PALEONTOLOGY

Brawn before brains in placental mammals after the end-Cretaceous extinction

Ornella C. Bertrand[1]*, Sarah L. Shelley[1,2], Thomas E. Williamson[3], John R. Wible[2], Stephen G. B. Chester[4,5,6], John J. Flynn[7,8,9,10], Luke T. Holbrook[11], Tyler R. Lyson[12], Jin Meng[7], Ian M. Miller[13,12], Hans P. Püschel[1], Thierry Smith[14], Michelle Spaulding[15], Z. Jack Tseng[16], Stephen L. Brusatte[1,3]*

Mammals are the most encephalized vertebrates, with the largest brains relative to body size. Placental mammals have particularly enlarged brains, with expanded neocortices for sensory integration, the origins of which are unclear. We used computed tomography scans of newly discovered Paleocene fossils to show that contrary to the convention that mammal brains have steadily enlarged over time, early placentals initially decreased their relative brain sizes because body mass increased at a faster rate. Later in the Eocene, multiple crown lineages independently acquired highly encephalized brains through marked growth in sensory regions. We argue that the placental radiation initially emphasized increases in body size as extinction survivors filled vacant niches. Brains eventually became larger as ecosystems saturated and competition intensified.

Mammals have the largest brains, absolutely and relative to body size, of all vertebrates, reaching an extreme in the hyperinflated brain of humans (*1*, *2*). The mammalian brain was assembled over 200 million–plus years of evolution, beginning with encephalization pulses—increases in brain size relative to body size—on the mammal stem lineage in the Mesozoic. These increases were associated with heightened olfaction and the origin of the neocortex, a new part of the cerebrum involved in higher cognition and sensory integration (*3*). Among extant mammals, the more than 6000 species of placentals (*4*) exhibit remarkable diversity of encephalization (*5*) and sensory abilities (*6*), the result of complex interplay between brain and body size changes over time and across taxa (*7*). It has long been recognized that the earliest fossils of extant placental orders (herein "placental crown orders") from the Eocene (56 million to 34 million years ago) had brains similar in structure to (*8*, *9*), but smaller than, those of their modern-day counterparts (*10*, *11*) and that relative brain size generally increased over the Cenozoic (*12*, *13*). However, much about the origin of the placental brain, and when and how it encephalized to modern levels, remains unclear.

In particular, little is known about the transition from the ancestral brains of Mesozoic mammals to the more modern brains of Eocene crown placentals. The principal gap in understanding is the Paleocene (66 million to 56 million years ago), the interval after the end-Cretaceous mass extinction, when placentals and close kin radiated into niches vacated by dinosaurs (*14*), ballooned in body size (*15*, *16*), and inaugurated the Age of Mammals (*17*, *18*). Jerison (*1*) posited that the "archaic" placentals replacing dinosaurs (herein "placental stem taxa," those that do not clearly belong to extant orders) were overgrown versions of Mesozoic mammals, which passively increased their absolute brain sizes to keep pace with body size expansion and then, later in the Eocene, actively encephalized to increase relative brain sizes. This hypothesis was based on a small sample of skulls, of uncertain Paleocene or Eocene age, whose brain cavities were measured with basic volumetric techniques unable to distinguish sensory regions. Recently, a broad study of mammals instead identified increases in relative brain size after the end-Cretaceous extinction (*7*), but this alternative hypothesis was inferred from phylogenetic comparative data that did not directly include Paleocene fossils. Testing these competing hypotheses has proven difficult because well-preserved Paleocene mammal skulls have been notoriously rare.

We assessed the early evolution of the placental brain with an expansive dataset of Mesozoic and Cenozoic mammals, including newly discovered Paleocene skulls from the San Juan Basin of New Mexico (*19*) and Denver Basin of Colorado (*20*). To do so, we used high-resolution computed tomography (CT) to measure the size of the brain and its individual sensory components (neocortex, olfactory bulbs, and cerebellar petrosal lobules involved in control of eye movements) (Fig. 1) (*21*). Our dataset includes 34 new CT scans of Paleogene taxa (17 Paleocene and 17 Eocene) (table S1), alongside data from previous work. We examined patterns over time and across taxa to quantify body size, brain size, and sensory regions change during the placental radiation and after the end-Cretaceous extinction. This enabled us to test the competing hypotheses for placental encephalization and more broadly to investigate when and how the modern placental brain and sensory repertoire emerged, and what role the end-Cretaceous extinction played.

We found that Mesozoic and Paleocene mammals had smaller brains relative to their body mass than those of Eocene stem taxa and crown orders (Fig. 1D). When expressed as a phylogenetic encephalization quotient (PEQ), a measure of relative brain size compared with its value predicted by allometry and phylogeny (*22*), Paleocene forms were less encephalized than Mesozoic and Eocene taxa (Fig. 2, A and B, and table S2). After the Paleocene low in PEQ, both average PEQ and variance significantly expanded in the Eocene, in both stem taxa and crown orders (Fig. 2, A and B). These results are robust to phylogenetic uncertainty (figs. S1 and S2 and tables S3 to S5), differences in body mass estimates (figs. S3 to S9 and tables S6 to S8), and whether placentals originated in the Cretaceous or immediately after the end-Cretaceous extinction (fig. S10). Our results are broadly in line with Jerison's "body-before-brain" hypothesis rather than the alternative but reveal an unexpected wrinkle. The earliest placentals were neither scaled up versions of Mesozoic mammals nor did they encephalize rapidly. Instead, their relative brain sizes actually decreased as they increased in body sizes more than in brain size while radiating after the end-Cretaceous extinction.

Proportions of sensory regions also changed markedly over time. The olfactory bulbs and petrosal lobules of Paleocene species and Eocene placental stem taxa essentially maintained their Mesozoic sizes, relative to both body mass and brain volume (endocranial volume) (Fig. 3, fig. S11, and table S2). The olfactory bulbs became a significantly smaller component of the brain, and the petrosal lobules became a larger component, in Eocene crown orders (Fig. 3, fig. S11, and table S2). Additionally, the neocortex enlarged over

[1]School of GeoSciences, University of Edinburgh, Grant Institute, Edinburgh, Scotland EH9 3FE, UK. [2]Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, PA, USA. [3]New Mexico Museum of Natural History and Science, Albuquerque, NM, USA. [4]Department of Anthropology, Brooklyn College, City University of New York, Brooklyn, NY, USA. [5]Department of Anthropology, The Graduate Center, City University of New York, New York, NY, USA. [6]New York Consortium in Evolutionary Primatology, New York, NY, USA. [7]Division of Paleontology, American Museum of Natural History, New York, NY, USA. [8]Department of Earth and Environmental Sciences, Columbia University, New York, NY, USA. [9]Ecology, Evolutionary Biology, and Behavior subprogram, PhD Program in Biology, The Graduate Center, City University of New York, New York, NY, USA. [10]PhD Program in Earth and Environmental Sciences, The Graduate Center, City University of New York, New York, NY, USA. [11]Department of Biological Sciences, Rowan University, Glassboro, NJ, USA. [12]Denver Museum of Nature & Science, Denver, CO, USA. [13]National Geographic Society, Washington, DC, USA. [14]Directorate Earth and History of Life, Royal Belgian Institute of Natural Sciences, Brussels, Belgium. [15]Department of Biological Sciences, Purdue University Northwest, Westville, IN, USA. [16]Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, CA, USA.
*Corresponding author. Email: ornella.bertrand@ed.ac.uk (O.C.B.); stephen.brusatte@ed.ac.uk (S.L.B.)

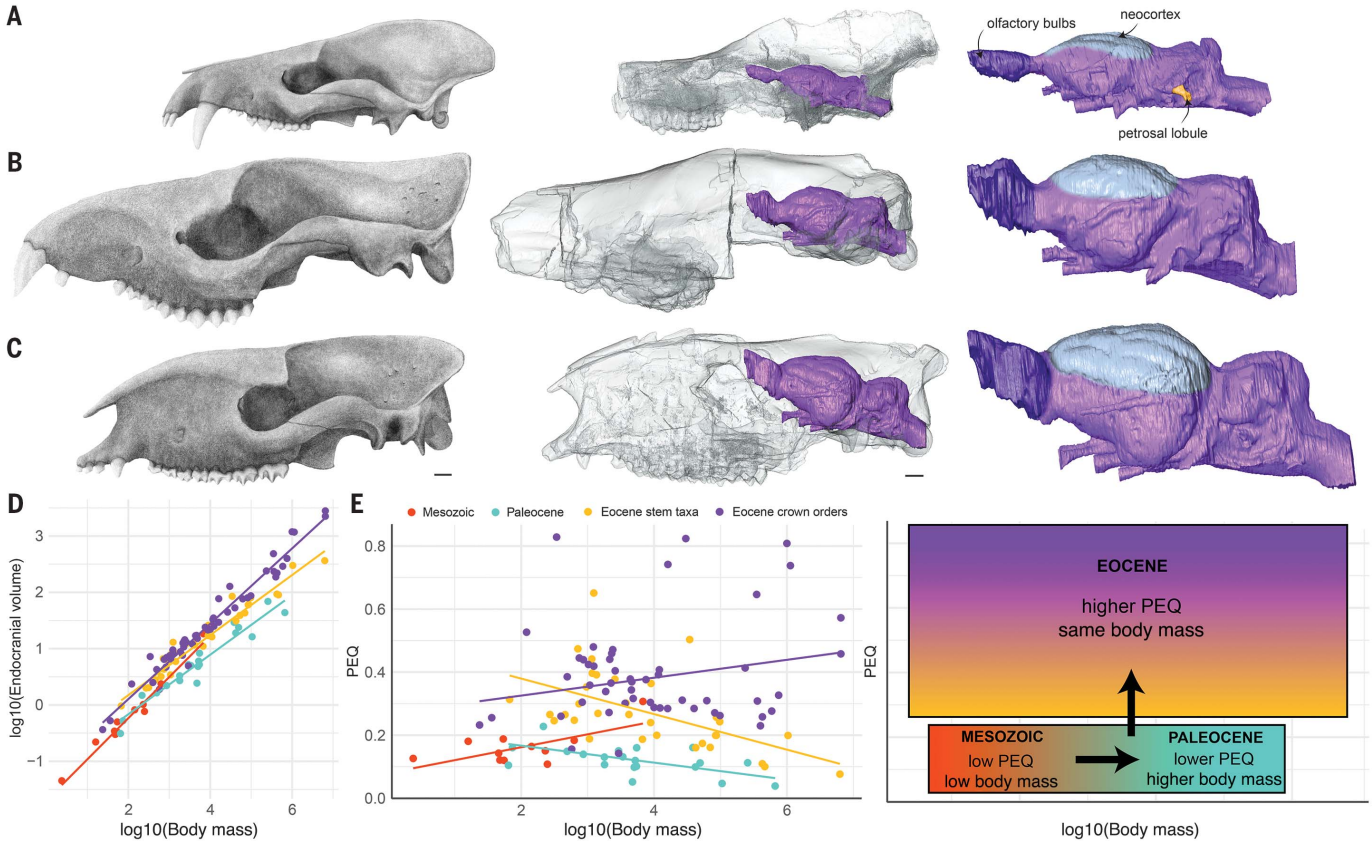

Fig. 1. Virtual endocasts of Cenozoic mammal exemplars used in this study with sensory regions highlighted and phylogenetic generalized least squares (PGLS) regressions for Mesozoic and early Cenozoic mammals. (**A**) Late Paleocene stem placental condylarth *Arctocyon primaevus* (IRSNB M2332). (**B**) Middle Eocene stem placental tillodont *Trogosus hillsii* (USNM 17157). (**C**) Middle Eocene crown placental perissodactyl *Hyrachyus modestus* (AMNH FM 12664). (**D**) Phylogenetically corrected PGLS regression of $\log_{10}$(Endocranial volume) versus $\log_{10}$(Body mass). (**E**) Phylogenetically corrected PGLS regression of PEQ versus $\log_{10}$(Body mass) and graphical summary of the results. The petrosal lobules are absent in (B) and (C). Scale bar, 10 mm. Body mass was measured in grams, and endocranial volume was measured in cubic centimeters.

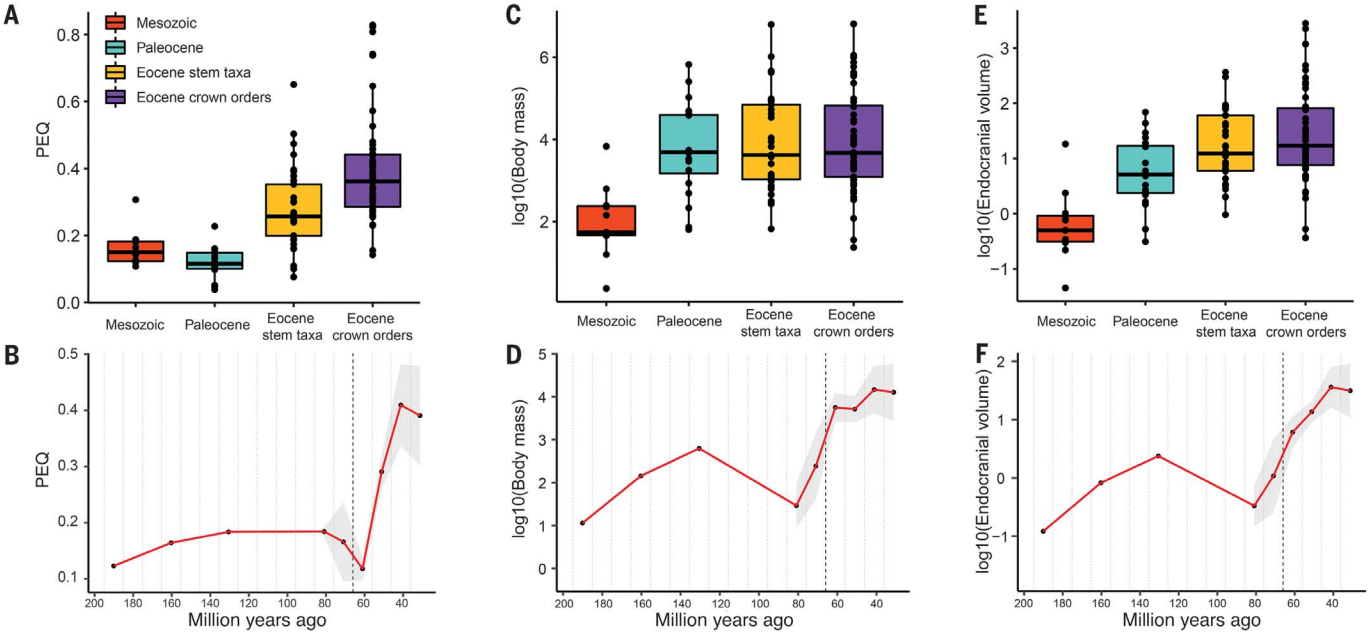

Fig. 2. PEQ, endocranial volume, and body mass of Mesozoic and early Cenozoic mammals. (**A**) Boxplot of PEQ for Mesozoic, Paleocene, Eocene stem taxa, and Eocene crown orders. (**B**) PEQ average through time per 10-million-year bins. (**C**) Boxplot of $\log_{10}$(Body mass). (**D**) $\log_{10}$(Body mass) average through time per 10-million-year bins for groups in (A). (**E**) Boxplot of $\log_{10}$(Endocranial volume) for groups in (A). (**F**) $\log_{10}$(Endocranial volume) average through time per 10-million-year bins. Body mass was measured in grams, and endocranial volume was measured in cubic centimeters.

time and covered significantly more of the brain surface in Eocene crown orders versus Paleocene and Eocene stem forms (Fig. 3 and table S2). Thus, the Eocene increase in relative brain size was underpinned by expansions of the petrosal lobules and especially the neocortex, but not the olfactory bulbs. Most of these changes occurred in the Eocene crown orders, helping explain why they had significantly higher PEQs than those of their Eocene stem contemporaries, despite insignificant differences in body mass among them (Fig. 2 and table S2). These results are also robust to phylogenetic uncertainty and placental origin timing (figs. S12 to S17 and tables S3 to S5).

Phylogenetic context helps untangle the trends and tempo of these changes. Both body mass and brain volume significantly increased from the Mesozoic to the Paleocene (Fig. 2, D and F, and table S9), as did the rate of change in both measures on the phylogeny (figs. S18 and S19), regardless of placental origin time (fig. S20). However, during the Paleocene, the majority of branches exhibited faster rates of body mass increase than brain volume increase (fig. S21), and although this largely held in the Eocene, crown orders accelerated to faster relative increases in brain volume rate compared with those of Eocene stem and Paleocene taxa. This discrepancy explains why there was a drop in PEQ in the Paleocene, followed by relative brain expansion in the Eocene.

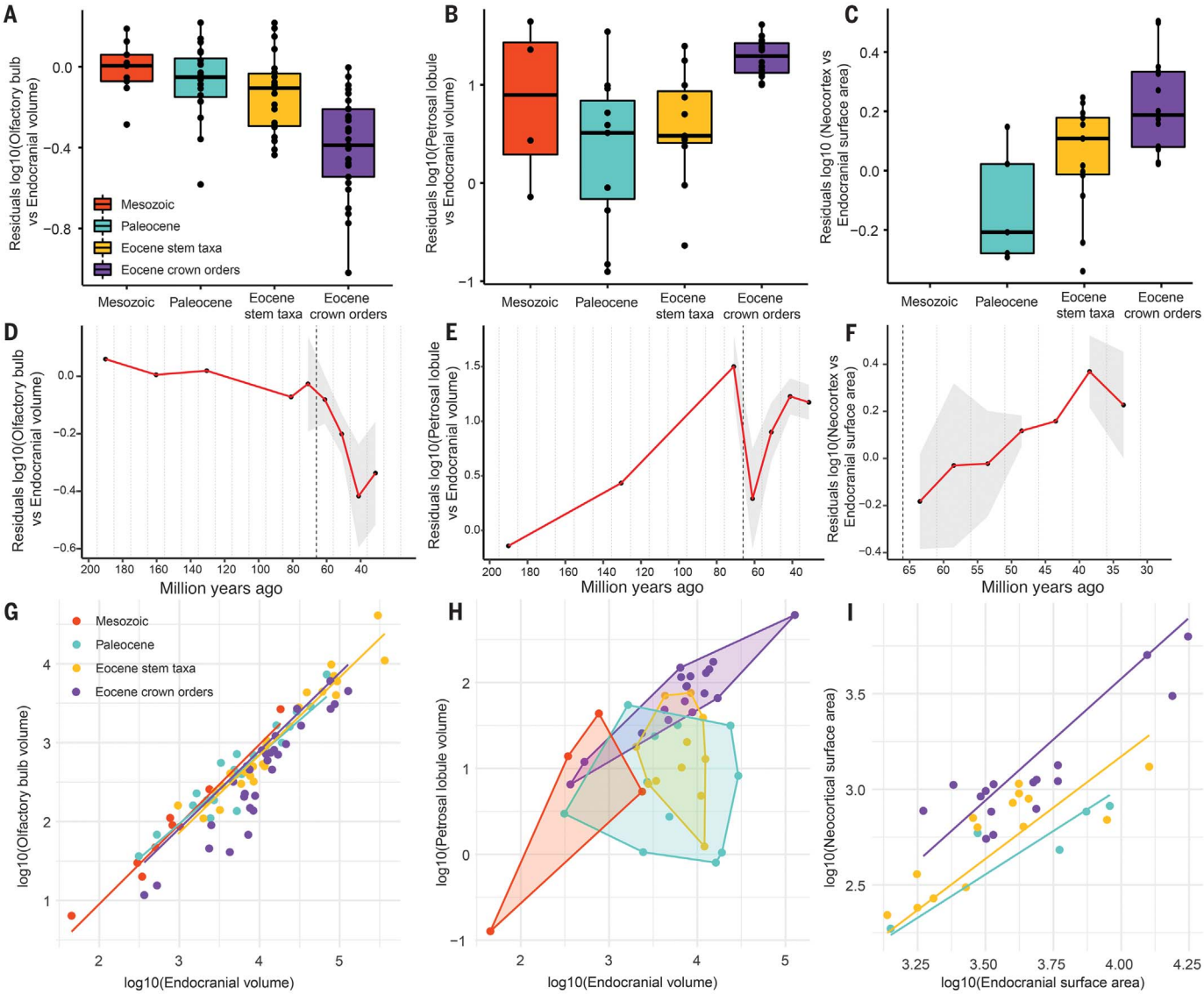

Fig. 3. Relative size of the olfactory bulbs, petrosal lobules, and neocortex of Mesozoic and early Cenozoic mammals. (**A**) Boxplot of the residuals from a PGLS regression of $\log_{10}$(Olfactory bulb volume versus Endocranial volume) for Mesozoic, Paleocene, Eocene stem taxa, and Eocene crown orders. (**B**) Boxplot of the residuals from a PGLS regression of $\log_{10}$(Petrosal lobule volume versus Endocranial volume) for the groups in (A). (**C**) Boxplot of the residuals from a PGLS regression of $\log_{10}$(Neocortical surface area versus Endocranial surface area) for the groups in (A). (**D**) Residuals of $\log_{10}$(Olfactory bulb volume versus Endocranial volume) average through time per 10-million-year bins. (**E**) Residuals of $\log_{10}$(Petrosal lobule volume versus Endocranial volume) average through time per 10-million-year bins. (**F**) Residuals of $\log_{10}$(Neocortical surface area versus Endocranial surface area) average through time per 5-million-year bins. (**G**) PGLS regression of $\log_{10}$(Olfactory bulb volume versus Endocranial volume) for the groups in (A). (**H**) PGLS regression of $\log_{10}$(Petrosal lobule volume versus Endocranial volume) for the groups in (A). (**I**) PGLS regression of $\log_{10}$(Neocortical surface area versus Endocranial surface area) for the groups in (A). Mesozoic neocortical data were unavailable. Volumetric measurements are in cubic millimeters, and surface area measurements are in square millimeters.

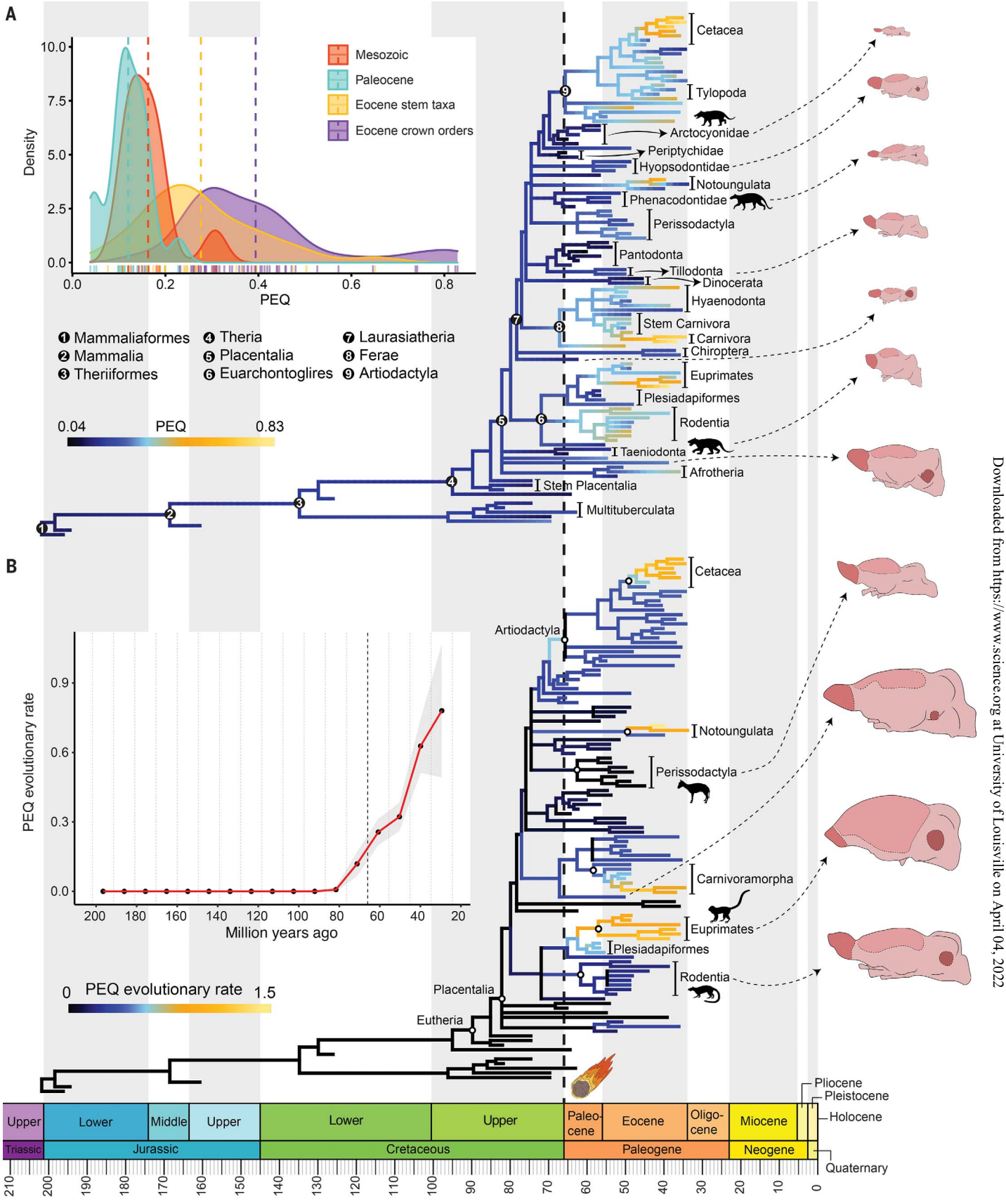

Fig. 4. PEQ evolutionary change across time and phylogeny in Mesozoic and early Cenozoic mammals. (**A**) PEQ density plot and ancestral state reconstruction mapped onto a phylogeny for Mesozoic, Paleocene, and Eocene mammals. (**B**) PEQ evolutionary rate mapped onto a phylogenetic

tree and averaged through time per 10-million-year bins. Virtual endocasts illustrated to the right with highlighted brain regions are scaled in terms of their PEQ and are, from top to bottom, *Arctocyon primaevus* (IRSNB M2332), *Hyopsodus paulus* (USNM 17980), *Meniscotherium chamense* (USNM 22673), *Trogosus hillsii* (USNM 17157), *Acmeodon secans* (KU 7912), *Ectoganus copei* (USNM 12714), *Leptictis* sp. (AMNH 62369), *Hyrachyus modestus* (AMNH FM 12664), *Metacheiromys marshi* (USNM 452349), *Smilodectes gracilis* (UM 32773), and *Paramys delicatus* (AMNH 12506). [Silhouettes are from http://phylopic.org (Euprimates, Perissodactyla, and Rodentia).]

Rates of change in body mass, brain volume, and PEQ were stable across most of the Mesozoic but increased dramatically at or near the origin of Placentalia, whether it occurred in the Cretaceous (Fig. 4B and figs. S18 and S19) or immediately after the end-Cretaceous extinction (figs. S20 and S22). This makes it difficult to differentiate the effects of the extinction itself, but because both dating approaches place the key pulses at or near the origin of Placentalia, this implies that fundamental changes to the mammalian brain and its allometric relationships happened around this event, perhaps associated with changes in metabolic rate and reproductive style (*23*). The body mass, brain volume, and PEQ rate increases for early Placentalia were not followed by stasis or decline; rather, high rates continued through the Paleocene and Eocene. Brain evolutionary rate increased in placentals, although it would take until the Eocene for those persistently high rates to assemble greatly encephalized modern placental brains with relatively large neocortices and petrosal lobules and small olfactory bulbs (figs. S23 to S26).

Phylogenetic character mapping reveals lineage-specific changes in body, brain, and sensory region sizes. The Paleocene decline in PEQ was the net result of several independent decreases in relative brain volume, largely because of independent increases in body mass in archaic groups such as "condylarths," pantodonts, and taeniodonts (Fig. 4 and figs. S18 to S20, S22, and S27 to S29). Then in the Eocene, there were several independent increases in PEQ, particularly in crown orders such as artiodactyls (including cetaceans), perissodactyls, carnivorans, euprimates, and rodents (Fig. 4 and figs. S18 to S20, S22, and S27 to S29). Omnivores and carnivores were statistically indistinguishable in PEQ compared with contemporary herbivores in the Paleocene, but both guilds significantly increased PEQ in the Eocene, with omnivores and carnivores eclipsing herbivores (fig. S30 and table S10). The two most speciose placental subclades experienced different fates: Raw body mass increased markedly in Paleocene-Eocene laurasiatherians (carnivorans, perissodactyls, and artiodactyls) but not in euarchontoglirans (rodents and primates). Both subclades underwent substantial encephalization (Fig. 4), but rates of change in both body mass and brain volume were higher in laurasiatherians (Fig. 4 and figs. S18 to S20 and S22).

Small relative brain size after the end-Cretaceous extinction—even more so a decline in encephalization—is surprising and counter to the convention that mammal brains have steadily gotten larger over time [(*10*–*13*), but see (*7*)]. Although relative brain size is but one aspect of cognition, and we lack information on neuron density and connectivity in virtually all fossil mammals, experimental evidence indicates that extant mammals with relatively larger brains are better problem solvers (*24*). There also is ample evidence that larger relative brain size is linked to greater behavioral flexibility and capacity to cope with new or altered environments (*25*–*28*). All of these skills, presumably, would have been beneficial after a mass extinction, yet the placentals that diversified as devastated ecosystems recovered and new food webs emerged did not develop relatively larger brains, which suggests that other factors were behind their radiation.

It appears that the postextinction placental radiation emphasized changes to body size rather than brain size, as survivors proliferated to fill vacant niches, no longer constrained to shrew to badger sizes by incumbent dinosaurs (*15*). Brain size increased as a result of body size expansion, and because there were no marked relative increases in key sensory regions (olfactory bulbs and petrosal lobules), the growth was primarily in regions that permit control of larger bodies (brain stem, diencephalon, and striatum) (*29*, *30*). This suggests that selection acted differently on brain and body size and adds to growing evidence that body size shifts, rather than pronounced alterations in brain size, drove much of the variation in mammalian encephalization (*7*, *31*). At the very least, relatively enlarged brains were not necessary for Paleocene placentals.

As the Paleocene transitioned to the Eocene, the mode of placental brain and body evolution shifted. Relative brain size greatly increased, in both average and variance, signaling a new regime in which brain size changes were more paramount than those in body size. Brains were not only becoming larger; growth was focused in regions involved in advanced senses as these mammals added better balance, vision, eye movement, head control, and sensory integration to their preexisting keen olfaction, thus greatly expanding the placental sensory toolkit. This corroborates arguments that mosaic evolution of brain regions, not merely changes in overall size, underlie the adaptive potential of the mammalian brain—not only across phylogeny (*32*) but also in deep time. Primarily, encephalization and sensory enhancements occurred in the crown orders, with predators developing significantly larger relative brain size than those of prey groups as ecosystems saturated. It was these crown placentals—among them the first horses, whales, dogs, bats, and euprimates—that achieved high PEQs, whereas the smaller-brained and more olfactory-driven stem taxa waned, with groups once so instrumental in the end-Cretaceous recovery and initial placental radiation—such as condylarths and pantodonts—ultimately succumbing to extinction.

REFERENCES AND NOTES

1. H. J. Jerison, *Evolution of the Brain and Intelligence* (Academic Press, 1973).
2. M. Tsuboi *et al*., *Nat. Ecol. Evol.* **2**, 1492–1500 (2018).
3. T. B. Rowe, T. E. Macrini, Z. X. Luo, *Science* **332**, 955–957 (2011).
4. C. J. Burgin, J. P. Colella, P. L. Kahn, N. S. Upham, *J. Mammal.* **99**, 1–14 (2018).
5. J. R. Burger, M. A. George Jr., C. Leadbetter, F. Shaikh, *J. Mammal.* **100**, 276–283 (2019).
6. B. Finlay, in *Encyclopedia of Neuroscience* (2009), vol. 2, pp. 337–345.
7. J. B. Smaers *et al*., *Sci. Adv.* **7**, eabe2101 (2021).
8. L. Radinsky, *Science* **194**, 626–627 (1976).
9. H. J. Jerison, *Biolinguistics* **6**, 383–392 (2012).
10. E. Lartet, *Comptes Rendus des Séances de l'Académie des Sciences* **66**, 1119–1122 (1868).
11. O. C. Marsh, *Ann. Mag. Nat. Hist.* **14**, 167–167 (1874).
12. H. J. Jerison, *Science* **133**, 1012–1014 (1961).
13. H. J. Jerison, *Science* **170**, 1224–1225 (1970).
14. D. M. Grossnickle, S. M. Smith, G. P. Wilson, *Trends Ecol. Evol.* **34**, 936–949 (2019).
15. J. Alroy, *Syst. Biol.* **48**, 107–118 (1999).
16. F. A. Smith *et al*., *Science* **330**, 1216–1219 (2010).
17. G. G. Simpson, *Biol. Rev. Camb. Philos. Soc.* **12**, 1–46 (1937).
18. K. D. Rose, *The Beginning of the Age of Mammals* (Johns Hopkins Univ. Press, 2006).
19. T. E. Williamson, *The Beginning of the Age of Mammals in the San Juan Basin, New Mexico: Biostratigraphy and Evolution of Paleocene Mammals of the Nacimiento Formation: Bulletin 8* (New Mexico Museum of Natural History and Science, 1996), vol. 8.
20. T. R. Lyson *et al*., *Science* **366**, 977–983 (2019).
21. H. Rambold, A. Churchland, Y. Selig, L. Jasmin, S. G. Lisberger, *J. Neurophysiol.* **87**, 912–924 (2002).
22. X. Ni, J. J. Flynn, A. R. Wyss, C. Zhang, *Sci. Adv.* **5**, eaav7913 (2019).
23. B. K. McNab, *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **151**, 5–28 (2008).
24. S. Benson-Amram, B. Dantzer, G. Stricker, E. M. Swanson, K. E. Holekamp, *Proc. Natl. Acad. Sci. U.S.A.* **113**, 2532–2537 (2016).
25. D. Sol, S. Bacher, S. M. Reader, L. Lefebvre, *Am. Nat.* **172** (Suppl. 1), S63–S71 (2008).
26. D. Sol, *Biol. Lett.* **5**, 130–133 (2009).
27. J. M. Ratcliffe, M. B. Fenton, S. J. Shettleworth, *Brain Behav. Evol.* **67**, 165–176 (2006).
28. J. T. van Woerden, E. P. Willems, C. P. van Schaik, K. Isler, *Evolution* **66**, 191–199 (2012).
29. S. Herculano-Houzel, K. Catania, P. R. Manger, J. H. Kaas, *Brain Behav. Evol.* **86**, 145–163 (2015).

30. S. Herculano-Houzel, *Curr. Opin. Behav. Sci.* **16**, 1–7 (2017).
31. J. B. Smaers, D. K. N. Dechmann, A. Goswami, C. Soligo, K. Safi, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 18006–18011 (2012).
32. R. A. Barton, P. H. Harvey, *Nature* **405**, 1055–1058 (2000).
33. O. C. Bertrand, Bertrand-Ornella/Brain_Evolution_Placental: Brain evolution in early Placental mammals. *Zenodo* (2022).

ACKNOWLEDGMENTS

We thank F. Mao, M. Hill Chase, R. O'Leary, M. Novacek, and S. Goldberg for scanning specimens and logistic support at the AMNH; A. Harrington and D. Boyer for providing access to several Euprimates virtual endocasts accessioned in Morphosource; S. Hoffman for providing access to the virtual endocast of *Vintana*; U. Lefèvre and the IRSNB for scanning *Arctocyon* and *Orthaspidotherium*; S. Anderson, P. dePolo, N. Egi, S. Holpin, and Z. Kynigopoulou for supplying postcranial measurements for several Paleocene and Eocene specimens; and T. Stubbs, B. Moon, and A. Meade for fruitful discussions about the evolutionary rates methods. We thank two anonymous reviewers for helpful comments that improved this manuscript. **Funding:** This work was supported by Marie Skłodowska-Curie Actions: Individual Fellowship, H2020-MSCA-IF-2018-2020, no. 792611 (O.C.B.); European Research Council (ERC) Starting Grant 756226 under the European Union's Horizon 2020 Research and Innovation Programme (S.L.B.); Philip Leverhulme Prize (S.L.B.); NSF DEB 1654952 (T.E.W. and S.L.B.); NSF DEB 1654949 (J.R.W. and S.L.S.); NSF DEB1456826 (L.T.H. and S.G.B.C.); Belgian Science Policy Office project BRAIN BR/121/A3/PalEurAfrica (T.S.); Lisa Levin Appel Family Foundation, M. Cleworth, Lyda Hill Philanthropies, David B. Jones Foundation, M. L. and S. R. Kneller, T. and K. Ryan, and J. R. Tucker as part of the Denver Museum of Nature & Science No Walls Community Initiative (T.R.L. and I.M.M.); and National Agency for Research and Development (ANID)/PFCHA/Doctorado en el extranjero Becas Chile/2018-72190003 (H.P.P.). Funding to J.J.F. and for scanning American Museum specimens was provided by the Microscopy and Imaging Facility, American Museum of Natural History Frick Fund, Division of Paleontology, American Museum of Natural History, and US National Science Foundation (DEB-1257572).

Author contributions: Conceptualization: O.C.B., S.L.B., S.L.S., T.E.W., and J.R.W. Methodology: O.C.B., S.L.B., S.L.S., J.J.F., Z.J.T., and H.P.P. Formal analyses: O.C.B., S.L.S., Z.J.T., and H.P.P. Investigation: O.C.B., S.L.B., S.L.S., T.E.W., and J.R.W. Results acquisition: O.C.B., S.L.B., S.L.S., T.E.W., and J.R.W. Raw data acquisition (specimens and CT data): O.C.B., S.L.B., S.L.S., T.E.W., J.R.W., S.G.B.C., J.J.F., L.T.H., T.R.L., J.M., I.M.M., T.S., M.S., and Z.J.T. Supervision: S.L.B. Writing, original draft: O.C.B. and S.L.B. Writing, review and editing: all authors. Visualization: O.C.B. and S.L.S. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** Code and data to run analyses using topology 1 (unconstrained) is provided with this article and is also available at (*33*). Raw data are available in the supplementary materials. All fossils are accessioned in public collections and, upon curator approval, should be available for study by qualified researchers. All (other) data needed to evaluate the conclusions in the paper are present in the paper or the supplementary materials. Raw CT scans of American Museum of Natural History specimens are available from the American Museum of Natural History under a materials transfer agreement with that institution. The 3D models of the brains will be stored in Morphosource at www.morphosource.org/projects/0000C1223?locale=en. Access to the 3D models will be approved by O.C.B. The endocasts cannot be described or figured without permission from O.C.B. or S.L.B.

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abl5584
Materials and Methods
Supplementary Text
Figs. S1 to S35
References (*34–295*)
MDAR Reproducibility Checklist
Tables S1 to S24
Data File S1

21 July 2021; accepted 1 February 2022
10.1126/science.abl5584

Science

Brawn before brains in placental mammals after the end-Cretaceous extinction

Ornella C. BertrandSarah L. ShelleyThomas E. WilliamsonJohn R. WibleStephen G. B. ChesterJohn J. FlynnLuke T. HolbrookTyler R. LysonJin MengIan M. MillerHans P. PüschelThierry SmithMichelle SpauldingZ. Jack TsengStephen L. Brusatte

Science, 376 (6588), • DOI: 10.1126/science.abl5584

Body first

Mammals have the largest ratio of brain to body size (encephalization) among vertebrates. It has been believed that this relationship emerged early on in mammalian evolution, with enlarging brains leading the way into new and diverse forms. However, Bertrand *et al*. looked at encephalization rates across mammals beginning in the Paleocene and found instead that body sizes were the first to increase, allowing for niche filling after the extinction of the dinosaurs (see the Perspective by Smith). It was only later, in the Eocene, that brain size began to increase, likely driven by a need for greater cognition in increasingly complex environments. This led to the highly encephalized brains of today, including those of humans. —SNV

Science (ISSN) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.