

Evolutionary and Preservational Constraints on Origins of Biologic Groups: Divergence Times of Eutherian Mammals

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Some molecular clock estimates of divergence times of taxonomic groups undergoing evolutionary radiation are much older than the groups' first observed fossil record. Mathematical models of branching evolution are used to estimate the maximal rate of fossil preservation consistent with a postulated missing history, given the sum of species durations implied by early origins under a range of species origination and extinction rates. The plausibility of postulated divergence times depends on origination, extinction, and preservation rates estimated from the fossil record. For eutherian mammals, this approach suggests that it is unlikely that many modern orders arose much earlier than their oldest fossil records.

The molecular clock hypothesis (1) sometimes yields estimated times of origin of major biologic groups that substantially predate their oldest known occurrences in the fossil record, especially when massive evolutionary radiations have occurred (2–7). A large discrepancy between a group's origin and its oldest observed fossil occurrence may imply an extraordinarily incomplete fossil record (3). If lineages continually branch, with few daughter branches surviving for tens of millions of years (8–10), much more diversity may be missing than suggested by a simple tally of gaps between postulated origins and oldest fossil appearances of lineages extant today (Fig. 1). Thus, postulated early divergence times may implicitly require much lower rates of origination and extinction than measured in the fossil record or unusually low rates of preservation during certain intervals of geologic time. To test divergence times, we must therefore have good estimates of rates of taxonomic evolution and of fossil preservation. Here we build upon the standard birth-death model (8, 9) that has been applied to a range of paleobiological problems (9, 11–13). To test the specific case of eutherian (placental) mammals, we use conservative hypotheses of diversity history, assuming monotonic increase in species diversity from the postulated time of origin of the

taxonomic group to the time it is first observed in the fossil record (Fig. 2), but the approach is more general.

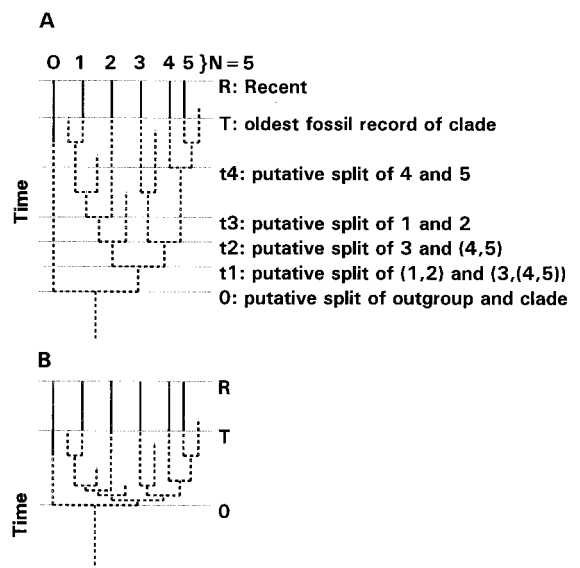
The question of interest is to estimate how low the rate of fossil preservation must be for all species of a group to escape detection over a specified interval of geologic time. To incorporate incomplete preservation of fossil taxa into our branching model, we treat preservation as a time-homogeneous Poisson process (14–17). Because the branching model explicitly considers only the divergence of species, not their morphological evolution, we assume that morphological divergence occurs soon enough after lineage splitting so that daughter species, if discovered, would be recognized as distinct from their ancestors. We contrast two alternatives: total lack of

preservation and preservation at least once. We consider a hypothesis of missing diversity plausible if the probability of complete nonpreservation of the group is at least 0.5. This is a conservative value.

We estimate the sum of missing species durations implied by a hypothesized divergence time. This sum increases with (i) the length of missing history, (ii) the diversity at the end of this interval, and (iii) the extinction rate in most diversity models (Fig. 3) (13, 18). Increases in all three parameters demand more extinct species evolving before the time that the group is first observed. Because the length of missing history and the minimal diversity at the group's first fossil appearance are given by the hypothesized time of origin and by observed fossils, the parameters that need to be constrained are extinction rate and preservation rate. For a group's summed species durations to be unobserved, the extinction rate, the preservation rate, or both must fall below some threshold (Fig. 3). We can thus place upper probabilistic bounds on the rates consistent with the hypothesis of early origins and unobserved diversity.

The known fossil record of modern eutherian mammals has a concentration of ordinal first appearances during the early Tertiary (19–21). There are no unequivocal, pre-Tertiary occurrences of modern eutherian orders or supraordinal groupings (22), and the low resolution of morphological and molecular phylogenies (19, 23) suggests that the orders arose within a short period of time, whether within or before the Tertiary. Some molecular clock calculations nevertheless suggest ordinal origins at widely spaced times during the Cretaceous, as much as 129 ± 18.5 million years (My) ago (4). This implies a missing history of 64 My for the group and a minimal diversity of nine species (the number of orders or supraordinal groupings) at the end of this interval (Table 1 and Fig. 3). Nine species is an absolute lower bound, as

Fig. 1. Hypothetical illustration of the missing diversity problem. Species 1 through 5 comprise the extant part of the group of interest, whose outgroup is O. Solid lines show the known fossil record. (A) Relatively even distribution of branching events. (B) Clustering of some branching events, as is often thought to occur in the early stages of an evolutionary radiation (41). In both cases, the tree topology, the length of the known fossil record, and the age of the common ancestor to the outgroup and the group of interest are the same. In (B), however, the interval of missing history is shorter and the sum of missing species durations is lower.



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REPORTS

it treats each major lineage as if it consisted of a single species. If the extinction rate were on the order of 0.1 per lineage-million-years (Lmy), a low value for mammals (14, 24, 25), then summed species durations would be on the order of 1000 Lmy (13). This large a sum of missing durations demands a preservation rate on the order of 7×10^{-4} Lmy $^{-1}$ or lower (17). If we take the nine lineages individually and assume no extinction or origination, then we have the absolutely minimal sum of missing durations of these lineages (the sum of postulated gaps), or 346 Lmy. This still requires a preservation rate of 2×10^{-3} Lmy $^{-1}$ or lower. Other treatments of the hypothesis, including several in which we minimized summed species durations by assuming no extinction and several in which we accepted that the modern eutherian fossil record starts at 85 My ago, which implies fewer than nine lineages at the start of the fossil record (4, 26), yield comparable results (Table 1 and Fig. 3).

Estimated preservation rates for Cenozoic mammals (14, 24) are at least two orders of magnitude higher than those required by the early-origins hypothesis, but one could expect that Cenozoic rates overestimate Cretaceous values: Cretaceous mammals were small (mostly under ~ 2 kg in body mass), whereas many Cenozoic species were larger (27). We therefore used known Late Cretaceous mammals to measure preservation rate. Because there are no unequivocal modern eutherians in the Cretaceous, we measured preservation and extinction rates for Late Cretaceous species in all other mammal groups known. We estimate that the extinction rate for Late Cretaceous mammals is $\sim 0.25 \pm 0.034$ Lmy $^{-1}$, lower than observed Cenozoic rates (14, 24, 25), and that the preservation rate is $\sim 0.03 \pm 0.0038$ to $\sim 0.06 \pm 0.0086$ Lmy $^{-1}$ (28).

This preservation rate is lower than similarly derived estimates for Cenozoic mam-

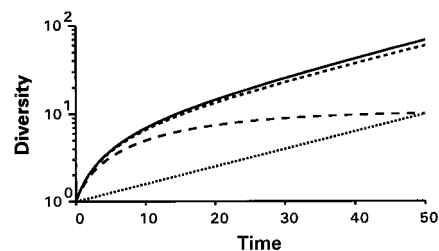


Fig. 2. Comparison of expected diversity in models (13), illustrated with $q = 0.25$ Lmy $^{-1}$, $T = 50$ My, $N = 10$ species, and $p = q + \ln(N)/T$, values similar to those in the empirical case we examine. Dotted line is exponential growth. Short-dashed line is diversity before time T conditioned upon survival of group to time T . Long-dashed line is diversity before time T conditioned upon diversity exactly equal to N at time T . Solid line is diversity before time T conditioned upon diversity greater than or equal to N at time T .

mals (14, 24, 29) but is higher than the rates required by the hypothesis of missing eutherian diversity (Table 1). Even with the most generous treatment of the hypothesis, the preservation rate required is about an order of magnitude lower than our estimates, and the probability of complete nonpreservation is

only 0.02 (Table 1). We therefore find it difficult to support an extensive missing history of modern eutherians. Only if most of the divergences occurred within the last few million years of the Cretaceous, implying a long lag after the postulated origin of modern eutherians (4), could one support pre-Tertiary

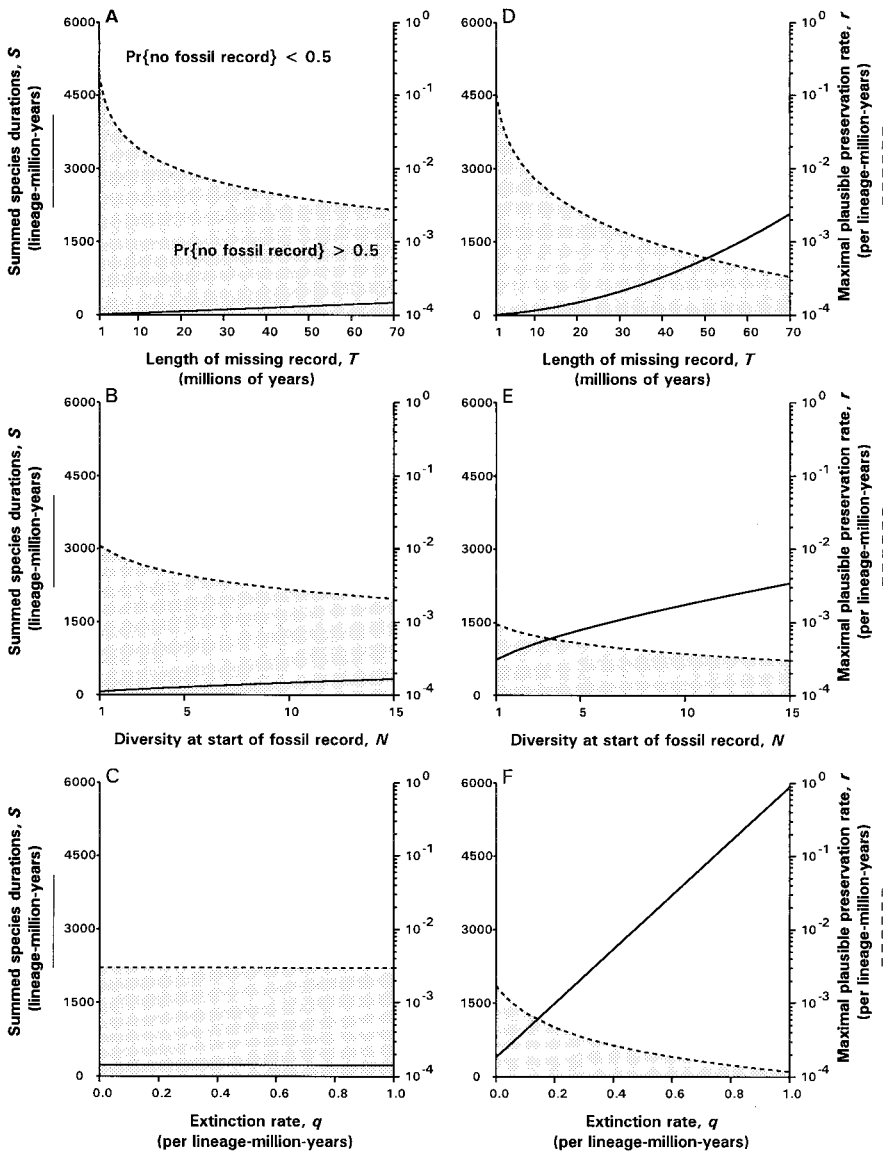


Fig. 3. Analysis of the hypothesis that many lineages of modern eutherians originated before the Tertiary (4, 13, 17). T is taken to be 64 My, N is taken to be 9 species, and q is taken to be 0.25 Lmy $^{-1}$ (see text). (A to C) Exponential diversity model; (D to F) diversity before time T conditioned upon minimal diversity of N at time T ; other diversity models yield results between these extremes. (A and D) Variation in T with $N = 9$ species and $q = 0.25$ Lmy $^{-1}$. (B and E) Variation in N with $T = 64$ My and $q = 0.25$ Lmy $^{-1}$. (C and F) Variation in q with $T = 64$ My and $N = 9$ species. Left-hand ordinate (solid line), expected sum of species durations, S (13). Right-hand ordinate (dashed line), preservation rate required to yield a probability of complete nonpreservation exactly equal to 0.5 (17). Shaded area beneath corresponds to probabilities of nonpreservation greater than 0.5, and thus to combinations of preservation rate and value of abscissa for which the corresponding amount of missing diversity is plausible. For example, in (D), $q = 0.25$ Lmy $^{-1}$ and $N = 9$ species. If $T = 40$ My, then $S = 918$ Lmy. This value of T implies that $r_{\max} = -\ln(0.5)/918 = 0.0008$ Lmy $^{-1}$. For this value of r , any value of T less than 40 My yields a probability of nonpreservation of the group greater than 0.5 (the shaded region), and, for this value of T , any value of r less than r_{\max} yields a probability of nonpreservation of the group greater than 0.5. As T increases so does S , and thus an ever smaller value of r is required to make group nonpreservation likely. The same is true for an increase in N with T and q fixed (B and E) or an increase in q with T and N fixed (C and F).

REPORTS

divergences of modern eutherian lineages (30) (Figs. 1B and 3D).

Several hypotheses could explain the discrepancy between our results and the postulate of missing eutherian history: (i) Cretaceous members of the modern eutherian orders are preserved and described, but they are not recognized because they are so primitive and lack most diagnostic features (3). This requires both that morphological evolution be largely decoupled from lineage splitting and molecular evolution and that eutherians experienced much lower rates of morphological change through the Cretaceous than during the Cenozoic, two conditions that may be testable. (ii) Modern eutherian lineages existed through the Cretaceous, but their preservation rates were generally lower than those

of species in other mammal groups. This difference in preservation rates would have to be more than an order of magnitude, for which we can offer no support (31). (iii) Modern eutherian lineages diversified in regions that have no known Late Cretaceous mammals (such as Africa, Australia, and Antarctica) and suddenly dispersed widely during the early Tertiary. This "Garden of Eden" hypothesis is testable with intensive exploration of the fossil record of the regions in question (32). (iv) The hypothesis of extensive missing history is wrong, because rates of molecular evolution are heterogeneous among lineages (33, 34) or, more importantly, over time (7, 33–37). If, as sometimes suggested, molecular evolutionary rates speed up during times of evolutionary radiation

(7, 33, 36, 37), then divergences during a Tertiary radiation might spuriously appear to have occurred earlier, especially if, as in (4), the molecular clock is calibrated with lineages that diverged long before the Tertiary (synapsids and diapsids), in what appears not to have been a remarkable radiation. This possibility, which is testable (38), is consistent with Kumar and Hedges's (4) analysis of major vertebrate lineages, which shows that estimated divergence times and oldest fossil occurrences agree fairly well for many gradually diversifying higher taxa but not for the rapidly diversifying, extant eutherian orders.

Our branching model approach is readily applicable to other cases, such as the postulated origins of a number of animal phyla some half-billion years before the Cambrian

Table 1. Analysis of the hypothesis that many modern eutherian lineages arose before the Tertiary (4, 13, 17). *N* is the minimal number of species present at the time the group is first found in the fossil record, *T* is the time between the postulated origin of the group and its first fossil appearance, *q* is the extinction rate, *S* is the expected summed species durations, *r*_{max} is the preservation rate that yields a probability of 0.5 that *S* will completely escape preservation, and *P* is the probability that *S* will completely escape preservation if *r* = 0.03 Lmy⁻¹ (see text) (that is, *P* = e^{-0.03*S*}). For the

bottom part of the table, *S* is the grand sum of summed species durations of the individual lineages. See (13) for exponential (E) and conditional (C) diversity models; the latter conditions upon minimal diversity of *N* at time *T*. Results of the other models (13) are within these extremes. We do not consider the "star phylogeny" model, in which all extant lineages diverge at the origin of the group, because it is inconsistent with the hypothesis we are testing. That model yields even greater summed species durations than those we present.

<i>N</i>	<i>T</i> (My)	Model	<i>q</i> = 0.0 Lmy ⁻¹			<i>q</i> = 0.1 Lmy ⁻¹			<i>q</i> = 0.5 Lmy ⁻¹		
			<i>S</i> (Lmy)	<i>r</i> _{max} (10 ⁻⁴ Lmy ⁻¹)	<i>P</i>	<i>S</i> (Lmy)	<i>r</i> _{max} (10 ⁻⁴ Lmy ⁻¹)	<i>P</i>	<i>S</i> (Lmy)	<i>r</i> _{max} (10 ⁻⁴ Lmy ⁻¹)	<i>P</i>
<i>Modern eutherian considered as a whole</i>											
9*	64†	C	401	17	6 × 10 ⁻⁶	939	7	6 × 10 ⁻¹³	3153	2	8 × 10 ⁻⁴²
9*	64†	E	233	30	9 × 10 ⁻⁴	233	30	9 × 10 ⁻⁴	233	30	9 × 10 ⁻⁴
14‡	64†	C	566	12	4 × 10 ⁻⁸	1216	6	1 × 10 ⁻¹⁶	3889	2	2 × 10 ⁻⁵¹
14‡	64†	E	315	22	1 × 10 ⁻⁴	315	22	1 × 10 ⁻⁴	315	22	1 × 10 ⁻⁴
7§	44§	C	227	31	1 × 10 ⁻³	454	15	1 × 10 ⁻⁶	1400	5	6 × 10 ⁻¹⁹
7§	44§	E	136	51	2 × 10 ⁻²	136	51	2 × 10 ⁻²	136	51	2 × 10 ⁻²
10	44§	C	300	23	1 × 10 ⁻⁴	562	12	5 × 10 ⁻⁸	1653	4	3 × 10 ⁻²²
10	44§	E	172	40	6 × 10 ⁻³	172	40	6 × 10 ⁻³	172	40	6 × 10 ⁻³
<i>Modern eutherians considered as individual lineages</i>											
9*¶		C	346	20	3 × 10 ⁻⁵	1337	5	4 × 10 ⁻¹⁸	5478	1	4 × 10 ⁻⁷²
9*¶		E	346	20	3 × 10 ⁻⁵	346	20	3 × 10 ⁻⁵	346	20	3 × 10 ⁻⁵
14‡¶#		C	487	14	5 × 10 ⁻⁷	1784	4	6 × 10 ⁻²⁴	7216	1	1 × 10 ⁻⁹⁴
14‡¶#		E	487	14	5 × 10 ⁻⁷	487	14	5 × 10 ⁻⁷	487	14	5 × 10 ⁻⁷

*Modern placental lineages that are implied by hypothesis (4) to have diverged during the Late Cretaceous and to have passed unpreserved into the Paleocene are Edentata, Sciuromnathi, Hystricognathi, Paenungulata, Cetartiodactyla, Perissodactyla, Carnivora, Lagomorpha, and Scandentia. †*T* is the difference between the postulated divergence time of Edentata [129 million years ago (Ma)] (4) and the oldest fossil record of undisputed modern placentals in the early Paleocene (21) at ~65 Ma (42). ‡Except as otherwise noted, we use the phylogenetic relationships in Kumar and Hedges's (4) hypothesis in order to test their postulated divergence times. The hypothesis in question omits a number of modern orders. Some of these can be inferred to extend into the Cretaceous if we accept Kumar and Hedges's divergence times and supraordinal groupings while incorporating additional interordinal relationships expressed in the widely cited, morphologically based phylogeny of Novacek (19). In this way, at least five additional lineages of modern placentals are inferred to have diverged during the Late Cretaceous: Macroscelidea, Lipotyphla, Primates (Dermoptera + Chiroptera), and Tubulidentata. Whether Pholidota should also be incorporated depends on how inclusive Edentata is in (4); we have left it out in order to be conservative. §If Kumar and Hedges's (4) divergence times and supraordinal groupings are accepted, and the beginning of the modern eutherian record is taken to correspond to the putative ungulatiforms at ~85 Ma (4, 26) or to the Campanian zambdalestids [putative lagomorphs (27)], or both, then *T* is reduced to 44 My and *N* is reduced to 7 lineages: Edentata, Sciuromnathi, Hystricognathi, Paenungulata, Ferungulata (sensu Kumar and Hedges), Lagomorpha, and Scandentia. ¶Three additional lineages must have diverged before 85 Ma if, as above, † the phylogeny of Novacek (19) is used to supplement the hypothesis of Kumar and Hedges (4): Macroscelidea, Primates, and (Dermoptera + Chiroptera). #The calculations in the top part of this table use only the oldest postulated divergence time. Here we treat the minimal number of lineages individually, each constrained with its own amount of missing time and with a minimal diversity of one species at the end of this time. The missing time, *T*, for an individual lineage is the difference between its postulated divergence time and the time of its oldest fossil record. For lineages added on the basis of Novacek's (19) phylogeny, ‡ the divergence time is the youngest time consistent with his phylogeny and with Kumar and Hedges's postulated divergence times (4). The divergence times, oldest fossil occurrences, and estimated absolute ages (42) of oldest fossil are: Edentata, 129 Ma, late Paleocene (21), 60.5 Ma; Sciuromnathi, 112 Ma, late Paleocene (21), 60.5 Ma; Hystricognathi, 109 Ma, early Eocene (21), 56.5 Ma; Paenungulata, 105 Ma, late Paleocene (43), 60.5 Ma; Ferungulata (sensu Kumar and Hedges), 92 Ma, early Paleocene (39, 44), 65 Ma; Cetartiodactyla, 83 Ma, late Paleocene (21), 60.5 Ma; Perissodactyla, 74 Ma, early Eocene (21), 56.5 Ma; Lagomorpha (excluding problematic zambdalestids), 90.8 Ma, early Paleocene (27), 65 Ma; Scandentia, 85.9 Ma, middle Eocene (21), 50 Ma; Macroscelidea, 112 Ma, early Paleocene (21), 65 Ma; Lipotyphla, 74 Ma, early Paleocene (21), 65 Ma; Primates, 85.9 Ma, early Paleocene (21), 65 Ma; (Dermoptera + Chiroptera), 85.9 Ma, late Paleocene (21), 60.5 Ma; Tubulidentata, 74 Ma, early Oligocene (21), 35.4 Ma. A number of these groups (Lagomorpha, Macroscelidea, and Primates) may have unequivocal first-fossil appearances that postdate those used here. Our acceptance of claims of earlier occurrences is conservative, because we thereby minimize implied gaps and thus favor the hypothesis of early origins of modern eutherians. In addition to the Perissodactyla and Cetartiodactyla, there must have been at least one continuous lineage of Ferungulata (sensu Kumar and Hedges, including Carnivora) that extends from the origin of this supraordinal grouping to the Paleocene. The gaps are minimized in the foregoing tabulation by taking the gap of this lineage to end at the first appearance of Carnivora. #Because the ~85-Ma Asian fossils in question are thought to be stem members of one or two modern eutherian lineages (4, 26) if they belong to these lineages at all, the number and duration of gaps for individual lineages are affected minimally by the interpretation of these fossils. Separate analyses are therefore not presented.

(2, 3) and the postulated origins of extant groups of flowering plants tens of millions of years before their oldest fossils (6, 7). The main value of this approach is that it maps out a field of preservation rates and rates of taxonomic evolution that can be measured and compared to hypothesized divergence times. Because these rates can be estimated directly with empirical data from the fossil record (14, 16, 24, 25), one can explicitly test an evolutionary hypothesis and its implications regarding rates of morphological, molecular, and taxonomic evolution.

References and Notes

1. E. Zuckerkandl and L. Pauling, in *Evolution Genes and Proteins*, V. Bryson and H. J. Vogel, Eds. (Academic Press, New York, 1965), pp. 97–165; W. M. Fitch, in *Molecular Evolution*, F. J. Ayala, Ed. (Sinauer, Sunderland, MA, 1976), pp. 160–178; M. Kimura, *J. Mol. Evol.* **26**, 24 (1987).
2. B. Runnegar, *Lethaia* **15**, 199 (1982); G. A. Wray, J. S. Levinton, L. M. Shapiro, *Science* **274**, 568 (1996); F. J. Ayala, A. Rzhetsky, F. J. Ayala, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 606 (1998); A. Seilacher, P. K. Bose, F. Pflüger, *Science* **282**, 80 (1998). For animal phyla, the gap may be partly explained by a major change in preservability corresponding with the advent of skeletons.
3. A. Cooper and R. Fortey, *Trends Ecol. Evol.* **13**, 151 (1998).
4. S. Kumar and S. B. Hedges, *Nature* **392**, 917 (1998).
5. S. B. Hedges et al., *ibid.* **381**, 226 (1996); M. S. Springer, *J. Mammal. Evol.* **4**, 285 (1997).
6. K. H. Wolfe et al., *Proc. Natl. Acad. Sci. U.S.A.* **86**, 6201 (1989); W. Martin, A. Gierl, H. Saedler, *Nature* **339**, 46 (1989); P. R. Crane et al., *ibid.* **342**, 131 (1989); W. Martin et al., *Mol. Biol. Evol.* **10**, 140 (1993); K. J. Systma and D. A. Baum, in *Flowering Plant Origin, Evolution and Phylogeny*, D. W. Taylor and L. J. Hickey, Eds. (Chapman & Hall, New York, 1996), pp. 314–340; J. A. Doyle and M. J. Sanderson, *Am. J. Bot.* **84** (suppl.), 132 (1997).
7. M. J. Sanderson, *Mol. Biol. Evol.* **14**, 1218 (1997).
8. C. U. Yule, *Philos. Trans. R. Soc. London Ser. B* **213**, 21 (1924); D. G. Kendall, *Ann. Math. Statist.* **19**, 1 (1948).
9. D. M. Raup, *Paleobiology* **11**, 42 (1985).
10. D. Normile, *Science* **281**, 774 (1998).
11. D. M. Raup, *Paleobiology* **4**, 1 (1978); *ibid.* **9**, 107 (1983); *ibid.* **17**, 37 (1991); _____ and J. W. Valentine, *Proc. Natl. Acad. Sci. U.S.A.* **80**, 2981 (1983); R. R. Strathman and M. Slatkin, *Paleobiology* **9**, 97 (1983); M. E. Patzkowsky, *ibid.* **21**, 440 (1995); M. Foote, *ibid.* **22**, 141 (1996).
12. We evaluate divergence times rather than branching topology. We are not concerned with determining whether the relative order of hypothesized origins is consistent with observed first appearances [M. A. Norell and M. J. Novacek, *Science* **255**, 1690 (1992); J. P. Huelsenbeck, *Paleobiology* **20**, 470 (1994); P. J. Wagner, *ibid.* **21**, 153 (1995); R. Hitchin and M. J. Benton, *ibid.* **23**, 20 (1997)]. Rather, we are interested in cases in which the absolute timing of postulated origins and of observed origins are already known to disagree.
13. We start by assuming that species originations and extinctions within a taxonomic group occur at stochastically constant per capita rates, p and q , per lineage-million-years. The hypothesized divergence times imply an interval of missing history of length T and a minimal diversity of N species at the end of this interval. We use lineage-million-years because each species has some chance of preservation throughout its lifetime, and so all species are multiplied by their durations to yield the sum of species durations, S , during the interval T . This is equivalent to

$$\int_0^T D_t dt$$

where D_t is the expected species diversity at time t . Several diversification models are plausible. Exponential growth, in which $D_t = e^{(p-q)t}$, includes the chance of total group extinction before time T . [With exponential growth, S depends only on $(p - q)$; the same value of S can thus result from higher rates, yielding many short-lived species, or lower rates, yielding fewer long-lived species.] A crucial aspect of the hypotheses we wish to test is a minimal diversity of N species at time T , when fossil taxa are first observed. The most appropriate model tracks expected diversity at time t conditioned upon a diversity at least equal to N at time T . Let t be the elapsed time since $t = 0$. Let $P(0, t, a)$ be the probability that a group is extinct at or before time t , given that its diversity is equal to a lineages at $t = 0$; $P(0, t, a) = [pt/(1 + pt)]^a$ if $p = q$, and $P(0, t, a) = \{q[e^{(p-q)t} - 1]/[pe^{(p-q)t} - q]\}^a$ if $p \neq q$ (9). Let $P(s, t, a)$ be the probability that a group survives at least until time t , given that its diversity is equal to a lineages at $t = 0$; $P(s, t, a) = 1 - P(0, t, a)$. Let $P(n, t, a)$ be the probability that a group's diversity is exactly equal to n lineages at time t , given that it is equal to a lineages at $t = 0$; for $a = 1$, $P(n, t, a) = (pt)^{n-1}/(1 + pt)^{n-1}$ if $p = q$ (9), and $P(n, t, a) = (1 - A)(1 - B)^{n-1}$ if $p \neq q$ (9), where $A = P(0, t, 1)$ and $B = pA/q$. For $a > 1$,

$$P(n, t, a) = [pt/(1 + pt)]^{a+n} \cdot \sum_{j=1}^{\min(a,n)} \binom{a}{j} \binom{n-1}{j-1} (pt)^{-2j} \text{ if } p = q \text{ (9)}$$

and

$$P(n, t, a) = \sum_{j=1}^{\min(a,n)} \binom{a}{j} \binom{n-1}{j-1} \cdot A^a \cdot B^{j-1} (1 - A)(1 - B)^{n-j} \text{ if } p \neq q$$

The last equation is a correction of equation (A18) from (9). Let $P(\geq n, t, a)$ be the probability that diversity is greater than or equal to n lineages at time t , given that it is equal to a lineages at $t = 0$. Then

$$P(\geq n, t, a) = 1 - P(0, t, a) - \sum_{m=1}^{n-1} P(m, t, a)$$

Let t and T be two points in time such that $t < T$, and let the group have diversity equal to one lineage at $t = 0$. Let $P(n, t, s, T)$ be the probability that diversity is exactly equal to n lineages at time t , given that the group survives at least until time T . Let $P(n, t, N, T)$ be the probability that diversity is exactly equal to n lineages at time t , given that diversity is exactly equal to N lineages at time T . And let $P(n, t, \geq N, T)$ be the probability that diversity is exactly equal to n lineages at time t , given that diversity is greater than or equal to N lineages at time T . Then, by the rules of conditional probability,

$$P(n, t, s, T) = P(n, t, 1) \cdot P(s, T - t, n) / P(s, T, 1);$$

$$P(n, t, N, T) = P(n, t, 1) \cdot P(N, T - t, n) / P(N, T, 1);$$

and

$$P(n, t, \geq N, T) = P(n, t, 1) \cdot P(\geq N, T - t, n) / P(\geq N, T, 1)$$

The corresponding expected (mean) diversities at time t are given by

$$D_t = E(n, t, s, T) = \sum_{m=1}^{\infty} m \cdot P(m, t, s, T);$$

$$D_t = E(n, t, N, T) = \sum_{m=1}^{\infty} m \cdot P(m, t, N, T);$$

and

$$D_t = E(n, t, \geq N, T) = \sum_{m=1}^{\infty} m \cdot P(m, t, \geq N, T)$$

14. M. Foote, *Paleobiology* **23**, 278 (1997). Preservation rate, r , per lineage-million-years, implicitly incorporates preservation and recovery.
15. C. R. Marshall, *ibid.* **16**, 1 (1990).
16. A. R. Solow and W. Smith, *ibid.* **23**, 271 (1997).

17. The probability that the group will be entirely unrepresented during the interval of time $(0, T)$ is equal to e^{-rS} , where S is the sum of species durations (13) and r is the preservation rate (14), and the probability that at least one member of the group will be preserved is equal to $1 - e^{-rS}$. If we demand a minimal probability of 0.5 for a hypothesis of missing diversity to be plausible, then r must be less than or equal to $-\ln(0.5)/S$.
18. We simplify the problem using the well-known positive correlation between origination and extinction rates and constrain the net growth rate $(p - q)$ to be equal to $\ln(N)/T$, thus forcing p to be equal to $q + \ln(N)/T$. For discussion of this correlation, see S. M. Stanley, in *Causes of Evolution*, R. M. Ross and W. D. Allmon, Eds. (Univ. of Chicago Press, Chicago, IL, 1990), pp. 103–127.
19. M. J. Novacek, *Nature* **356**, 121 (1992). This phylogeny is similar to that of J. Shoshani and M. C. McKenna, *Mol. Phylogenet. Evol.* **9**, 572 (1998).
20. M. J. Benton, *J. Mol. Evol.* **30**, 409 (1990); R. L. Carroll, *Vertebrate Paleontology and Evolution* (Freeman, New York, 1988); C. M. Janis, K. M. Scott, L. L. Jacobs, Eds. *Evolution of Tertiary Mammals of North America* (Cambridge Univ. Press, Cambridge, 1998).
21. R. C. Stucky and M. C. McKenna, in *The Fossil Record*, M. J. Benton, Ed. (Chapman & Hall, London, 1993), vol. 2, pp. 739–771.
22. A number of Cretaceous fossils have been interpreted as modern eutherians, but none of these interpretations is without controversy. Claims that the Cretaceous eutherians *Batodon* [M. J. Novacek, *Contrib. Sci. Los Angeles Co. Mus.* **283**, 1 (1976); L. Krishtalka and R. M. West, *Milwaukee Publ. Mus. Contrib. Biol. Geol.* **27**, 1 (1979)] and *Paranyctoides* [R. C. Fox, *Spec. Pub. Carnegie Mus. Nat. Hist.* **9**, 9 (1984)] are lipotyphlans have been regarded as weak [P. M. Butler, in *The Phylogeny and Classification of the Tetrapods*, M. J. Benton, Ed. (Clarendon, Oxford, 1988), pp. 117–141]. Cretaceous “zhelestids,” recently claimed to be ungulatormorphs (26), basal ferungulates (sensu Kumar and Hedges), or archontans (4), may instead be archaic eutherians allied with either *Prokennalestes* (39) or zalamdalestids [P. M. Butler, *Biol. Rev. Cambridge Philos. Soc.* **65**, 529 (1990)].
23. W. W. de Jong, *Trends Ecol. Evol.* **13**, 270 (1998).
24. M. Foote and D. M. Raup, *Paleobiology* **22**, 121 (1996).
25. S. M. Stanley, *ibid.* **11**, 13 (1985); L. M. Van Valen, *Evol. Theory* **1**, 1 (1973); *ibid.* **7**, 127 (1985).
26. J. D. Archibald, *Science* **272**, 1150 (1996); L. A. Nesson, J. D. Archibald, Z. Kielan-Jaworowska, *Bull. Carnegie Mus. Nat. Hist.* **34**, 40 (1998).
27. J. Alroy, *Science* **280**, 731 (1998).
28. We used the theoretical relationships among extinction rate, preservation rate, and the form of stratigraphic range-frequency distributions. The proportion of species confined to single horizons, f_0 , is equal to $q/(r + q)$, thus $r = q(1 - f_0)/f_0$, and the observed mean stratigraphic range of species that span more than one horizon is equal to $1/q$ (14). If, instead, we include single-horizon species by assigning them some arbitrarily short duration, we obtain a shorter mean duration, and thus a higher estimate of extinction rate and preservation rate (14, 16, 24). Our primary approach, therefore, is conservative. We based our estimates on a global data set of the geographic and biostratigraphic occurrences of Late Cretaceous mammal species and the correlations of the stratigraphic horizons from which they are known (supplemental data can be found at www.sciencemag.org/feature/data/985988.shl) (40). If all occurrences that cannot be assigned with confidence to a species are treated as distinct species confined to single horizons (which maximizes f_0 and thus minimizes r), then there are 460 species and $f_0 = 0.9$. If these uncertain occurrences are excluded, then there are 226 species and $f_0 = 0.8$. Our estimates of f_0 are quite robust; we find similar values when alternative schemes are used for stratigraphic correlation. For Late Cretaceous mammals, absolute biochronology is best worked out for North America (40). The 41 species from North America that are known from more than one stratigraphic horizon have a mean range of $\sim 4 \pm 0.40$ My; thus we estimate q to be $\sim 0.25 \pm 0.034$ Lmy $^{-1}$ and r to be $\sim 0.03 \pm 0.0038$ to $\sim 0.06 \pm 0.0086$ Lmy $^{-1}$, reflecting the two estimates of f_0 (all standard errors based on bootstrap resampling of these 41 species).

Because of the small number of species and the uncertainty in absolute dating, there is uncertainty in our estimate of extinction rate. But because the relation between estimated extinction rate and estimated preservation rate is linear, the value of q would have to be more than an order of magnitude lower than our estimate in order to affect our conclusions substantially. Taxonomic rates this low are incompatible with rates estimated for Cenozoic mammals (14, 24, 25) and for even the most slowly evolving groups of animals (25).

29. Because of the difference between Cenozoic and Cretaceous preservation rates, we do not recommend using Cenozoic occurrences to place confidence limits (15) on stratigraphic ranges for mammal taxa that may extend into the Cretaceous [see also (10)]. Moreover, confidence limits are more difficult to estimate for higher taxa than for single species, because the probability of group preservation per unit time is potentially greatly affected by changes in diversity [R. Bleiweiss, *Geology* **26**, 323 (1998); C. R. Marshall and R. Bleiweiss, *ibid.* **27**, 95 (1999)].

30. M. Messer *et al.*, *J. Mammal. Evol.* **5**, 95 (1998).

31. It is also likely that preservation rate fluctuates over time, because sea level and other factors change. Modeling of time-heterogeneous preservation (14, 24), however, shows that fluctuating preservation rate is not likely to distort substantially either the overall probability of species preservation or our estimates of preservation rate.

32. M. S. Springer *et al.*, *Nature* **388**, 61 (1997); M. J. Stanhope *et al.*, *Mol. Phylogenet. Evol.* **9**, 501 (1998); M. J. Stanhope *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 9967 (1998).

33. P. D. Gingerich, *Mol. Biol. Evol.* **3**, 205 (1986).

34. R. J. Britten, *Science* **231**, 1393 (1986).

35. J. H. Gillespie, *Proc. Natl. Acad. Sci. U.S.A.* **81**, 8009 (1984); *Genetics* **113**, 1077 (1986); *Mol. Biol. Evol.* **3**, 138 (1986); M. M. Miyamoto and W. M. Fitch, *ibid.* **12**, 503 (1995).

36. M. Goodman, *Prog. Biophys. Mol. Biol.* **37**, 105 (1981).

37. D. M. Raup, in *Rates of Evolution*, K. S. W. Campbell and M. F. Day, Eds. (Allen & Unwin, London, 1986), pp. 1–14.

38. If molecular rates are faster during evolutionary radiations, this may reflect two end-member mechanisms that have been suggested previously: (i) Adaptive change within species is faster during the rapid occupation of new adaptive zones (41), and many molecular substitutions are selective rather than neutral (35, 36); or (ii) a punctuational model applies to molecular evolution, with change concentrated at lineage splitting; thus, rapid speciation during evolutionary radiation (41) causes faster molecular rates (37). These mechanisms are testable with data from extant groups for which fossil diversity, genealogical relationships, and fossil divergence times are reliably known: Each pair of living species is separated by a divergence time, a number of cladogenetic events (patristic distance), a morphological distance, and a molecular distance. If morphological divergence provides a measure of adaptive change, the first hypothesis implies a positive partial correlation between molecular and morphological distance, with divergence time and patristic distance held statistically constant. The second hypothesis implies a positive partial correlation between molecular and patristic distance, with divergence time and morphological distance held constant.

39. M. C. McKenna and S. K. Bell, *Classification of Mammals Above the Species Level* (Columbia Univ. Press, New York, 1997).

40. Occurrence data are from a compilation of faunal lists and synonymies, extensively supplemented with observations by J.P.H. This database is heavily influenced by the rich fossil record of North America, but also includes the known faunas of South America, Europe, Asia (Mongolia, India, and western Asia), and Madagascar. Biostratigraphic correlation for species outside North America was based largely on information in the references consulted for faunal lists. For North American species, these sources were supplemented by the following: J. A. Lillegraven, *Contrib. Sci. Los Angeles Co. Mus.* **232**, 1 (1972); _____ and L. M. Ostresh Jr., *Geol. Soc. Am. Spec. Pap.* **243**, 1 (1990); M. B. Goodwin and A. L. Deino, *Can. J. Earth*

Sci. **26**, 1384 (1989); R. R. Rogers, C. C. Swisher III, J. R. Horner, *ibid.* **30**, 1066 (1993); C. C. Swisher III, L. Dingus, R. F. Butler, *ibid.*, p. 1981; F. M. Gradstein *et al.*, in *Geochronology, Time Scales and Global Stratigraphic Correlation*, W. A. Berggren, D. V. Kent, M.-P. Aubry, J. Hardenbol, Eds. [Society for Sedimentary Geology (SEPM), Tulsa, OK], pp. 95–126. To determine whether a species is known from a single horizon, it is generally necessary to have only a relative biochronology. We did not base our relative chronology solely on faunal associations of mammals, but also used local and regional stratigraphic relations, radiometric dates, and correlations with marine sequences based largely on regional strandline stratigraphy, as derived from sources cited above. North American localities were arranged into 14 resolvable stratigraphic intervals, and the localities of other continents were resolved to between 1 and 3 intervals, depending on the region. We treated each of these intervals operationally as a horizon. This approach is conservative insofar as it lumps distinct horizons into one unit, overestimating the proportion of species confined to single horizons and thus underestimating preservation rate. Our approach is also conservative insofar as we generally considered spe-

cies with uncertain stratigraphic ranges as single-horizon taxa. To estimate average stratigraphic ranges of North American species, for which the biochronology is best understood, we assigned absolute ages to the 14 stratigraphic intervals, mainly using correlations with ammonite zones and radiometric dates. See supplemental data at www.sciencemag.org/feature/data/985988.shl.

41. S. M. Stanley, *Macroevolution* (Freeman, San Francisco, 1979).

42. W. B. Harland *et al.*, *A Geologic Time Scale 1989* (Cambridge Univ. Press, Cambridge, 1990).

43. E. Gheerbrant, J. Sudre, H. Cappetta, *Nature* **383**, 68 (1996).

44. R. C. Fox and G. P. Youzwyshyn, *J. Vertebr. Paleontol.* **14**, 382 (1994).

45. We thank J. Alroy, R. J. Asher, J. Flynn, D. Jablonski, C. R. Marshall, R. R. Rogers, P. J. Wagner, and J. R. Wible for discussion, and R. H. De Simone, D. Jablonski, C. R. Marshall, D. M. Raup, and two anonymous referees for reviews. This research was supported by NSF (grant EAR-9506568) and NASA (grant NAGW-1693).

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The Density of Hydrous Magmatic Liquids

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Density measurements on several hydrous (≤ 19 mole percent of H_2O) silicate melts demonstrate that dissolved water has a partial molar volume (\bar{V}_{H_2O}) that is independent of the silicate melt composition, the total water concentration, and the speciation of water. The derived value for \bar{V}_{H_2O} is 22.9 ± 0.6 cubic centimeters per mole at $1000^\circ C$ and 1 bar of pressure, whereas the partial molar thermal expansivity ($\partial \bar{V}_{H_2O} / \partial T$) and compressibility ($\partial \bar{V}_{H_2O} / \partial P$) are $9.5 \pm 0.8 \times 10^{-3}$ cubic centimeters per mole per kelvin and $-3.2 \pm 0.6 \times 10^{-4}$ cubic centimeters per mole per bar, respectively. The effect of 1 weight percent dissolved H_2O on the density of a basaltic melt is equivalent to increasing the temperature of the melt by $\sim 400^\circ C$ or decreasing the pressure of the melt by ~ 500 megapascals. These measurements are used to illustrate the viability of plagioclase sinking in iron-rich basaltic liquids and the dominance of compositional convection in hydrous magma chambers.

The density of a silicate melt affects a wide range of magmatic processes, including melt segregation and transport, melt recharge and mixing in chambers, the viability of convection and crystal settling, and the mechanics of eruption. Water is an important component to include in models of melt density, as it can range up to 8 weight % in magmatic liquids (1), which translates to ~ 25 mol % because of the low molecular weight of H_2O as compared to the average molecular weight of magmatic liquids. Before this study, the only direct density measurements available for hydrous silicate melts were performed on molten albite ($NaAlSi_3O_8$) (2, 3). The large partial molar volume of the H_2O component (total water dissolved as molecular H_2O and as hydroxyl ions), \bar{V}_{H_2O} , in albite melt (3) results in a low density for the H_2O component (0.78 g/cm^3) as

compared to the density range of magmatic liquids (2.3 to 2.8 g/cm^3). This leads to a dramatic effect of dissolved water on melt density. For example, if the value for $\bar{V}_{H_2O}(T, P)$ (T , temperature; P , pressure) derived from albite liquid is applied to the Bishop Tuff rhyolite, then the effect on melt density of adding 1 weight % H_2O (at $750^\circ C$ and 300 MPa) is equivalent to increasing the temperature by $620^\circ C$ or decreasing the pressure by 260 MPa (the results are different for a basalt, which is less compressible and more thermally expansive than a rhyolite).

The outstanding question is whether the values for $\bar{V}_{H_2O}(T, P)$ derived for molten albite (3) can be applied to all igneous liquids or whether there is a compositional dependence to $\bar{V}_{H_2O}(T, P)$. An indirect method for determining \bar{V}_{H_2O} , which has been applied to a variety of silicate melts, is based on fitting a thermodynamic model to the solubility of water. The pressure dependence of the solu-

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