Divergence Times of Eutherian Mammals

In the continuing debate about the timing of the origin of major extant placental clades, both proponents of a divergence after the Cretaceous-Tertiary (K-T) boundary and those advocating divergence deep within the Cretaceous too often miss what the Late Cretaceous record of placentals actually shows. For example, Foote *et al.* (*1*) are correct that many Late Cretaceous reports of extant ordinal and superordinal placental taxa are now questioned (*2*). They are incorrect, however in extending this statement to all such taxa, notably the "zhelestids." Foote *et al.* essentially dismiss "zhelestids" as being "archaic eutherians allied with either *Prokennalestes* or zalambdalestids," thus placing them outside the clade leading to extant placentals. These assertions are not based on the most recent, extensive phylogenetic studies, but rather come from English language publications that cite older, preliminary Russian descriptions of "zhelestids." Recent fieldwork has yielded extensive marine invertebrate faunas overlying the "zhelestid" sites, thus demonstrating a minimum age of 85 million years ago (Ma) (*3*). Recent monographic studies and phylogenetic analyses strongly support the hypothesis that "zhelestids" form a series of stem taxa relative to early Tertiary archaic ungulates (so-called condylarths) that in turn are ancestral to a number of extinct and extant placental orders (*4*). Conversely, some molecular studies have used the "zhelestids" as evidence that some extant orders extend well back into the Late Cretaceous (*5*). Such conclusions, however, are unfounded. The most recent studies of "zhelestids" place them as a series of Late Cretaceous stem taxa most likely related to later ungulates, but the extant orders are not said to extend well into the Late Cretaceous. Thus, the fossil evidence (at least for now) supports the argument that there were some superordinal clades of extant placentals present by the Late Cretaceous, but such evidence cannot be used to extend extant ordinal appearances into the Late Cretaceous. In fact, another empirical study (*6*) that statistically examined the actual first appearances of extant orders in the fossil record does support the contention by Foote *et al.* that extant orders did not appear until shortly after the K-T boundary. Neither of these studies, however, contain data regarding the timing of appearance of superordinal clades of placentals.

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Traditionally, the adaptive radiation of eutherian mammals was thought to have begun about 65 Ma near the K-T boundary (*1, 2*), (herein referred to as the "K-T" hypothesis). Recent molecular studies, however, have suggested that lineage splitting began deep in the Cretaceous at least 100 Ma (*3–5*) (the "early origin" hypothesis). If the latter hypothesis is correct, a gap exists in the fossil record of modern eutherians (*6*). Foote *et al.* (*7*) use mathematical models to estimate the rate of preservation required to explain such a gap. They conclude that it would have to be at least "an order of magnitude" lower than the preservation rate for Cenozoic eutherians. Stating that such a rate difference would be "unlikely," they suggest that the gap does not exist (preservation rate = zero) and that molecular time estimates are biased. But several critical aspects of the model of Foote *et al.* are flawed, and a reassessment of the fossil and molecular evidence of eutherian mammals supports the early origin hypothesis.

The existence of a single modern eutherian fossil from deep in the Cretaceous would indicate that the preservation rate is not zero (*8*), and would reject the K-T hypothesis. The eutherian fossil record (Fig. 1) includes uncontested eutherian mammals as early as late Aptian (112 Ma), and possible eutherians from the earliest Cretaceous, 143 Ma (*9, 10*). Foote *et al.* do not contest the existence of eutherians from the Cretaceous, but consider their assignment to modern orders or superorders as controversial. However, the most recent and comprehensive works concerning these fossils, especially of ungulatomorphs (*11, 12*), support this link to modern eutherians, whereas studies cited by Foote *et al.* as critical of such a link are nearly a decade old (*13*). Foote *et al.* themselves incorporated such fossils in one version of their model (*7*, p. 1310).

The duration of the gap in the fossil record of modern eutherians is a critical parameter of the model by Foote *et al.* Two different upper bounds were used in their report for this gap: 65 Ma (classical K-T hypothesis) and 85 Ma (recognizing Central Asian fossils discussed above). However, the use 65 Ma to calibrate the upper bound is incorrect if any Cretaceous eutherian nests within the crown group. The presence of Late Cretaceous (Maastrichtian; 74 to 65 Ma) leptictids, arctocyonids, pantodonts, notoungulates, and condylarths (*14*), regardless of their assignment to order or superorder of modern eutherians, indicates that the lineage splitting was already well under way before the end of the Cretaceous. As clarification of the second upper bound, we note that earliest ungulatomorph fossils are late Turonian (90 to 89 Ma) or Coniacian (89 to 87 Ma; midpoint = 88 Ma) (*12*).

In all cases, Foote *et al.* (*7*) used one of our molecular time estimates (129 Ma; Fig. 1) as a single lower bound for the earliest split among modern orders of eutherians (*5*). Apparently, they did not consider the variance of this estimate. Although we analyzed a large number of nuclear genes, only three were available for xenarthrans. As we noted, time estimates based on such a small number of genes may be unreliable. Our other time estimates were based on as many as 333 genes, and their variances were much smaller (Fig. 1). The earliest statistically defensible molecular time estimate is the upper bound (105 Ma) of the 95% confidence interval (112 ± 7 Ma) for the split between sciurognath rodents and other eutherians, excluding xenarthrans (Fig. 1). Thus, the adjusted gap for the difference between the earliest molecular time estimate (105 Ma) and earliest fossil evidence of a modern eutherian (88 Ma) is only 17 (not 44 or 64) million years (My) (*7*). Moreover, this gap occurs during a period when eutherians not currently allocated to modern clades are known to have existed (Fig. 1B) but are rare as fossils (*9, 10*).

In their model, Foote *et al.* assume fossil preservation to be "time homogeneous." However, the sudden appearance of most eutherian orders in the early Tertiary fossil record, immediately following the extinction of dinosaurs, suggests a relationship between these two events. The simplest explanation is that mammals filled niches left vacant by reptiles (*1, 2*). A corollary to this hypothesis is that the observed rarity of Cretaceous eutherians is in part a result of large reptiles dominating the ecological landscape (*1*). A low rate of preservation is to be expected if species diversity and population sizes were low. Also, Foote *et al.* assumed that diagnostic morphological divergence occurs immediately after lineage splitting, which biased their results in favor of the K-T hypothesis. But the existence of cryptic species and "liv-
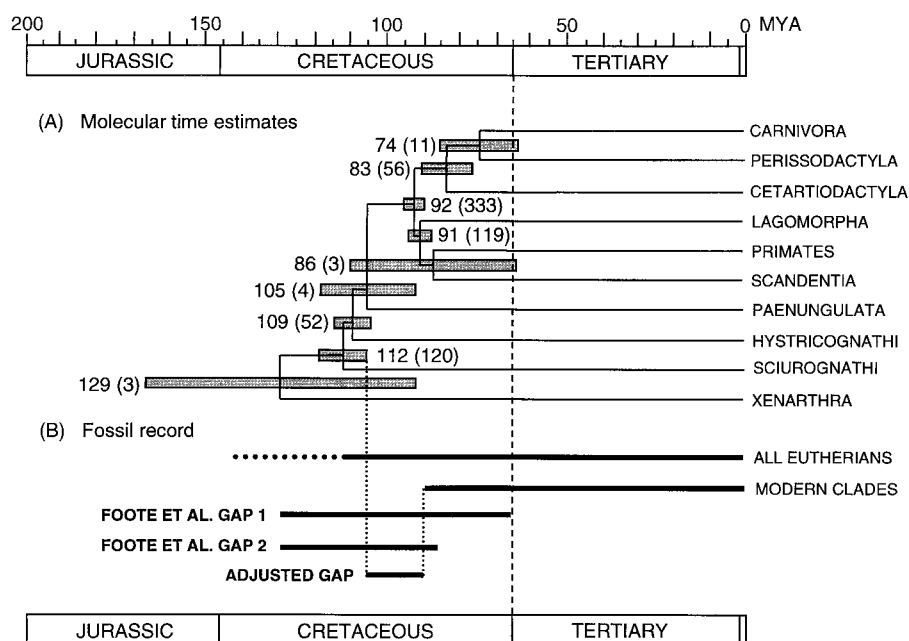
Fig. 1. Time scale for eutherian mammals. (**A**) Molecular estimates of divergence time (*4*). Mean divergence time (Ma) and number of nuclear genes (in parentheses) is given for each node, along with the 95% confidence interval of the mean (gray bar). (**B**) Fossil record (*9–12, 14*). For all eutherians, the solid line indicates uncontested fossil history whereas the dotted line represents a possible early record of a eutherian (*10*). Modern clades include the central Asian ungulatomorphs (*11, 12*). "Foote *et al*. Gap 1 and Gap 2" refers to the two fossil gaps used in the model of Foote *et al*. (*7*). Adjusted gap is difference between the earliest molecular time estimate (considering 95% confidence intervals) and the earliest representative of a modern clade.

ing fossils" (*2*) suggests that morphological differentiation and lineage-splitting are not necessarily coupled. Moreover, the smaller body size of early eutherians (*15*) makes them less likely to be recognizable as members of modern orders.

Other biases in the fossil record include environment (habitat), geographical distribution, preservation potential, and extrinsic factors such as lithofacies variation, postdepositional processes, and distribution of well-studied areas (*16*). Cretaceous eutherians apparently did not occur in a diversity of habitats (*10–12*). Also, sea levels were higher in the Cretaceous, which reduced the area of exposed land available for mammals (*3*). Higher sea levels isolated continents and restricted dispersal of terrestrial organisms (*17*). The wide distribution of eutherian mammals in the early Tertiary, in part, may have been a consequence of continental fusions (*3*) that occurred with the large drop in sea level near the K-T boundary. The rarity of Cretaceous eutherians may thus be the result of any or all of these factors (or others).

Foote *et al*. (*7*) used all Cretaceous mammals to model preservation rate. In doing so, they biased their analysis because metatherians and multituberculates are more abundant than eutherians in the Cretaceous fossil record (*14*). Even in general terms, it is not clear that any one species or group can be used to model preservation of another species or group. For example, humans and chimpanzees are closely related species, yet differ considerably in rates of fossil preservation. Fossils on the human lineage (for example, *Australopithecus* spp., *Homo* spp.) are numerous, yet those for chimpanzees are virtually unknown.

Foote *et al*. (*7*) suggest that the molecular time estimates are incorrect because of rate differences among and within lineages. However, we explicitly tested rate heterogeneity in our studies (*3, 5*) and excluded lineages and genes that did not pass this test. In addition, we measured divergence time with all data and found no consistent directional bias, even in taxa and genes that were excluded (*5*). Variation in the rate of molecular evolution does exist in some cases, but none of the studies cited by Foote *et al*. have demonstrated nuclear genome-wide rate variation of the type or magnitude required in this case nor are their suggested mechanisms supported (*18*).

In conclusion, there is clear evidence that Cretaceous eutherians are rarely preserved, while Tertiary eutherians are abundant in the fossil record. The result presented by Foote *et al*. (*7*) of preservation probabilities is unnecessary even without the problems discussed above, because this pattern is already established. Moreover, such a pattern is compatible with the early origin hypothesis and with the biolog-

ical consequences expected from the K-T extinction of the dinosaurs. Nonetheless, we welcome additional molecular and paleontological evidence to better understand the enigmatic early history of eutherian mammals.

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Foote *et al*. (*1*) have coined the phrase "'Garden of Eden' hypothesis" to label one way of reconciling an anomaly that exists between the times of origin of the extant eutherian orders as estimated from the fossil

record and the substantially older dates indicated for these events by molecular clock data. Vertebrate paleontological evidence puts the times of appearance of most of the earliest representatives of the extant eutherian orders as being soon after the Mesozoic-Cenozoic boundary, 65 Ma, when the nonavian dinosaurs had become extinct (*1, 2*). On the other hand, molecular clock estimates place these fundamental divisions amongst the eutherians significantly earlier, around the mid-Cretaceous (*1, 3*).

Foote *et al*. (*1*) give a detailed stochastic argument as to why the fossil record should be relied on in this matter. They then present four hypotheses to account for the discrepancy. The third of these is that the extant eutherian orders had, in fact, originated at the times estimated by molecular clock evidence, but that these events occurred in areas where there was no Late Cretaceous mammalian paleontological record. They explicitly single out Africa, Australia, and Antarctica as potential areas where these previously undocumented events could have happened. This is their "'Garden of Eden' hypothesis."

During the Mesozoic, microcontinents or terranes were splitting off from the northern edge of eastern Gondwana, northward of modern Australia, and drifting north to collide with southeast Asia. The West Burma terrane, for example, is shown as part of the eastern Gondwana in the Late Jurassic [figure 16A in (*4*)] and part of southeast Asia by Late Cretaceous [figure 16C in (*4*)]. This scenario implies a maximum transit time of 80 million years. Such terranes could easily have served as "Noah's Arks" (*sensu* McKenna, *5*).

The Erinaceidae are first represented in the Northern Hemisphere in the Paleocene (*2*). *Ausktribosphenos nyktos* occurs in the Australian late Early Cretaceous (Aptian) (*6*). It is a possible placental mammal with a dentition remarkably similar to Early Cenozoic erinaceids emplaced in a more primitive jaw (*7*). The jaw is slightly more structurally advanced than in the penecontemporaneous, undoubted placental *Prokennalestes trofimovi* from the late Early Cretaceous of Mongolia (*7, 8*). "The following features of the Erinaceidae listed by Novacek, Bown, and Schankler [*9*] . . . are shared with *Ausktribosphenos nyktos*: progressive reduction in molar size from M_1 to M_3; molars semi-rectangular in outline with some degree of exodaenodonty (i.e. bases of trigonid and talonid cusps are significantly lower on the labial than lingual side of the posterior premolars and anterior molars); M_1 paraconid salient and anteriorly projecting, elongating the prevallid shearing wall; and hypoconulids markedly reduced on M_{1-2}." (*7*).

Although *A. nyktos* is only about 50 million years older than the oldest Northern Hemisphere erinaceids, there is no earlier record of mammals of any kind in Australia. Therefore, the splitting of the stocks which gave rise to the available specimens of *A. nyktos* and the earliest Northern Hemisphere erinaceids could have easily taken place 10 to 30 million years before the age of the oldest known germane fossils. Also, the transit time estimate is a maximum.

Thus, it would seem that the "Garden of Eden" hypothesis may have merit, because (i) relevant fossils of the age expected appear to exist on one of the source continents explicitly specified in the original statement of the hypothesis, and (ii) a plausible mechanism can account for the timing and direction of movement out of the "Garden of Eden" during the Cretaceous for at least one extant eutherian family.

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Response: We thank **Archibald** for discussing the relationships of Late Cretaceous "zhelestids." Recent phylogenetic analyses place this group with varying degrees of confidence. Archibald seems sure of their position; others (*1*) are less certain, partly because the material is fragmentary. We did not "dismiss" the group; we emphasized this uncertainty by stating that they may be archaic placentals [note 22 in (*2*)]. More important, we presented analyses in which we accepted both Archibald's interpretation of "zhelestids" and his estimate of their age, thus implying fewer lineages at the start of the modern placental fossil record (≥7 rather than ≥9) and a smaller gap in this record (44 My rather than 64 My) [note § in table 1 in (*2*)]. Our main conclusion, that a gap as large as required by some molecular clock studies (*3*) is implausible (a conclusion with which Archibald agrees), stood, regardless of how we treated "zhelestids."

Contrary to Archibald's suggestion, we did not contend that no extant orders or supraordinal groupings of placentals could have been present in the Late Cretaceous. Rather, we showed that observed, Late Cretaceous extinction and preservation rates are highly inconsistent with size of the gap (64 My) and the number of terminal Cretaceous lineages (≥9) required by conditions stated by Kumar and Hedges (*3*). As we also showed, however, the gap can be supported statistically if the number of lineages and the size of the gap are much smaller than stated [(figure 3 in (*2*)]. This result does not mean that there necessarily were modern placentals during the Cretaceous, only that we cannot rule it out because our approach constrains the maximum plausible number of lineages, but not the minimum. Nevertheless, as Archibald points out, there may be other, phylogenetic, reasons to believe that no extant orders extended into the Cretaceous (*1*).

Many approaches are consistent in casting doubt on the deep Cretaceous origins of living placental groups, including the analysis of first appearances that Archibald mentions, but which we have had no chance to evaluate, the consideration of "ghose lineages" implied by some morphological phylogenies (*1*), our modeling of diversification and direct measurement of Late Cretaceous rates of extinction and fossil preservation, and possibly even the assessment of molecular data in light of the variation and uncertainty in rate estimates (*4*). Our modeling results are not highly sensitive to the interpretations given to particular fossil groups such as "zhelestids." This robustness reflects the huge discrepancy between actual rates of preservation and hypothetical rates required by a putative major gap.

We thank **Hedges and Kumar** for clarifying their view regarding the "earliest statistically defensible molecular time estimate" for the origin of modern eutherians. We agree that the discrepancy between fossil and molecular dates seems smaller when we consider

the variation in molecular rate estimates (4), but, as we will show, the discrepancy is still unacceptably large. Hedges and Kumar misrepresent our work by suggesting that our conclusions were based in any way on the preservability of Cenozoic mammals. We arrived at our conclusions through a comparison between empirical preservation rates of Cretaceous mammals and the rates required by the early origins hypothesis. Although we mentioned Cenozoic preservation rates, we did not use them in our argument. Rather, we explicitly offered reasons why it would be unwise to apply Cenozoic preservation rates to the Cretaceous. Far from overlooking the increase in abundance of fossil eutherians from the Cretaceous to the Tertiary, we designed our analysis specifically to accommodate this fact. We would like to make two principal points: (i) Eutherian and noneutherian preservation rates do differ in the Cretaceous, but this difference is too small to rescue the early-origins hypothesis, and (ii) even if we accept Hedges and Kumar's calibration of the postulated Cretaceous gap in the modern eutherian record, a calibration that is replete with problems, the gap is still implausible given our knowledge of eutherian preservation rates during the Cretaceous.

Hedges and Kumar associate us with what they call the K-T hypothesis and portray us as suggesting "that the gap does not exist." We did not, however, conclude that no extant orders or supraordinal groupings of eutherians could have been present in the Late Cretaceous, that is, that there is no gap in the record. Rather, we used our data on Late Cretaceous extinction and preservation rates to argue against a very large gap and against a large number of terminal Cretaceous lineages. As we showed, the postulated gap can be supported statistically by our approach if the number of lineages and the size of the gap are substantially smaller than implied by the work of Kumar and Hedges (3). The plausible combinations of gap size and number of lineages can be calculated by the method we present. There are additional, phylogenetic, reasons to believe that few if any modern eutherians extend into the Cretaceous (1), but such reasons did not form a basis of our argument.

Hedges and Kumar point out that one possible explanation for the discrepancy between our results and theirs is the violation of our working assumption that diagnostic morphological features evolve shortly after cladogenesis. The alternative, that morphological evolution is slow and is decoupled from cladogenesis and molecular change, is potentially testable. This point has important implications for evolutionary rates, which is, after all, the question in which we are ultimately interested. We make the very same point in our report (2, p. 1310).

Hedges and Kumar agree with us (2, p. 1310) that the discrepancy between our results and theirs could arise in principle if Cretaceous eutherians had substantially lower preservation rates than Cretaceous noneutherians. To support this possibility, they point out that "metatherians and multituberculates are more abundant than eutherians in the Cretaceous fossil record." But the lower frequency of eutherian fossils could reflect two end-member causes: a smaller original number of species or a lower within-species rate of fossil preservation.

Let us attempt to distinguish between these causes. We have taken the data we used to estimate preservation rate for Late Cretaceous mammals as a whole and have divided them into eutherian and noneutherian subsets. If we include occurrences that cannot be assigned with confidence to a named species as distinct species confined to single stratigraphic horizons, then there are 368 noneutherian species and 92 eutherian species. If we ignore such uncertain occurrences, then the numbers are 178 and 58. The frequency of noneutherian species confined to single horizons is equal to 0.89 if we treat uncertain occurrences as distinct, single-horizon species, and 0.78 of we disregard uncertain occurrences. Following the method outlined in our report and elsewhere (5) and using our previous extinction rate estimate of 0.25 per lineage-million-years (Lmy), these two results imply a preservation rate of 0.031 to 0.073 Lmy^{-1}. For eutherians, the frequency of single-horizon species is 0.91 or 0.86, depending on the treatment of uncertain occurrences, and the corresponding estimates of preservation rate are 0.024 and 0.040 Lmy^{-1}. Thus, the maximal difference between estimated preservation rates of eutherian and noneutherian mammals is less than a factor of two. As we explained in our original report and as we elaborate below, a difference this small is not sufficient to account for the discrepancy between our results and the Kumar-Hedges date for the origin of modern eutherians.

Hedges and Kumar criticize our choice of 65 Ma as the start of the modern eutherian fossil record. No claims for fossil remains of crown-group eutherians before the Tertiary are without controversy. In each case, either the phylogenetic position or the age has been questioned (6). We trust that the difference between this cautionary statement and the bolder statement that no such claims are true (a statement we did not make) is clear. There has been some dispute as to whether a particular group of Late Cretaceous mammals, the "zhelestids," are in fact modern eutherians [note 22 in (2)]. We cannot agree with Hedges and Kumar that this or any controversy should be ignored merely because some of the relevant work is "nearly a decade old." Nevertheless, a more recent and comprehen-

sive phylogenetic study (1) than the ones cited by Hedges and Kumar concluded that the position of "zhelestids" was too difficult to judge with confidence, at least partly because of the fragmentary nature of the material. Because of the controversy surrounding "zhelestids," we chose to calibrate our model in two alternative ways, treating them as archaic eutherians or as modern eutherians. Our purpose was to demonstrate that our substantive conclusions were not materially affected by the treatment of this group.

Although we object, on the grounds of likelihood, to the practice of selecting an extreme value such as the 95% confidence limit as the most reasonable value with which to work, let us, for the sake of discussion, use 105 Ma as Hedges and Kumar's estimate for the time of origin of modern eutherians. Let us also accept that the "zhelestids" are modern eutherians. And let us also accept Hedges and Kumar's estimate that the age of "zhelestids" is 88 Ma, rather than the more commonly cited 85 Ma (7). We are then left with a gap of 17 My in the history of modern placentals and at least seven independent modern placental lineages at the start of the fossil record, according to dates presented in (3) and in figure 1 of the comment by Hedges and Kumar. Seven lineages is a highly conservative number, because it treats each order or supraordinal grouping as if it consisted of a single species. Following the methods of our conditional diversity model and applying our empirical extinction rate estimate of 0.25 Lmy^{-1}, this calibration implies a missing sum of species durations of 172 Lmy. The corresponding maximal plausible preservation rate is 0.004 Lmy^{-1}; the actual preservation rate would have to be this low or lower in order for us to accept the gap with even a minimal confidence level of 0.5. Even our lowest estimate of preservation rate for eutherians alone (0.024 Lmy^{-1}) is six times higher than this critical value, a value derived by accepting all of Hedges and Kumar's contentions. With a preservation rate of 0.024 Lmy^{-1}, the probability that a sum of species durations of 172 Lmy will go unobserved is only 0.016. As a statement of support for a postulated, major gap in the modern eutherian record (a postulate that bears important evolutionary implications), this possibility is not compelling.

We can be more generous still in our treatment of Hedges and Kumar's hypothesis. If we assume an exponential diversity model (which is unrealistically conservative because we know that diversity must have reached a minimal level according to their hypothesis), and if we assume a species extinction rate of zero (which is also unrealistically conservative, given the evidence for abundant extinction in every group of organisms ever studied), we then calculate a missing sum of species durations of 52 Lmy. The corresponding maximal plausible preservation rate

is 0.013 Lmy^{-1} (still a factor of two below our lowest empirical estimate), and the probability that 52 Lmy will escape preservation given our lowest estimate of preservation rate (0.024 Lmy^{-1}) is only 0.29. Thus, even if we accept all of Hedges and Kumar's contentions regarding the gap, and even if we make the most favorable assumptions we can possibly make, then we are still left with a higher probability that their postulated gap is not real than that it exists.

We offered in our report several possible reasons to explain the discrepancy between our results and those of Kumar and Hedges and offered suggestions for their testing. We discussed violations of the molecular clock as only one alternative, one that we think has particularly important implications if true. We did not claim to have unequivocal support for any one of these alternatives. In particular, we did not claim that "molecular time estimates are incorrect" but that they may be incorrect in this particular case. Hedges and Kumar state that they tested for rate variation and are skeptical that there exists documented variation in molecular rates of evolution "of the type or magnitude required in this case." In this regard, the test (8) Kumar and Hedges cite (3) uses constancy as a null hypothesis and, more importantly, relates to variation among lineages. What is especially at issue is systematic temporal variation within lineages (9), that is, an acceleration in rates at about the same time in a number of independent lineages.

We have stated explicitly what the rates of evolution and preservation would have to be in order for us to accept the plausibility of a specified gap in the history of modern eutherians or any other group. We would likewise welcome from Hedges and Kumar an explicit statement regarding the type and magnitude of variation in molecular rates that would lead them to discard the early origins hypothesis.

We welcome the attempt by **Rich *et al.*** to test one hypothesis that might account for the discrepancy between the early origins scenario and our finding (2) that a hidden diversification of the extant placental mammal orders deep in the Cretaceous is unlikely. They focused on our hypothesis (iii) that one or more regions without known Late Cretaceous mammals could have served as a "Garden of Eden" where modern placental orders could have originated. We initially suggested that the "Garden of Eden" hypothesis was testable with intensive fieldwork to recover Late Cretaceous mammals from these regions. Rich *et al.* have not corroborated the "Garden of Eden" hypothesis because (i) the fossil mammals they discuss may not be relevant to the origin of modern placental orders; (ii) even if the fossils are modern placentals, this would imply only a few missing lineages rather than the large number of lineages required by the

early origins scenario that we orginally sought to test.

Rich *et al.* suggest that our "Garden of Eden" hypothesis is corroborated because fossils relevant to the origin of an extant placental mammal family, the Erinaceidae (hedgehogs and gymnures), occur in the Early Cretaceous of Australia. We actually intended our "Garden of Eden" hypothesis to describe a scenario in which numerous lineages of extant placentals might originate in the Cretaceous without a known fossil record, not just one or a few lineages of them. The particular dispersal scenario that Rich *et al.* envision is only relevant if such early fossils, described under the name *Ausktribosphenos nyctos*, do indeed bear on the origin of a group nested deep within modern placental mammals, implying a substantial pre-Cenozoic radiation of modern placentals.

A. nyctos does not necessarily bear on the origin of modern orders of placental mammals. Rich *et al.*'s characterization of this species as a "possible placental" with dental similarities to erinaceids is their preferred hypothesis. In their more comprehensive studies (10, 11), this group was unable to reject alternative hypotheses that *A. nyctos* is a sister-group to all placentals (extant and extinct) or that *A. nyctos* belongs to a lineage of mammals that evolved tribosphenic-like molars independent of the Tribosphenida (that is, placentals, marsupials, and related taxa). Several authors (12, 13) have criticized the assignment of *A. nyctos* to the Placentalia because of extremely primitive features of its lower jaw and some peculiarities in tooth shape and wear, which suggest that *A. nyctos* may instead be an unusual symmetrodont (that is, a "pretribosphenic" mammal). Jaws of *A. nyctos* possess a faint trough where postdentary jawbones probably attached as in the most primitive mammals, unlike the condition in extant mammals and multituberculates where the postdentary bones occur as middle ear ossicles (13). If *A. nyctos* were a true placental mammal, either stem or more derived, then its retention of postdentary bones in the lower jaw would require that these bones became incorporated into an isolated middle ear convergently in marsupials and placentals, contrary to current views (14, 15). Additionally, if one accepts the molar cusp homologies proposed by Rich *et al.* (10, 11), which assume that *A. nyctos* has true tribosphenic molars, then *A. nyctos* has three lower molar crests not present in other mammals with tribosphenic teeth, such as placentals. Other hypotheses of cusp homology, which assume a "pretribosphenic" ancestry of *A. nyctos*, might better account for the pattern of tooth cusps and crests.

Even if one accepts the conclusion by Rich *et al.* that *Ausktribosphenos* is not only a tribosphenid but also a true erinaceid pla-

cental, it is unnecessary to postulate a hidden Cretaceous radiation of modern placentals in Australia or elsewhere. The order Insectivora, which includes the Erinaceidae, consistently appears near the base of the placental mammal tree in both morphological (16) and molecular (17) phylogenies. An early first occurrence of Insectivora requires the postulation of only a few other lineages (perhaps only three) of extant placentals that would have to survive through the Late Cretaceous without leaving a known fossil record. Our results (1) are consistent with a small amount of "missing history," so long as the number of lineages and their summed duration remain small, but they strongly contradict a hidden radiation of dozens of lineages for tens of millions of years, as the molecular clock implies. The occurrence of insectivorans in the Early Cretaceous need not imply deep origins of the full range of extant placental mammals.

A. nyctos is an important fossil find because it occurs in a relatively poorly sampled part of the fossil record both geographically and temporally, but by itself *A. nyctos* does not corroborate the "Garden of Eden" hypothesis.

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