

Impacts of the Cretaceous Terrestrial Revolution and KPg Extinction on Mammal Diversification

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Previous analyses of relations, divergence times, and diversification patterns among extant mammalian families have relied on supertree methods and local molecular clocks. We constructed a molecular supermatrix for mammalian families and analyzed these data with likelihood-based methods and relaxed molecular clocks. Phylogenetic analyses resulted in a robust phylogeny with better resolution than phylogenies from supertree methods. Relaxed clock analyses support the long-fuse model of diversification and highlight the importance of including multiple fossil calibrations that are spread across the tree. Molecular timetrees and diversification analyses suggest important roles for the Cretaceous Terrestrial Revolution and Cretaceous-Paleogene mass extinction in opening up ecospace that promoted interordinal and intraordinal diversification, respectively. By contrast, diversification analyses provide no support for the Eocene delayed rise of present-day mammals hypothesis.

The ~5400 described species of living mammals evolved to occupy diverse ecological niches and include arboreal, fossorial, volant, aquatic, and terrestrial forms, some of which exhibit 100 million-fold differences in body mass (1, 2). Mammals exhibit striking examples of ecomorphological convergence that has led to contentious debates in modern

systematics (3–5). The diversity of living and extinct mammalian species is documented by an ~220 million year fossil record and has evolved against the backdrop of radical alterations in terrestrial floras during the Cretaceous Terrestrial Revolution (KTR), the Cretaceous-Paleogene (KPg) mass extinction, continental rearrangements, and changes in key environmental parameters such as average global temperature. However, the impact of these drivers on taxonomic diversification, particularly near the KPg boundary, remains controversial (6–8).

Previous molecular studies have elucidated mammalian interordinal relationships (9–11). One study (8) that examined relationships and divergence times among all living mammalian families employed matrix representation with parsimony (MRP) supertrees, and was compromised by including numerous source phylogenies with overlapping data (12, 13). The supertree study (8) proposed that there was a dramatic upturn in diversification rates in the Eocene ~55–50 million years ago (Mya), but this hypothesis was inferred from a topology that contained numerous polytomies, and was dated with a combination of local molecular clocks and pure birth interpolation for internal nodes. Even with these limitations this timetree (8) underpins numerous studies in comparative biology (14–17). Here we report an analysis of relationships, divergence times, and diversification patterns

among 97-99% of mammalian families (1, 2) on the basis of a molecular supermatrix that includes 164 mammals, five outgroups, and 26 gene fragments (tables S1, S2). The resulting DNA and protein alignments comprise 35,603 base pairs (bp) and 11,010 amino acids (AA), respectively. Divergence time estimates from molecular data employed a large assemblage of fossil calibrations (table S3).

Phylogenetic relationships from maximum likelihood (ML) and Bayesian methods are well resolved across the mammalian tree. More than 90% of the nodes have bootstrap support $\geq 90\%$ and posterior probabilities ≥ 0.95 (Fig. 1, figs. S1-S4, table S4). AA and DNA ML trees are in agreement for 163/168 internal nodes (figs. S1-S4). The MRP supertree (8) failed to recover $\sim 30\%$ of our well-supported nodes (Fig. 1). These disagreements occur in some of the most speciose mammalian clades, including bats, rodents, and carnivorans, and may potentially impact the conclusions of numerous studies that have relied on the MRP topology. Our phylogeny improves upon previous resolution (8), and provides a character matrix-based framework for re-evaluating early mammalian divergence times.

Results derived from coalescence methods (18-19) were broadly similar to ML and Bayesian supermatrix methods, but in some cases failed to recover well-substantiated clades such as Amniota, Haplorhini, and Odontoceti (13, figs. S5-S8). Coalescence methods assume that discrepancies between individual gene trees and the species tree are solely the result of incomplete lineage sorting, but our results suggest otherwise and highlight difficulties of applying coalescence methods to deep-level phylogenetic problems where differences between individual gene trees often result from problems such as long branch attraction (13).

Rates of molecular evolution range over an order of magnitude for mammalian lineages (20, 21) and present an exceptional challenge for estimating divergence times. Mammals also have a fossil record that provides numerous constraints for calibrating relaxed clocks (22). Accordingly we selected minimum and maximum constraints for 82 different nodes (table S3). Unlike previous studies (8-11), outgroup representation in our analyses provided well-constrained fossil calibrations that precede mammalian diversification and allowed us to bracket controversial interordinal divergences with both older and younger calibrated nodes. Further, we employed relaxed clock molecular dating methods that utilized eight different combinations of molecule type (DNA versus AA), evolutionary rate (autocorrelated versus independent rates), and hard- versus soft-bounded constraints.

Molecular timetree analyses that used subsets of constraints that were either temporally restricted (deep versus shallow nodes) or topologically confined to groups with fast (rodents) or slow (cetaceans) rates of molecular evolution

resulted in poor estimates of divergence times that are in direct conflict with the fossil record (13, table S5). For example, the fossil record provides robust support for the origin of crown-group mysticetes (baleen whales) no later than 20.4 million years ago (23), but soft-bounded analyses with only rodent constraints suggested an age as young as four million years for Mysticeti. These results demonstrate that lineage-specific rate variation can have severe effects on resulting divergence dates when fossil calibrations are sparse and/or unevenly distributed throughout the tree, and suggest that appropriate caution should accompany molecular timetree analyses for taxonomic groups with extensive rate variation and a poor fossil record.

By contrast, all eight relaxed clock analyses that utilized the full suite of fossil constraints yielded divergence time estimates that are largely consistent with each other and with the fossil record (tables S6 and S7). The mean date for the split between placentals and marsupials is ~ 190 Mya (table S6) and accords well with the discovery of a stem eutherian from the Jurassic (24). Our analyses suggest that only 29-32 mammalian lineages, nearly all of which are stem branches leading to extant orders, may have crossed the KPg boundary (Fig. 1, table S8). Several orders have point estimates of basal diversification that precede the KPg, but only in the case of Eulipotyphla are the composite credibility intervals entirely within the Cretaceous (Table 1, Fig. 2A). This inference is consistent with the Long Fuse Model of mammalian diversification (10, 25), which postulates interordinal diversification in the Cretaceous followed by intraordinal diversification that is mostly restricted to the Cenozoic (Fig. 2A), although conflicts do remain with the Cretaceous eutherian fossil record (7). By contrast, the MRP supertree analysis (8) estimated that $\sim 50\%$ more placental lineages with extant descendants survived the mass extinction at the end of the Cretaceous, and also recovered confidence intervals for basal cladogenic events in seven placental orders that are entirely in the Cretaceous.

Taxon sampling in our data set was chosen to index deeper nodes in Mammalia, and with minor augmentation is complete or nearly so for lineages with extant descendants that diversified in the Cretaceous, Paleocene, and Eocene up through the end of the Lutetian (40.4 Mya; middle Eocene) (13, table S9). Lineage-through-time (LTT) plots from molecular timetrees were analyzed with two statistical methods to detect diversification rate shifts (Fig. 2, B and C) (13, 17, 26). Analyses with both DNA and AA timetrees identified rate increases in the Cretaceous, either at ~ 100 Mya and/or ~ 83 Mya, followed by a rate decrease at ~ 78 Mya (ΔAIC_{RC} test, table S10). This increase in the mammalian diversification rate corresponds to interordinal cladogenesis, and is apparent in diversification plots (Fig. 2D). This is consistent with Benton's hypothesis that the KTR (125-80

Mya), during which the angiosperm component of floras increased from 0 to 80%, was a key event in the diversification of mammals and birds (27).

By contrast, there was no statistical support for a rate increase at or near the KPg boundary. However, the finding that basal cladogenesis for the majority of orders occurred in the Cenozoic, and that only one order has a 95% credibility interval that is entirely restricted to the Cretaceous, supports the hypothesis (28) that modern mammalian orders originated or only acquired their definitive ordinal characteristics after the KPg mass extinction that resulted in the final demise of non-avian dinosaurs. Whereas previous molecular studies have suggested intraordinal divergences as far back as the early Cretaceous, our results are in better agreement with the fossil record (7) and suggest that we are unlikely to find crown rodents or primates in rocks that are older than the latest Cretaceous (base of the Maastrichtian, 70.6 Mya).

The delayed rise of present-day mammals hypothesis (8) suggests that diversification rates in the direct ancestors of extant mammals were relatively low in the Paleocene before increasing in the Eocene, possibly in response to abiotic drivers (Paleocene-Eocene Thermal Maximum, early Eocene Climatic Optimum) and/or the extinction of Paleocene species that had previously inhibited the ancestors of present-day mammals (8). Our results contradict this hypothesis. No significant rate increases were detected during the early or middle Eocene (Fig. 2). Importantly, diversification rates in the ancestors of present-day mammals were not repressed by Paleocene lineages that subsequently went extinct (8).

The results reported here provide a robust molecular phylogeny for mammalian families and a solid foundation for resolving the remainder of the mammalian hierarchy below the family level. Molecular timetree analyses based on this phylogeny and a comprehensive set of fossil constraints resulted in divergence time estimates that contradict the 'delayed rise of placental mammals' hypothesis. Rather, our results are consistent with the hypothesis that both the KTR and the KPg mass extinction played important roles in the early diversification and adaptive radiation of mammals. The KTR increased ecospace diversity, possibly precipitating interordinal diversification, whereas the KPg mass extinction made more of this ecospace available for mammals, promoting the emergence of crown-group orders with their distinctive morphological adaptations.

References and Notes

1. D. E. Wilson, D. M. Reeder, *Mammal Species of the World*, 3rd Edition (Johns Hopkins University Press, Baltimore, MD, 2005).
2. R. M. Nowak, *Walker's Mammals of the World*, 6th Edition (Johns Hopkins University Press, Baltimore, MD, 1999).
3. J. D. Pettigrew, *Science* **14**, 231(1986).
4. R. M. Adkins, R. L. Honeycutt, *Proc. Natl. Acad. Sci. U.S.A.* **88**, 10317 (1991).
5. M. S. Springer et al., *Nature* **388**, 61 (1997).
6. S. B. Hedges, P. H. Parker, C. G. Sibley, S. Kumar, *Nature* **381**, 286 (1996).
7. J. R. Wible, G. W. Rougier, M. J. Novacek, R. J. Asher, *Nature* **447**, 1003 (2007).
8. O. R. P. Bininda-Emonds et al., *Nature* **446**, 507 (2007).
9. W. J. Murphy et al., *Science* **294**, 2348 (2001).
10. M. S. Springer, E. Eizirik, W. J. Murphy, S. J. O'Brien, *Proc. Natl. Acad. Sci. U.S.A.*, **100**, 1056 (2003).
11. R. W. Meredith et al., *J. Mammal. Evol.*, **15**, 1 (2008).
12. A. de Queiroz, J. Gatesy, *Trends Ecol Evol.* **22**, 34 (2007).
13. See supporting material on Science Online.
14. T. J. Davies et al. *Proc. Natl. Acad. Sci. U.S.A.*, **105**, 11556 (2008).
15. N. Cooper, A. Purvis, *Am. Nat.* **175**, 727 (2010).
16. W. Thuiller, et al. *Nature* **470**, 531 (2011).
17. T. Stadler, *Proc. Natl. Acad. Sci. U.S.A.*, **108**, 6187 (2011).
18. L. Liu, L. Yu, D. K. Pearl, S. V. Edwards, *Syst. Biol.* **58**, 468 (2009).
19. L. Liu, L. Yu, L. Kubatko, D. K. Pearl, S. V. Edwards. *Mol. Phylogenet. Evol.* **53**, 320 (2009).
20. C. R. Marshall, E. C. Raff, R. A. Raff, *Proc. Natl. Acad. Sci. U.S.A.*, **91**, 12283 (1994).
21. R. W. Meredith, J. Gatesy, W. J. Murphy, O. A. Ryder, M. S. Springer, *PLoS Genetics* **5**, e1000634 (2009).
22. M. J. Benton, P. C. J. Donoghue, R. J. Asher, in *The Timetree of Life*, S. B. Hedges, S. Kumar, Eds. (Oxford Univ. Press, New York, 2009), pp 35-86.
23. E. M. G. Fitzgerald, *Cranbrook Inst. Sci. Misc. Publ.* **1**, 25 (2005).
24. Z.-X. Luo, C.-X. Yuan, Q.-J. Meng, *Nature* **476**, 442 (2011).
25. J. D. Archibald, D. H. Deutschman, *J. Mammal. Evol.* **8**, 107 (2001).
26. D. L. Rabosky, *Evol. Bioinform. Online* **2006**, 257 (2006).
27. M. J. Benton, *Philos. Trans. R. Soc. Lond. B* **365**, 3667 (2010).
28. L. Van Valen, *Evolution* **25**, 420 (1973).
29. W. J., Murphy, T. Pringle, T. Crider, M. S. Springer, W. Miller, *Genome Res.* **17**, 413 (2007).
30. H. Nishihara, S. Maruyama, N. Okada, *Proc. Natl. Acad. Sci. U.S.A.*, **106**, 5235 (2009).
31. D. E. Wildman et al., *Proc. Natl. Acad. Sci. U.S.A.*, **104**, 14395 (2007).
32. Z. C. Hou, R. Romero, D. E. Wildman, *Mol. Phylogenet. Evol.* **52**, 660 (2009).
33. B. M. Hallstrom, A. Janke, *Mol. Biol. Evol.* **27**, 2804 (2010).

34. M. S. Springer, C. W. Krajewski, R. W. Meredith, in *The Timetree of Life*, S. B. Hedges, S. Kumar, Eds. (Oxford Univ. Press, New York, 2009), pp. 466-470.
35. M. R. Dawson, L. Marivaux, C. Li, K. C. Beard, G. Metais, *Science* **311**, 1456 (2006).
36. R. L. Honeycutt, in *The Timetree of Life*, S. B. Hedges, S. Kumar, Eds. (Oxford Univ. Press, New York, 2009), pp. 490-494.
37. C. M. Deschamps, A. I. Olivares, E. C. Vieytes, M. G. Vucetich, *J. Vertebr. Paleontol.* **27**, 683 (2007).
38. E. Eizirik, W. J. Murphy, in *The Timetree of Life*, S. B. Hedges, S. Kumar, Eds. (Oxford Univ. Press, New York, 2009), pp. 504-507.
39. C. M. Miller-Butterworth *et al.*, *Mol. Biol. Evol.* **24**, 1553 (2007).
40. E. C. Teeling, in *The Timetree of Life*, S. B. Hedges, S. Kumar, Eds. (Oxford Univ. Press, New York, 2009), pp. 499-503.
41. J. Gatesy, in *The Timetree of Life*, S. B. Hedges, S. Kumar, Eds. (Oxford Univ. Press, New York, 2009), pp. 511-515.
42. O. Madsen *et al.*, *Nature* **409**, 610 (2001).
43. W. J. Murphy *et al.*, *Nature* **409**, 614 (2001).
44. H. Amrine-Madsen, K.-P. Koepfli, R. K. Wayne, M. S. Springer, *Mol. Phylogenet. Evol.* **28**, 225 (2003).
45. E. C. Teeling *et al.*, *Science* **307**, 580 (2005).
46. J. E. Janecka *et al.*, *Science* **318**, 792 (2007).
47. M. S. Springer *et al.*, *Syst. Biol.* **56**, 673 (2007).
48. A. Rambaut, Se-Al: Sequence Alignment Editor, 2.0a11. <http://evolve.zoo.ox.ac.uk> (1996).
49. A. Löytynoja, N. Goldman, *Science* **320**, 1632 (2008).
50. D. Posada, *Mol. Biol. Evol.* **25**, 1253 (2008).
51. S. Guindon, O. Gascuel, *Syst. Biol.* **52**, 696 (2003).
52. F. Abascal, R. Zardoya, D. Posada, *Bioinformatics* **21**, 2104 (2005).
53. Z. Yang, *Computational Molecular Evolution* (Oxford Univ. Press, Oxford, 2006).
54. A. Stamatakis, *Bioinformatics* **22**, 2688 (2006).
55. M. Miller, The CIPRES Portals. CIPRES. 2009-08-04. URL: http://www.phylo.org/sub_sections/portal. Accessed: 2009-08-04; <http://www.webcitation.org/5imQlJeQa>.
56. J. P. Huelsenbeck, F. Ronquist, *Bioinformatics* **17**, 754 (2001).
57. F. Ronquist, J. P. Huelsenbeck, *Bioinformatics* **19**, 1572 (2003).
58. J. C. Wilgenbusch, D. L. Warren, D. L. Swofford, AWTY: A system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. <http://ceb.csit.fsu.edu/awty> (2004).
59. J. A. A. Nylander, J. C. Wilgenbusch, D. L. Warren, D. L. Swofford, *Bioinformatics* **24**, 581 (2008).
60. Z. Yang, *Mol. Biol. Evol.* **24**, 1586 (2007).
61. B. Rannala, Z. Yang, *Syst. Biol.* **56**, 453 (2007).
62. R. W. Meredith, M. A. Mendoza, K. K. Roberts, M. Westerman, M. S. Springer, *J. Mamm. Evol.* **17**, 75 (2010).
63. M. S. Springer, R. W. Meredith, J. E. Janecka, W. J. Murphy, *Phil. Trans. R. Soc. B* **366**, 2478 (2011).
64. F. M. Gradstein, J. G. Ogg, in *The Timetree of Life*, S. B. Hedges, S. Kumar, Eds. (Oxford Univ. Press, New York, 2009), pp. 26-34.
65. D. L. Rabosky, *Evolution* **60**, 1152 (2006).
66. O. R. P. Bininda-Emonds *et al.*, *Syst. Biol.* **52**, 724 (2003).
67. S. A. Price, O. R. P. Bininda-Emonds, J. L. Gittleman, *Biol. Rev. Camb. Philos. Soc.* **80**, 445 (2005).
68. J. Gatesy, P. Arctander, in *Antelopes, Deer, and Relatives: Fossil Record, Behavioral Ecology, Systematics, and Conservation*, E. Vrba, G. Schaller, Eds. (Yale University Press, New Haven, Connecticut, 2000), pp. 143-155.
69. R. Grenyer, A. Purvis, *J. Zool. (Lond.)* **260**, 245 (2003).
70. J. Gatesy, M. S. Springer, in *Phylogenetic Supertrees: Combining Information to Reveal the Tree of Life, Computational Biology, Volume 4*, O. R. P. Bininda-Emonds, Ed. (Kluwer, Netherlands, 2004), pp. 369-388.
71. M. O. Woodburne *et al.*, *J. Vertebr. Paleontol.* **13**, 483 (1993).
72. T. Rowe, T. H. Rich, P. Vickers-Rich, M. Springer, M. O. Woodburne, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1238 (2008).
73. F. J. Goin, M. R. Sanchez-Villagra, M. A. Abello, R. F. Kay, *Palaeontology* **50**, 1267 (2007).
74. F. J. Goin, A. M. Candela, M. A. Abello, E. V. Oliveira, *Zool. J. Linn. Soc.* **155**, 867 (2009).
75. F. J. Goin, in *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*, R. F. Kay, Ed. (Smithsonian Institution, Washington, DC, 1997), pp. 187-206.
76. L. G. Marshall, *J. Paleontol.* **50**, 402 (1976).
77. O. A. Reig, J. A. W. Kirsch, L. G. Marshall, in *Possums and Opossums: Studies in Evolution*, M. Archer, Ed. (Surrey Beatty and Sons, Chipping Norton, New South Wales, 1987), pp. 1-90.
78. I. Horovitz *et al.*, *PLoS ONE* **4**, e8278 (2009).
79. W. D. Turnbull, E. L. Lundelius, Jr., M. Archer, *Bull. Am. Mus. Nat. Hist.* **279**, 513 (2003).
80. L. R. S. Schwartz, *Palaeontology* **49**, 991 (2006).
81. D. Megirian, P. Murray, L. Schwartz, C. von der Borch, *Aust. J. Earth Sci.* **51**, 701 (2004).
82. H. Godthelp, M. Archer, R. Cifelli, S. J. Hand, C. F. Gilkeson, *Nature* **256**, 514 (1992).
83. M. Archer *et al.*, *Aust. Mammal.* **21**, 1 (1999).
84. S. Wroe, *Palaeontology* **42**, 501 (1999).
85. W. Miller *et al.*, *Genome Res.* **19**, 213 (2009).
86. J. Long, M. Archer, T. F. Flannery, S. J., *Hand Prehistoric Mammals of Australia and New Guinea: One Hundred Million Years of Evolution* (Univ. New South Wales Press, Sydney, 2002).
87. K. J. Travouillon, M. Archer, S. J. Hand, H. Godthelp, *Alcheringa* **1**, (Special Issue), 323 (2006).
88. S. Wroe, in *Predators with Pouches: The Biology of Marsupial Carnivores*, M. Jones, C. Dickerman, M. Archer, Eds. (CSIRO, Collingwood, Australia, 2003), pp. 102-123.
89. J. A. Case, R. W. Meredith, J. Person, *Mus. No. Ariz. Bull.* **65**, 659 (2009).
90. B. P. Kear, N. S. Pledge, *Aust. J. Zool.* **55**, 331 (2008).
91. B. P. Kear, B. N. Cooke, M. Archer, T. F. Flannery, *J. Paleontol.* **81**, 1147 (2007).
92. T. J. Gaudin, D. G. Branham, *J. Mamm. Evol.* **5**, 237 (1998).
93. M. J. Benton, P. C. J. Donoghue, *Mol. Biol. Evol.* **24**, 26 (2007).
94. A. A. Carlini *et al.*, in *Abstracts, IV International Congress of Systematic and Evolutionary Biology*, B. Cox, J. Reveal, Eds. (University of Maryland, College Park, Maryland, 1990), p. 325.

95. A. A. Carlini, G. J. Scillato-Yané, S. F. Vizcaíno, M. T. Dozo, *Ameghiniana* **29**, 176 (1992).
96. M. C. McKenna, A. R. Wyss, J. J. Flynn, *Am. Mus. Novit.* **3536**, 1 (2006).
97. M. O. Woodburne, W. J. Zinsmeister, *Science* **218**, 284 (1982).
98. S. A. Marenssi, M. A. Reguero, S. N. Santillana, S. F. Vizcaíno, *Antarct. Sci.* **6**, 3 (1994).
99. K. D. Rose, R. J. Emry, T. J. Gaudin, G. Storch, in *The Rise of Placental Mammals: Origin and Relationships of the Major Extant Clades*, K. D. Rose, J. D. Archibald, Eds. (Johns Hopkins Univ. Press, Baltimore, Maryland, 2005) pp. 106-126.
100. S. F. Vizcaíno, G. J. Scillato-Yané, *Antarct. Sci.* **7**, 407 (1995).
101. R. D. E. MacPhee, M. A. Reguero, *Am. Mus. Novit.* **3689**, 1 (2010).
102. L. P. Bergqvist, É. A. L. Abrantes, L. S. Avilla, *Geodiversitas* **26**, 323 (2004).
103. P. Vignaud *et al.*, *Science* **418**, 152 (2002).
104. A.-E. Lebatard *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 3226 (2008).
105. P. Tassy, in *Lothagam: The Dawn of Humanity in Eastern Africa*, M. G. Leakey, J. M. Harris, Eds. (Columbia Univ. Press, New York, 2003), pp. 331-358.
106. J. Shoshani, P. Tassy, *Quat. Int.* **126-128**, 5 (2005).
107. M. Pickford, L. J. Hlusko, *Kirtlandia* **56**, 106 (2007).
108. S. H. Ambrose, C. M. Nyamai, E. M. Mathu, M. A. J. Williams, *Kirtlandia* **56**, 53 (2007).
109. D. P. Domning, *Proc. San Diego Soc. Nat. Hist* **29**, 177 (1994).
110. M. Voss, *N. Jb. Geol. Paläont. Abh* **249**, 257 (2008).
111. D. P. Domning, in *Evolution of Tertiary Mammals of North America, Volume 2*, C. M. Janis, G. F. Gunnell, M. D. Uhen, Eds. (Cambridge Univ. Press, New York, 2008), pp. 629-638.
112. M. C. McKenna, S. K. Bell, *Classification of Mammals above the Species Level* (Columbia Univ. Press, New York, 1997).
113. R. Tabuce, R. J. Asher, T. Lehmann, *Mammalia* **72**, 2 (2008).
114. D. M. Avery, *J. Hum. Evol.* **41**, 113 (2001).
115. E. R. Seiffert, E. L. Simons, T. M. Ryan, T. M. Bown, Y. Attia, *J. Vertebr. Paleontol.* **24**, 963 (2007).
116. E. Gheerbrant, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 10717 (2009).
117. J. Meng, *Bull. Am. Mus. Nat. Hist.* **285**, 93 (2004).
118. R. J. Asher *et al.*, *Science* **307**, 1091 (2005).
119. C. Li, J. Meng, Y. Wang, *Bull. Carnegie Mus. Nat. Hist* **39**, 97 (2007).
120. K. D. Rose *et al.*, *Proc. Biol. Sci.* **275**, 1203 (2008).
121. T. P. Eiting, G. F. Gunnell, *J. Mamm. Evol.* **16**, 151 (2009).
122. G. Storch, B. Sigé, J. Habersetzer, *Paläontol. Zeit (Hambg.)* **76**, 189 (2002).
123. G. F. Gunnell, N. B. Simmons, *J. Mamm. Evol.* **12**, 209 (2005).
124. P. Hulva, I. Horáček, P. Benda, *BMC Evol. Biol.* **7**, 165 (2007).
125. B. K. Lim, *Chiroptera Neotropical* **15**, 391 (2009).
126. N. B. Simmons, J. H. Geisler, *Bull. Am. Mus. Nat. Hist.* **235**, 1 (1998).
127. G. S. Morgan, N. J. Czaplewski, *J. Mammal.* **84**, 729 (2003).
128. N. J. Czaplewski, G. S. Morgan, S. A. McLeod, in *Evolution of Tertiary Mammals of North America, Volume 2*, C. M. Janis, G. F. Gunnell, M. D. Uhen, Eds. (Cambridge Univ. Press, New York, 2008), pp. 174-197.
129. M. A. Cozzuol, *J. S. Am. Earth Sci.* **21**, 185 (2006).
130. X.-M. Wang, R. H. Tedford, in *The Terrestrial Eocene-Oligocene Transition in North America*, D. R. Prothero and R. J. Emry, Eds. (Cambridge Univ. Press, New York, 1996), pp. 433-452.
131. M. Spaulding, J. J. Flynn, *J. Vertebr. Paleontol.* **29**, 1212 (2009).
132. H. N. Bryant, *J. Paleontol.* **67**, 1032 (1993).
133. J. Krause *et al.*, *BMC Evol. Biol.* **8**, 220 (2008).
134. R. M. Hunt, in *Evolution of Tertiary Mammals of North America, Volume 1*, C. M. Janis, K. M. Scott, L. L. Jacobs, Eds. (Cambridge Univ. Press, New York, 1998), pp. 196-227.
135. K. D. Rose, *The Beginning of the Age of Mammals* (Johns Hopkins Univ. Press, Baltimore, Maryland, 2006).
136. J. A. Finarelli, *J. Mamm. Evol.* **15**, 231 (2008).
137. X. Wang, M. C. McKenna, D. Dashzeveg, *Am. Mus. Novit.* **3483**, 1 (2005).
138. W. Banyue, Q. Zhanxiang, *Bull. Am. Mus. Nat. Hist.* **279**, 116 (2003).
139. J. J. Sato *et al.*, *Mol. Phylogenet. Evol.* **53**, 907 (2009).
140. J. A. Baskin, *Evolution of Tertiary Mammals of North America, Volume 1*, C. M. Janis, K. M. Scott, L. L. Jacobs, Eds. (Cambridge Univ. Press, New York, 1998), pp. 152-173.
141. M. Wolsan, B. Lange-Badré, *Acta Palaeontol. Pol.* **41**, 277 (1996).
142. M. Wolsan, *Acta Palaeontol. Pol.* **44**, 223 (1999).
143. J. J. Sato *et al.*, *Zool. Sci.* **20**, 243 (2003).
144. M. Wolsan, in *Abstracts of Plenary, Symposium, Poster and Oral Papers Presented at Ninth International Mammalogical Congress (IMC 9): Roles of Mammalogy on Coexistence of Wild Mammals and Human, July 31-August 5, 2005, Sapporo, Hokkaido, Japan* (Science Council of Japan and Mammalogical Society of Japan, Tokyo, 2005), pp. 372-373.
145. T. A. Deméré, A. Berta, P. J. Adam, *Bull. Am. Mus. Nat. Hist.* **279**, 32 (2003).
146. G. D. Wesley-Hunt, J. J. Flynn, *J. Syst. Palaeontol.* **31**, 1 (2005).
147. J. A. Holliday, Dissertation (The Florida State Univ. College of Arts and Sciences, 2007).
148. E. Barycka, *Mamm. Biol.* **72**, 257 (2007).
149. G. Veron, M. Colyn, A. E. Dunham, P. Taylor, P. Gaubert, *Mol. Phylogenet. Evol.* **30**, 582 (2004).
150. R. M. Hunt, R. H. Tedford, in *Mammal Phylogeny: Placentals*, F. S. Szalay, M. J. Novacek, M. C. McKenna, Eds. (Springer-Verlag, New York, 1993), pp. 53-73.
151. S. M., Goodman, R. M. Rasoloarison, J. U. Ganzhorn, *Zoosystema* **26**, 129 (2004).
152. Flynn, J. J., in *Carnivore Behavior, Ecology, and Evolution, Volume 2*, J. L. Gittleman, Ed. (Cornell Univ. Press, New York, 1996), pp. 542-581.
153. E. R. Seiffert, E. L. Simons, Y. Attia, *Nature* **422**, 421 (2003).
154. S. Bajpai *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 11093 (2008).
155. K. D. Rose *et al.*, *J. Human Evol.* **56**, 366 (2009).
156. J. I. Bloch, M. T. Silcox, D. M. Boyer, E. J. Sargis, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 1159 (2007).
157. G. V. R. Prasad *J. Biosci.* **34**, 649 (2009).

158. E. R. Seiffert et al., *Science* **310**, 300 (2005).
159. B. A. Williams, R. F. Kay, E. C. Kirk, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 4797 (2010).
160. K. C. Beard, T. Qi, M. R. Dawson, B. Wang, C. Li, *Nature* **368**, 604 (1994).
161. J. B. Rossie, X. Ni, K. C. Beard, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 4381 (2006).
162. R. F. Kay et al., *J. Human Evol.* **54**, 323 (2008).
163. R. F. Kay, B. J. MacFadden, R. H. Madden, H. Sandeman, F. Anaya, *J. Vertebr. Paleontol.* **18**, 189 (1998).
164. R. Tabuce et al., *Proc. R. Soc. B* **276**, 4087 (2009).
165. T. Harrison, P. Andrews, *J. Human Evol.* **56**, 479 (2009).
166. N. M. Young, L. MacLachy, *J. Hum. Evol.* **46**, 163 (2004).
167. J. A. Finarelli, W. C. Clyde, *Paleobiology* **30**, 614 (2004).
168. M. I. Jensen-Seaman, K. A. Hooper-Boyd, in *Encyclopedia of Life Sciences (ELS)* (Wiley, Chichester, 2008).
169. E. R. Seiffert, E. L. Simons, *J. Human Evol.* **41**, 577 (2001).
170. E. R. Seiffert, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 5000 (2006).
171. E. R. Seiffert, J. M. G. Perry, E. L. Simons, D. M. Boyer, *Nature* **461**, 1118 (2009).
172. Y. Tong, *Vert. Palasiatica* **26**, 214 (1988).
173. M. O. Woodburne, G. F. Gunnell, R. K. Stucky, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 13399 (2009).
174. M. J. Benton, P. C. J. Donoghue, R. J. Asher, in *The Timetree of Life*, S. B. Hedges, S. Kumar, Eds. (Oxford Univ. Press, New York, 2009), pp. 35-86.
175. A. V. Lopatin, *Paleontol. J.* **33**, 182 (1999).
176. R. Ziegler, *N., Jb. Geol. Paläont. Abh.* **246**, 183 (2007).
177. A. V. Lopatin, *Paleontol. J.* **40**, S205 (2006).
178. S. Bajpai, P. D. Gingerich, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 15464 (1998).
179. M. D. Uhen, *Annu. Rev. Earth Planet. Sci.* **38**, 189 (2010).
180. M. A. O'Leary, J. Gatesy, *Cladistics* **24**, 397 (2008).
181. J. M. Theodor, *J. Paleont.* **78**, 39 (2004).
182. E. B. Davis, in *The Evolution of Artiodactyls*, D. R. Prothero, S. Foss, Eds. (Johns Hopkins Univ. Press, Baltimore, Maryland, 2008), pp. 227-240.
183. R. E. Drake, J. A. Van Couvering, M. H. Pickford, G. H. Curtis, J. A. Harris, *J. Geol. Soc. Lond.* **145**, 479 (1988).
184. C. M. Janis, E. Manning, in *Evolution of Tertiary Mammals of North America, Volume 1*, C. M. Janis, K. M. Scott, L. L. Jacobs, Eds. (Cambridge Univ. Press, New York, 1998), pp. 491-507.
185. M. Bisconti, *J. Vertebr. Paleontol.* **30**, 943 (2010).
186. R. Kellogg, *Proc. U.S. Natl. Mus.* **61**, 1 (1922).
187. T. A. Deméré, A. Berta, M. R. McGowen, *J. Mammal. Evol.* **12**, 99 (2005).
188. M. Steeman et al., *Syst. Biol.* **58**, 573 (2009).
189. F. G. Marx, *J. Mammal. Evol.* **18**, 77 (2011).
190. N. Solounias, J. C. Barry, R. L. Bernor, E. H. Lindsay, S. M. Raza, *J. Vertebr. Paleontol.* **15**, 806 (1995).
191. I. A. Vislobokova, A. V. Lavrov, *Paleontol. J.* **43**, 326 (2009).
192. D. R. Prothero, in *The Evolution of Artiodactyls*, D. R. Prothero, S. Foss, Eds. (Johns Hopkins Univ. Press, Baltimore, Maryland, 2008), pp. 221-226.
193. M. J. Orliac, A. Pierre-Olivier, S. Ducrocq, *Zool. Scripta* **39**, 315 (2010).
194. J. M. Harris, L. Li-Ping, in *The Evolution of Artiodactyls*, D. R. Prothero, S. Foss, Eds. (Johns Hopkins Univ. Press, Baltimore, Maryland, 2008), pp. 130-150.
195. E. D. Mitchell, *Can. J. Fish. Aquat. Sci.* **46**, 2219 (1989).
196. E. M. G. Fitzgerald, *Mem. Mus. Vic.* **62**, 67 (2005).
197. R. E. Fordyce, *J. Vertebr. Paleontol.* **22**, 54A (2002).
198. G. Bianucci, W. Landini, *Zool. J. Linn. Soc.* **148**, 103 (2006).
199. O. Lambert, G. Bianucci, C. de Muizon, *C. R. Palevol.* **7**, 361 (2008).
200. J. H. Geisler, A. E. Sanders, *J. Mammal. Evol.* **10**, 23 (2003).
201. M. D. Uhen, *J. Syst. Palaeontol.* **6**, 433 (2008).
202. L. G. Barnes, *Syst. Zool.* **25**, 321 (1976).
203. M. D. Uhen, R. E. Fordyce, L. G. Barnes, in *Evolution of Tertiary Mammals of North America, Volume 2*, C. M. Janis, G. F. Gunnell, M. D. Uhen, Eds. (Cambridge Univ. Press, New York, 2008), pp. 566-606.
204. L. J. Flynn, L. L. Jacobs, in *Evolution of Tertiary Mammals of North America, Volume 2*, C. M. Janis, G. F. Gunnell, M. D. Uhen, Eds. (Cambridge Univ. Press, New York, 2008), pp. 377-390.
205. R. J. Emry, W. W. Korth, *J. Vertebr. Paleontol.* **27**, 693 (2007).
206. D. Anderson, in *Evolution of Tertiary Mammals of North America, Volume 2*, C. M. Janis, G. F. Gunnell, M. D. Uhen, Eds. (Cambridge Univ. Press, New York, 2008), pp. 311-325.
207. L. Marivaux, M. Vianey-Liaud, J.-J. Jaeger, *Zool. J. Linn. Soc.* **142**, 105 (2004).
208. G. Storch, C. Seiffert, *J. Vertebr. Paleontol.* **27**, 189 (2007).
209. T. Galewski, J.-F. Mauffrey, Y. L. R. Leite, J. L. Patton, E. J. P., Douzery, *Mol. Phylogenet. Evol.* **34**, 601 (2005).
210. B. D. Patterson, P. M. Velazco, *J. Mammal. Evol.* **15**, 181 (2008).
211. M. G. Vucetich, D. H. Verzi, J.-I. Hartenberger, *C. R. Acad. Sci. Paris Earth Planet. Sci.* **329**, 763 (1999).
212. J. J. Flynn, C. C. Swisher III, in *Geochronology, Time-Scales, and Global Stratigraphic Correlation, SEPM*, W. A. Berggren, D. V. Kent, J. Hardenbol, Eds. (Soc. for Sedimentary Geology, Tulsa, Oklahoma, Special Publication 54, 1995), pp. 317-333.
213. J. J. Flynn, A. R. Wyss, *Trends Ecol. Evol.* **13**, 449 (1998).
214. K. E. Campbell, Jr., C. D. Frailey, L. Romero-Pittman, *Nat. Hist. Mus. Los Angeles County, Sci. Ser.* **40**, 3 (2004).
215. C. D. Frailey, K. E. Campbell, Jr., *Nat. Hist. Mus. Los Angeles County, Sci. Ser.* **40**, 71 (2004).
216. D. H. Verzi, E. C. Vieytes, C. I. Montalvo, *Geobios* **37**, 795 (2004).
217. M. A. Zárate, et al., *J. So. Am. Earth Sci.* **23**, 81 (2007).
218. J. J. Flynn, A. R. Wyss, D. A. Croft, R. Charrier, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **195**, 229 (2003).
219. C. Argot, *Zool. J. Linn. Soc.* **140**, 487 (2004).
220. J. J. Flynn et al., *J. So. Am. Earth Sci.* **26**, 412 (2008).
221. P.-O. Antoine et al., in *4th European Meeting on the Palaeontology and Stratigraphy of Latin America*, E. Diaz-Martínez, I. Rábano, Eds. (Cuadernos del Museo Geominero, n° 8, Instituto Geológico y Minero de España, Madrid, 2007), pp. 19-24.
222. L. Marivaux et al., *J. Vertebr. Paleontol.* **25**, 214 (2005).

223. A. J. Winkler, L. MacLachy, M. Mafabi, *Palaeontol. Electron.* **8**, 24A (2005).
224. L. J. Flynn, L. L. Jacobs, in *Evolution of Tertiary Mammals of North America, Volume 2*, C. M. Janis, G. F. Gunnell, M. D. Uhen, Eds. (Cambridge Univ. Press, New York, 2008), pp. 391-405.
225. H. M. Sallam, E. R. Seiffert, M. E. Steiper, E. L. Simons, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 16722 (2009).
226. R. L. Antonanzas, S. Sen, P. Mein, *Zool. J. Linn. Soc.* **142**, 423 (2004).
227. J.-L. Hartenberger, *C. R. Acad. Sci. Paris Earth Planet. Sci.* **326**, 439 (1998).
228. M. Vianey-Liaud, J.-J. Jaeger, J.-L. Hartenberger, M. Mahboubi, *Palaeovertebrata*, **23**, 93 (1994).
229. L. J. Flynn, L. L. Jacobs, in *Evolution of Tertiary Mammals of North America, Volume 2*, C. M. Janis, G. F. Gunnell, M. D. Uhen, Eds. (Cambridge Univ. Press, New York, 2008), pp. 428-455.
230. T. Martin, *Bull. Carnegie Mus. Nat. Hist.* **39**, 127 (2007).
231. T. Tsubamoto, M. Takai, N. Egi, *J. Vertebr. Paleontol.* **24**, 657 (2004).
232. C. M. Janis, M. R. Dawson, L. J. Flynn, in *Evolution of Tertiary Mammals of North America, Volume 2*, C. M. Janis, G. F. Gunnell, M. D. Uhen, Eds. (Cambridge Univ. Press, New York, 2008), pp. 263-292.
233. Z. Kielan-Jaworowska, R. L. Cifelli, Z.-X. Luo. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure* (Columbia Univ. Press, New York, 2004).
234. S. G. Lucas, Z., Luo, *J. Vertebr. Paleontol.* **13**, 309 (1993).
235. P. M. Datta, *J. Vertebr. Paleontol.* **25**, 200 (2005).
236. J. A. Clarke, C. P. Tambussi, J. I. Noriega, G. M. Erickson, R. A. Ketchum, *Nature* **433**, 305 (2005).
237. M. Laurin, *Zool. J. Linn. Soc.* **101**, 59 (1991).
238. S. P. Modesto, R. R. Reisz, *J. Vertebr. Paleontol.* **22**, 851 (2002).
239. J. H. Hutchison, *Geobios* **7**, 211 (1974).
240. L. W. van den Hoek Ostende, *Proc. Kon. Ned. Akad. v. Wetensch.* **100**, 27 (1997).
241. R. Ziegler, *Acta Palaeontol. Pol.* **48**, 617 (2003).
242. B. Sigé, J.-Y. Crochet, A. Insole, *Géobios Mém. spécial* **1**, 141 (1977).
243. K. J. Lloyd, J. J. Eberle, *Acta Palaeontol. Pol.* **53**, 539 (2008).
244. L. W. van den Hoek Ostende, *Scripta Geol.* **122**, 1 (2001).
245. M. J. Phillips, T. H. Bennett, M. S. Y. Lee, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 17089 (2009).
246. R. W. Meredith, M. Westerman, M. S. Springer, *Mol. Phylogenet. Evol.* **51**, 554 (2009).
247. A. L. Roca et al., *Nature* **429**, 649 (2004).
248. C. J. Douady, E. J. P. Douzery, *Mol. Phylogenet. Evol.* **28**, 285 (2003).
249. S. Dubey, N. Salamin, S. D. Ohdachi, P. Barriere, P. Vogel, *Mol. Phylogenet. Evol.* **44**, 126 (2007).
250. T. J. Gaudin, R. J. Emry, J. R. Wible, *J. Mammal. Evol.* **16**, 235 (2009).
251. F. A. Perini, C. A. M. Russo, C. G. Schrago, *J. Evol. Biol.* **23**, 311 (2010).
252. J. B. Lack, Z. P. Roehrs, C. E. Stanley, Jr., M. Ruedi, R. A. Van Den Bussche, *J. Mammal.* **91**, 976 (2010).
253. G. N. Eick, D. S. Jacobs, C. A. Matthee, *Mol. Biol. Evol.* **22**, 1869 (2005).
254. A. L. Russell, S. M. Goodman, I. Fiorentino, A. D. Yoder, *J. Mammal.* **89**, 209 (2008).
255. K. E. Jones, O. R. P. Bininda-Emonds, J. L. Gittleman, *Evolution* **59**, 2243 (2005).
256. N. Lewis-Oritt, R. A. Van Den Bussche, R. J. Baker, *J. Mammal.* **82**, 748 (2001).
257. L. J. Hollar, M. S. Springer, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 5716 (1997).
258. S. Stoffberg, D. S. Jacobs, I. J. Mackie, C. A. Matthee, *Mol. Phylogenet. Evol.* **54**, 1 (2010).
259. G. Li, *J. Mammal.* **88**, 736 (2007).
260. E. A. Oakenfull, H. N. Lim, O. A. Ryder, *Cons. Gen.* **1**, 341 (2000).
261. E. Willerslev et al., *BMC Evol. Biol.* **9**, 95 (2009).
262. J. E. Norman, M. V. Ashley, *J. Mol. Evol.* **50**, 11 (2000).
263. P. Cui, *BMC Genomics* **8**, 241 (2007).
264. C. Montgelard, F. M. Catzeflis, E. Douzery, *Mol. Biol. Evol.* **14**, 550 (1997).
265. M. Orliac, J.-R. Boissarie, L. MacLachy, F. Lihoreau, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 11871 (2010).
266. T. E. Roberts, H. C. Lanier, E. J. Sargis, L. E. Olson, *Mol. Phylogenet. Evol.* (2011), doi:10.1016/j.ympev.2011.04.021.
267. C. A. Matthee, B. J. van Vuuren, D. Bell, T. J. Robinson, *Syst. Biol.* **53**, 433 (2004).
268. H. C. Lanier, L. E. Olson, *Mol. Phylogenet. Evol.* **53**, 1 (2009).
269. S. Horn et al., *PLoS ONE* **6**, e14622 (2011).
270. C. A. Matthee, T. J. Robinson, *Mol. Biol. Evol.* **14**, 20 (1997).
271. C. Montgelard, E. Forty, V. Arnal, C. A. Matthee, *BMC Evol. Biol.* **8**, 321 (2008).
272. H. M. Sallam, E. R. Seiffert, E. L. Simons, *Palaeontology* **53**, 803 (2010).
273. Y. Kimura, *Naturwissenschaften* **98**, 87 (2011).
274. S. A. Jansa, T. C. Giarla, B. K. Lim, *J. Mammal.* **90**, 1083 (2009).
275. M. Vianey-Liaud, H. G. Rodrigues, L. Marivaux, *Zool. J. Linn. Soc.* **160**, 531 (2010).
276. M. Nunome, S. P. Yasuda, J. J. Sato, P. Vogel, H. Suzuki, *Zool. Scripta* **36**, 537 (2007).
277. J. M. Mercer, V. L. Roth, *Science* **299**, 1568 (2003).
278. D. Huchon, E. J. P. Douzery, *Mol. Phylogenet. Evol.* **20**, 238 (2001).
279. J. E. Horvath et al., *Genome Res.* **18**, 489 (2008).
280. M. Shekelle, R. Meier, I. Wahyu, Wirdateti, N. Ting, *Int. J. Primatol.* **31**, 1083 (2010).
281. F. Delsuc, S. F. Vizcaino, E. J. P. Douzery, *BMC Evol. Biol.* **4**, 11 (2004).
282. C. J. Douady, F. Catzeflis, J. Raman, M. S. Springer, M. J. Stanhope, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 8325 (2003).
283. R. J. Asher et al., *BMC Evol. Biol.* **10**, 69 (2010).
284. M. Kuntner, L. J. May-Collado, I. Agnarsson, *Zool. Scripta* **40**, 1 (2011).
285. C. Poux, O. Madsen, J. Glos, W. W. de Jong, M. Vences, *BMC Evol. Biol.* **8**, 102 (2008).

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Supporting Online Material

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Materials and Methods

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References

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occurred near or after the KPg mass extinction event, ~65.5 Mya, for almost all orders. Diversification rate shifts detected by (B) TreePar and (C) Laser are denoted with green (rate increase) and red (rate decrease) arrows for rate shifts that were identified in analyses with both AA and DNA timetrees (table S10). (D) Sliding window analysis of the net diversification rate (originations/lineage/window) based on mean divergence estimates from eight different analyses.

Fig. 1. Phylogenetic timetree of mammalian families (13) created on the basis of an analysis of the AA matrix (autocorrelated rates, hard-bounded constraints) of 164 mammals, rooted with five vertebrate outgroups (chicken, zebrafish, green anole, frog, zebrafish; see SOM for trees with outgroups). All nodes were strongly supported (BS $\geq 90\%$, BPP ≥ 0.95) in AA and DNA analyses except for nodes that are denoted by solid blue circles (conflict between DNA and AA trees) or solid black circles (DNA and AA trees agree, but with BS $< 90\%$). Strongly supported nodes that disagree with Bininda-Emonds et al. (8) are indicated with solid red circles. Several nodes that remain difficult to resolve (e.g., placental root) have variable support between studies of rare genomic changes (29, 30), as well as genome-scale datasets (31–33), suggesting that diversification was not fully bifurcating or occurred in such rapid succession that phylogenetic signal tracking true species relationships may not be recoverable with current methods. The KPg boundary is denoted by the transition from gray background (= Mesozoic) to white background (= Cenozoic). Color-coded branches in Placentalia correspond to Laurasiatheria (green), Euarchontoglires (blue), Xenarthra (orange), and Afrotheria (pink). See table S11 for ordinal affiliations of mammalian families. Mammal paintings are by Carl Buell.

Fig. 2. Timescale of major mammalian divergence events during the past 110 My. (A) Colored circles represent cladogenic events leading to the four major groups of placental mammals (light blue) and interordinal splits within Euarchontoglires (dark blue), Laurasiatheria (green), Afrotheria (pink), and Marsupialia (dark purple). The split between ornithorhynchids and tachyglossids is shown in light purple (Monotremata). Basal divergences within crown-group placental and marsupial orders are shown in orange (also see Table 1). 95% composite credibility intervals are shown for ordinal divergences as horizontal bars. Basal cladogenesis

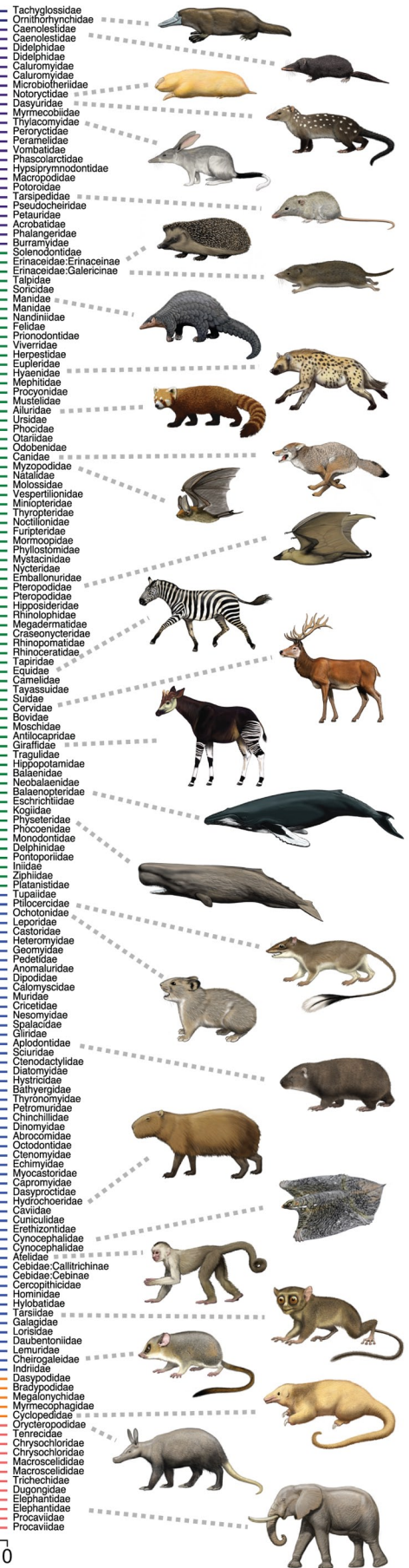
Table 1. Divergence times estimated in this study for major ordinal and superordinal groups, and comparison to the results of the MRP supertree (8). 95% credibility intervals are listed in parentheses. Asterisks denote orders. Indentations in taxon names denote hierarchical relationships.

Taxon	Supermatrix mean Div. Time	MRP (8) Div. Time	Difference
Mammalia	217.8 (203.3–238.2)	166.2 (Fixed)	–51.6
Monotremata*	36.7 (22.4–103.1)	63.6 (52.2–75.0)	26.9
Theria	190.0 (167.2–215.3)	147.4 (141.8–153.1)	–42.6
Marsupialia	81.8 (67.9–97.2)	82.5 (71.4–93.7)	0.7
Paucituberculata*	11.7 (7.2–16.2)	33.2 (26.3–40.1)	21.5
Didelphimorphia*	31.4 (23.0–38.4)	56.2 (45.9–67.7)	24.8
Peramelemorphia*	28.0 (21.1–37.1)	36.2 (30.6–41.8)	8.2
Dasyuromorphia*	30.0 (22.1–41.7)	31.3 (16.2–55.8)	1.3
Diprotodontia*	52.8 (42.4–64.0)	54.1 (52.4–55.8)	1.3
Placentalia	101.3 (92.1–116.8)	98.5 (93.2–108.1)	–2.8
Xenarthra*	65.4 (58.4–71.5)	70.5 (65.6–75.4)	5.1
Afrotheria	80.9 (74.4–96.5)	90.4 (87.3–93.6)	9.5
Afrosoricida*	68.2 (56.8–88.0)	82.4 (78.3–86.4)	14.2
Macroscelidea*	49.1 (37.7–57.2)	47.5 (39.9–55.6)	–1.6
Paenungulata	64.3 (56.0–76.6)	75.8 (72.4–79.2)	11.5
Hyracoidea*	6.1 (3.9–8.3)	18.6 (17.8–19.5)	12.5
Proboscidea*	5.3 (1.8–8.0)	19.5 (7.6–31.4)	14.2
Sirenia*	31.4 (25.0–34.4)	52.2 (37.9–66.5)	20.8
Boreoeutheria	92.0 (82.9–107.6)	96.1 (92.9–98.4)	4.1
Laurasiatheria	84.6 (78.5–93.0)	87.8 (85.0–90.5)	3.2
Eulipotyphla*	77.3 (70.7–85.8)	82.5 (79.8–85.3)	5.2
Chiroptera*	66.5 (62.3–71.3)	71.2 (68.0–74.3)	4.7
Perissodactyla*	56.8 (55.1–61.0)	55.8 (51.1–60.5)	–1.0
Pholidota*	25.3 (16.9–35.7)	19.1 (7.3–46.9)	–6.2
Carnivora*	54.7 (47.4–60.6)	63.4 (59.8–67.1)	8.7
Cetartiodactyla*	65.4 (62.3–68.5)	70.7 (67.6–73.7)	5.3
Euarchontoglires	83.3 (74.1–97.8)	91.8 (90.0–93.8)	8.5
Primates	82.0 (73.7–97.4)	88.5 (85.9–91.0)	6.5
Primates*	71.5 (64.3–78.4)	84.5 (81.9–87.1)	13.0
Dermoptera*	7.4 (4.5–13.2)	15.0 (10.2–19.9)	7.6
Scandentia*	55.9 (45.0–63.9)	31.7 (29.9–34.7)	–24.2
Glires	79.5 (71.5–94.1)	88.9 (87.8–90.1)	9.4
Rodentia*	69.0 (64.1–74.8)	82.8 (80.2–85.4)	13.8
Lagomorpha*	50.2 (47.4–56.9)	64.3 (60.0–68.7)	14.1
Mean difference (absolute values) for orders=			11.1

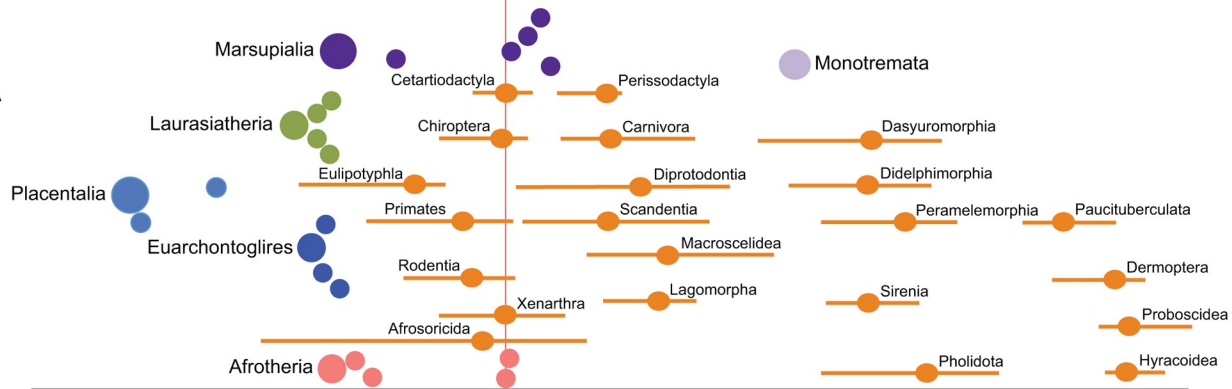
Monotremata

Marsupialia

Placentalia



200 175 150 125 100 75 50 25 0

A**B****C****D**