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

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Abstract: 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 via 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.

One-Sentence Summary: Placental mammals had a smaller brain-to-body-size ratio after the dinosaur extinction but later, through competition, developed the largest vertebrate brains.

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 years of evolution, beginning with encephalization pulses— increases in brain size relative to body size—on the mammal stem lineage in the Mesozoic.

5 These increases were associated with heightened olfaction and the origin of the neocortex, a novel part of the cerebrum involved in higher cognition and sensory integration (3). Among extant mammals, the 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
10 fossils of extant placental orders (herein ‘placental crown orders’) from the Eocene (56-34 Ma) 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.

15 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 (66-56 Ma), the interval following 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)
20 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, 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 assess 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 use high-resolution computed tomography (CT) to measure the size of the brain and its individual sensory components (neocortex, olfactory bulbs, cerebellar petrosal lobules involved in control of eye movements (21) (Fig. 1). Our dataset includes 34 new Paleogene CT scans (17 Paleocene, 17 Eocene; table S1), alongside data from previous work. We examine patterns over time and across taxa in order 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 ask 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 Eocene stem taxa and crown orders (Fig. 2c). When expressed as a phylogenetic encephalization quotient (PEQ), a measure of relative brain size compared to its value predicted by allometry and phylogeny (22), Paleocene forms were less encephalized than Mesozoic and Eocene taxa (Fig. 2a,b; table S2). Following the Paleocene low in PEQ, both average PEQ and variance significantly expanded in the Eocene, in both stem taxa and crown orders (Figs. 2a,b,

4a). These results are robust to phylogenetic uncertainty (figs. S1-S2; tables S3-S5), body mass estimates (Figs. S3-S9; Tables S6-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 size actually decreased as they increased in body size 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; table S2). The olfactory bulbs became a significantly smaller component of the brain, and the petrosal lobules a larger component, in Eocene crown orders (Fig. 3; fig. S11; table S2). Additionally, the neocortex enlarged over time, and covered significantly more of the brain surface in Eocene crown orders versus Paleocene and Eocene stem forms (Fig. 3; 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 their Eocene stem contemporaries, despite insignificant differences in body mass among them (Fig. 2; table S2). These results are also robust to phylogenetic uncertainty and placental origin timing (figs. S12-S17; tables S3-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. 2d-g; table S9), as did the rate of change in both measures on the phylogeny (figs. S18-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 while this largely held in the Eocene, crown orders accelerated to faster relative increases in brain volume rate compared to 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.

5 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, figs. S18-S19) or immediately after the end-Cretaceous extinction (figs. S20, S22). This makes it difficult to differentiate the effects of the extinction itself, but because both dating approaches place the key pulses at/near the origin of Placentalia, this implies that
10 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
15 persistently high rates to assemble greatly encephalized modern placental brains with relatively large neocortices and petrosal lobules and small olfactory bulbs (figs. S23-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 due to independent increases in body mass in
20 'archaic' groups like 'condylarths', pantodonts, and taeniodonts (Fig. 4, figs. S18-S20, S22, S27-S29). Then, in the Eocene, there were several independent increases in PEQ, particularly in crown orders like artiodactyls (including cetaceans), perissodactyls, carnivorans, euprimates, and rodents (Fig. 4, figs. S18-S20, S22, S27-S29). Omnivores/carnivores were statistically indistinguishable in PEQ compared to contemporary herbivores in the Paleocene, but both guilds

significantly increased PEQ in the Eocene, with omnivores/carnivores eclipsing herbivores (fig. S30; table S10). The two most speciose placental subclades experienced different fates: raw body mass increased markedly in Paleocene-Eocene laurasiatherians (carnivorans, perissodactyls, artiodactyls) but not in euarchontoglires (rodents, 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; figs. S18-S20, S21).

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 novel or altered environments (25-28). All of these skills, presumably, would have been beneficial after a mass extinction, yet the placentals diversifying as devastated ecosystems recovered and new food webs emerged did not develop relatively larger brains, suggesting other factors were behind their radiation.

It appears that the post-extinction placental radiation emphasized body size rather than brain size changes, 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, petrosal lobules), the growth was primarily in regions permitting control of larger bodies (brain stem, diencephalon, 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, but growth focused in regions involved in advanced senses, as these mammals added better balance, vision, eye movement, head control, and sensory integration to their pre-existing 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 prey groups as ecosystems saturated. It was these crown placentals—among them the first horses, whales, dogs, bats, and euprimates—that achieved high PEQs, while the smaller-brained and more olfactory-driven stem taxa waned, with groups once so instrumental in the end-Cretaceous recovery and initial placental radiation—like ‘condylarths’ and pantodonts—ultimately succumbing to extinction.

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Supplementary Materials

Materials and Methods

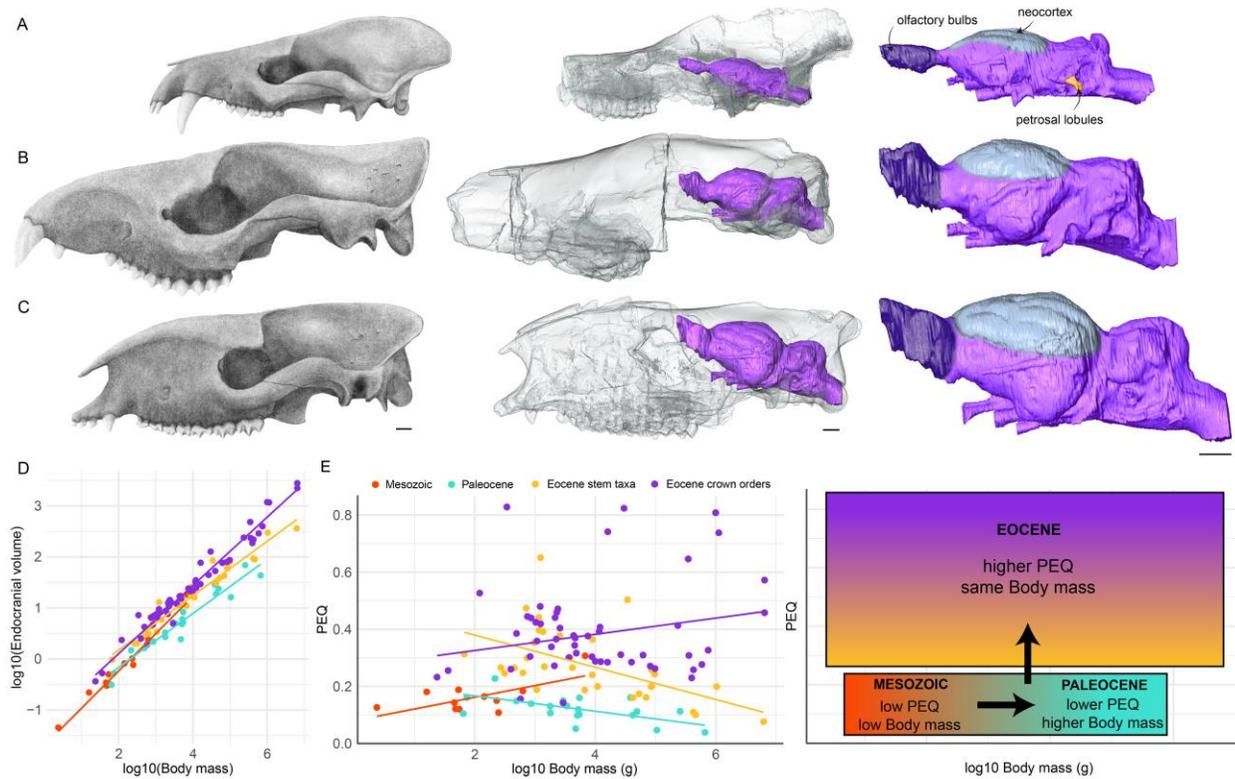
Sensitivity analyses results

Figs. S1 to S35

Captions for Tables S1 to S24

References (33–295)

Code and data files



5 **Fig. 1. Virtual endocasts of Cenozoic mammal exemplars used in this study with sensory**
regions highlighted and 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
10 **corrected PGLS regression of endocranial volume vs. body mass. (E) Phylogenetically**
corrected PGLS regression of PEQ vs. \log_{10} (body mass) and graphical summary of the results. The
petrosal lobules are absent in (C) and (D). Scale = 10mm.

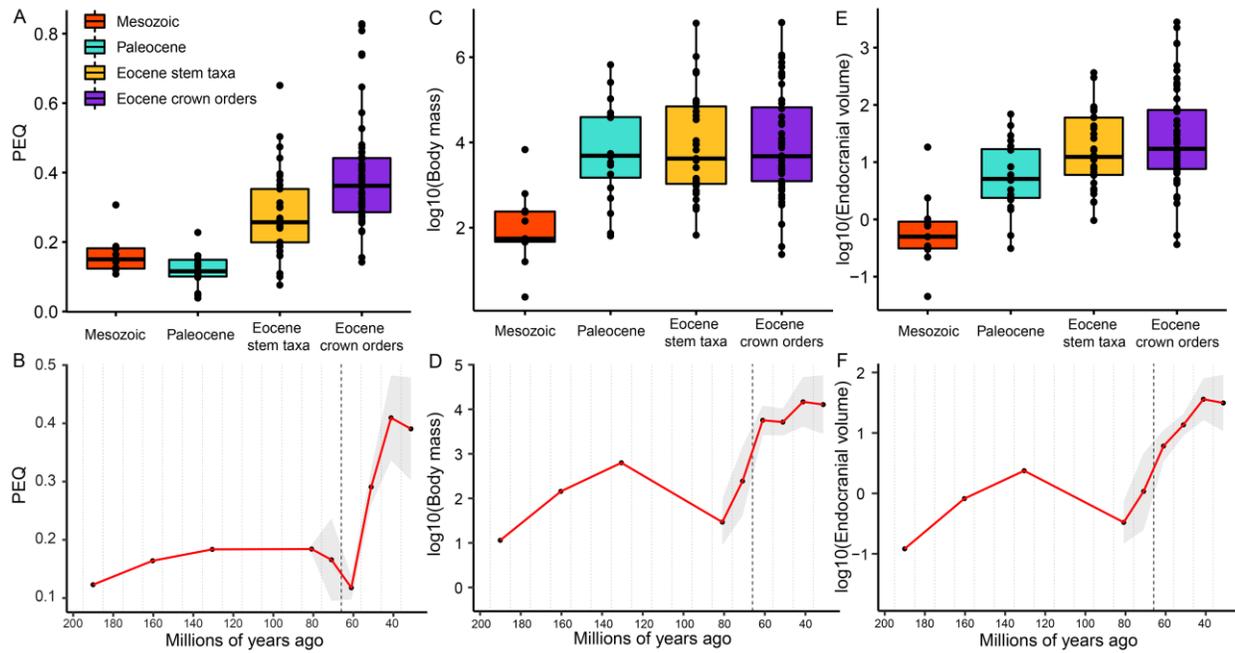


Fig. 2. Phylogenetic encephalization quotient (PEQ), endocranial volume and body mass of Mesozoic and early Cenozoic mammals. (A) Boxplot of PEQ for Mesozoic, Paleocene, Eocene stem taxa and Eocene crown orders. (B) PEQ average through time per 10-million-year bins. (C) Boxplot of \log_{10} (body mass). (D) Boxplot of \log_{10} (endocranial volume) for groups in (A). (E) \log_{10} (body mass) average through time per 10 million year bins for groups in (A). (F) \log_{10} (endocranial volume) average through time per 10 million year bins.

5

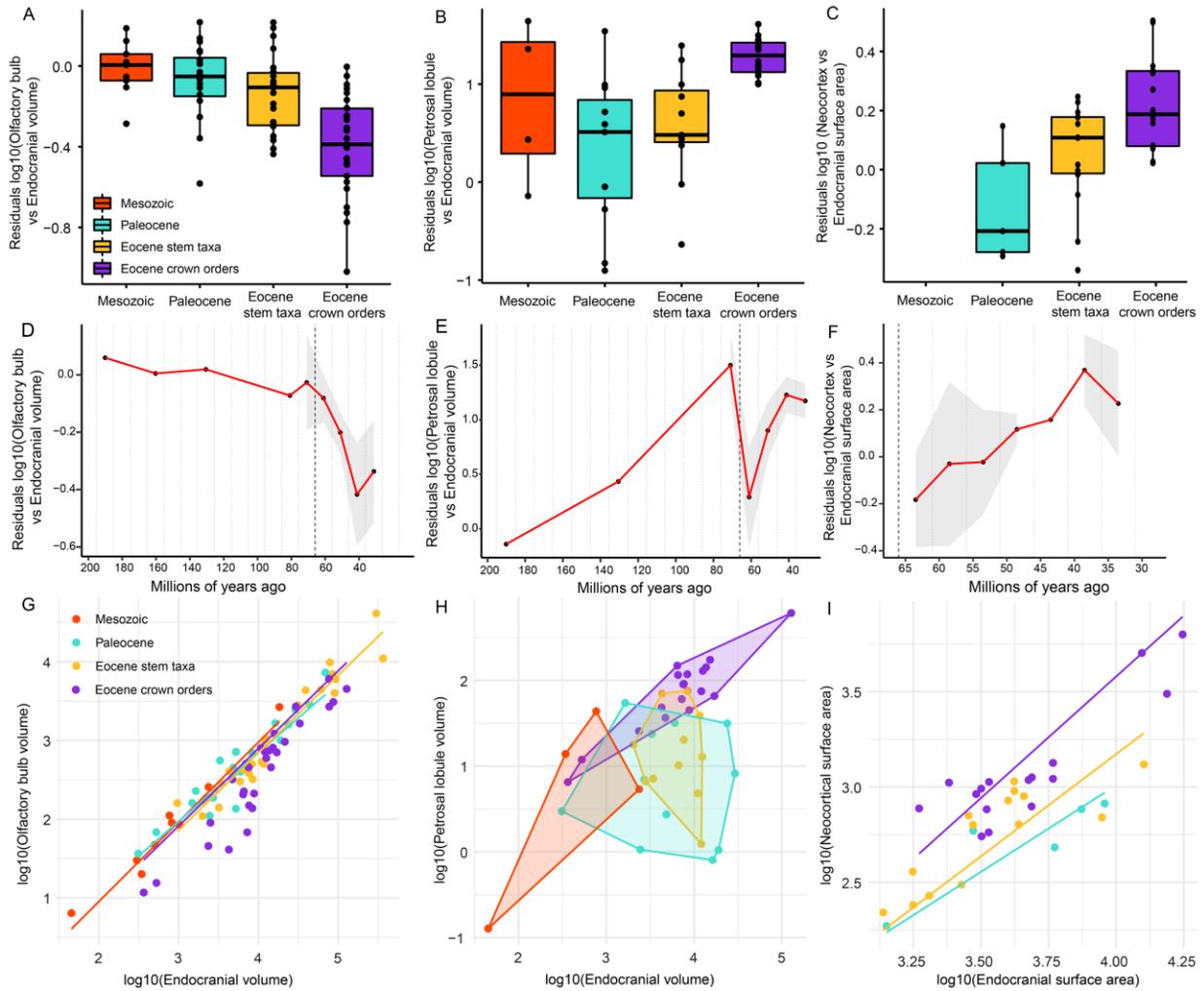


Fig. 3. Relative size of the olfactory bulbs, petrosal lobules, and neocortex of Mesozoic and early Cenozoic mammals.

(A) Boxplot of the residuals from a PGLS regression of \log_{10} (olfactory bulb volume vs. 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 vs. endocranial volume) for the groups in (A). (C) Boxplot of the residuals from a PGLS regression of \log_{10} (neocortical surface area vs. endocranial surface area) for the groups in (A). (D) Residuals of \log_{10} (olfactory bulb volume vs. endocranial volume) average through time per 10-million-year bins. (E) Residuals of \log_{10} (petrosal lobule volume vs. endocranial volume) average through time per 10 million year bins. (F) Residuals of \log_{10} (neocortical surface area vs. endocranial surface area) average through time per 5 million years bins. (G) PGLS regression of \log_{10} (olfactory bulb volume vs. endocranial volume) for the groups as (A). (H) PGLS regression of \log_{10} (petrosal lobule volume vs. endocranial volume) for the groups in (A). (I) PGLS regression of \log_{10} (neocortical surface area vs. endocranial surface area) for the groups in (A).

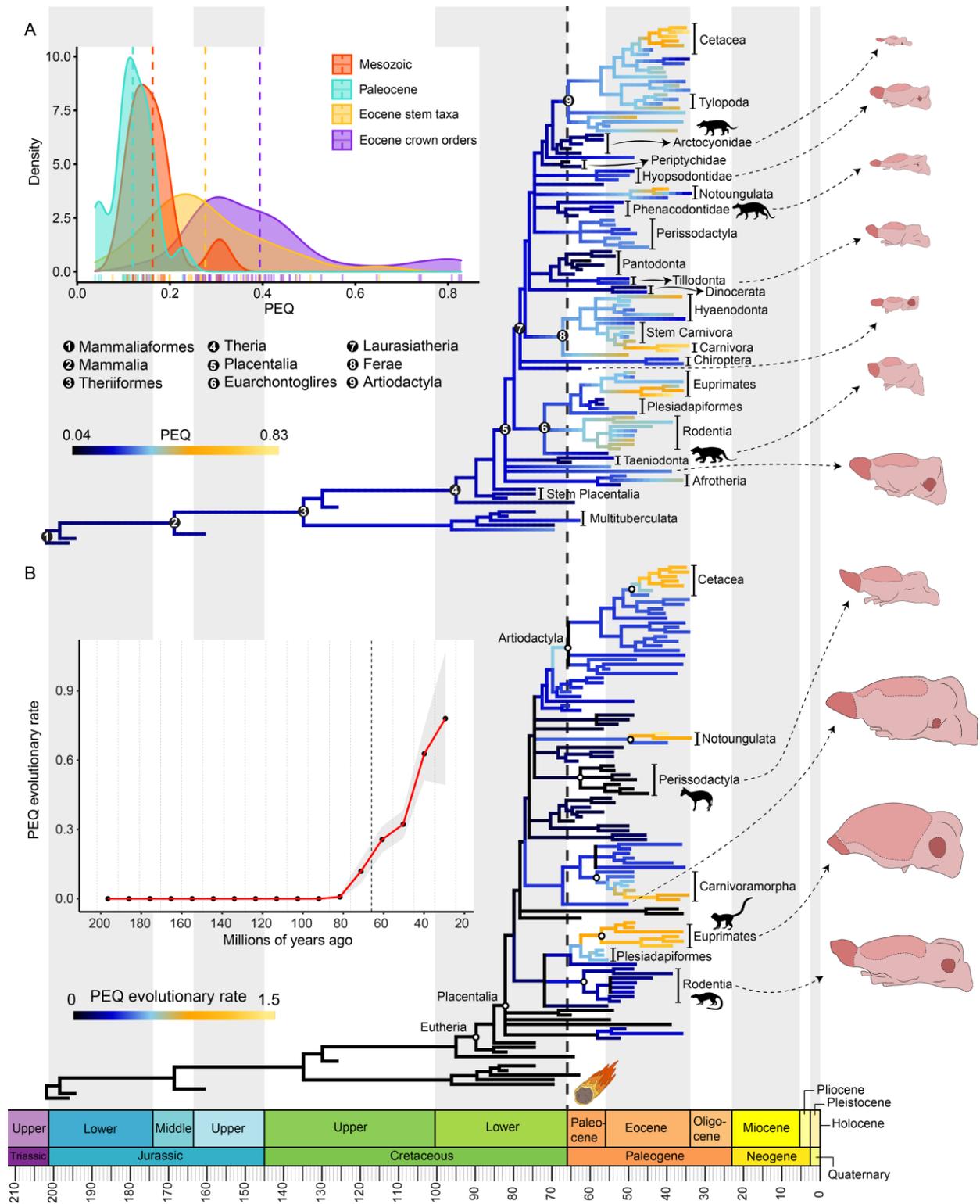


Fig. 4. Phylogenetic encephalization quotient (PEQ) evolutionary change across time and phylogeny in Mesozoic and early Cenozoic mammals. (A) PEQ density plot and ancestral state reconstruction mapped onto a phylogeny for Mesozoic, Paleocene and Eocene mammals. **(B)** PEQ evolutionary rate mapped onto a phylogenetic tree and averaged through time per 10-million-year bins. Virtual endocasts illustrated to the right with highlighted brain regions are

5 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), *Paramys delicatus* (AMNH 12506), and *Smilodectes gracilis* (UM 32773). Silhouettes from <http://phylopic.org/> (i.e., Euprimates, Perissodactyla and Rodentia).