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RESEARCH ARTICLE

The Placental Mammal Ancestor and the Post–K-Pg Radiation of Placentals

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To discover interordinal relationships of living and fossil placental mammals and the time of origin of placentals relative to the Cretaceous-Paleogene (K-Pg) boundary, we scored 4541 phenomic characters de novo for 86 fossil and living species. Combining these data with molecular sequences, we obtained a phylogenetic tree that, when calibrated with fossils, shows that crown clade Placentalia and placental orders originated after the K-Pg boundary. Many nodes discovered using molecular data are upheld, but phenomic signals overturn molecular signals to show Sundatheria (Dermoptera + Scandentia) as the sister taxon of Primates, a close link between Proboscidea (elephants) and Sirenia (sea cows), and the monophyly of echolocating Chiroptera (bats). Our tree suggests that Placentalia first split into Xenarthra and Epitheria; extinct New World species are the oldest members of Afrotheria.

It is disputed whether orders of placental mammals, the very diverse group of species that includes humans, evolved before or after the significant extinction horizon known as the Cretaceous-Paleogene (K-Pg) event 66 to 65 million years ago (Ma) (1, 2). Different models have been proposed to describe ordinal-level diversification either before (short-fuse model), near (long-fuse model), or after (explosive model) this boundary (3). The ~5100 living placental species collectively exhibit extreme size ranges (1.5-g bumblebee bat to 190,000-kg blue whale); dramatic locomotor diversity (e.g., running, flying, and swimming); and diverse degrees of encephalization (4). Moreover, extinct species in the placental fossil record are even more numerous and exhibit a broader range of adaptations (5). Given this diversity, it is of interest to determine the phenotype of the ancestral placental mammal.

The hypothesis that the oldest members of crown Placentalia [the clade of all living placental mammals (6)] were present by ~100 Ma in the Mesozoic Era has been supported by molecular clock analyses (7–9), which suggest that at least 29 mammalian lineages (7), including the stem lineages of Primates and Rodentia, appeared in Late Cretaceous ecosystems (8) and survived the massive K-Pg extinction event. However, fossil evidence has not corroborated this hypothesis, despite discovery of abundant, well-preserved, small vertebrates (10). By contrast, phenomic phylogenies incorporating fossils have placed ordinal and intraordinal specia-

tion of Placentalia after the K-Pg extinction event (11).

Determining placental origins and relationships has met with the practical challenge of codifying phenomic data on a scale comparable to that for genomic data to produce a maximally informed phylogenetic tree. We built a phenomic character matrix (4541 characters; 403 constant and 482 parsimony uninformative) using MorphoBank (12). The matrix contains newly scored characters for 86 species representing all living placental orders plus 40 fossil species, with more than 12,000 annotated images supporting the phenomic homologies. These data were examined with molecular sequences compiled from 27 nuclear genes from GenBank (table S1).

Placental orders originated after the K-Pg boundary. A single tree emerged from our combined phenomic-molecular parsimony analysis (Fig. 1; hereafter, "combined tree"); we also performed extensive sensitivity analyses using other tree-searching methods (13). We applied multiple fossil ages for the oldest members of the clades sampled and ghost lineage analysis (14) to this tree to determine minimum divergence dates using fossils alone (13). Results support the monophyly of most traditional orders originally identified on the basis of phenotypes, as well as interordinal groupings discovered using molecular sequence data (Fig. 1 and Table 1). Twenty nodes (over 40%) are congruent in partitioned molecular and phenomic analyses (fig. S2).

When time-calibrated, this tree indicates that none of the six, very complete Mesozoic fossil species (e.g., *Ukhaatherium*, *Maelestes*, and *Zalambdalestes*) sampled falls within crown clade Placentalia. Instead, these Mesozoic fossils emerge as nonplacental members of Eutheria or at lower nodes. This tree suggests that interordinal and ordinal diversification occurred within the first few hundred thousand years after the K-Pg event, and the first members of modern placental orders began appearing 2 to 3 million years (My) later during the Paleocene. All recent clock-based estimates for the ages of key clades, with few exceptions, are substantially older than indicated by the fossil record (7, 8, 15). Ghost lineage estimates are minimum divergence dates and may underestimate the timing of actual splits.

We find that only the stem lineage to Placentalia crossed the K-Pg boundary and then speciated in the early Paleocene. We estimate that the minimum age of the diversification of crown Placentalia is just younger than the K-Pg boundary, or ~36 My younger than molecular clock–based mean estimates derived from supertree (15) and supermatrix (7) analyses. We do not find support for the hypothesis that 29 to 39 (7, 15) mammalian lineages, including Afrotheria, Rodentia, Primates, Lipotyphla, Xenarthra,

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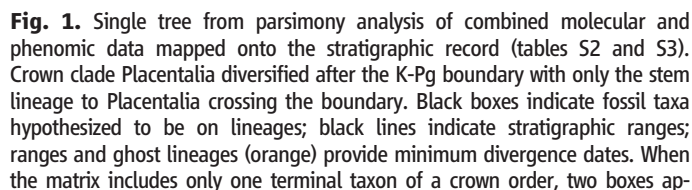†Present address: Department of Organismal Biology and Anatomy, University of Chicago, 1027 East 57th Street, Chicago, IL 60637, USA.
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Fig. 1. Single tree from parsimony analysis of combined molecular and phenomic data mapped onto the stratigraphic record (tables S2 and S3). Crown clade Placentalia diversified after the K-Pg boundary with only the stem lineage to Placentalia crossing the boundary. Black boxes indicate fossil taxa hypothesized to be on lineages; black lines indicate stratigraphic ranges; ranges and ghost lineages (orange) provide minimum divergence dates. When the matrix includes only one terminal taxon of a crown order, two boxes ap-pear: the oldest hypothesized member of the crown clade (the younger date) and the oldest hypothesized taxon on the stem to the crown clade (the older date). Crown clades (except Eutheria and Metatheria) are defined (table S4). Space immediately younger than 65 Ma not to scale showing early Paleo-cene interordinal diversification of Placentalia. Crown clades Marsupialia and Monotremata also diversified post K-Pg boundary. Bremer support (BS) (table S8) above nodes, jackknife values below nodes.

Table 1. Comparison of divergence dates for mammalian clades (tables S2 and S3) between our combined data analysis, a combined data supertree [Bininda-Emonds et al. (15)], and a molecules-only supermatrix [Meredith et al. (7)]. Ranges and ghost lineages are illustrated in Fig. 1; date calculations are described in (14). Names listed specify crown clades (table S4); older dates in (7, 15) are negative differences (bold). −, no data; NA, not applicable because clade not found in our study.

Taxon		Oldest crown clade member (this study)		Oldest crown clade member—Age midpoint (range) and difference from our study			
Higher clades	Orders	Taxon	Clade age (range) (Ma)	Bininda-Emonds et al. (Ma)	Difference	Meredith et al. (Ma)	Difference
Mammalia Linnaeus 1758		Dryolestida [Martin et al. (38)]	166.2 (167.7–164.7)	166.2*	1.5	217.8 (203.3–238.2)	**−50.1**
Monotremata Bonaparte 1838		*Obdurodon insignis*	20.0 (28.4–11.6)	63.6 ± 11.4	**−35.2**	36.7 (22.4–103.1)	**−8.4**
Theria Parker & Haswell 1897		*Sinodelphys szalayi*	127.5 (130.0–125.0)	_	_	190.0 (167.2–215.3)	**−60.0**
Marsupialia Illiger 1811		*Peradectes minor*	64.85†	82.5 ± 11.1	**−17.7**	81.8 (67.9–97.2)	**−17.0**
Placentalia Owen 1837		*Protungulatum donnae*	64.85†	101.3 ± 7.4	**−36.5**	101.3 (92.1–116.8)	**−36.5**
	Xenarthra Cope 1889	*Riostegotherium yanei*	58.3 (57.5–59.0)	72.5 ± 5.1	**−13.5**	65.4 (58.4–71.5)	**−6.4**
Epitheria McKenna (21)		*Protungulatum donnae*	64.85†	_	_	NA	_
Afrotheria Stanhope et al. (39)		*Prodiacodon crustulum*	64.85†	93.4 ± 3.0	**−28.6**	80.9 (74.4–96.5)	**−16.1**
Paenungulata Simpson (40)		*Simpsonotus praecursor*	61.8 (62.5–61.0)	_	_	64.3 (56.0–70.6)	**−1.8**
	Hyracoidea Huxley 1869	*Prohyrax hendeyi*	17.3 (23.0–11.6)	19.1 ± 0.8	**−3.9**	6.1 (3.9–8.3)	16.9
	Macroscelidea Butler 1956	*Miorhynchocyon* sp.	21.2 (22.4–20.0)	50.7 + 7.6	**−28.3**	49.1 (37.7–57.2)	**−26.7**
Tethytheria McKenna (21)		*Eritherium azzouzorum*	58.7	_	_	_	_
	Proboscidea Illiger 1811	*Primelephas gomphotheroides*	14.2 (23.0–5.3)	19.5 ± 12.1	**−3.5**	5.3 (1.8–8.0)	17.7
	Sirenia Illiger 1811	*Eotheroides aegyptiacum*	44.5 (48.6–40.4)	52.2 ± 14.4	**−3.6**	31.4 (25.0–34.4)	17.2
Boreoeutheria Springer & de Jong (41)		*Protungulatum donnae*	64.85†	_	_	92.0 (82.9–107.6)	**−27.2**
Laurasiatheria Waddell et al. (42)		*Protungulatum donnae*	64.85†	91.8 ± 2.6	**−27.0**	84.6 (78.5–93.0)	**−19.8**
	Lipotyphla Haeckel 1866	*Litolestes ignotus*	58.3 (58.9–57.8)	84.2 ± 2.1	**−22.5**	77.3 (70.7–85.8)	**−15.6**
	Chiroptera Blumenbach 1779	*Archaeonycteris praecursor*	55.5	74.9 ± 3.3	**−19.4**	66.5 (62.3–71.3)	**−11.0**
	Perissodactyla Owen 1848	*Hyracotherium angustidens*	52.9 (55.4–50.3)	58.2 ± 4.9	**−2.8**	56.8 (55.1–61.0)	**−1.4**
	Pholidota Weber 1904	*Smutsia gigantea*	5.0 (7.3–2.6)	19.9 ± 20.7	**−12.6**	25.3 (16.9–35.7)	**−18.0**
	Carnivora Bowditch 1821	*Hesperocyon gregarius*	43.3 (46.2–40.4)	67.1 ± 3.8	**−20.9**	54.7 (47.4–60.6)	**−8.5**
	Artiodactyla Owen 1848	*Cainotherium* sp.	44.9 (55.8–33.9)	74.1 ± 3.1	**−18.3**	65.4 (62.3–68.5)	**−9.6**
Euarchontoglires Murphy et al. (88)		*Purgatorius coracis*	64.85†	94.5 ± 2.0	**−29.7**	83.3 (74.1–97.8)	**−18.5**
Euarchonta Wadell et al. (42)		*Purgatorius coracis*	64.85†	_	_	82.0 (73.7–97.4)	**−17.2**
	Primates Linnaeus 1758	*Teilhardina brandti*	53.1 (55.8–50.3)	87.7 ± 2.7	**−31.9**	71.5 (64.3–78.4)	**−15.7**
	Dermoptera Illinger 1811	No crown clade fossils	No crown clade fossils	13.0 ± 5.2	_	7.4 (4.5–13.2)	_
	Scandentia Wagner 1855	*Eodendrogale parvum*	42.9 (48.6–37.2)	32.7 ± 2.6	15.9	55.9 (45.0–63.9)	**−7.3**

(Continued on next page)

Taxon		Oldest crown clade member (this study)		Oldest crown clade member—Age midpoint (range) and difference from our study			
Higher clades	Orders	Taxon	Clade age (range) (Ma)	Bininda-Emonds et al. (Ma)	Difference	Meredith et al. (Ma)	Difference
Glires Linnaeus 1758		*Mimotona wana*	63.4 (65.0–61.7)	–	–	79.5 (71.5–94.1)	**−14.5**
	Rodentia Bowditch 1821	*Sciuravus* sp.	56.8	85.3 ± 3.0	**−28.5**	69.0 (64.1–74.8)	**−12.2**
	Lagomorpha Brandt 1885	Leporidae [Rose *et al.* (*43*)]	53.0	66.8 ± 5.1	**−13.8**	50.2 (47.4–56.9)	2.8

*Fixed calibration point.   †Age between 65.0 and 64.7 Ma, in the Cenozoic portion of Chron C29r, 230 to 420 ky above the K-Pg boundary (*1, 2*).
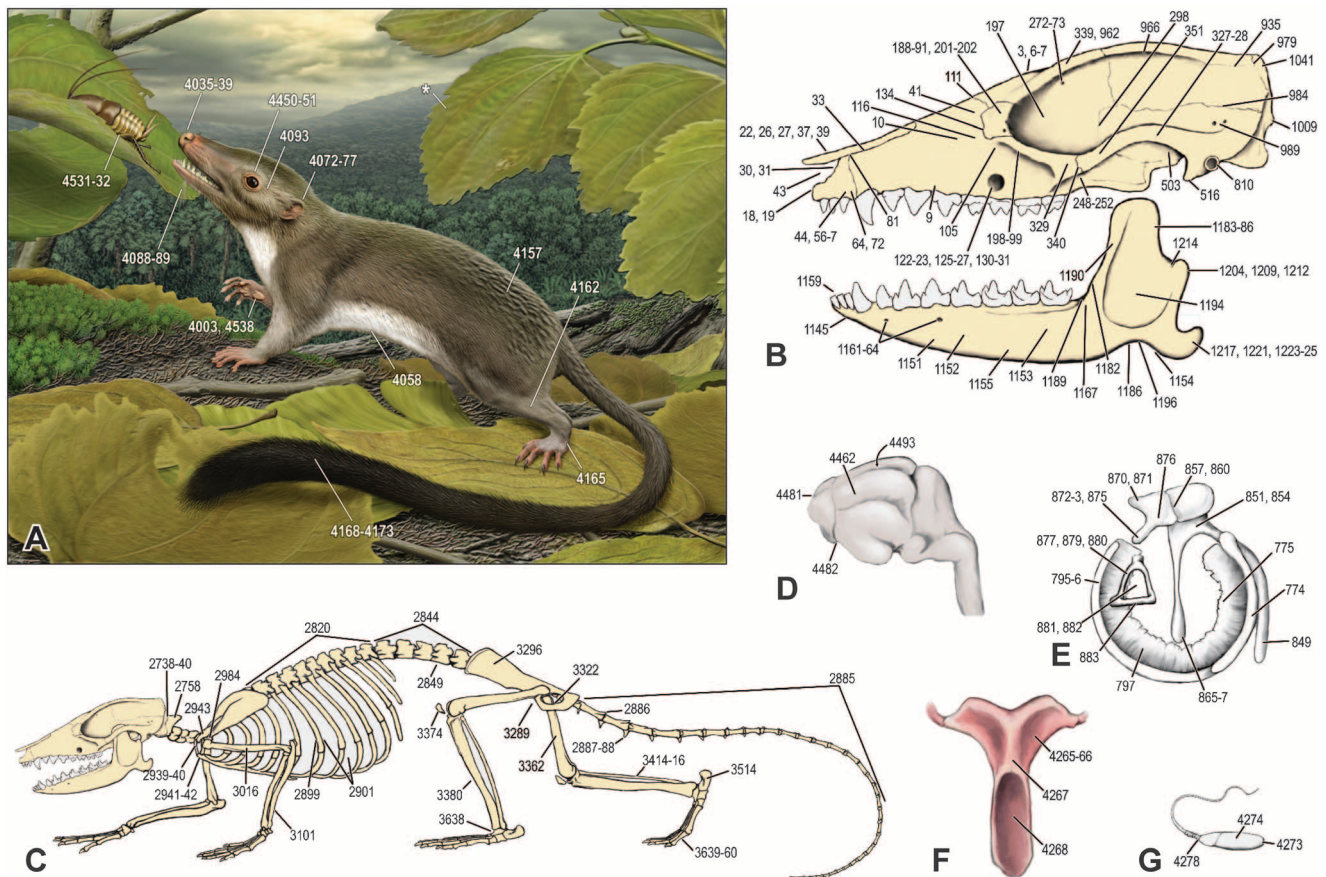
Fig. 2. Reconstructions of the phenotype of the hypothetical placental ancestor derived from the combined data matrix optimized onto the tree in Fig. 1. The mammal is shown in an early Paleocene ecosystem. (**A**) External body, posture, and diet of insectivory; asterisk depicts the plant *Paranymphaea crassifola* of the early Paleocene. (**B**) Cranium and dentary bone, (**C**) skeleton, (**D**) brain in left lateral view, (**E**) ear ossicles and ectotympanic bone, (**F**) uterus, and (**G**) sperm cell. Numbers designate a subset of the numerous phenomic characters used to build these reconstructions (appendix S1).

Artiodactyla, and Chiroptera, each crossed the K-Pg boundary.

We recognize *Protungulatum donnae* as the oldest undisputed species within crown Placentalia (Fig. 1), and this species dates to the earliest Paleocene (*13*) within an interval extending from the K-Pg boundary to ~200,000 to ~400,000 years later (*16, 17*). Integration of fossils as primary data in the phylogeny indicates that ~10 interordinal speciation events might have occurred in as little as 200,000 years. Most of the fossil species sampled across Placentalia fall either within ordinal crown clades or on the immediate stem to ordinal crown clades (exceptions are stem taxa to Glires, Tethytheria, and Euungulata).

Our results also imply that the total clade Eutheria (all species more closely related to Placentalia than to any other living species) is younger than estimated from prior studies. The Cretaceous fossil *Eomaia scansoria* (125 Ma) has previously been called a placental (*18*) or eutherian (*11, 18, 19*); however, we find with 100% jackknife support that *Eomaia* falls outside of Eutheria as a stem taxon to Theria. The oldest age of Eutheria in our study is constrained by taxa such as *Maelestes* and is 91 Ma. The age of Theria is 127.5 Ma, a clade that some molecule-based estimates previously suggested to be 190 Ma (*7*).

Phenomic topologies dominate for key clades. We resolve the basal diversification within Placentalia, a historically unstable node (20), as a split between Xenarthra and Epitheria (all other placentals; 89% jackknife and Bremer support of 14 steps). These clades were previously predicted to be monophyletic on the basis of phenomic data alone (21). The phenomic data–only tree (fig. S2A) supports the clade Sundatheria [Scandentia (treeshrews) + Dermoptera (flying lemurs)] as the sister taxon of Primates, a topology that prevails in the combined analysis, in contrast to molecules-only trees that favored Dermoptera in this role (7, 22).

The existence of two clades within bats (Chiroptera), one that echolocates (Microchiroptera) and one that does not (Megachiroptera), emerges from the phenomic-only analysis (fig. S2A), in contrast to molecule-based results (fig. S2B) (7, 23, 24). Microchiroptera in our combined data tree has low support, most likely because the molecules-only and phenomic-only trees each had 100% jackknife support for mutually incompatible hypotheses. In the combined tree, the phenomic signal is upheld relative to the molecular signal. The arrangement of two Eocene fossil bats (*Onychonycteris* + *Icaronycteris*) as a sister clade to extant Microchiroptera also differs from prior results (25). Molecules alone, here (figs. S2B and S3 to S6) and in prior studies (7), do not support Tethytheria. Phenomic data alone do support Tethytheria, and the combined data tree retains Tethytheria with relatively strong support, which corroborates previous combined data analyses (26).

Regarding extinct species, many fossil hoofed mammals are part of Laurasiatheria, and extinct relatives of Carnivora known as Creodonta lack deep linkages to African taxa (27). Endemic South American ungulates are split between Pan-Euungulata and Afrotheria (28). The fossil *Rhombomylus* has lagomorph (rabbit) affinities (29), which implies that loss of incisors occurred independently in Rodentia and Lagomorpha. Extinct Palaeanodonta (*Metacheiromys*) falls closer to Pholidota than to Xenarthra (30), and *Moeritherium* is a member of Tethytheria.

Reconstructing the placental ancestor and its dental formula. Integration of data for both fossil and living species permits reconstruction of ancestral nodes across the placental tree by using optimizations (Fig. 2 and appendix S1). We reconstructed the hypothetical placental ancestor using synapomorphic and symplesiomorphic characters. It weighed between 6 and 245 g (character 2026), was insectivorous (characters 4531 and 4532) and scansorial (character 4538), and single young were born hairless with their eyes closed (character 4290). Females had a uterus with two horns (character 4265) and a placenta with a trophoblast (character 4295), and males produced sperm with a flat head (character 4274) and had abdominal testes (characters 4228 and

4229) positioned just caudal to the kidneys. The brain was characterized by the presence of a corpus callosum (character 4493), an encephalization quotient greater than 0.25 (character 4460), facial nerve fibers that passed ventral to the trigeminal sensory column (character 4492), and a cerebral cortex that was gyrencephalic (character 4462) with distinctly separate olfactory bulbs (character 4482). A hemochorial placenta (character 4313) optimizes unambiguously to the base of Placentalia (31). The basal placental also lacked an endodermal cloaca (character 4226), having separate anal and urogenital openings.

Osteologically (Fig. 2), the placental ancestor had a triangular, perforate stapes (characters 878 and 882) and lacked epipubic bones (character 3290). Reconstructing soft tissues not preserved in fossils is best done by optimization (32) when both soft tissues and osteology have built the underlying tree. The path of the internal carotid artery sometimes leaves channels on adjacent bones and is frequently reconstructed in fossils (33). We find that this artery (scored as a soft tissue character in living species) optimizes as present in the ancestor of Placentalia; however, the three osteological correlates of the artery are each
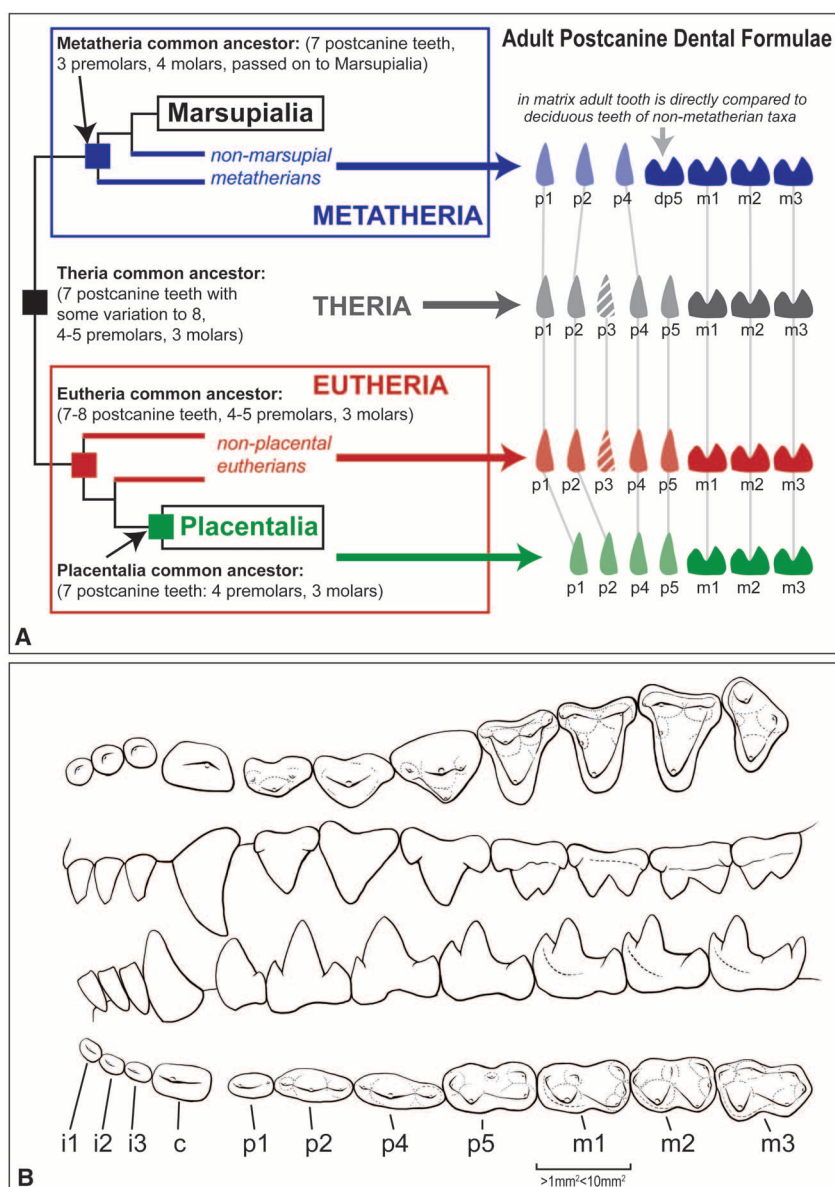

Fig. 3. (A) Split between Placentalia and Marsupialia and homologies of hypothesized adult postcanine dental formulae. Gray lines indicate adult teeth compared for cladistic scoring. **(B)** Reconstructions of the dentition of the hypothetical placental ancestor based on optimization (appendix S1, see also figs. S11 to S14). Views are left side. From top to bottom: occlusal upper teeth, labial upper teeth, labial lower teeth, and occlusal lower teeth. p, premolar; dp, deciduous premolar; m, molar.

absent (appendix S1). Thus, the conservative hypothesis is that the artery was present in the placental ancestor but did not leave an osteological correlate.

We have implemented a revised postcanine tooth formula for clades within Theria and reconstructed the dentition of the hypothetical placental ancestor (Fig. 3A). Complexities of homology arise in Theria regarding the number of premolars [any postcanine tooth with two generations (deciduous or "baby" teeth and permanent or "adult" teeth) or a postcanine tooth anterior to a tooth with two generations (*34*)]. Molars, by contrast, have a single generation and are posterior to teeth that are replaced. Metatheria (and Marsupialia) primitively have seven postcanine teeth, three of which are premolars. The common ancestor of Placentalia also had seven postcanine teeth, but four of these were premolars, and some nonplacental eutherians had as many as five premolars (*11*).

The primitive dental formula for Theria optimizes on our tree (Fig. 3) to be seven postcanine teeth: four premolars and three molars (Fig. 3A). Both Metatheria and Placentalia have each lost the third premolar (p3/P3) during evolution. We hypothesize that the first tooth in the molar series in Metatheria is homologous to the deciduous p5 (dp5) of eutherians, including placentals (*34, 35*). What has been lost in Metatheria is the p5 locus tooth replacement. The implication for phylogenetic work is that a tooth at the fourth postcanine locus of an adult metatherian (the retained dp5) must be compared directly with a tooth in the dentition of a juvenile placental (the dp5). Accordingly, we revise the postcanine dental formula for Theria such that the primitive adult dentition for Placentalia consists of upper and lower p1, p2, p4, p5, m1, m2, and m3 [see (*33*)]. The reconstructed ancestral placental dentition lacks lower fourth and upper fourth and fifth incisors (characters 1327, 1388, and 1391), lacks canine dimorphism (characters 1404 and 1428), and has small stylar shelves on the upper molars (characters 2330 and 2476) (Fig. 3B and appendix S1).

Biogeography and placental paleoenvironments. Our relatively younger age estimate for Placentalia means that there is no basis for linking placental interordinal diversification to the Mesozoic fragmentation of Gondwana (*8*). The most ancient members of Afrotheria included in our tree are extinct South American ungulates and the North American fossil *Leptictis dakotensis*, which suggests that Afrotheria did not originate in Africa. The oldest afrotherian is the North American leptictid *Prodiacodon crustulum*, whose antiquity constrains Afrotheria's minimum age and extends several afrotherian lineages into the early Paleocene (Fig. 1). Members of Afrotheria would have been present in two regions of

the New World by the early Paleocene. Given that afrotheres are not found in the Mesozoic and that South America was an island continent for most of the Late Cretaceous and Cenozoic, a vicariant explanation for this pattern is precluded. Afrotheres would have had to disperse either from North to South America, or the reverse, in the Paleocene, and then to Africa.

The early Paleocene diversification of placentals occurred in a radically transformed terrestrial ecosystem lacking nonavian dinosaurs and other species terminated at the K-Pg event (*10*). Maximum K-Pg extinction estimates for plants are 57% of megaflora and 30% of pollen-producing plants from North American localities (*36*). In some areas, insects and plants were substantially affected by the K-Pg event (*37*), and such changes may have left available to the insectivorous placental ancestor a different diet than would have existed in the Mesozoic. This interval of dramatic environmental transformation would have bracketed several interordinal speciation events within Placentalia. The incompleteness of the fossil record will always constrain what we can infer about the past, but integration of phenomic and genomic data have here corroborated the hypothesis that ordinal and interordinal diversification of Placentalia most closely fits the explosive model (*3*) and that there was no Cretaceous Terrestrial Revolution (*7*) for Placentalia.

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