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The Fossil Record of North American Mammals: Evidence for a Paleocene Evolutionary Radiation

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Abstract.— Paleontologists long have argued that the most important evolutionary radiation of mammals occurred during the early Cenozoic, if not that all eutherians originated from a single common post-Cretaceous ancestor. Nonetheless, several recent molecular analyses claim to show that because several interordinal splits occurred during the Cretaceous, a major therian radiation was then underway. This claim conflicts with statistical evidence from the well-sampled latest Cretaceous and Cenozoic North American fossil record. Paleofaunal data confirm that there were fewer mammalian species during the latest Cretaceous than during any interval of the Cenozoic, and that a massive diversification took place during the early Paleocene, immediately after a mass extinction. Measurement data show that Cretaceous mammals were on average small and occupied a narrow range of body sizes; after the Cretaceous–Tertiary mass extinction, there was a rapid and permanent shift in the mean. The fact that there was an early Cenozoic mammalian radiation is entirely compatible with the existence of a few Cretaceous splits among modern mammal lineages. [Body mass; Cenozoic; Cretaceous; diversification; extinction; Mammalia; molecular clock.]

Over the past few years, there has been an explosion of interest in the early evolutionary radiation of mammals. Traditional scenarios based mostly on paleontological data have been challenged by inferences based on the calibration of molecular phylogenies to numerical time (Hedges et al., 1996; Janke et al., 1997; Springer, 1997; Cooper and Fortey, 1998; Kumar and Hedges, 1998). Some of these new molecular studies (e.g., Kumar and Hedges, 1998) purport not just to overthrow traditional higher-order phylogenetic groupings, but also to show that a major diversification of therian mammals began much earlier than previously thought, perhaps even in the Early Cretaceous.

If the fate of some other recent debates in mammalian molecular systematics is a guide, then some of the novel topologies undergirding these results may be incorrect. For example, Sullivan and Swofford (1997) have shown that a heated debate over the possible polyphyly of rodents (e.g., D'Erchia et al., 1996) rested on inadequate analyses. Regardless of topologies, most of the "Cretaceous radiation" research suffers from using just one or two "clock" calibration points (Hedges et al., 1996; Cooper and Penny, 1997; Janke et al., 1997; Kumar and Hedges, 1998). Such calibrations often yield anomalous results that are defended by assertions that all of the conflicting, paleontologically inferred dates of origin are simply too young.

For example, Hedges et al. (1996: 227) justify their decision to use a single Carboniferous calibration point with a non sequitur—that there is a "long time span between the earliest [mammalian] fossils. . . and the first appearance of the modern orders." In other words, because the modern mammal orders seem to Hedges et al. to have appeared long after they diverged, the authors can justify using a Carboniferous calibration point instead, and because the Carboniferous point is reasonable, they can infer that the modern mammal orders appeared long after they actually diverged. Tautological reasoning like this makes it impossible to move on to a reasoned discussion of the relative reliability of molecular clocks and paleontological data. For example, if the first appearances of modern mammal orders are even vaguely close to their true divergence times, this strongly suggests a speed up in the molecular clock

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of Hedges et al. (1996) sometime during the 245 million years (MY) between the Carboniferous and the Cretaceous–Tertiary (K-T) boundary.

Even the better studies have crucial flaws. Despite having employed multiple calibration points and trying to correct for variation in the clock speed, Springer (1997) arrived at a clock rate with alarmingly broad 95% confidence limits of ± 13% ("XR adjusted") or ± 15% ("MRR adjusted"). Furthermore, all but one of the calibration points fell within the Cenozoic, forcing the interordinal divergence times to be based largely on extrapolation instead of interpolation. This one Cretaceous point was a supposed figure of 130 million years ago (MYA) for the marsupial–placental split. However, the original source (Novacek, 1993) did not discuss the 130 MYA date, which was read off of an artistically rendered text figure that clearly implied the absence of any concrete evidence for a split before 98 MY. The younger date has been confirmed by more recent research (Cifelli et al., 1997). Changing to a 98 MYA estimate—a minimum figure like all of the other ones used by Springer (1997)—increases the clock rate, and therefore decreases all the estimated divergences, by 12%.

Despite such concerns, my purpose is not to challenge the inference that the basal splits among many therian orders occurred sometime during the Cretaceous. Instead, I will make three simple points. First, the modern paleontological literature has never implied that all therian or even eutherian orders diverged from one common ancestor after the Cretaceous. Any claim to the contrary is a misinterpretation that makes the molecular results seem more novel than they really are. Second, most molecular studies have failed to define the idea of "radiation" or "diversification" in a rigorous manner, leading to inferences from data that are not really relevant to the debate. Finally, clearer definitions imply that only two biological patterns are of interest in this discussion: changes through time in the overall number of species, and changes through time in the distribution of morphologies (or other attributes) across those species.

The fossil record does provide clear-cut evidence regarding both of these patterns. It shows that Cretaceous mammals were taxonomically depauperate and morphologically uniform, and that the most important radiation in the history of therian mammals did occur in the earliest Paleocene. According to all interpretations, this radiation must have involved multiple, phylogenetically independent lineages and therefore is far more likely to have involved ecological release rather than a key evolutionary innovation. The bulk of this paper will be devoted to the empirical problem of establishing that there was a Paleocene radiation.

Fossils Versus Molecules

Cretaceous Splits among Mammal Orders: Do Fossils and Molecules Really Disagree?

Apart from possible lipotyphlan insectivores (Novacek, 1993), no representatives of a modern therian order have ever been clearly shown to occur in the Cretaceous. Claims of Cretaceous xenarthrans were based on misidentified multituberculates (Krause, 1993). Claims of Cretaceous primates were based on earliest Paleocene finds of plesiadapiforms, which occur together with reworked Cretaceous mammals (Lofgren, 1995); the affinity of plesiadapiforms and primates is contentious and the two are at best sister groups (Beard, 1993). Claims of Cretaceous marsupials in the broad sense are valid, the relevant fossils having been known since the 19th century, but the Cretaceous forms have no clear-cut affinities with the modern, ordinal- level marsupial groupings (Johanson, 1996). Claims of Cretaceous "ungulatomorphs" are irrelevant because even if ungulates are monophyletic, they are a clade of at least six orders, not a single order,

and may easily not have started to diversify until the earliest Cenozoic (Archibald, 1996).

Nonetheless, traditional, paleontologically based phylogenies imply that some basal splits among therians did take place during the Cretaceous. The eutherian-metatherian split dates to at least 98 MYA (Cifelli et al., 1997). The Carnivora (Fox and Youzwyshyn, 1994) and Mesonychia (a possible sister group of the Cetacea; Thewissen, 1994) both appear in the earliest Paleocene. If "Archonta" and "Ungulata" are truly clades, they too definitely occur at this time (Novacek, 1993). The sister grouping of the Lagomorpha and Rodentia is controversial, but there is substantial paleontological evidence for the existence during the latest Cretaceous of a separate clade that includes these two orders (Meng et al., 1994). Several orders are depauperate and rarely fossilized (e.g., Tubulidentata, Pholidota, Macroscelida, Scandentia, and Dermoptera), so there is little to argue against speculations that they might have originated in the Cretaceous. None of these conclusions is contentious among paleontologists. For example, the widely reproduced phylogenies of Romer (1966) and Novacek (1993) show multiple eutherian lineages separating from each other in the late Cretaceous. Together, the most current paleontological evidence suggests that at least 7 or 8, and probably 10 or 20 living therian lineages do extend back into the Cretaceous.

In fact, with appropriate corrections for the previously mentioned error in calibration, the most methodologically sound analysis (Springer, 1997) implies that only five eutherian orders had split from their sister groups by the K-T boundary (65 MYA): Xenarthra, Insectivora, Primates (the only member of "Archonta" included in that study), Lagomorpha, and Rodentia. Far from overturning the traditional view, molecular studies confirm what the fossil record already has suggested—not just these five orders but also several others do date back to the Cretaceous.

What Would It Mean to Demonstrate a Cretaceous Diversification?

This remarkable lack of substantive disagreement raises a key question: what exactly is the problem supposedly addressed by the latest molecular studies? For example, Cooper and Penny (1997: 1109) claimed there were "incremental changes during a Cretaceous diversification of birds and mammals rather than an explosive radiation in the Early Tertiary," which might imply that molecular data allow us to infer the tempo of speciation and adaptation. But in discussing the Paleocene, Cooper and Fortey (1998: 152) declared that "the explosive phases of evolution so amply demonstrated by the fossil record may, in many cases, have been preceded by an extended period of inconspicuous innovation." In other words, the molecular data only imply "innovations" (equated with divergences among modern orders), that may have had no consequences for the observed taxonomic and morphological diversity of mammals.

This weaker interpretation leaves little to argue about. All parties agree that several basal splits occurred during the Cretaceous, which means that no one can argue seriously for the importance of a key evolutionary innovation in a single early Paleocene lineage as the driving mechanism for a radiation. Not only that, but mammalian paleontologists have shown remarkably little interest in the question of when exactly the modern mammal orders diverged. Instead, Simpson (1952), Lillegraven (1972), Savage and Russell (1983), and Stucky (1990) all focused on the pace of taxonomic diversification. These studies directly counted orders, families, and genera in different time

intervals, living or not. Meanwhile, paleontologists who work on the early evolution of mammal orders have tended to focus on documenting morphological transitions instead of exact dates of origin (e.g., Meng et al., 1994; Thewissen, 1994).

Thus, the crucial empirical issue that might be tested by molecular data is not when exactly the modern mammalian orders split from each other, but whether taxonomic and morphological diversity exploded in the early Paleocene instead of the Cretaceous. However, this traditional paleontological concern simply has not been addressed by the molecular studies. The number of species that were present at different times can in theory be inferred from comprehensive molecular phylogenies (e.g., Nee et al., 1992, 1994). But this requires sampling either all living species or at least all living lineages that are believed to extend beyond a certain point in time. None of the molecular analyses of mammalian diversification have made any effort to guarantee this kind of comprehensive sampling. Therefore, it is impossible to conclude from these studies whether the rate of diversification was the same or different during the Cretaceous and Cenozoic.

Meanwhile, molecular workers have granted that phylogenetic topologies may say little or nothing about the timing of the major morphological transitions that distinguish living orders (e.g., Cooper and Fortey, 1998). They even have used this argument to suggest that paleontologists have failed to recognize a greater diversity of surviving lineages in the Cretaceous because Cretaceous mammals had not yet evolved the diagnostic morphological features of their living descendants. Indeed, all Cretaceous mammals were terrestrial and ecologically generalized, and, as I will show, all of them occupied a narrow range of the size spectrum. The important point is not that this might excuse the mismatch between paleontological and molecular data. To the contrary, it shows that molecular workers have already conceded that the fossil record is the best means of documenting morphological radiations.

If they are not directly addressing taxonomic or morphological diversity, what is the evolutionary import of molecular clock studies? I would suggest that in fact they have little to say about the theoretical problem of evolutionary radiations, and instead are of interest mostly to mammalogists who want to know when particular mammalian clades originated. Nonetheless, it is still important to show just what the fossil record really does say about the evolutionary radiation of mammals.

Taxonomic Diversity

The most important features of a large evolutionary radiation that can be inferred from a phylogeny are these: (1) the number and timing of evolutionary divergences and the tempo of taxonomic diversification implied by these facts; and (2) the distribution of such attributes as morphology, physiology, behavior, and biogeography across a phylogeny, which might imply the tempo of ecological diversification. Although none of these general issues have yet been addressed directly by molecular studies of the mammalian radiation, all of them may be addressed by the fossil record. Here I will reanalyze augmented versions of two data sets to show exactly what the differences were between Cretaceous and Cenozoic mammal faunas in North America. Most of the issues regarding data preparation have been discussed elsewhere (Alroy, 1992, 1994, 1996, 1998a, 1998b), so I will focus instead on new analyses and results. I first will treat the problem of taxonomic diversification, and then discuss morphological evolution in terms of body mass distributions.

Data

The faunal data used here are an extension of a previously discussed compi-

lation of North American mammalian fossil localities ranging in age from about 98 MYA (mid-Cretaceous) to 0.1 MYA (late Pleistocene), which now number 4385. Because most of these localities pertain to a single quarry or a small outcrop, each serves as paleontological "snapshot," representing a short period of time in a restricted geographical area. Each locality is documented by a taxonomically standardized, species-level faunal list and whenever possible is placed in a local stratigraphic section (the lists may be reviewed at http://www.nceas.ucsb.edu/~alroy/nampfd.html).

Instead of being pegged into a traditional time scale, the faunal lists are subjected to a multivariate ordination that is constrained by the stratigraphy. In previous studies, the ordination was governed by a parsimony criterion aimed at minimizing the number of temporal overlaps between species and/or genera. In the current analysis, I have modified the parsimony analysis into a maximum likelihood approach. The new method seeks to find the combination of age- range boundaries and "nuisance" sampling parameters for each taxon that is most likely to predict the observed pattern of overlap. Although the algorithmic details are of interest, the parsimony and likelihood approaches yielded such similar results that the exact choice of an ordination method is not relevant here.

The arrangement of lists implies a relative "event sequence" of taxonomic first and last appearances that is numbered from oldest to youngest and calibrated to numerical time by use of geochronological age estimates (Alroy, 1992, 1994, 1996, 1998b). The current version of the data set includes 198 stratigraphic sections, 1223 genera, 3234 species, and 153 geochronological calibration points. As previously, the statistical analyses focus only on the relatively well-sampled western region of the United States and Canada. Lists older than 80 MYA are too few to allow full-blown analyses of trends in diversity and morphology, but the lists have been retained for the purpose of constructing a chronological framework.

The calibrated event sequence can be used directly to infer counts of the species that existed at any of several arbitrary, evenly spaced moments in geological time. Together, such counts would constitute a diversity curve for the entire interval. Furthermore, counts of species appearing or disappearing between sampling points can be used to estimate speciation and extinction rates. Before doing so, however, a key problem must be solved: Each interval is represented by a different number of fossils, as shown by variation in the number of faunal lists per MY (Alroy, 1996, 1998b). Such variations are exactly the "obvious deficiencies" that make a "literal reading of the fossil record" so dangerous (Cooper and Fortey, 1998).

Far from being an intractable handicap, however, variation in sampling intensity may be removed. The best method is to standardize sampling in each interval by drawing faunal lists at random until reaching a predefined limit. The limit is set by the total number of faunal lists that are drawn; the cutoff is made as high as possible, given that all or nearly all of the intervals should be able to reach it. After lists are drawn in each interval and the temporal durations of taxa are recomputed on the basis of these lists, the procedure is iterated 100 times to yield average diversity and turnover rates.

In this paper the subsampling procedure keeps track of the number of faunal lists, instead of taxonomic records, that are drawn in each trial. This is because alpha (within-locality) diversity is much higher during the Cenozoic than during the Cretaceous, such that in the Cenozoic sampling the same number of fossils is likely to yield a larger number of distinct taxonomic records. Conversely, 10 records in the Cenozoic are likely to represent far fewer actual fossils than 10 records in the Cretaceous, but any 10 lists

in each interval are likely to represent about the same number of fossils.

In a previous analysis using an earlier version of the data set, I analyzed the Cenozoic data only and separated the diversity counts by 1.0 MY (Alroy, 1996). Because the calibration of the time scale is poorer in the Cretaceous, in the present study I used a longer bin size, 2.5 MY. The latest Cretaceous bin and all but one of the Cenozoic bins were able to meet a standardized sampling cutoff of 60 lists per bin (24 per MY). The undersampled Cenozoic bin is for 42.5–40.0 MYA, for which only 22 lists were available. In the earlier study, I set a cutoff of 85 taxonomic records per 1.0 MY. Because each Cenozoic list averaged about 6.8 taxonomic records, that was equivalent to only 12.5 lists per MY.

The current study's relatively intense sampling is likely to recover any substantial differences between the Cretaceous and Cenozoic. Unfortunately, even though the 60-list sampling level is adequate for the last temporal bin of the Cretaceous, it is not for any of the preceding intervals. However, this lack of data should have little effect on the results because (1) my discussion will focus on contrasts between the last, fully sampled Cretaceous interval and the Cenozoic; (2) all available lists from all of the Cretaceous intervals before the last one will be sampled; and (3) computing full temporal ranges for the taxa ("ranging through") will extend ranges into this ultimate Cretaceous interval for some taxa that were present but not directly sampled.

Results

The diversity data (Fig. 1) establish three key patterns. First, regional standing diversity was much lower during the Cretaceous than at any point during the Cenozoic (Fig. 1A). For example, standing diversity was about 23 species per 60 faunal lists across the time plane at 67.5 Ma, but the total was never lower than 41 after 65 MYA, and averaged 86 across the 25 Cenozoic time planes.

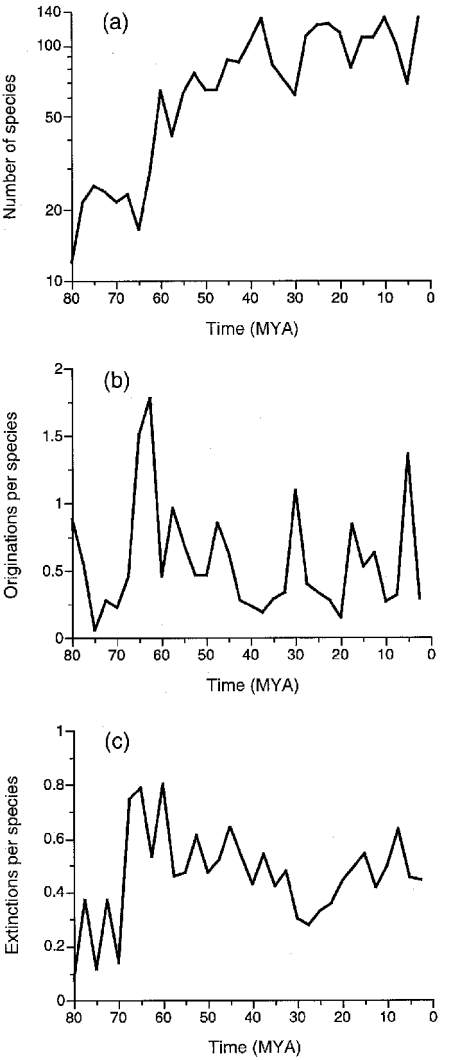

FIGURE 1. North American mammalian diversity, origination (new appearance) rates, and extinction rates for the late Cretaceous and Cenozoic. Data are based on multivariate ordination and standardized sampling of faunal lists. Data for lists going back to 98 MYA are available but are not shown because they are not sufficient for analytical purposes. (a) Standing diversity. The y-axis is log transformed to show the lack of either a log-linear (exponential) or asymptotic (simple logistic) pattern; instead, an offset between two logistic curves at about 65 MYA is indicated. (b) Origination rates. Anomalously high rate for the 40.0–37.5 MYA interval is not shown because it is an artifact of undersampling in the preceding interval. (c) Extinction rates. Anomalously low rate for the 42.5–40.0 MYA interval is not shown because it is a sampling artifact.

Second, there was an abrupt transition between the two diversity levels. Diversity surged shortly after the K-T boundary, reached a plateau by no later than 45 MYA, and then fluctuated dynamically within relatively narrow limits. The lack of any true net diversification after this point can be shown in a simple way by focusing on the 18 data points from 45 MYA on, for which no significant correlation between time and standing diversity can be demonstrated (Spearman's rank-order correlation $rs = -0.253$; $t = 1.045$; n.s.).

The S-shaped pattern seen in this semilog plot is consistent with neither a simple exponential growth model, which predicts a linear curve, nor a simple logistic model, which predicts an asymptotic curve with no visible lag in this kind of plot. Moreover, the pattern is not an artifact of poor sampling during most of the Cretaceous: Better sampling would only raise the first several data points relative to the fully-sampled (but very low) 67.5–65 MYA data point, which would create the appearance of a Cretaceous decline in the diversity and therefore make the subsequent Paleocene diversification seem even more dramatic. Further evidence for a dynamic Cenozoic equilibrium has been presented previously (Alroy, 1996, 1998b). This study's additional data suggest that distinct Cretaceous and Cenozoic equilibria were offset by the Paleocene radiation.

Finally, both origination and extinction rates increased dramatically around the K-T boundary: there were 0.75 extinctions/species per 2.5 MY bin just before 65 MYA, and 1.51 originations/species per 2.5 MY just afterwards. Both curves remained high during the Paleocene (roughly 65–55 MYA); the three relevant data points average 0.60 extinctions and 1.07 originations per species per 2.5 MY. However, these high values do little to obscure the singular nature of the K-T event.

Several further details could be discussed. For example, there is weak evidence that Cretaceous turnover rates were on average lower than Cenozoic turnover rates. There also is significant evidence that origination rates are negatively correlated with standing diversity levels. This monotonic relationship underlies the Cenozoic's dynamic equilibrium and partially explains why origination rates are much more variable than extinction rates. Finally, the major Cenozoic North American mammal orders had different diversity trajectories, suggesting that they were obeying different dynamic rules (Alroy, 1996, 1998b).

The important point, however, is not the exact nature of the evolutionary dynamic, but rather the fact that these abundant and essentially unbiased data refute the two main inferences one might wish to draw from some of the recent molecular phylogenetic studies. First, diversification was not a slow and steady process: The early Paleocene witnessed an immense evolutionary radiation that went unmatched anywhere else in mammalian history. This remarkable pattern is visible even in the coarse 2.5 MY bin data reported here. The closest matches to the 1.51 originations/species per 2.5 MY rate for the earliest Paleocene are rates of just over 1 origination/species per 2.5 MY for the intervals beginning at 62.5, 57.5, 30, and 5 MYA. The remaining 18 Cenozoic intervals average only 0.45 originations/species per 2.5 MY, even if one includes the anomalously high rate for the 40–37.5 MYA bin, which is an artifact of undersampling in the preceding time interval. In other words, the early Paleocene origination rates were at least three times greater than background. Data computed with finer bin sizes (Alroy, 1996, 1998b) yield essentially the same result, and furthermore strongly suggest that the most rapid phase of the radiation was confined to the very first 1.0 MY of the Paleocene. Because only a fraction of first appearances in the Paleocene record might reasonably be attributed to anagenesis instead of cladogenesis (Archibald, 1993), there is no

way to discount this result as a taxonomic artifact.

Second, contrary to some speculations based on molecular data (e.g., Cooper and Penny, 1997), there was in fact a mammalian mass extinction at the K-T boundary. The lengthy 2.5 MY bins used in this study obscure the intensity of the event and also intensify some later (background) rates that do not pertain to short-term extinction episodes (e.g., for the 60–57.5 MYA bin). Nonetheless, the bin that includes the K-T boundary still has virtually the highest extinction rate in the time series (Fig. 1C). Moreover, in the best available stratigraphic section, fully characteristic latest Cretaceous faunas from just meters below the K-T boundary are replaced just above the boundary by almost completely different Paleocene faunas (Archibald, 1982). The best of these Cretaceous assemblages (Flat Creek 5) includes 24 species, which is an almost complete inventory of the regional fauna. Of these species, just three have well-established Paleocene records (*Mesodma formosa, M. thompsoni, Cimolestes incisus*), and five more have possible Paleocene descendants: *M. hensleighi, C. propalaeoryctes, C. stirtoni, Batodon tenuis,* and *Gypsonictops illuminatus* (Lillegraven, 1969; Archibald and Bryant, 1990; Fox and Youzwyshyn, 1994). Therefore, even the most liberal estimate suggests that as many as two-thirds of all mammal species went extinct during a relatively short interval bracketing the K-T impact event.

Morphological Disparity

If taxonomic diversity was lower during the Cretaceous than during the Cenozoic, and if this transition was rapid and confined mostly to the early Paleocene, then the only remaining arena for a possible "Cretaceous radiation" would have to be ecology. The best way to capture ecological variation among fossil forms is to measure morphological disparity (sensu Foote, 1993), but this quantity is hard to measure across the entire range of mammalian orders because of the great anatomical differences among them. For example, the only cheek tooth that is found in every toothed mammal is the first lower molar. Thus, it would be nearly impossible to construct a disparity measure for all groups of mammals based on homologous morphological features of cheek teeth (but see Jernvall et al., 1996, for "ungulates"). Worse, these very cheek teeth are the only easily preserved and identified parts of the mammalian skeleton. Constructing morphospaces for, say, the postcranium would therefore not be feasible in a general analysis of all fossil mammals (but see Janis and Wilhelm, 1993, for large mammals).

Fortunately, there is one very easily quantified morphological feature of overwhelming ecological importance for mammals: body mass, which is correlated strongly not just with every linear measurement of the mammalian skeleton but also with dietary, locomotor, and life history variables. Despite important residual variation among species in such features, body mass distributions do capture a considerable amount of ecological information (Legendre, 1986). In this section I will outline Cretaceous and Cenozoic trends in body mass distributions, showing again that a profound biotic transition did occur at the K-T boundary.

Data

The raw data discussed here have been described previously (Alroy, 1998a), so I will omit many details of data preparation. The latest version of the data set consists of body mass estimates for 1815 North American fossil mammal species based on a compilation of published measurements for 19,363 individual lower first molars (m-1-s). Separate regression equations are available for each of the major mammalian orders (e.g., Legendre, 1986; Damuth, 1990; Bloch et al., 1998), and for the others I used a generic all-

mammal equation (Legendre, 1986). All of these equations have very high *r*-squared values; most of them relate the log of m-1 length times width to the log of body mass, although for ungulates the log of m-1 length was used as the independent variable (see Damuth, 1990). Although no account is taken of such factors as sexual dimorphism, geographic variation, or within-species anagenetic change, these all are inconsequential in light of the study's shrew-to-mammoth size range.

The data were used to compute body mass distributions for 1.0-MY-long temporal bins. The taxonomic age-ranges that were used to determine the presence and absence of species in bins were based on the same multivariate ordination of faunal lists described earlier. Species were considered to be present in a bin if they ranged anywhere into it, which does occasionally result in the lumping together of species that never actually co-existed. The relatively short 1.0 MY bin length largely avoids this problem, but the data for the 66–65 MYA interval do lump classic latest Cretaceous faunas together with a few small, earliest Paleocene ("Pu0") faunas.

Trends in the size distribution were quantified in two ways. First, I computed the mean body mass across all species in each bin (Fig. 2A), which is an important variable because there is a strong trend toward size increase (Alroy, 1998a). Second, I computed the standard deviation of the same body mass values (Fig. 2B), which is important because it is a direct measure of disparity (this latter term is typically equated with such measures of morphological variation as the range, variance, or standard deviation; Foote, 1993).

Some caveats are in order. First, it is possible to compute all of these statistics separately for individual fossil localities, which would avoid the problem of lumping species together in a temporal bin. However, preliminary analyses indicate that after correcting

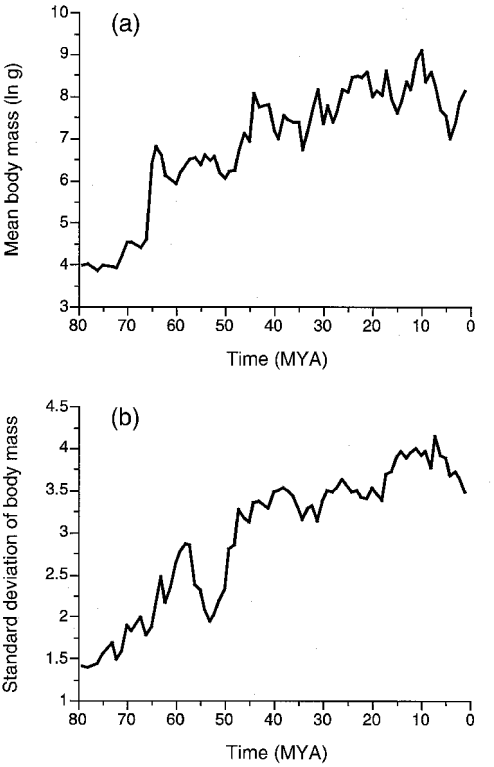

FIGURE 2. Trends through time in North American mammalian body mass distributions. All species falling into each 1.0 MY bin are considered. (a) Mean body mass. (b) Standard deviation of body mass.

such locality-specific data for sampling effects, one arrives at almost exactly the same patterns that are seen in the lumped data. Second, additional features of the distribution also might be quantified, including the skewness and kurtosis. However, these statistics are noisy and add little to the key conclusions. Finally, these trends apparently are governed by a complex, nonrandom dynamic operating within evolutionary lineages (Alroy, 1998a). However, I will constrain my discussion to the pattern itself, instead of the underlying evolutionary processes, because the raw data alone are sufficient to show that a Paleocene radiation occurred.

Results

The body mass curves (Fig. 2) show four clear-cut patterns: (1) Cretaceous mammals were small and occupied a very narrow range of the size spectrum (67–66 MYA bin: $n = 20$, mean ± SD mass = 4.40 ± 1.98 ln [natural log] g); (2) there was little change in the Cretaceous fauna during a period of at least 9 MY (76–75 MYA bin: $n = 20$, mass = 3.86 ± 1.44 ln g, i.e., about the size of an elephant shrew); (3) there was an abrupt shift in the mean just around the K-T boundary, which resulted from the extinction of many small mammals and the addition of many medium-sized mammals (65–64 MYA bin: $n = 40$, mass = 6.42 ± 1.88 ln g); and (4) there was a steady expansion in the size range throughout the Cenozoic; mean body mass was forced to track this upwards trend because the lower limit to size was static (Fig. 1 in Alroy, 1998a).

Was the K-T shift a true evolutionary event, or was it merely the side-effect of immigration (specifically from Eurasia) in the wake of a major mass extinction? Immigration might seem important because, for example, mean mass is 4.29 ln g in the Flat Creek 5 assemblage (latest Cretaceous) and 5.60 ln g, already much higher, in the apparently earliest Paleocene component of the Bug Creek Anthills fauna (see Lofgren, 1995). A few of the larger Bug Creek species are indeed most likely immigrants (e.g., *Catopsalis joyneri, Stygimys kuszmauli*, and one or more of the three ungulates: Archibald, 1982, 1993; Archibald and Bryant, 1990). However, some in situ speciation may already have occurred at this point, and in any case mean mass was still 0.8 ln g short of the average for the whole 65–64 MYA interval. Given that the later, post-Bug Creek Anthills shift was almost certainly due to a rapid, in situ radiation, the overall transition seems to have been less an effect of immigration than of trends within lineages combined with differential speciation of large forms. Regardless of the exact cause, the Cretaceous–Paleocene shift certainly had a more important long-term effect than any other sudden transition during the Cenozoic: By the 1–0 MYA interval, mean mass had increased by only another 1.70 ln g.

Discussion

One possible criticism of the preceding results is that they pertain to just a single continent. After all, only the North American record is relatively complete and well studied through both the latest Cretaceous and all of the Cenozoic. Thus, one could argue that molecular studies imply that a significant Cretaceous radiation did take place, but happened not to do so on this particular continent. But even apart from the fact that the best molecular clock data merely imply a few interordinal splits instead of a true evolutionary radiation, it is not true that the bulk of living eutherian diversity has its deep roots entirely outside of North America. Basal members of the Carnivora, Insectivora, Primates, Artiodactyla, Perissodactyla all appeared in North America during the early Cenozoic. Basal lagomorphs, rodents, and cetaceans fail to do so, but on the other hand the fossil record demonstrates that these groups originated in Asia during the Paleocene, not the Cretaceous, and that some major lineages within these orders (e.g., Geomyoidea, Sciuromorpha) did originate in North America. There are many minor groups that do seem to have originated in times and places where the fossil record is not strong, but it simply is not reasonable to suggest that North America witnessed less than its fair share of mammalian evolution. Instead, as a typical continent that long served as a crossroads for migrating lineages, North America is well-qualified to serve as a testing ground for models of mammalian evolutionary radiation.

If we accept even such a limited defense of the North American data, there are few ways to avoid this study's major conclusions: In terms of both taxonomic diversity and body mass distributions, the single most important radiation of mammals occurred not during the Cretaceous, but during the early Paleocene. Far from being a "literal reading of the fossil record," these are statistically ro-

bust results based on standardized sampling regimes. They show the folly of denying the Paleocene radiation on the basis of loosely calibrated molecular clocks. A more fruitful line of inquiry would be to take advantage of this obviously important event by exploring its impact on molecular evolution. For example, if the extraordinary early Paleocene burst of speciation and morphological evolution was correlated with intense selection at the molecular level, that may have created a simultaneous speed-up in the molecular clock across most or all early Paleocene lineages. In turn, such an effect might account for some of the much-touted, but biologically inconsequential discrepancies between molecular and paleontological data.

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