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Response to Comment on “Impacts of the Cretaceous Terrestrial Revolution and KPg Extinction on Mammal Diversification”

William J. Murphy,^{1*} Jan E. Janecka,¹ Tanja Stadler,² Eduardo Eizirik,³ Oliver A. Ryder,⁴ John Gatesy,⁵ Robert W. Meredith,⁵ Mark S. Springer^{5*}

Bininda-Emonds and Purvis reanalyzed our mammalian phylogenetic supermatrix and claim that our results are not significantly different from their delayed-rise hypothesis. We show that our divergence times are ~11 million years later for placental inter- and intraordinal divergences—consistent with a post-Cretaceous-Paleogene (KPg) radiation of most modern mammalian orders—and find no support for the early Eocene delayed-rise hypothesis.

In their comment (1), Bininda-Emonds and Purvis claim that (i) our macroevolutionary analyses “were not made using their supermatrix trees,” (ii) macroevolutionary differences between Meredith *et al.* (2) and Bininda-Emonds *et al.* (3) “are either simply not present or not statistically significant,” and (iii) Meredith *et al.*'s (2) results “confirm, rather than conflict with” their delayed-rise hypothesis for mammalian diversification. We address each of these claims below.

Although we were critical of their matrix representation with parsimony (MRP) supertrees (2), we were not critical of supertree methods in general. We grafted up to 10 lineages onto our time trees for macroevolutionary analyses, but this approach avoided the black-box procedure of MRP supertree construction, as well as data duplications and the use of input trees based on taxonomies, as in Bininda-Emonds *et al.* (3). All of the lineages in the time tree of Fig. 1 (2) are from our supermatrix tree, and the few grafted lineages were derived from maximum likelihood-based analyses of primary sequence data.

Bininda-Emonds *et al.* (3) identified a Cretaceous diversification spike using formal diversification analyses, but previous studies had also indicated clustering of interordinal divergences within the Cretaceous [e.g., (4–6)]. Because the spike of Bininda-Emonds *et al.* (3) is ~11 million years earlier than the spike identified by Meredith *et al.* (2), our results are not equivalent. Bininda-Emonds and Purvis' (1) reanalysis of

our mammalian tree using a generalized additive model (GAM) approach supports this statement: GAM differs from our methodology but reveals the same difference of ~11 million years between the spikes. GAM has advantages and disadvantages (7) compared to fitting explicit models of diversification directly, but because both approaches indicate a Cretaceous interordinal spike at ~82 million years ago (Ma) with our data, the choice of approach is secondary. Bininda-Emonds and Purvis' (1) denial of the 11-million year difference ignores their own GAM results.

The mean difference between Meredith *et al.*'s (2) basal intraordinal diversification dates and those of Bininda-Emonds *et al.* (3) is also ~11 million years. Bininda-Emonds *et al.*'s (3) older divergence dates imply that intraordinal diversification was well under way in the Cretaceous. By contrast, we recovered the vast majority of basal intraordinal cladogenic events after the Cretaceous-Paleogene (KPg) boundary, with only a single order (Eulipotyphla) having a credibility interval that was entirely within the Cretaceous. This diversification pattern, wherein the vast majority of crown mammalian orders originated near or after the KPg extinction, is more consistent with the mammalian fossil record and the long-fuse diversification model (2, 6). Specifically, we suggested that most “modern mammalian orders originated or only acquired their definitive ordinal characteristics after the KPg mass extinction.” We never claimed that there was a significant quantitative increase in the diversity of extant mammalian lineages after the KPg extinction and explicitly stated that there was “no statistical support for a rate increase at or near the KPg boundary.” Nonetheless, the absence of a significant quantitative diversification pulse at or near the KPg boundary says nothing about the qualitative, morphological diversification of mammals into different dimensions of newly emerging ecospace that may have become available at this time. By

contrast with our results, Bininda-Emonds *et al.*'s (3) time tree pushes much of this morphological diversification back into the Cretaceous; to argue otherwise is inaccurate.

Finally, Bininda-Emonds *et al.* (3) argued that the rate of net diversification began to accelerate from the early Eocene onward and referred to this delayed-rise hypothesis as one of the “pivotal macroevolutionary events” for extant mammalian lineages. Our results provide no support for this hypothesis, wherein rates began to increase in response to the extinction of archaic Paleocene lineages or to climatic events such as the “Cenozoic thermal maximum and subsequent Early Eocene Climatic Optimum” (3). Instead, our time trees suggest that diversification rates remained constant from ~78 to 40.4 Ma (Fig. 1). Our analyses did not address the possibility of diversification rate changes after 40.4 Ma, but an increase (or more complicated pattern of increases and decreases) may be postulated to get from ~93 lineages with extant descendants at 40.4 Ma to ~6000 present-day species (8). Bininda-Emonds *et al.* (3) stated that the net diversification rate “remained low until the late Palaeocene, after which it increased more or less continuously until the Miocene epoch,” but the part of mammalian history for which their tree “is at least 85% resolved and for which no dates were interpolated to minimize biases caused by ‘soft’ polytomies or interpolation” (3) only extends from 166.2 to 50.0 Ma. Bininda-Emonds *et al.*'s (3) lineage through time (LTT) plot shows no detectable increase in slope until after 50 Ma when supertree resolution drops below 85% (Fig. 1). Importantly, the only apparent increases in diversification rate between 50 and 40.4 Ma are artifacts of polytomies in muroids, caviomorphs, and hipposiderids (Fig. 1). Stadler's (7) statistical analysis of Bininda-Emonds *et al.*'s (3) supertree detected no rate increases in the “resolved” region of the supertree and only detected rate changes in regions that are saturated with polytomies and interpolated dates, i.e., an increase at 33 Ma and decreases at 30, 8.55, and 3.35 Ma. Accurately testing diversification rate changes in the latter part of the Cenozoic will require further analysis of primary sequence data supporting a fully resolved species-level phylogeny for the vast majority of mammals. The poorly resolved supertree of Bininda-Emonds *et al.* (3) that conflicts sharply in topology with our supermatrix tree (2) is inadequate for this purpose.

In summary, Bininda-Emonds and Purvis (1) asserted that macroevolutionary differences between Meredith *et al.* (2) and Bininda-Emonds *et al.* (3) “are either simply not present or not statistically significant,” but this claim is false and, instead, there are fundamental differences between the two studies that have profound implications for the overall pattern of mammalian diversification. Interordinal and intraordinal diversification are both ~11 million years more ancient in their time tree, and any evidence for a delayed rise of

¹Department of Veterinary Integrative Biosciences, Texas A&M University, College Station, TX 77843, USA. ²Institut für Integrative Biologie, Eidgenössische Technische Hochschule Zurich, 8092 Zurich, Switzerland. ³Faculdade de Biociências, PUCRS, Porto Alegre, RS 90619-900, Brazil. ⁴San Diego Zoo Institute for Conservation Research, Escondido, CA 92027, USA. ⁵Department of Biology, University of California, Riverside, CA 92521, USA.

*To whom correspondence should be addressed: mark.springer@ucr.edu (M.S.S.); wmmurphy@cvm.tamu.edu (W.J.M.)

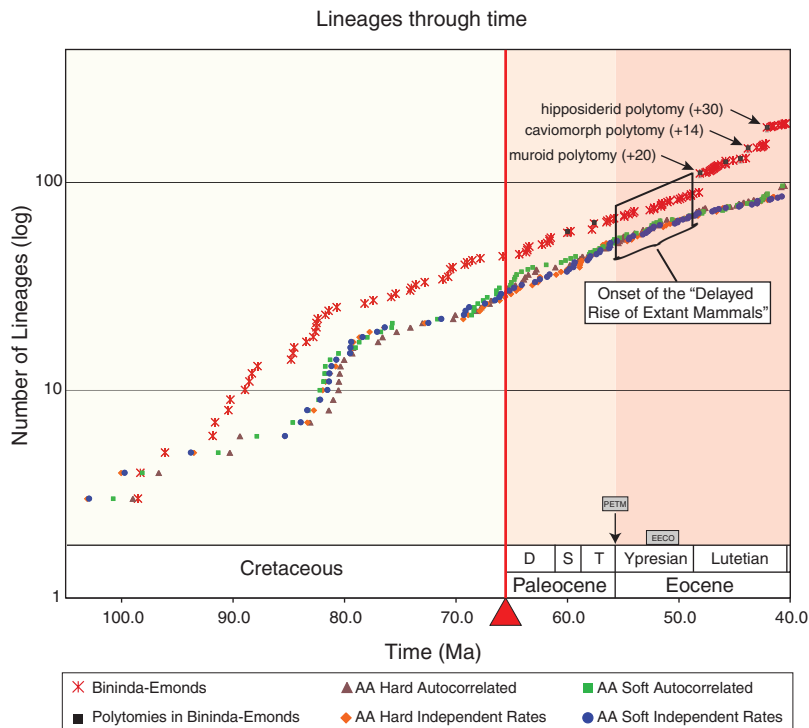


Fig. 1. LTT plots comparing the four amino acid time trees from Meredith *et al.* (2) to the MRP time tree of Bininda-Emonds *et al.* (3). The LTT plot has been truncated to show the time period from ~105 Ma to the end of the Lutetian (40.4 Ma). At 40.4 Ma, there are 191 tips present in the Bininda-Emonds *et al.* (3) time tree, but only 116 internal nodes, so that 74 of 191 lineages (38.7%) result from excess splitting at polytomies. Bininda-Emonds *et al.* (3) postulated that net diversification began to accelerate from the early Eocene onward (“delayed rise of extant mammals”), but the LTT plot shows no indication of a rate increase until after the early Eocene (Ypresian, 55.8 to 48.6 Ma), which corresponds to the region of Bininda-Emonds *et al.*’s (3) LTT plot that is laden with polytomies and interpolated dates. The three largest polytomies occur in Muroidea (20 excess lineages), Caviomorpha (14 additional lineages), and Hipposideridae (30 additional lineages) and result in artificial jumps in the LTT plot. Together, these three polytomies comprise 86.5% of the 74 lineages that result from excess splitting at nonbifurcating nodes. Bininda-Emonds *et al.* (3) also attempted to rectify problems with interpolated dates and poor resolution by using “only those lineages for which neither the beginning nor end dates were interpolated, and which did not start at a polytomy,” but this nonrandom deletion of unresolved and interpolated lineages from their supertree does not provide a satisfactory solution to the manifest problems inherent in their overall analysis. Dates for Paleocene-Eocene Thermal Maximum (PETM) (~55.8 Ma) and Early Eocene Climatic Optimum (EECO) (~53 to 50 Ma) are from Woodburne *et al.* (9). Red vertical line, KPg mass extinction event; D, Danian; S, Selandian; T, Thanetian.

mammals during the Eocene is either absent or artificial (Fig. 1). Given the deficiencies of their overall methodology, we prefer the macroevolutionary inferences derived from our analysis.

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