

Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary

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Estimates of the time of origin for placental mammals from DNA studies span nearly the duration of the Cretaceous period (145 to 65 million years ago), with a maximum of 129 million years ago¹ and a minimum of 78 million years ago². Palaeontologists too are divided on the timing. Some^{3–5} support a deep Cretaceous origin by allying certain middle Cretaceous fossils (97–90 million years old) from Uzbekistan with modern placental lineages, whereas others^{6,7} support the origin of crown group Placentalia near the close of the Cretaceous. This controversy has yet to be addressed by a comprehensive phylogenetic analysis that includes all well-known Cretaceous fossils and a wide sample of morphology among Tertiary and recent placentals⁶. Here we report the discovery of a new well-preserved mammal from the Late Cretaceous of Mongolia and a broad-scale phylogenetic analysis. Our results exclude Cretaceous fossils from Placentalia, place the origin of Placentalia near the Cretaceous/Tertiary (K/T) boundary in Laurasia rather than much earlier within the Cretaceous in the Southern Hemisphere^{8,9}, and place afrotherians and xenarthrans in a nested rather than a basal position^{8,9} within Placentalia.

Placentals represent most living mammals (1,135 out of 1,229 genera) and are found on all continents and in all oceans¹⁰. Placentals and their extinct stem lineage constitute the Eutheria. More than 4,000 extinct eutherian genera have been named that represent the 65 million years of the Cenozoic, and the majority of these have been assigned to modern placental lineages¹¹. In contrast, only about 40 eutherian genera are known from the 80 million years of the Cretaceous^{4,6,11}. The relationships of these Cretaceous taxa to modern placentals are highly contentious. At one extreme, three-quarters of Cretaceous eutherians are assigned to the placental crown group^{4,11}; at the other, all Cretaceous eutherians fall outside Placentalia⁶.

Mammalia Linnaeus, 1758

Theria Parker and Haswell, 1897

Eutheria Gill, 1872

Cimolestidae Marsh, 1889

Maelestes gobiensis gen. et sp. nov.

Etymology. *Mae* is the acronym for Mongolian Academy of Sciences–American Museum of Natural History Expeditions; *lestes* (Greek), robber, often used for insectivore-like mammals; *gobiensis*, occurring in the Gobi Desert.

Holotype. PSS-MAE 607 (Figs 1 and 2; Palaeontological and Stratigraphy Section, Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar): an incomplete skull, left mandible, atlas, axis, twelve thoracic vertebrae, eight partial ribs, incomplete scapula, clavicle, humerus, proximal radius and ulna, and incomplete astragalus (see Supplementary Figs 1–5).

Age and locality. Late Cretaceous Djadokhta Formation, Ukhaa Tolgod (between Camel Humps and Sugar Mountain), Mongolia. Recent age estimates of Djadokhta Formation are 75–71 million years¹².

Diagnosis. Upper dentition: I², C¹, P⁵, M³. Lower dentition: I₃, C₁, P₅, M₃ (Figs 1 and 2). Differs from other Mongolian Djadokhta Formation eutherians (asioryctitheres *Kennalestes*, *Asioryctes*¹³ and *Ukhaatherium*¹⁴, and zalambdalestids *Zalambdalestes* and *Barunlestes*¹⁵) in having five upper and lower premolars, three subequal procumbent lower incisors, palatal vacuity between maxilla and palatine, postglenoid foramen behind postglenoid process, transpromontorial internal carotid artery, and small prootic canal. Resembles *Kennalestes* and *Asioryctes*¹³ in having hypoglossal foramen housed in an opening larger than jugular foramen and petrosal roof for external acoustic meatus. Differs from Central Asian Late Cretaceous asioryctitheres *Bulaklestes*, *Daulestes* and *Uchkudukodon*¹⁶ in having five upper and lower premolars, single-rooted lower canine, penultimate upper premolar with three roots, upper molars much wider than long with narrower stylar shelves, and lower molars with protoconid subequal to metaconid. Differs from Central Asian Late Cretaceous ‘zhelestids’ (*Sheikhdzheilia*, *Eozhelestes*, *Aspanlestes*, *Zhelestes* and *Parazhelestes*)^{3,17,18} and North American and Central Asian Late Cretaceous *Paranyctoides*^{3,18} in having upper molars with weak conules, metacone much smaller than paracone, metacone and paracone with adjoined base, and lower molars with narrower talonids and no labial postcingulid. Resembles North American Late Cretaceous cimolestids⁴ *Cimolestes* and *Batodon*^{19,20} in having lower canine and first lower premolar single-rooted. Resembles *Cimolestes* in having subequal procumbent lower incisors (two preserved in *Cimolestes propalaeoryctes*)¹⁹. Resembles *Batodon*^{18,19} in having upper molars with narrow stylar shelves and pre- and post-cingula, and lower molars with transverse protocristid and entoconid approximating hypoconulid. Differs from *Cimolestes* and *Batodon*^{19,20} in having five upper and lower premolars, upper molars with weak conules, and lower molars with more compressed trigonids and protoconid subequal to metaconid.

Our phylogenetic analysis (see below) allies *Maelestes* with two slightly younger western North American taxa, the cimolestids⁴ *Cimolestes* and *Batodon* (Fig. 3); these are known primarily by incomplete dentitions and jaws^{4,19,20}, and have been linked with placental carnivorans⁴. *Maelestes* is the sister of *Batodon*, the smallest Cretaceous eutherian, which has molars roughly 60% the size of *Maelestes*. The dentition of *Maelestes* shows an odd mix of resemblances to other Late Cretaceous Asian taxa, with premolars like the zhelestid *Zhelestes*¹⁸, upper molars like the asioryctithere *Kennalestes*¹³, and lower molars like the zalambdalestid *Zalambdalestes*¹⁵. *Maelestes* is the first Cretaceous eutherian with a marsupial-like palatal vacuity (Fig. 1)—a rare feature, even among extant placentals (for example, some

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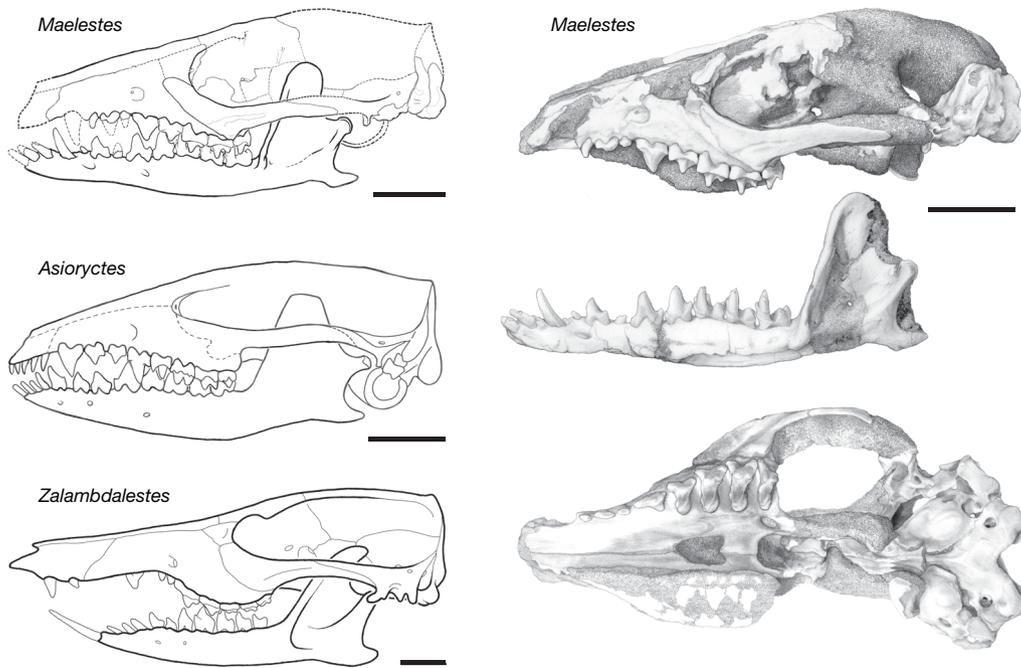


Figure 1 | *Maelestes gobiensis* gen. et sp. nov. (holotype, PSS-MAE 607) skull and mandible in comparison to other Djadokhta eutherians. Left panel: reconstructions of *Maelestes*, *Asioryctes* and *Zalambdalestes*, the last two of which are redrawn from ref. 15. Right panel: incomplete *Maelestes* skull in left lateral (top) and ventral (bottom) views, and left *Maelestes*

mandible in lateral view (middle). The large opening in the palate between the palatines and maxillae is a palatal vacuity. *Maelestes* probably had some upper incisors, but only a small non-tooth-bearing fragment of the premaxilla is preserved. Scale bars, 5 mm.

hedgehogs and elephant shrews). The preserved postcranial elements of *Maelestes* are similar to those of the asioryctitherian *Ukhaatherium* from Ukhaa Tolgod, which resemble, but are more generalized than, those of placental insectivores²¹.

We reconstructed the phylogenetic relationships of *Maelestes* by parsimony analysis of 408 morphological characters (127 dental, 212 craniomandibular and 69 postcranial) across 69 taxa (see

Supplementary Information), including 4 stem therians, 3 metatherians, 31 Cretaceous eutherians (all but the most incomplete and poorly preserved taxa), 20 extinct Tertiary placentals and 11 extant placentals. The Tertiary and extant taxa were chosen to sample the 4 major placental lineages recovered by some recent DNA studies^{8,9}: 5 afrotherians, 3 xenarthrans, 10 euarchontaglirans and 13 laurasiatherians. We did not include any of the Jurassic and Cretaceous Gondwanan mammals (*Ambondro*, *Asfaltomylos*, *Ausktribosphenos* and *Bishops*), which are regarded by some as eutherians²², because most recent analyses place these taxa in a Southern Hemisphere clade, Australosphenida, that is more distantly related to placentals than the stem therians and metatherians used here as outgroups^{4,23}.

Our strict consensus tree (Fig. 3) recognizes at least nine lineages of Mesozoic eutherians and does not support the inclusion of any Cretaceous eutherians within a placental lineage. Although branch support for many basal nodes is weak, we examined various competing hypotheses of association^{3-6,11} using a Wilcoxon rank sum (also known as Templeton) test, and found all (except *Purgatorius* with Primates, and Palaeocene and Eocene 'condylarths' with Cetartiodactyla) to be significantly rejected using our morphological data set (see Supplementary Information). Of the five basal-most eutherians in our tree, all are from Asia except *Montanalestes*, which is from western North America; this supports an Asian origin of Eutheria and its sister group Metatheria (marsupials and their stem lineage), because the basal-most members of both clades are Asian⁴.

Most Late Cretaceous eutherians fall into three morphologically distinct clades. The basal-most of these, the Zhelestidae (Fig. 3), is the most widespread temporally and geographically, occurring in Uzbekistan, western North America and Spain. Zhelestids are known mainly from their incomplete dentitions^{3,4,17,18}. They have robust upper molar protocones, shifted labially in some forms, which are among the features used to support the view that zhelestids are a paraphyletic stem lineage to 'condylarths' (basal ungulates)^{3-5,18}. In contrast, our analysis (Fig. 3) shows that upper molar resemblances were acquired convergently in zhelestids and 'condylarths', and that a minimum of 25 additional steps are required to produce a zhelestid-'condylarths'

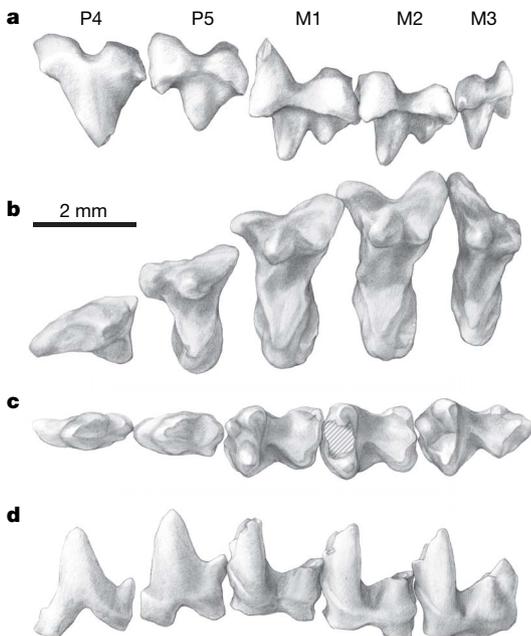


Figure 2 | *Maelestes gobiensis* gen. et sp. nov. (holotype, PSS-MAE 607) left upper and lower penultimate and ultimate premolars (P4, P5) and molars (M1, M2, M3). Uppers are shown in labial (a) and occlusal (b) views; lowers are shown in occlusal (c) and labial (d) views.

clade. Furthermore, our results (Fig. 3) highlight the need for representative taxonomic as well as morphological sampling in phylogenetic analyses, because the two ‘condylarths’ from the early Palaeocene (*Protungulatum* and *Oxyprimus*), aligned with zhelestids elsewhere^{3,4,18}, do not appear with late Palaeocene–early Eocene ‘condylarths’ (*Hyopsodus*, *Meniscotherium* and *Phenacodus*) or even within the placental crown group. Our results support *Hyopsodus*, *Meniscotherium* and *Phenacodus* as the oldest ungulate-like clade of crown placentals, which form the sister clade to the early Eocene dichobunid cetartiodactylan *Gujaratia pakistanensis*. Other morphological analyses have placed North American ‘condylarths’ with Afrotheria^{24,25}, which adds an extra 30 steps to our optimal trees.

The other two Late Cretaceous clades include some forms represented by fairly complete skulls and skeletons. Zalambdalestidae is the more proximate of the two to Placentalia (Fig. 3). Zalambdalestids are endemic to Asia; they are dentally specialized with enlarged evergrowing anteriormost lower incisors (*Zalambdalestes* in Fig. 1) that have enamel restricted anteriorly, as occurs in Glires (rodents and lagomorphs)^{3,15} as well as in various other mammals¹⁵. This dental specialization has been used elsewhere³ to support a zalambdalestid–Glires clade. In contrast, our analysis (Fig. 3) indicates that the specialized lower incisors of Zalambdalestidae and Glires were acquired convergently (confirming some earlier results^{15,26}). An extra 35 steps from the most parsimonious trees are needed to place zalambdalestids with Glires. The third Late Cretaceous clade is dentally more generalized than the other two. Included are Asioryctitheria^{14,16} (*Asioryctes* in Fig. 1), endemic to Asia, together with the cimolestid lineage that contains *Maelestes*, *Batodon* and *Cimolestes* (Fig. 3).

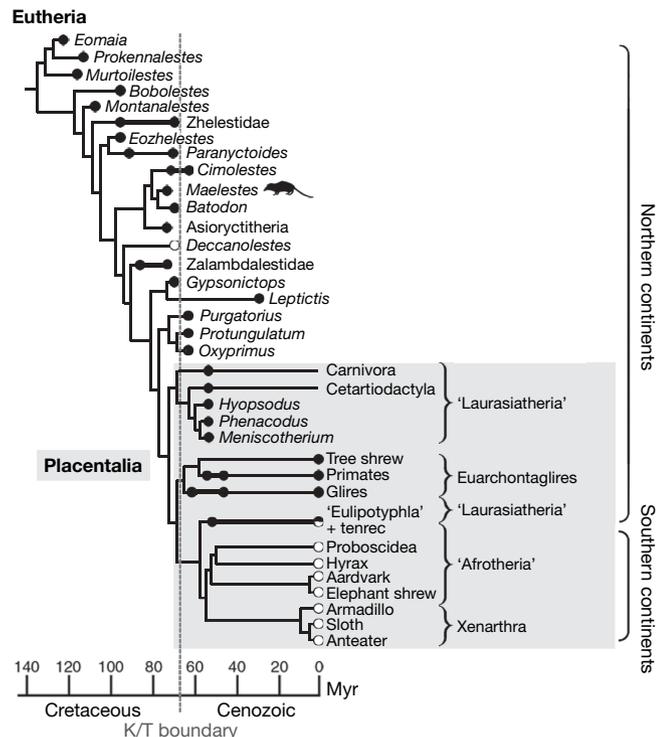


Figure 3 | Relationships of *Maelestes* to other eutherians. Simplified eutherian part of the strict consensus of three most parsimonious trees (2,296 steps; see Supplementary Information). Broken line, K/T boundary at 65 million years. Filled circle taxa, Laurasian (northern continents); open circle taxa, Gondwanan (southern continents). Circles and circles with thicker black lines indicate temporal occurrence of studied specimens. The grey box delimits Placentalia, the oldest member of which is the early Palaeocene *Mimotona*. Placentalia originates at or near the K/T boundary in Laurasia. *Deccanolestes* from the latest Cretaceous of India is nested among Asian clades and is more parsimoniously interpreted as an independent southern migration. The animal silhouette spotlights *Maelestes*.

Three models of origin and diversification of the modern placental orders have been characterized²⁷: ‘explosive’ (interordinal and ordinal originations near the K/T boundary); ‘long fuse’ (interordinal divergence deep in the Cretaceous with intraordinal diversification near the K/T boundary); and ‘short fuse’ (interordinal, ordinal and intraordinal diversifications deep in the Cretaceous, but without a fossil record). Some recent molecular studies^{2,8,9,28} are consistent with the short- or long-fuse models (deep Cretaceous origin), and a recent supertree approach²⁹ is consistent with the short-fuse model, although it has been argued that this model is statistically unlikely^{7,27}. Some palaeontologists^{6,7} prefer the explosive model (K/T boundary origin and diversification), despite the paucity of supporting phylogenetic analyses. Our analysis, which to date provides the best sample of relevant taxa and morphological characters, supports the explosive model. The immediate outgroup to Placentalia is a clade of *Protungulatum*, *Oxyprimus* and *Purgatorius*, best known from the Bug Creek Anthills of Montana, originally reported as latest Cretaceous but now accepted as basal Palaeocene⁴. All known fossil placentals are younger than this (Fig. 3), although some extension of ghost lineages into the Cretaceous is likely.

Within Placentalia, our results (Fig. 3) identify Euarchoptaglires and Xenarthra—two of the four major placental lineages identified in some recent DNA studies^{8,9}. Our morphological dataset does not fully support the other two lineages, Afrotheria and Laurasiatheria, as monophyletic, with the afrotherian tenrec *Potamogale* nested within laurasiatherian Eulipotyphla and eulipotyphlans more closely related to xenarthrans and the remaining afrotherians than to other laurasiatherians (carnivorans and cetartiodactylans). Afrotheria is a novel molecular clade^{8,9} that unites the modern placental clades Hyracoidea (hyraxes), Proboscidea (elephants), Sirenia (manatees), Tubulidentata (armadillos), Macroscelidea (elephant shrews), Tenrecidae (tenrecs) and Chrysochloridae (golden moles)—groups usually aligned with other ungulate- and insectivore-like lineages in morphological taxonomies¹¹. Our analysis, however, captures a core Afrotheria (hyrax, the Eocene proboscidean *Moeritherium*, armadillo and elephant shrew).

The highly nested position for Afrotheria and Xenarthra (the South American clade of armadillos, sloths and anteaters) in our tree (Fig. 3) is strikingly different from most recent molecular results^{8,9} (but resembles mitogenomic analyses²⁸ as well as from combined molecular and morphological results²⁴), which identify these groups as the basal-most placental clades, supporting a Southern Hemisphere origin for Placentalia. The nested position for Xenarthra is also a departure from previous classifications that place this clade at the base of Placentalia¹¹. Given that the basal placental clades and immediate outgroups in our tree are from the Northern Hemisphere (Fig. 3), our analysis supports a laurasian origin for Placentalia, with subsequent appearance of afrotherians as recovered here in Africa and xenarthrans in South America. A laurasian origin has been argued as most parsimonious even if afrotherians and xenarthrans are at the base of Placentalia⁷. The only Cretaceous Gondwanan form in our tree—*Deccanolestes* from the latest Cretaceous of India—is nested among Asian clades and, therefore, is most parsimoniously an immigrant from the north, as proposed elsewhere³⁰.

Elucidating the origin and diversification of placentals is facilitated by palaeontological and neontological approaches. We see the progressive convergence of tree topologies resulting from recent molecular, morphological and combined data sets as highly encouraging. However, the temporal framework for the origination of Placentalia ranges, potentially, from the Early Cretaceous to the early Palaeocene. Some recent molecular clock studies^{8,9,28} and a recent supertree approach²⁹ support origin dates for Placentalia close to 100 million years. But other clock studies vary widely for this node, with dates that exceed 140 million years¹ or that approach palaeontological estimates of less than 80 million years². Other analyses^{7,26}, including our own, support an origin in the vicinity of the K/T boundary. These competing hypotheses imply substantially different palaeogeographical

scenarios that have crucial impacts on the areas of origin, dispersion and diversification of some of the major clades of living mammals.

Received 21 February; accepted 17 April 2007.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank A. Davidson for specimen preparation; P. Bowden for illustration; N. B. Simmons, J. J. Flynn, R. L. Cifelli, J. G. Mead and H. L. Kafka for specimens; and J. D. Archibald, K. C. Beard, J. I. Bloch, R. L. Cifelli, M. R. Dawson, T. J. Gaudin, J. A. Hopson, I. Horovitz, Z. Kielan-Jaworowska, Z.-X. Luo, G. Metais, M. A. O'Leary, K. D. Rose and S. P. Zack for discussions. This work was supported by the NSF (J.R.W., G.W.R., M.J.N. and R.J.A.), the Carnegie Museum of Natural History, and the American Museum of Natural History.

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