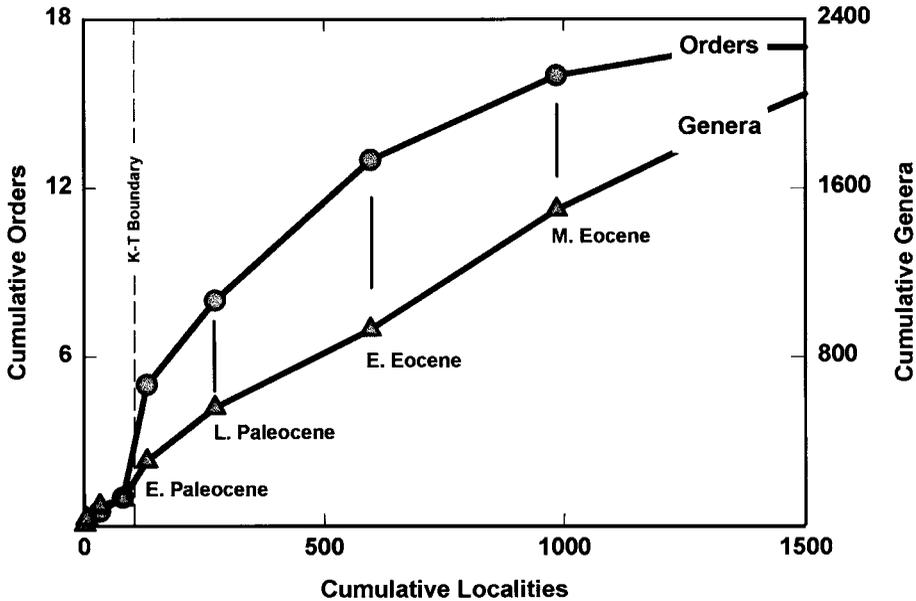


Fig. 5. Quantile-Quantile plots comparing the cumulative distributions of orders and genera versus sampling localities. The number of described genera rises linearly as a function of the number of localities sampled (triangles, $p = .131$ added Sums-of-Squares F-test for non-linearity). The number of orders described shows a pronounced jump at the K/T boundary (circles, $p < .001$, added Sums-of-Squares F-test for non-linearity). The vertical dashed line marks the K-T boundary, and early Cenozoic values are labeled.

Simple calculations from the locality data (the proportion of new orders discovered in each time period) imply that π ranges from .005 to .08 (Fig. 1). The wider range of values used in the simulations encompassed the entire range of behaviors of the simulation. Although many comparisons were made, we present the results from the best-fit simulations ($\pi = .005$) for ranges of both 105 and 60 million years (Fig. 6). The observed pattern of ordinal appearances is steeper than expected under the null models. The probabilities of observing an increase of 15 orders in the 16 million year window from early Paleocene into early middle Eocene were very low ($p = .001$ and .024 for the 105 and 60 million year ranges, respectively). Both quantitative analyses of the locality data reject the idea that the increase in orders can be explained by increasing numbers of localities.

DISCUSSION

The quantitative evaluation of the fossil record together with the Monte Carlo simulations demonstrate that the rapid increases in described orders between 65 and 49 mya cannot be explained by inadequate sampling. Our findings suggest that the appearance and early diversification of most if not all extant placental orders occurred in the first 16 or so million years of the Cenozoic (Explosive or Long Fuse models, Fig. 3A and 3B, respectively), contra some recent molecular studies arguing for a diversification beginning before the end of the Cretaceous (Short Fuse Model, Fig. 3C). Furthermore, even if some of the possible new ordinal-level taxa based on molecular studies (e.g., whales

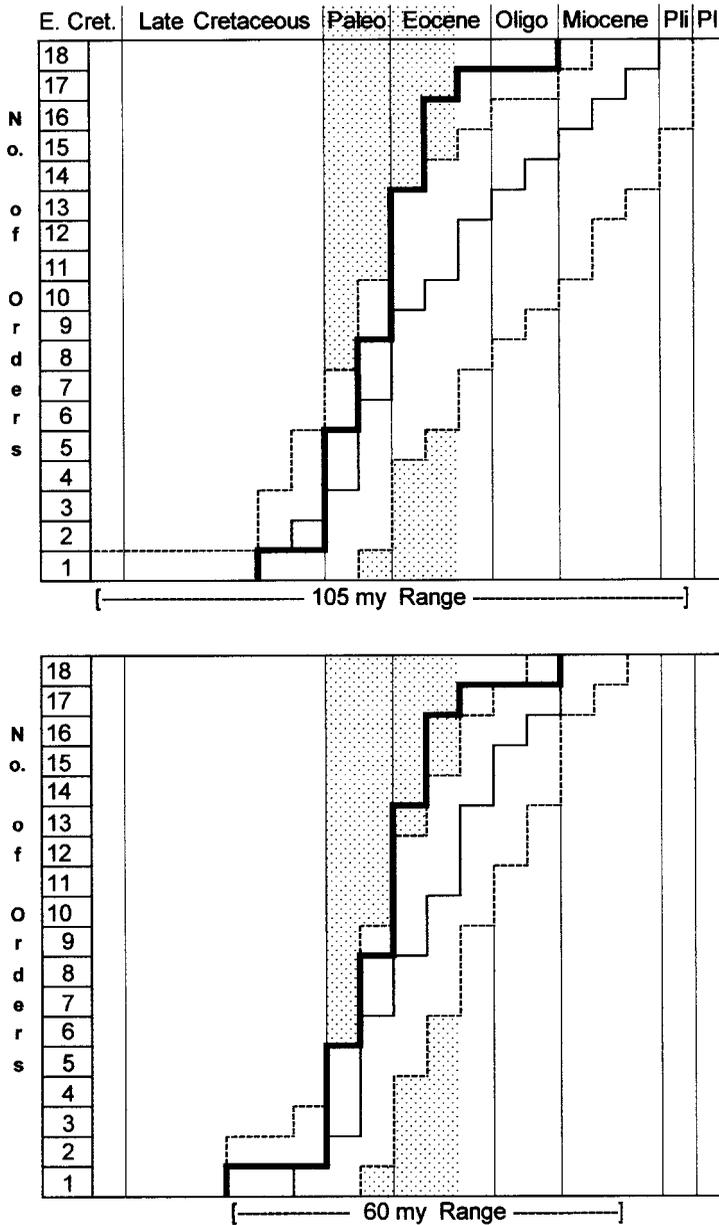


Fig. 6. Step cumulative curves for placental ordinal appearances. In both upper (105 million year range) and lower (60 million year range) graphs, the thick line is the step cumulative curve observed for placental ordinal appearances. The gray shading delimits the 16 million-year time interval for the appearances of 15 of the 18 placental orders. Thin line and dashed lines are median and 95% confidence intervals, respectively, of a cumulative plot of the number of discovered orders through time resulting from a randomization of 1000 replicates with π (the probability that an order was present at any locality) = .005. In both graphs the observed cumulative plot lies outside the 95% interval except in the latest Cretaceous and early Paleocene.

with artiodactyls, and chrysochlorids with tenrecids) continue to be supported, the fossil evidence of their origin is still no earlier than the early Tertiary. Finally, our results cannot be used to argue for or against the extension of superordinal taxa (e.g., Paenungulata including Proboscidea, Sirenia, and Hyracoidea) into the Cretaceous. There is, however, some agreement between the fossil record and molecular data on such possible extensions into the Cretaceous (e.g., the probable presence of ungulatormorphs as represented by “zhelestids”).

The work presented here is in broad agreement with several other recent studies suggesting the sudden appearance of orders in the early Cenozoic (Alroy, 1999; Foote *et al.*, 1999). Alroy (1999, p. 113) used an empirically based, random subsampling method to explore species diversity, concluding that species diversity “surged shortly after the K-T boundary. . . . Moreover, the pattern is not an artifact of poor sampling during most of the Cretaceous.” In contrast, Foote *et al.* (1999) took a more theoretical approach linking the origination of large lineages to implied rates of speciation, extinction, and fossil preservation. Their model, while attractively mechanistic, makes several assumptions about speciation rates, the relationship between species diversity and ordinal appearances, and rates of preservation. Our q-q plots (Fig. 5) suggest that there is not a clear relationship between the appearance of genera and orders.

The work presented here combines empirical data on sampling effort with simple models of ordinal appearances. As a result, it strikes a middle ground between empiricism and theory. Like Foote *et al.* (1999) our tests were conservative, because the null models were constructed so as to maximize the chance that the null model was consistent with the observed pattern (for example, using a restricted 60 million-year range for the ordinal appearances in the Monte Carlo simulations). Our work provides additional support for the rapid appearance of extant orders in the early Cenozoic because it combines a new tally of global sampling effort with a simple and robust theoretical model. Although the Late Cretaceous and early Tertiary mammalian record is far from complete, it is certainly adequate enough (Benton *et al.*, 2000) to address such broad questions as the timing of origin of most extant placental orders.

Our results that the timing of the origin and diversification of most, if not all, 18 extant placental orders is correctly bracketed within the early Cenozoic is at odds with the much older origin and diversification for some of these orders based on molecular data. We feel that much of the discrepancy results from an overly confident assumption of a “clock-like accumulation of sequence differences in some genes” (Kumar and Hedges, 1998, p 917). There are two related issues. The first issue is that there is more variation in rates of change between different genes, and especially between different taxa using the same gene, than is usually acknowledged. The second issue is that rates of change in genes may be linked more to changes in morphology than is often recognized.

The issue of rate variation between different genes and different taxa is not new, but has received more attention recently with increased disparities between molecules and morphology. In a recent commentary, Strauss (1999) indicated that there is far more variation in at least mitochondrial “clocks” than had formerly been recognized. Even more germane to our study, Huelsenbeck *et al.* (2000, p. 1889) “uncovered significant rate variation across lineages for the mammalian mitochondrial DNA sequence sets.”

Bromham *et al.* (1999) reported that the molecular date estimates vary by as much as 100%. For example, these authors provide four molecularly based dates for the split

between metatherians and eutherians that range from a low of 104 Ma up to a high of 257 Ma. Discrepancies can arise because of the choice of sequences, calibration dates, or phylogenetic methods (Bromham *et al.*, 1999). These differences demonstrate significant variation in molecular estimates, but do not shed any light on whether they are consistently biased. Bromham *et al.* (1999, p. 116) argue that despite the observed variability, “a sloppy clock is better than no clock.” This is an attractive idea but it is valid *only* if the estimates are unbiased. If the estimates are biased (consistently under or over predicting) then confidence intervals will be of no use (*contra* Bromham *et al.*, 1999). Further complications occur because of the relative tests that are frequently used to argue for a clock-like behavior of molecular evolution. Bromham *et al.* (2000, p. 296) concluded “that relative rate tests are unlikely to detect moderate levels of lineage-specific rate variation . . . for most commonly used sequences in molecular dating analyses, and . . . that this lack of power is likely to result in substantial error in the estimation of dates of divergence.”

Unlike for problems with different rates of molecular evolution, less attention has been paid to possible links between morphologic and molecular change. This may well be the result of the assumption of near constancy in the rate of molecular change as compared to morphologic change. The relatively few cases are intriguing. For example, Bromham *et al.* (1996) found evidence for a correlation between both body size and generation time versus rates of molecular evolution. In another detailed study, Omland (1997) examined rates of molecular and morphologic evolution across a wide array of plant and animal taxa (dwarf dandelions, the plant *Sedum*, the birch family, beetles, dabbling ducks, caniform carnivores, salamanders, and echinoids). He found considerable correlation between rates of molecular and morphologic change. 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. During such tremendous episodes of biotic reorganization, both molecular and morphologic evolution might be expected to increase somewhat in concert (also see Alroy, 1999). This hypothesis explains our results, namely that extant placental orders originated and diversified in the early Cenozoic rather than the Late Cretaceous, and argues that rates of morphologic and molecular change may be more synchronized than is usually recognized.

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