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Combined data analysis of fossil and living mammals: a Palaeogene sister taxon of Placentalia and the antiquity of Marsupialia

Paúl M. Velazco[a,b]*, Alexandra J. Buczek[a], Eva Hoffman[a], Devin K. Hoffman[c], Maureen A. O'Leary[a,d] and Michael J. Novacek[a]

[a]*Division of Paleontology, American Museum of Natural History, New York, NY, 10024, USA;* [b]*Department of Biology, Arcadia University, Glenside, PA, 19038, USA;* [c]*Department of Geosciences, Virginia Tech, Blacksburg, VA, 24060, USA;* [d]*Department of Anatomical Sciences, Renaissance School of Medicine, Stony Brook University, Stony Brook, NY, 11794, USA*

Abstract

The Cretaceous–Palaeogene (KPg) boundary, one of Earth's five major extinction events, occurred just before the appearance of Placentalia in the fossil record. The Gobi Desert, Mongolia and the Western Interior of North America have important fossil mammals occurring just before and after the KPg boundary (e.g. *Prodiacodon*, *Deltatheridium*) that have yet to be phylogenetically tested in a character-rich context with molecular data. We present here phylogenetic analyses of >6000 newly scored anatomical observations drawn from six untested fossils and added to the largest existing morphological matrix for mammals. These data are combined with sequence data from 27 nuclear genes. Results show the existence of a new eutherian sister clade to Placentalia, which we name and characterize. The extinct clade Leptictidae is part of this placental sister clade, indicating that the sister clade survived the KPg event to co-exist in ancient ecosystems during the Palaeogene radiation of placentals. Analysing the Cretaceous metatherian *Deltatheridium* in this character-rich context reveals it is a member of Marsupialia, a finding that extends the minimum age of Marsupialia before the KPg boundary. Numerous shared-derived features from multiple anatomical systems support the assignment of *Deltatheridium* to Marsupialia. Computed tomography scans of exquisite new specimens better document the marsupial-like dental replacement pattern of *Deltatheridium*. The new placental sister clade has both Asian and North American species, and is ancestrally characterized by shared derived features such as a hind limb modified for saltatorial locomotion.

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Introduction

One of the most comprehensive morphological studies of phylogenetic relationships emerged from the collaborative work of a team of palaeontologists and mammalogists investigating the mammal tree of life (O'Leary et al., 2013). Working in annual conference meetings and through the collaborative web application MorphoBank, these authors standardized anatomical terminology and resolved longstanding disagreements on homology to identify over 4541 discrete morphological characters from osteology and soft tissues. They then scored these characters for 86 species, including 40 key fossils, and documented their work with labelled images and annotations. By combining this morphological matrix with published molecular sequences these authors produced a well-tested, parsimony-based tree of relationships derived from multiple sources, producing a particularly thorough example of the application of combined analysis (Kluge, 1989, 1998; Nixon & Carpenter, 1996). Results of O'Leary et al. (2013) showed that no placental mammal fossils tested pre-dated the Cretaceaous–Palaeogene (KPg) boundary, one of Earth's five major extinction events. Those authors also showed that although many clades in the combined tree derived from a signal in the molecular data partition, this large

*Corresponding author:
E-mail address:* pvelazco@amnh.org

morphological dataset overturned several molecules-only results.

Given its comprehensiveness, building on this matrix with new morphological data collection is an important approach to ongoing phylogeny testing through combined data analysis. Because of the time-consuming nature of the morphological data collection, it is important to select carefully which taxa might be most impactful for future work. O'Leary et al. (2013) highlighted (see the Supplementary Materials of that paper) several fossils that were a high priority for further testing based on their morphology, antiquity and completeness. Here we add some of these fossils and report on their impact on the combined data mammal tree analysed with parsimony. Our study contributes >6000 newly scored and illustrated anatomical observations made on six previously unsampled fossil taxa (O'Leary et al., 2013).

As a prelude to discussing the new phylogenetic results, we note that applying the convention of crown clades and total clades (de Queiroz, 2007) has been particularly useful in the study of higher-level mammalian relationships, especially when the position of fossil species relative to living species is an intensive research topic. This convention has helped ensure that clade names are unambiguous and that palaeontologists and molecular biologists investigating phylogenetics are talking about "the same thing" when calling a species "a placental mammal" or "a marsupial" [see discussion in O'Leary et al., 2013 (Supplementary Materials)]. To review the key points, Mammalia, and the three major clades with living species nested within Mammalia, have each been defined as crown clades with associated total clades, the latter containing fossil species that are on the stem branch to the crown clade in question. Particularly relevant to our results below are the crown clades Placentalia and Marsupialia within Mammalia. These clades contain the living placental and marsupial mammals, respectively, and—of course—each of these clades contains many, well-documented fossil species. The total clade of Placentalia is called Eutheria, and that of Marsupialia, Metatheria. Thus, all placental mammals are eutherians, but not all eutherians are placentals. Likewise, all eutherians that are not placentals are extinct. An important research focus has been testing which fossils, and of what age, fall inside a crown clade like Placentalia as opposed to outside of it on the placental stem in the total clade Eutheria (O'Leary et al., 2013; Wible et al., 1995, 2004, 2007, 2009).

One noteworthy result of O'Leary et al. (2013) was that, of the taxa sampled, the clade Placentalia contained no fossil taxa from the Cretaceous. Thus, a priority for additional taxon sampling in combined data analyses has been to select fossil taxa thought to be ancient or basal branches of the total clades Eutheria

and Metatheria, to investigate whether any of these extinct species actually belonged to the crown clades themselves.

Four of the new fossils we add here come from Late Cretaceous localities: the metatherian *Deltatheridium pretrituberculare*, and the eutherians *Prokennalestes trofimovi*, *Kennalestes gobiensis* and *Gypsonictops hypoconus*. Moreover, in the case of *Deltatheridium pretrituberculare*, several new specimens discovered from recent field work in the Cretaceous of Mongolia made this taxon a priority for inclusion. We also sampled two fossil eutherians from the early Palaeogene: *Prodiacodon puercensis* and *Palaeictops bicuspis* because they are members of Leptictidae, a fossil clade whose anatomical variation captures important aspects of early mammalian diversification (Novacek, 1986; Velazco & Novacek, 2016) and in many papers has been associated with the Cretaceous taxon *Gypsonictops* (Novacek, 1986).

It previously has been shown that the extinct taxon *Deltatheridium*, from the Late Cretaceous of Mongolia, was the sister taxon of the crown clade Marsupialia, and that both were part of the larger clade Metatheria (Rougier et al., 1998). Although not emphasized in the publication of O'Leary et al. (2013), which discussed many issues regarding placental mammals, that dataset also incorporated numerous characters from prior phylogenetic analyses of marsupials (Horovitz, 2000; Horovitz & Sánchez-Villagra, 2003). The matrix also sampled living and fossil metatherians to a roughly similar degree as the study sampled most placental mammal clades; thus, two extant marsupials were included in O'Leary et al. (2013) and, among placental clades, five extant chiropterans and four extant rodents were sampled as representatives of the two most diverse clades of placentals. Below we discuss in more detail findings related to marsupials, particularly in the context of the discovery of a new, juvenile fossil specimen of *D. pretrituberculare*.

Materials and methods

Taxon sample

We selected six new fossil taxa for study (Table 1) because of their relevance to the problem of metatherian and eutherian diversification. The stratigraphic ages of the first appearances of the six newly added fossil species are listed in Table 1 [see also the Supplementary Materials of O'Leary et al. (2013) for first appearances of all other species in the tree]. These six fossil species were scored for any of the 4541 phenomic characters in O'Leary et al. (2013) that were preserved. The new species were scored from direct observation. We did not modify the published characters, nor did we add new characters. The numbers of cells scored for each of the new fossil taxa are in Table 1 (characters not scored were not preserved or were inapplicable).

Table 1
Numbers of characters scored *de novo* for six fossil species in this analysis; images of the character states for these scorings also have been added to the database MorphoBank

Fossil taxa	Ages of the first appearances	Cells scored	Material
Deltatheridium pretrituberculare	Late Cretaceous, Campanian (Dingus et al., 2008)	1387	Partial cranium (4), petrosal (1), dentaries (8), postcranial skeleton (1), ulna (2), and upper and lower teeth
Prokennalestes trofimovi	Early Cretaceous, Aptian/Albian (Lopatin & Averianov, 2017)	871	Petrosal (1), partial dentaries (5), and upper and lower teeth
Kennalestes gobiensis	Late Cretaceous, Campanian (Dingus et al., 2008)	1138	Partial cranium (3), partial dentaries (3), and upper and lower teeth
Prodiacodon puercensis	Middle Palaeocene, early Tiffanian (Halverson & Eberle, 2018)	936	Partial cranium (1), partial dentaries (2), partial pelvis (1), partial femur (1), partial tibia (1), calcaneus (1), astragalus (1),
Palaeictops bicuspis	Early Eocene, Wasatchian (Velazco & Novacek, 2016)	957	Partial cranium (1), partial dentaries (3), and upper and lower teeth
Gypsonictops hypoconus	Late Cretaceous, Maastrictian (Archibald & Clemens, 1984)	917	Partial dentaries (6), and upper and lower teeth

Ages correspond to numbers in Figure 1 (following O'Leary et al., 2013: tables S2 and S3).

Character sample: morphological data

Characters were scored and documented in the web application and database MorphoBank (O'Leary & Kaufman, 2011), Project P3871, and the matrix and additional phylogenetic files are freely viewable online. This project was created by duplicating Project P773 (O'Leary et al., 2013) so that the additional taxa could be added for simultaneous analysis of new data with published data. The six new fossil taxa were examined using light microscopy, digitally photographed, and >900 new images were loaded to the matrix from O'Leary et al. (2013). Photographs documenting the character states were loaded to MorphoBank so that the homology assessments for the new taxa were thoroughly documented for maximum repeatability. Computed tomography (CT) scans of *D. pretrituberculare* and *Zalambdalestes lechei* also are presented here as additional important new information. Information on the CT data collection and processing can be found in Table S1. Images from the scans are deposited in MorphoBank Project P3871.

Character sample: molecular data

The molecular dataset of 27 nuclear genes for the combined data analysis was that used in O'Leary et al. (2013: Supplementary Materials). The O'Leary et al. (2013) dataset included genes used in previous higher-level mammalian phylogenetic analyses (Madsen et al., 2001; Meredith et al., 2011; Murphy et al., 2001a,b) and x-linked zinc finger protein (zfx). The final matrix analysed here consisted of 4541 discrete morphological characters; 27 nuclear genes (37 kbp); and 92 species, of which 46 were fossils. All of the DNA characters for all fossils were replaced with "?".

Phylogeny reconstruction

The combined matrix of 41 401 characters, was prepared in a text editing program for phylogenetic analysis. On the basis of first principles, we consider the combined data parsimony analysis to be the most effective means of analysing this dataset (Farris, 1983). However, we recognize that often there is keen interest in using large, newly collected, primary datasets for reanalysis under a range of partitions and statistical algorithms as the basis for new publications. Thus, we preempt this trend by providing and briefly discussing alternative trees from model-based methods and certain data partitions (i.e. molecular and morphological data) for the reader's information (Appendix; Figs A1–A3, S1–S5).

Maximum parsimony (MP) analyses were performed in the program TNT (Goloboff & Catalano, 2016). Characters were considered unordered and were assigned equal weights. We conducted a new technology search including sectorial searches, ratchet, tree drifting and tree fusing. The search was set to stop after finding the minimum length 40 times. After the initial search, TBR arrangements were searched with the tree in memory. We rooted the tree along the branch leading to *Morganucodon*. Nodal support in all analyses was assessed using 1000 jackknife replicates (Farris et al., 1996). Additional Bremer Support indices (Bremer, 1994) were calculated for our main tree. We plotted the main tree against minimum stratigraphic age drawn from the literature for each terminal (Table 1). Because we are focused on the basal nodes of Placentalia and Marsupialia for this study, we present a summary tree of those nodes in Fig. 1 and the full tree in Fig. A1.

For the additional model-based analyses, computational limitations of these approaches regarding our dataset must first be described. The Mkv model used by model-based algorithms to infer phylogenies from morphological data has been shown to be too unrealistic and inadequate to analyse these types of datasets (Goloboff et al., 2019). The MP analyses run with implied or equal weights
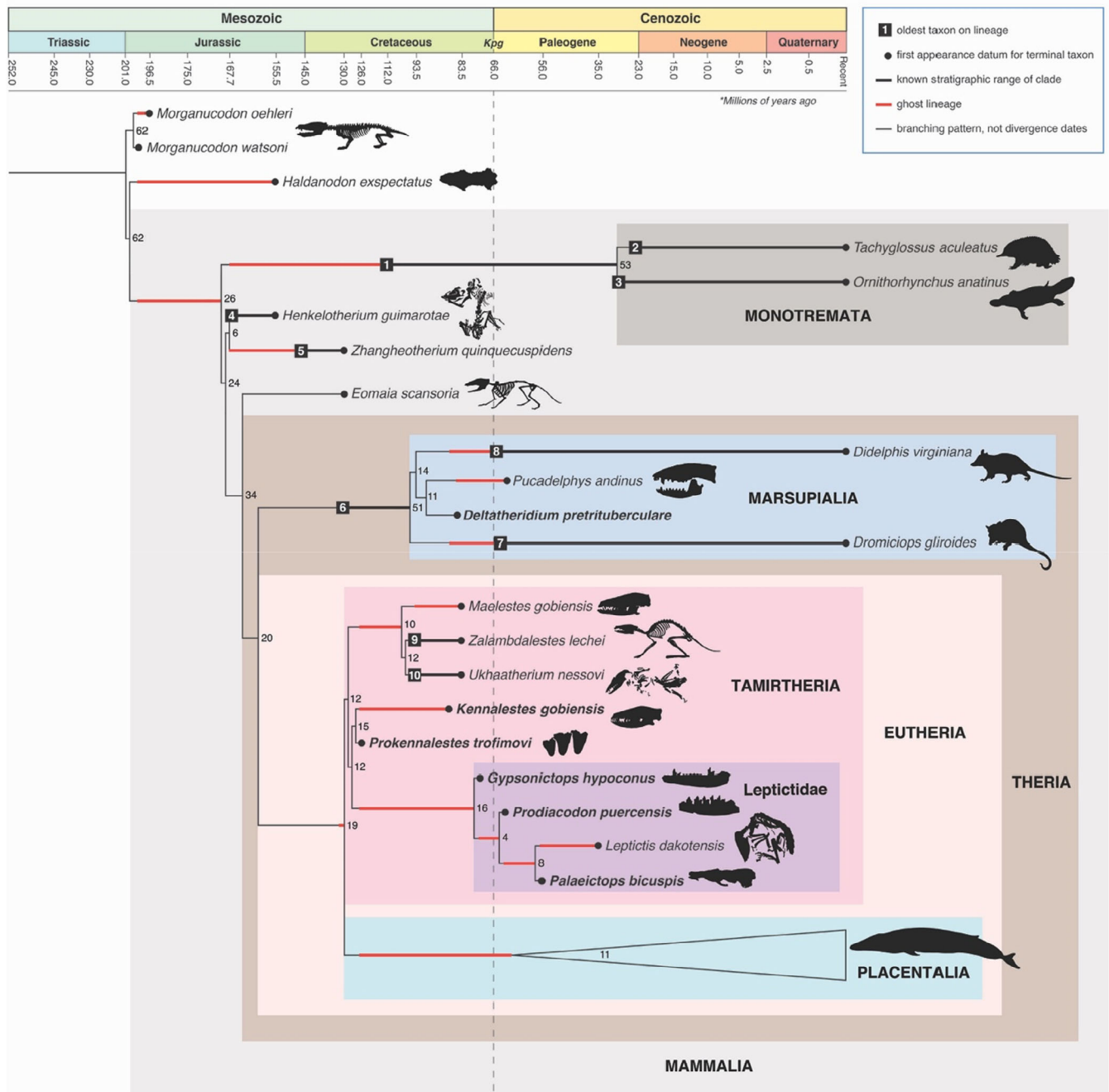
Fig. 1. Single most parsimonious tree based on combined data parsimony analysis (see full tree in Fig. A1) mapped against stratigraphy. The oldest taxa nested within Placentalia (*Purgatorius, Leptacodon* and *Protungulatum*) are ~65 Myr old and post-date the KPg boundary (see discussion on dating in Supplementary Materials of O'Leary et al., 2013). The sister taxon of Placentalia, Tamirtheria, is an extinct and diverse clade containing members ranging from the Late Cretaceous to the Eocene. The oldest taxon within Marsupialia, *Deltatheridium pretrituberculare*, predates the KPg boundary. Nodal numbers indicate Bremer support (Bremer, 1994). The oldest taxa on particular lineages (boxed numbers) are listed in Table 1, with additional data in O'Leary et al. (2013: tables S2 and S3).

performed as well as or better than model-based algorithms when analysing morphological data (Goloboff et al., 2018). Maximum parsimony algorithms also can accommodate morphological characters with more than ten states and characters with polymorphisms. Both of these occur in our dataset. Model-based phylogenetic methods, however, are unable to accommodate polymorphic morphological characters. Because Phylip, the RAxML preferred alignment format, does not permit polymorphic scoring, multistate character scorings were changed to "?". Additionally, character states above nine had to be changed to "?" to accommodate the algorithm. Thus, phylogenetic analyses ultimately were performed on two datasets: the unmodified dataset including characters with more than ten states

and polymorphisms and on the modified dataset that excluded character states >9 and polymorphic character states. In constructing the modified dataset the changes affected 768 polymorphic scorings and 56 scorings with character states >9. Using these two datasets, we performed a total of eight analyses in order to evaluate the performance of the different algorithms and the effects of the exclusion of characters with more than ten states and polymorphisms.

Maximum-likelihood (ML) analyses were performed with RAxML-HPC2 v.8.2.12 (Stamatakis, 2014) on the CIPRES portal (Miller et al., 2010). The ML analyses included 1000 rapid bootstrap pseudoreplicates followed by a search for the tree that maximizes the likelihood function (the "-f a" option). The searches used the default value of 25 rate categories and estimates of all free model parameters. The search for the ML tree used the GTRGAMMA model for nucleotides and the MK + gamma model for the phenomic data. By default, the bootstrap searches used the CAT approximation. As for the parsimony analyses, in all searches we rooted the tree along the branch leading to *Morganucodon*.

In order to study character optimization on the parsimony analysis of combined data, we obtained both the ACCTRAN and DELTRAN optimizations using the "DescribeTrees" option in PAUP* v.4.0a (Swofford, 2003). We report unambiguous synapomorphies as those common to both ACCTRAN and DELTRAN optimization strategies. These optimizations are available as Supplementary Materials in the public database, MorphoBank, Project P3871.

Results

A parsimony search of the phenomic dataset combined with the molecular data including 41 401 characters for 92 taxa (46 extinct, 46 extant) resulted in a single tree of length 128 104 steps (CI: 0.3854; RI: 0.4070; Figs 1, A1). The tree was rooted with the clade *Morganucodon*. *Haldanodon exspectatus* appears as the next branch, as sister taxon to Mammalia [BS (Bremer support index): 26; J (Jackknife pseudoreplicate frequencies): 100]. Monotremata is monophyletic (BS: 53; J: 100), appearing as the sister taxon of Theriimorpha (BS: 24; J: 100), a group that includes *Eomaia* and the sister taxa *Henkelotherium* + *Zhangeotherium* (BS: 6; J: 83). Marsupialia is monophyletic (BS: 51; J: 100) and sister to Eutheria (BS: 19; J: 66). The analysis supports the hypothesis that *D. pretrituberculare* is a member of Marsupialia, with strong support for a sister relationship with *Pucadelphys* (BS: 11; J: 82). A eutherian clade was recovered along the stem to Placentalia containing extinct Mesozoic and Paleogene members. Within this clade *Maelestes* is sister to *Ukhaatherium* + *Zalambdalestes* (BS: 12; J: 94) and *Kennalestes* + *Prokennalestes* is sister to Leptictidae (BS: 16; J: 97). The basal split within Placentalia occurs between Xenarthra (BS: 29; J: 100) and Epitheria (BS: 16, J: 60). Afrotheria is weakly supported (BS: 24; J: 63). Boreoeutheria is weakly supported in this analysis (BS: 21; J: 76). We recover Euarchontoglires (BS: 26; J: 95), Euarchonta (BS: 47; J: 100) with Sundatheria (BS: 66; J: 100), comprising Scandentia (BS: 168; J: 100) + Dermoptera (BS: 136; J: 100), as sister taxon to Primates (BS: 63; J: 100). We recover

Laurasiatheria (BS: 24; J: 76) with Lipotyphla (BS: 51; J: 100) as the basal branch. Within Ostentoria, we recover Ferae, Carnivoramorpha and Carnivora (BS: 11; J: 68). Within Chiroptera, we recover Microchiroptera (BS: 8; J: 43). The extinct Eocene taxa *Icaronycteris* and *Onychonycteris* form a well-supported clade (BS: 19; J: 100) that appears as a sister taxon to Microchiroptera. We find that the sister taxa to Euungulata, within the clade Pan-Euungulata, are extinct. These include the most basal member of Pan-Euungulata, *Protungulatum donnae*, and the second branch, a clade comprising *Aphelisus*, *Hyopsodus*, *Phenacodus*, *Didolodus* and *Protolipterna*. Within Euungulata (BS: 24; J: 100), we find *Mesonyx* and *Rodhocetus* as the basal-most branches. We recover Perissodactyla (BS: 21; J: 100) and Cetacea (BS: 17; J: 100), with *Basilosaurus* and *Artiocetus* as successive sister taxa to extant cetaceans. Cetancodonta is weakly supported (BS: 8; J: 32), with *Archaeotherium*, *Bos*, *Sus* and *Lama* as successive sister taxa.

The ML tree of the combined data matrix (Fig. A3) is largely in agreement with the central point on parsimony-based trees (Appendix; Figs 1, A1–A2): a eutherian clade exists on the stem to Placentalia that contains Palaeogene taxa. However, for the position of some major clades the tree differs from MP. For example, condylarths were recovered within Laurasiatheria by MP (Appendix; Figs A1–A2) as suggested by a wide array of studies (e.g. Buckley, 2015; Halliday et al., 2017), whereas the combined ML analysis placed a clade of condylarths as the sister to crown Placentalia (Fig. A3). The differences between our MP and ML trees do not reside in the use of a modified (multistate character scorings and character states >9 were changed to "?") or unmodified matrix, but rather in how the ML and MP programs analysed the morphological data. This is because when the modified combined matrix was analysed under MP, it recovered the same topology as the unmodified matrix (Appendix; Figs A1–A3).

Results regarding the clade Placentalia

None of the newly added fossil species falls within Placentalia, indicating again that the oldest known members of Placentalia tested here post-date the KPg boundary, and corroborating those results from O'Leary et al. (2013). Ten extinct species form a new sister clade to Placentalia, which we name below. Results show that several species in the new placental sister clade belong to lineages that survived the KPg boundary to persist well into the Cenozoic (Fig. 1). Thus, as placental mammals radiated in the early Palaeogene into familiar clades such as Cetacea and Primates, nonplacental eutherian congeners existed in the same ecosystems. Although some suggestion that

members of Leptictidae might fall outside Placentalia emerged in previous work (Wible et al., 2007, 2009), this result previously has not been upheld by such a character-rich phylogenetic test of the phylogeny, and not with such a speciose clade. In the following section we formally name this eutherian clade.

Systematic palaeontology

    Mammalia Linnaeus, 1758
    Theria Parker and Haswell, 1897
    Eutheria incertae sedis Gill, 1872
    Tamirtheria unranked, stem-based clade

Etymology. For the late Tamir Nasankhuu, the long-standing chief technician and Mongolian member of the American Museum of Natural History-Mongolian Academy of Sciences expeditions.

Age and geographical range. Late Cretaceous of Mongolia and North America; Palaeocene–Oligocene of North America.

Definition and clade membership. All species more closely related to *Ukhaatherium nessovi* than to *Elephas maximus*: *Maelestes gobiensis, Zalambdalestes lechei, Ukhaatherium nessovi, Kennalestes gobiensis, Prokennalestes trofimovi* and Leptictidae.

Diagnosis. Eutherian sister taxon of Placentalia, differs from Placentalia in 43 unambiguous synapomorphies (Fig. 2; Supplementary Material on MorphoBank Project P3871) including presence of a suprameatal fossa on the squamosal; a dental ramus with a masseteric fossa and condyloid crest; a V-shaped premaxilla-maxilla suture on the palate; an ectopterygoid process; P5 with a wide stylar shelf; M1 with a postparaconule crista, parastylar groove, and metaconule; M2 with a preparaconule crista and a premetaconule crista, M3 with a metaconule; scapula coracoid process <0.5× the dimension of the glenoid fossa; absence of an anterior concavity on the humerus supinator crest; flat ulnar facet rim on the radial head; distal contact of the tibia and fibula extended to near the midshaft of the tibia; and an astragalar ectal facet continuous with the astragalar lateral facet, among other features.

Discussion. Small mammals with a sectorial dentition, long canines and a postcranial skeleton modified with a fibula that is in close contact with the tibia through midshaft. Tamirtherians also primitively retain epipubic bones (bones in the anterior abdominal wall), also found in Marsupialia, among other mammals (Novacek et al., 1997). Among tamirtherians, epipubic bones are present in *Zalambdalestes lechei* and *Ukhaatherium nessovi* and absent in the Oligocene *Leptictis*. In the other members of the group the structure is not preserved.

Preserved as skulls, dentitions and skeletons, Tamirtheria, along with Placentalia, form the total clade, Eutheria. All known tamirtherians are extinct. The phylogenetic position of the tamirtherian *Gypsonictops* extends the minimum age of the clade Leptictidae into the late Mesozoic (Fig. 1). Tamirtheria persisted alongside the newly diversifying placental orders such as primates, bats and rodents in the early Palaeogene. Like tamirtherians, the Mesozoic clade Multituberculata survived the KPg event to persist until the latest Eocene (Prothero, 1994). Whether competition among the increasingly specialized placental clades limited the success of these Cretaceous relic taxa, as has been posited for Multituberculata (Krause, 1986; Ostrander, 1984), is currently unknown. Our tree also indicates that Asioryctitheria, previously conceived as a basal eutherian clade with *Ukhaatherium, Kennalestes* and *Asioryctes* (Novacek et al., 1997), is paraphyletic with its members in different clades of Tamirtheria.

The substantial contact between the tibia and fibula (here represented by character 3414; Fig. 2) reported in *Zalambdalestes* has been described as being similar to that in rabbits (Kielan-Jaworowska, 1978; Novacek et al., 1997; Rose, 2006), the latter having specialized hind limbs for saltatorial locomotion. This condition is a synapomorphy of Tamirtheria, as it is also well-represented in *Leptictis*, and present to a lesser degree in *Prodiacodon*. Reversals from this derived condition may have occurred in the clade in such taxa as *Ukhaatherium*; the distal fibula of *Ukhaatherium* and its contact with the tibia are not well-known (Horovitz, 2003), although the shape of its fibula overall differs from that of *Zalambdalestes*.

Examination of other dental changes on the shortest tree indicates that the loss of the lower third premolar (p3) is a synapomorphy of Theria, and that *Gypsonictops, Prokennalestes* and *Maelestes* have each regained a tooth at the lower third premolar (p3) locus (note, the tooth locus terminology follows that of O'Leary et al., 2013: fig. 3]). This pattern thus is an example of a complex structure—a tooth—reappearing evolutionarily, in contrast to a Dollo's Law-type preconception that the evolution of complex structures is irreversible (Collin & Miglietta, 2008).

Results regarding the clade Marsupialia

Our tree produced the novel result that the clade Marsupialia contains a Late Cretaceous fossil, *Deltatheridium pretrituberculare*. Long-recognized as a metatherian, but not necessarily as a marsupial (Rougier et al., 1998), the position of *Deltatheridium* inside Marsupialia is supported by numerous unambiguous synapomorphies at multiple nodes, including the node Marsupialia, and nodes more highly nested within that clade. Our study supports the hypothesis that *Deltatheridium pretrituberculare* is part of a fossil sister
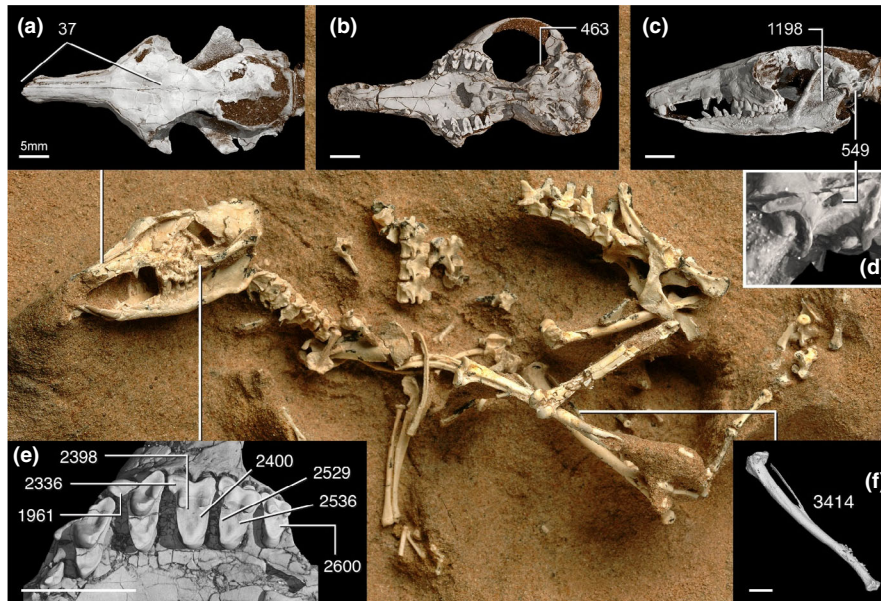
Fig. 2. Computed tomography scans of specimens and an associated skeleton [PSS-MAE 131, centre and (f)] of the extinct eutherian mammal and tamirtherian, *Zalambdalestes lechei*, with shared derived features of Tamirtheria illustrated from the skull, dentition and postcrania. Characters: 37 (a), nasal bones elongate relative to skull length; 463 (b), presence of the ectopterygoid process; 549 (c and d), presence of a suprameatal fossa; 1198 (c) presence of a condyloid crest in the masseteric fossa, and (e) numerous features of crests and cusps of the upper molars; and 3414 (f) tibia and fibula in contact proximally. (a–d) PSS-MAE 108; (e) PSS-MAE-130. Character numbers are those in the matrix (Methods and online at MorphoBank project P3871).

clade to *Didelphis* (Fig. 1). Regardless of whether some of these synapomorphies may show homoplasy elsewhere in the tree, their cumulative impact results in this novel, but highly supported, position of *Deltatheridium*. No member of Marsupialia previously had been shown to pre-date the KPg boundary, but this result indicates that Marsupialia has a nested member that is *c.* 80 Myr old (Dingus et al., 2008).

Over 75 unambiguous morphological synapomorphies support the clade Marsupialia with *Deltatheridium pretrituberculare* nested within it. Thirty-five unambiguous synapomorphies support the clade of the two fossil species *Pucadelphys* + *Deltatheridium*. These come from the cranial, dental and postcranial partitions, and include: the presence of a W-shaped frontonasal suture (character 38: state 2); a posterior masseteric shelf that is nearly vertical (1202: 1); the absence of a medial expansion of the dentary condyle (1208: 0); an angular process of the dentary that is at least as large as the dentary itself (1224: 2); the presence of a parastylar groove on M1 (2336: 1); an M1 parastylar lobe that is hook-like and that curves around the postmetacrista of the preceding tooth (2341: 0); and the absence of a parafibula (3417: 0).

Additionally, the sister-taxon relationship between the extant marsupial *Didelphis* and the clade *Pucadelphys* + *Deltatheridium* is strongly supported by 55 unambiguous synapomorphies from the cranial, dental and postcranial systems. These include: elongate nasal bones (37: 2); presence of a paracanine fossa (106: 1); absence of contact between the lacrimal and the maxilla in the orbital wall (218: 0); a pterygoid canal positioned such that it is visible in ventral view of the skull (413: 1); presence of the condyloid fossa on the exoccipital (906: 1); a triangular anterior process on the dentary (1223: 0); presence of the upper dP5 stylocone (1863: 0); presence of a stylocone on upper M2 (2487: 0); presence of stylar cusp D on upper M2 (2495: 0); a sigmoid-shaped clavicle (2946: 2); an ischial process that flares laterally (3329: 1); absence of contact between the fibula and the calcaneus (3431: 0); and a well-developed lateral tubercle on the astragalus (3482: 1). These characters, and other synapomorphies, are illustrated and labelled in MorphoBank projects 773 and 3871.

Further important information that emerged from CT scans of a newly discovered metatherian fossil, while not directly incorporated into the phylogenetic analysis, points to an important new phenomic character set. The scans exposed exquisite new details of a marsupial-like dental eruption pattern preserved in new Mongolian fossils of *Deltatheridium* (Fig. 3). The sequence of tooth eruption observed in the new fossils of the extinct Cretaceous taxon *Deltatheridium* presented here for the first time, lends further support for its phylogenetic position inside Marsupialia (Fig. 3). *Deltatheridium* had been described as resembling living marsupials in replacing deciduous teeth with
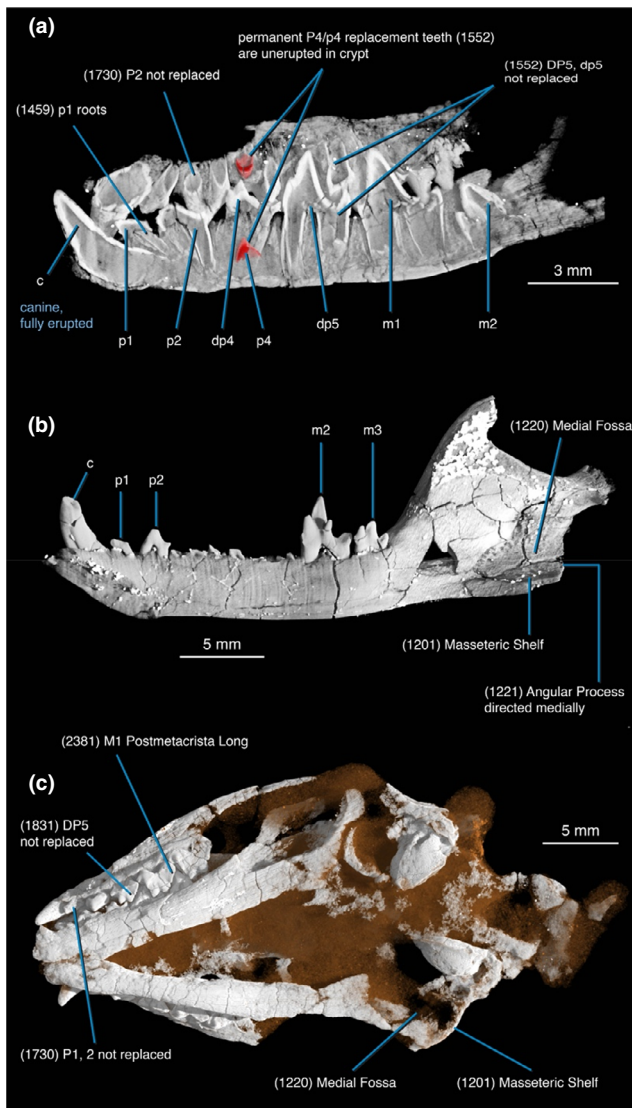
Fig. 3. Computed tomography scans of *Deltatheridium pretrituberculare*, a Late Cretaceous member of Marsupialia illustrating derived morphological features that it shares with Marsupialia (numbered characters). (a) Digital cutaway of maxilla and dentary (PSS-MAE 221), juvenile individual preserving the following marsupial feature: canine teeth fully erupted but the permanent fourth premolar (P4/p4) teeth still in crypts. These teeth have yet to develop adult morphology. (b) Medial view of the dentary (PSS-MAE 133) and (c) ventral view of dentary and skull (PSS-MAE 221), both showing derived marsupial features present in this fossil (see Supplementary Information). Note dental nomenclature here follows O'Leary et al. (2013: fig. 3), wherein C/c, P/p1, P/p2, DP/dp4, P/p4, DP/dp5, M/m1, M/m2, M/m3 correspond to C/c, P/p1, P/p2, DP/dp3, P/p3, M/m1, M/m2, M/m3, M/m4 of previous work (Rougier et al., 1998).

permanent teeth only at the fourth upper and lower premolar loci (P4/p4) (Rougier et al., 1998). The canine in marsupials erupts only once as a permanent tooth and it erupts before the permanent P4/p4 teeth erupt. Previously data existed only from a single fossil specimen of *Deltatheridium* from which it was

concluded that the permanent P4/p4 erupted in *Deltatheridium* before the canine fully erupted (Rougier et al., 1998). The latter pattern would make *Deltatheridium* unlike marsupials in the relative timing of the canine and P4/p4 eruption.

However, evidence in a new juvenile specimen of *Deltatheridium pretrituberculare* indicates that the canine has fully erupted, but the permanent P4/p4 teeth are incipiently developed, unerupted and still in their crypts (Fig. 3). Thus, *Deltatheridium* has a more marsupial-like dental replacement pattern than previously recognized. This replacement pattern compares closely with that of fossil and living didelphoid marsupials, some dasyurid marsupials, and the Cretaceous–Palaeocene metatherian taxon *Alphadon* (Cifelli et al., 1996; Rougier et al., 1998). Further underscoring the marsupial-like delayed maturity seen in *Deltatheridium* is the observation that the P4/p4 replacement teeth themselves are not even fully formed in the upper and lower jaws in this specimen (Fig. 3a). Examination of other dental changes on the tree indicates that the loss of the lower third premolar (p3) is a synapomorphy of Theria and that *Gypsonictops*, *Prokennalestes* and *Maelestes* each have regained a tooth at the lower third premolar (p3) locus.

Discussion

Tests of phylogenetic hypotheses often proceed by additions to taxon-rich or character-rich matrices. Our results are based on additions to a character-rich matrix: we added >6000 new morphological observations taken from six fossil species to a matrix with 4541 morphological (osteological and soft tissue) characters. This matrix previously had been assembled by a collaborative team in O'Leary et al. (2013), a paper that revised and sourced the new, large matrix from many published matrices including characters from matrices explicitly focused on Marsupialia (Horovitz, 2000; Horovitz & Sánchez-Villagra, 2003).

Our addition of six fossils to this character-rich matrix further refines our understanding of the timing of placental diversification relative to the KPg boundary, a topic of debate (Meredith et al., 2011; O'Leary et al., 2013; Phillips, 2016; Springer et al., 2017). The new tree presents critical calibrations for higher mammalian clades. The tree topology (Fig. 1; Supplementary Information) indicates that *Protungulatum donnae*, which dates to just after the KPg boundary (O'Leary et al., 2013), is the oldest species known within Placentalia. Continued addition of taxa and characters to this large matrix will provide an important ongoing test of mammalian phylogeny, not only the addition of more marsupials, both living and fossil species, but also ongoing eutherian fossil discoveries from Cretaceous rocks.

The extinct clade Leptictidae, now outside of Placentalia, has been hypothesized to fall in a number of different places on the mammalian tree (Asher, 2018), including *Leptictis* being among the oldest Afrotherians (O'Leary et al., 2013). We show here, however, that Leptictidae belongs neither to Afrotheria nor even to Placentalia. The oldest fossils associated with Afrotheria, *Thomashuxleya externa* and *Carodnia vieirai,* thus are South American. Tamirtherian fossils are known from Asia and western North America, regions that were in relatively close contact in the latest Cretaceous, with the latter separated by an epicontinental sea from the rest of North America (Matthews et al., 2016). Previously, Placentalia was considered to have a single (O'Leary et al., 2013) or multiple (Rougier et al., 1998) outgroups from Asia alone, but our results show a more complex history with early eutherian speciation occurring on at least two continents.

That the North American Leptictidae is phylogenetically nested within an Asian eutherian radiation is consistent with other evidence for a degree of floral and faunal continuity between Asia and North America in the Late Cretaceous (Russell, 1993). Close relationships between Asian and North American taxa during this interval are observed in multiple plant lineages (Wen et al., 2016); in ceratopsian (Farke et al., 2014), hadrosaurid (Prieto-Marquez, 2010) and coelurosaurian (Ding et al., 2020) dinosaurs, including tyrannosaurids (Brusatte & Carr, 2016); in alligatoroid crocodilians (Massonne et al., 2019); and in polyglyphanodontian (Gauthier et al., 2012) and iguanian (DeMar et al., 2017) lizards. Thus, our new findings about the distribution of ancient mammals are consistent with a larger biogeographical pattern.

Acknowledgements

Conflict of interest

None declared.

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APPENDIX

Results of the combined, molecular and phenomic analyses

Here we present the results and comparison of eight maximum parsimony (MP) and maximum-likelihood (ML) analyses performed on different combinations and versions of the phenomic and molecular matrices. We analysed two versions of the phenomic matrix. One included multistate character scorings and character states >9, and the other included what we refer to as "the modified dataset," that is a version of the phenomic matrix in which multistate character scorings and character states >9 were changed to "?". The exclusion of multistate character scorings and character states >9 was necessary to run the matrix under the RAxML algorithm. The eight analyses performed were: (A) MP analysis using a combined phenomic and molecular dataset, (B) MP analysis using a modified version of the phenomic dataset combined with the molecular dataset, (C) ML analysis using a modified version of the phenomic dataset combined with the molecular dataset, (D) MP analysis of the molecular dataset, (E) ML analysis of the molecular dataset, (F) MP analysis of the phenomic dataset, (G) MP analysis of the modified phenomic dataset, and (H) ML analysis of the modified phenomic dataset. We tried to analyse the combined dataset using Bayesian Inference, but it was computationally unfeasible due to the size of the dataset. The branch support values for analysis (A) are given by Bremer support indices (BS) and Jackknife pseudoreplicate frequencies (J); for analyses (B) and (G) by J (modified [M]); for analyses (C), (E) and (H) by bootstrap values (B); and for analyses (D) and (F) by J.

Combined data

A parsimony search of the phenomic dataset combined with the molecular data using 41 401 characters for 92 taxa (46 extinct, 46 extant) resulted in a single tree of length 128 104 steps (CI: 0.3854; RI: 0.4070; Figs 1, A1), which is the primary result of our analysis as discussed in the main paper. The parsimony search of the modified dataset and the molecular data resulted in a single tree of length 128 019 steps (CI: 0.379; RI: 0.407; Fig. A2). A ML analysis of the same modified phenomic matrix + molecular data resulted in a tree with a likelihood value of −632600.100826 (Fig. A3). All trees are in general agreement concerning the overall tree structure. The trees were rooted with the clade *Morganucodon*. *Haldanodon exspectatus* appears as the next branch, as sister taxon to Mammalia (BS: 26; J: 100; J [M]: 100; B: 100). Monotremata is monophyletic (BS: 53; J: 100; J [M]: 100; B: 100), appearing as the sister taxon of Theriimorpha (BS: 24; J: 100; J [M]: 85; B: 99), a group that includes *Eomaia*

and the sister taxa *Henkelotherium* + *Zhangeotherium* (BS: 6; J: 83; J [M]: 85; B: 84). Marsupialia is monophyletic (BS: 51; J: 100; J [M]: 100; B: 100) and sister to Eutheria (BS: 19; J: 66; J [M]: 65; B: 85). All of the analyses support the hypothesis that *Deltatheridium pretrituberculare* is a member of Marsupialia. With a strong support for a sister relationship with *Pucadelphys* (BS: 11; J: 82; J [M]: 87; B: 82). Both MP analyses recover a eutherian clade along the stem to Placentalia containing extinct Mesozoic and Paleogene members. Within this clade *Maelestes* is sister to *Ukhaatherium* + *Zalambdalestes* (BS: 12; J: 94; J [M]: 95) and *Kennalestes* + *Prokennalestes* is sister to Leptictidae (BS: 16; J: 97; J [M]: 95). This clade in the ML tree is paraphyletic. Both MP analyses recover identical topologies for all Placentalia members (see below for ML). The basal split within Placentalia occurs between Xenarthra (BS: 29; J: 100; J [M]: 100) and Epitheria (BS: 16, J: 60; J [M]: 58). Afrotheria is weakly supported in both parsimony analyses (BS: 24; J: 63; J [M]: 62). Boroeutheria is weakly supported in both analyses (BS: 21; J: 76; J [M]: 70). We recover Euarchontoglires (BS: 26; J: 95; J [M]: 94), Euarchonta (BS: 47; J: 100; J [M]: 100) with Sundatheria (BS: 66; J: 100; J [M]: 100), comprising Scandentia (BS: 168; J: 100; J [M]: 100) + Dermoptera (BS: 136; J: 100; J [M]: 100), as sister taxon to Primates (BS: 63; J: 100; J [M]: 100). We recover Laurasiatheria (BS: 24; J: 76; J [M]: 72) with Lipotyphla (BS: 51; J: 100; J [M]: 100) as the basal branch. Within Ostentoria, we recover Ferae, Carnivoramorpha and Carnivora in both MP analyses with identical topologies (BS: 11; J: 68; J [M]: 74). Within Chiroptera, we recover Microchiroptera in both MP analyses (BS: 8; J: 43; J [M]: 49). In both MP analyses, the extinct Eocene taxa *Icaronycteris* and *Onychonycteris* form a clade (BS: 19; J: 100; J [M]: 100) that appears as a sister taxon to Microchiroptera. We find, in both MP analyses, that the sister taxa to Euungulata, within the clade Pan-Euungulata, are extinct. These include the most basal member of Pan-Euungulata, *Protungulatum donnae*, and the second branch, a clade comprising *Aphelisus*, *Hyopsodus*, *Phenacodus*, *Didolodus* and *Protolipterna*. Within Euungulata (BS: 24; J: 100; J [M]: 100), we find *Mesonyx* and *Rodhocetus* as the basal-most branches in both analyses. We recover Perissodactyla (BS: 21; J: 100; J [M]: 100) and Cetacea (BS: 17; J: 100; J [M]: 100), with *Basilosaurus* and *Artiocetus* as successive sister taxa to extant cetaceans. Cetancodonta is weakly supported (BS: 8; J: 32; J [M]: 32), with *Archaeotherium*, *Bos*, *Sus* and *Lama* as successive sister taxa.

Important differences occur within the clades when the parsimony and ML analyses are compared. The ML analysis recovered *Protungulatum donnae*, and a clade comprising *Aphelisus*, *Hyopsodus*, *Phenacodus*, *Didolodus* and *Protolipterna* sister to crown Placentalia. Both MP analyses found these taxa as the basal-most members of Pan-Euungulata. The ML analysis also fails to recover Epitheria. However, the ML analysis recovers a weekly supported Atlantogenata (B: 35) which includes Xenarthra + Afrotheria. There are differences between the parsimony and ML trees regarding the placement of *Notharctus* within Primates, with the ML analysis supporting a clade of *Notharctus* + *Lemur* (B: 96), whereas the parsimony analyses favour *Lemur* and *Notharctus* as successive sister taxa to the remaining primate taxa. Within Glires the position of *Tribosphenomys* differs in the different analyses; both MP analyses recover *Tribosphenomys* as the most basal member of the clade in both analyses, whereas the ML analysis recovers *Tribosphenomys* as sister to Duplicidentata + *Rhombomylus*.

Both MP analyses recover *Sinopa* as sister to Carnivoramorpha (BS: 23; J: 100; J [M]: 100). However, the ML analysis recovers *Sinopa* nested within Carnivoramorpha, sister to the clade including both species of *Vulpavus* (B: 97).

The ML tree of the combined data matrix (Fig. A3) is largely in agreement with the central point on parsimony-based trees: a eutherian clade exists on the stem to Placentalia that contains Palaeogene taxa. In addition, when the modified matrix was analysed under MP, it recovered the same topology as the unmodified matrix.
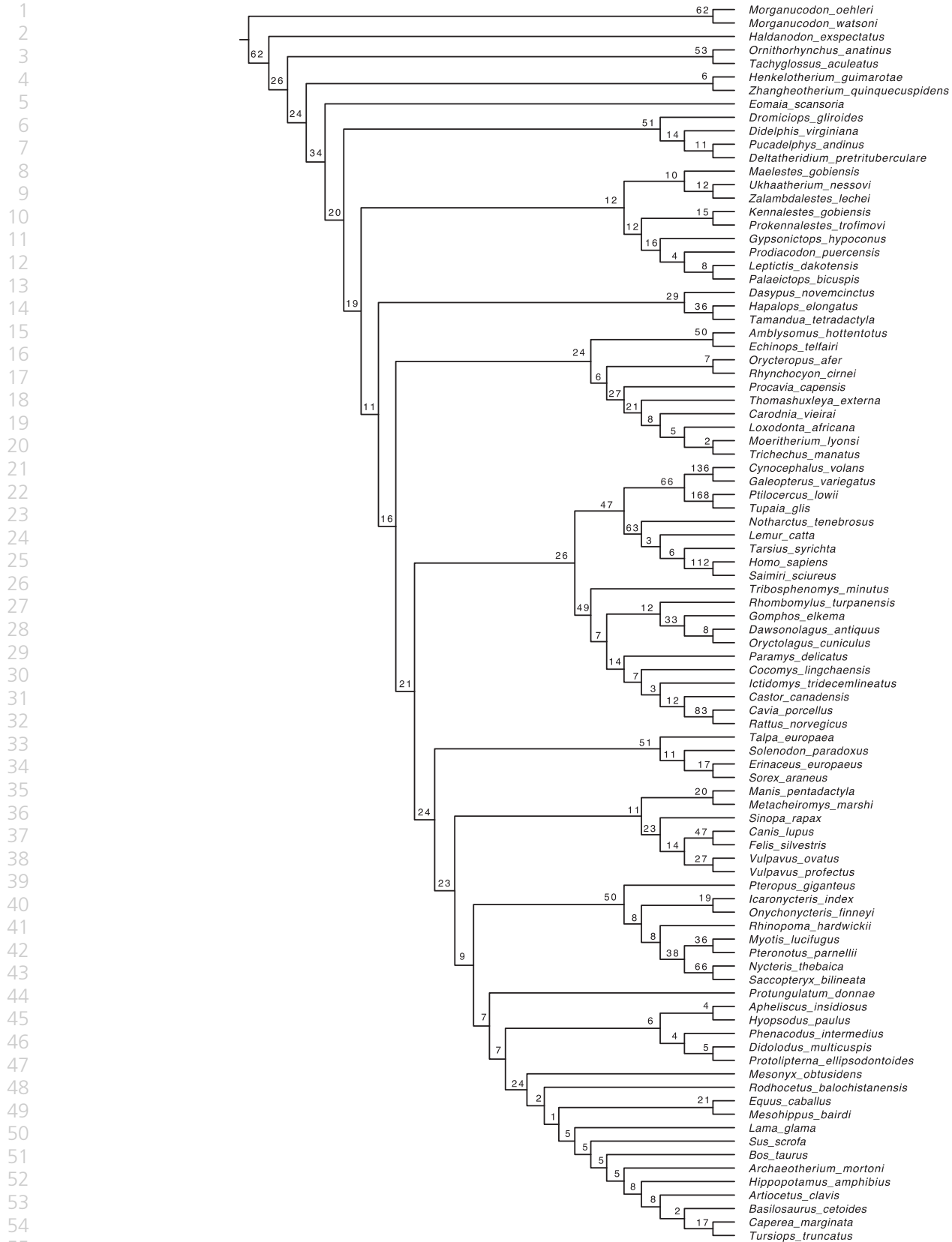
Fig. A1. Single most parsimonious tree resulting from parsimony analysis of combined data Nodal numbers indicate Bremer support (Bremer, 1994). This tree is summarized with stratigraphy in Figure 1.

Fig. A2. Maximum parsimony tree computed on the combined matrix using the "the modified dataset" —a phenomic matrix for which polymorphic scorings and multistate character scorings were changed to "?" so that the matrix would run under the RAxML algorithm. Nodal numbers are Jackknife pseudoreplicate frequencies.

Molecular data

A parsimony search using 36 860 characters for 46 extant taxa resulted in a single tree of length 97 787 steps (CI: 0.4366; RI: 0.3974; Fig. S1) (see also O'Leary et al., 2013, where the identical analysis was performed). An ML search for the same matrix and number of taxa produced a tree with a likelihood of −474 260.690809 (Fig. S2). Both trees differ in arrangements of several clades. The trees were rooted at the branch leading to Monotremata (J: 100, B: 100). Marsupialia is recovered in both analyses (J: 100, B: 100). The basal branch of Placentalia (J: 100, B: 100) differs, with parsimony supporting Xenarthra (J: 100) as the sister taxon of Epitheria, and the ML analysis supporting a basal position within Placentalia for Afrotheria (B: 100). Within Afrotheria, the MP analysis recover Sirenia as sister taxon to a clade including Hyracoidea + Proboscidea (J: 73; + Sirenia: J: 100). Afrosoricida is recovered only by the ML analysis (B: 83), whereas the parsimony analysis places Tubulidentata and Chrysochloridae as the successive sister taxa of Macroscelidea + Tenrecidae (J: 53). In the ML analysis, Tubulidentata and Macroscelidea are successive sister taxa of Afrosoricida. This entire clade receives J of 98 (MP) and 100% ML bootstrap support. We recover Boreoeutheria (J: 99, B: 100). Within this clade Euarchontoglires receives strong support (J: 99, B: 100). The parsimony analysis recovers Sundatheria (J: 88) as the sister taxon of Glires (J: 91); however, the ML analysis support an alternative grouping of Scandentia (B: 100) with Glires (B: 86). In the ML analysis, Dermoptera (B: 100) appears as the sister taxon of Primates (B: 100; + Dermoptera: B: 88). Within Primates, relationships are identical among both analyses (*Lemur* and *Tarsius* as successive sister taxa to *Homo* + *Saimiri*) and are strongly supported. However, within Glires, relationships within Rodentia (J: 100) differ with Hystricognathi and Sciuromorpha as successive sister taxa to Caviomorpha + Myomorpha (J: 100) in the parsimony analysis. The ML analysis, however, offer weak support for a sister taxon relationship between Caviomorpha and Sciuromorpha (B: 38), and more robust support for a sister taxon relationship between Hystricognathi and Myomorpha (B: 98). We find strong support for Laurasiatheria (J: 100, B: 100), with Lipotyphla as the basal branch (J: 100, B: 100). Relationships within Lipotyphla differ among the analyses, with parsimony supporting *Talpa* and *Solenodon* as successive sister taxa to *Sorex* + *Erinaceus*, while the ML analysis switch the order of *Solenodon* and *Talpa*. Ostentoria is supported in both analyses (J: 84, B: 99), as is Carnivora (J: 100, B: 100). Ostentoria is the sister taxon of Chiroptera + Euungulata, a clade receiving weak support (J: 52, B: 46). Chiroptera is well-supported (J: 100, B: 100), as is Yinpterochiroptera (J: 100, B: 100) and Yangochiroptera (J: 100, B: 100). Relationships within Yangochiroptera are identical in all analyses. We recover Euungulata with weak support (J: 62, B: 43), with *Equus* as the sister taxon of Artiodactyla (J: 100, B: 100). Cetacea (J: 100, B: 100) is monophyletic, as is Cetancodonta (J: 100, B: 100) and the topology of Artiodactyla is identical (*Bos*, *Sus* and *Lama*) as successive sister taxa to Cetancodonta) and strongly supported in both analyses.

Morphological data

A parsimony search of the unmodified phenomic dataset using 4541 phenomic characters for 92 taxa (46 extinct, 46 extant) resulted in four trees of length 28 389 steps (CI: 0.191; RI: 0.445; Fig. S3). The parsimony search of the modified matrix resulted in two trees of length 28 311 steps (CI: 0.191; RI: 0.445; Fig. S4). A ML analysis of the same modified matrix resulted in a tree with a likelihood value of −181 970.953262 (Fig. S5). The MP strict consensus trees (unmodified and modified matrices) and the ML tree are in general agreement concerning the overall tree structure. The trees were rooted with the clade *Morganucodon*.
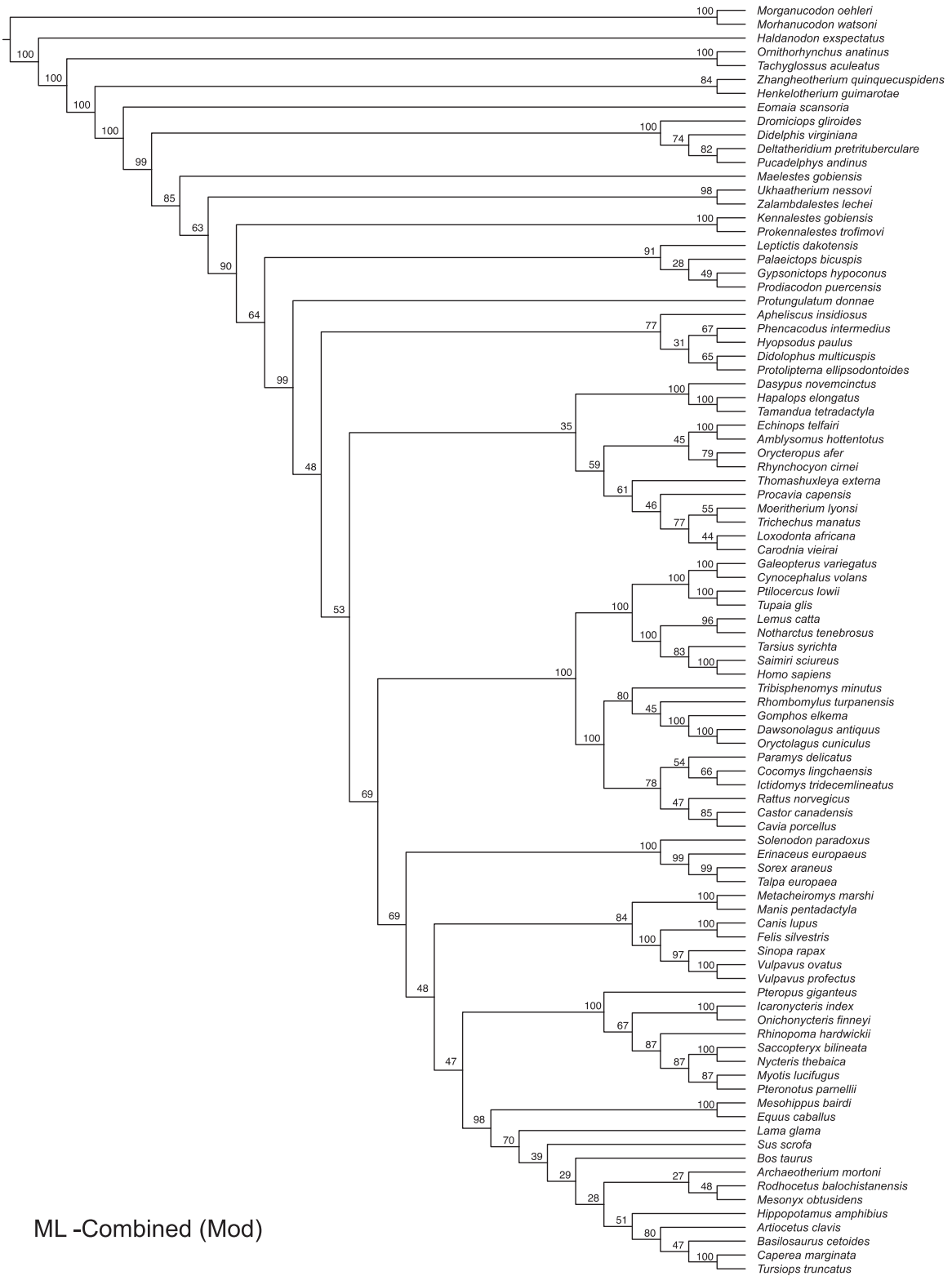
ML -Combined (Mod)

0.07

Fig. A3. RAxML tree computed on the modified combined data matrix. Note, the RAxML algorithm cannot accommodate our morphological characters that include polymorphisms, and, as such, could only compute on a modified version of this part of the matrix with a reduced number of observations. Nodal numbers are bootstrap values.

Haldanodon exspectatus appears as the next branch, as sister taxon to Mammalia (J: 100; J [M]: 100; B: 100). Monotremata is monophyletic (J: 100; J [M]: 100; B: 100), appearing as the sister taxon of Theriimorpha (J: 100; J [M]: 100; B: 100), a group that includes *Eomaia* and the sister taxa *Henkelotherium + Zhangheotherium*, a group well-supported in the parsimony tree (J: 93; J [M]: 91; B: 87). Marsupialia is monophyletic (J: 100; J [M]: 100; B: 100) with *Dromiciops* and *Didelphis* as successive sister taxa to *Deltatheridium + Pucadelphys* (J: 93; J [M]: 96; B: 98). Both MP analyses recover a weekly supported clade including the extinct Mesozoic taxon *Maelestes* sister to *Ukhaatherium + Zalambdalestes* (J: 98; J [M]: 95) and *Kennalestes + Prokennalestes* (J: 100; J [M]: 100). Placentalia is weakly supported in both MP analyses (J: 6; J [M]: 3). In the ML analysis the extinct Mesozoic taxa *Maelestes*, *Ukhaatherium* and *Zalambdalestes* form a weakly supported sister taxon (B: 57) to Placentalia (B: 69). In both MP analyses, the basal split within Placentalia is between a weekly supported grouping of Lipotyphla plus Leptictidae and *Rhynchocyon* and the remaining placental taxa. The basal split within Placentalia in the ML analysis is similar with the difference that the Mesozoic taxa *Kennalestes + Prokennalestes* are recovered as sister to Leptictidae (B: 83). Our phenomic data do not recover Euarchontoglires. Instead, our phenomic analyses weakly support Archonta (J: 51; J [M]: 52; B: 67), with Sundatheria, Scandentia (J: 100; J [M]: 100; B: 100) + Dermoptera (J: 100; J [M]: 100; B: 100), as the sister taxon to Primates (J: 100; J [M]: 100; B: 100). Within Chiroptera (J: 100; J [M]: 100; B: 100), we recover Microchiroptera (J: 100; J [M]: 100; B: 100). In all analyses, the extinct Eocene taxa *Icaronycteris* and *Onychonycteris* form a clade (J: 100; J [M]: 100; B: 100). This group appears as sister taxon to Microchiroptera in both the parsimony and ML analyses. There are differences between the parsimony and ML analyses regarding the placement of *Notharctus* within Primates, with the ML analysis supporting a clade of *Notharctus + Lemur* (B: 69), whereas the parsimony analyses favor *Notharctus* and *Lemur* as successive sister taxa to the remaining primate taxa. All analyses recover Edentata (Pholidota, Xenarthra, + Tubulidentata; J: 100; J [M]: 96; B: 99), as the sister group of Archonta (J: 51; J [M]: 52; B: 67). We recover Ferae,

Carnivoramorpha and Carnivora in all analyses with identical topologies and strong support (J: 100; J [M]: 100; B: 100). *Protungulatum donnae* appears as the sister taxon of a clade that includes artiodactyls, perissodactyls, cetaceans, extinct ungulates, rodents and lagomorphs. Carnivoramorpha is the sister taxon of this clade. All of the analyses agree regarding the position of a clade of extinct ungulates, including *Apheliscus*, *Didolodus*, *Hyopsodus*, *Phenacodus* and *Protolipterna* (J: 71; J [M]: 66; B: 79) placing them as the next branch within the clade. Although we recover Glires with a strong support (J: 100; J [M]: 100; B: 100) in all analyses as the next branch, the internal structure of the clade differs. The topology of crown Rodentia is identical in the MP analysis with the unmodified data and the ML analyses (J: 46; B: 81). The MP analysis with the modified data recovers crown Rodentia as a polytomy. In all analyses, *Rhombomylus* and *Tribosphenomys* are successive sister taxa to Duplicidentata (J: 100; J [M]: 100; B: 100). However, the positions of these taxa vary among all trees, with *Tribosphenomys* appearing to be more closely related to Duplicidentata in the MP unmodified dataset, *Rhombomylus* sister to Duplicidentata in the ML analysis, and a polytomy of both species in relation to Duplicidentata. Tethytheria is recovered in all analyses (J: 60; J [M]: 63; B: 92), with *Carodnia* and *Thomashuxleya* as successive sister taxa (ML), forming a polytomy with Tethytheria clade (MP unmodified dataset), or forming a basal polytomy with Tethytheria and Euungulata. In the ML analysis we recover *Procavia* as the sister taxon to *Thomashuxleya* (B: 34), whereas in both parsimony analyses *Procavia* is the sister taxon of Euungulata. Within Euungulata, we recover Perrisodactyla (J: 87; J [M]: 87; B: 95) in all trees, as well as Cetaceamorpha (J: 17; J [M]: 24; B: 56), Cetaceamorpha + *Mesonyx* (J: 4; J [M]: 7). In both MP analyses, *Archaeotherium* and *Mesonyx* appear as successive sister taxa to Cetaceamorpha, but both branches are reversed in the ML analysis. The ML analysis supports Perrisodactyla + Artiodactyla (B: 28), with *Lama + Bos* as sister taxon to a clade including *Sus + Hippopotamus*. Both MP analyses recover *Archaeotherium*, *Hippopotamus*, *Sus* and *Lama + Bos* as successive sister taxa to the Cetaceamorpha + *Mesonyx* clade.