

The earliest known eutherian mammal

Qiang Ji*, Zhe-Xi Luo†, Chong-Xi Yuan*, John R. Wible‡, Jian-Ping Zhang‡ & Justin A. Georgi†

* Chinese Academy of Geological Sciences, Beijing 100037, China

† Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, USA

‡ Geoscience University of China, Beijing 100083, China

The skeleton of a eutherian (placental) mammal has been discovered from the Lower Cretaceous Yixian Formation of northeastern China. We estimate its age to be about 125 million years (Myr), extending the date of the oldest eutherian records with skull and skeleton by about 40–50 Myr. Our analyses place the new fossil at the root of the eutherian tree and among the four other known Early Cretaceous eutherians, and suggest an earlier and greater diversification of stem eutherians that occurred well before the molecular estimate for the diversification of extant placental superorders (104–64 Myr). The new eutherian has limb and foot features that are known only from scansorial (climbing) and arboreal (tree-living) extant mammals, in contrast to the terrestrial or cursorial (running) features of other Cretaceous eutherians. This suggests that the earliest eutherian lineages developed different locomotory adaptations, facilitating their spread to diverse niches in the Cretaceous.

Placental mammals are the most diverse and dominant group of the three extant mammal lineages (Placentalia, Marsupialia and the egg-laying Monotremata)^{1,2}. All extant placentals, including our own order, Primates, are a subgroup of eutherians^{1,3}, which consist of extant placentals plus all extinct mammals that are more closely related to extant placentals (such as humans) than to extant marsupials (such as kangaroos). Here we describe a well-preserved eutherian mammal from the Early Cretaceous with bearing on the timing of the phylogenetic diversification and the locomotory evolution of the earliest eutherians.

Systematic palaeontology

Class Mammalia
 Subclass Boreosphenida
 Infraclass Eutheria
incertae sedis
Eomaia scansoria gen. et sp. nov.

Etymology. Eo (Greek): dawn; maia (Greek): mother; *Eomaia* for the earliest known eutherian mammal; *scansoria* (Latin) for the specialized skeletal features for climbing.

Holotype. CAGS01-IG1-a, b (Fig. 1; Chinese Academy of Geological Sciences, Institute of Geology), part and counterpart of a skeleton with an incomplete, flattened skull partially represented by impressions (dashed lines in Fig. 1), and nearly all of the post-cranium, with some preserved soft tissues, such as costal cartilages and fur.

Locality and horizon. Dawangzhangzi Locality, Lingyuan County, Liaoning Province, China. The holotype is from lacustrine silty shales of the Yixian Formation.

Geological age and fauna. The main fossiliferous horizon of the Yixian Formation was dated as 124.6 Myr (ref. 4) and correlated to the lower Barremian stage of the Mesozoic timescale⁵. The age of *Eomaia scansoria* is ~125 Myr and no younger than Mid Barremian. The Yixian Formation elsewhere in western Liaoning has yielded three other mammals, the spalacotheriid *Zhangheotherium*^{6,7}, the eutriconodont *Jeholodens*⁸, and the gobiconodontid *Repenomamus*⁹. The associated fauna in the Yixian Formation includes diverse fossil vertebrates, invertebrates and plants (reviewed in ref. 10).

Diagnosis. Among eutherians previously known from the late Early Cretaceous, *Eomaia scansoria* differs from *Prokennalestes*^{11,12} in lacking the labial mandibular foramen in the masseteric fossa and in having a larger metastylar and metaconal region on upper molar

M³; differs from *Murtoilestes*^{13,14} in having less-developed conules on the upper molars; and differs from both *Murtoilestes* and *Prokennalestes* in having an anteroposteriorly shorter molar trigonid and a longer talonid basin; differs from *Montanalestes*¹⁵ in having a paraconid lower than the metaconid; differs from the Late Cretaceous zhelestids^{16,17} and the Palaeocene ungulatomorphs in lacking an inflated protocone and swollen lower molar cusps. *E. scansoria* differs from *Montanalestes*¹⁵ and all Late Cretaceous eutherians^{16–19} in retaining the primitive Meckel's sulcus on the mandible, and from most eutherians including placentals (but not *Prokennalestes*¹¹, *Montanalestes*¹⁵ and several asioryctitherians¹⁹) in having a slightly in-turned angular process of the mandible. *E. scansoria* differs from *Deltatheridium*^{20,21} and other metatherians²² (including marsupials) in having a typical eutherian dental formula, 5.1.5.3/4.1.5.3 (incisors, canine, premolars, molars) (Fig. 2); differs from most marsupials in lacking the hypoconulid shelf and having nearly equal distance between the talonid cusps^{20–23}; differs from stem boreosphenidans^{24,25} in possessing a larger entoconid of nearly equal size to the hypoconid; differs from nontribosphenic therians^{6,7,26,27} in having a tricuspid talonid in occlusion with protocone; differs from *Ausktribosphenos* and *Bishops* (eutherians by some^{28,29}, but endemic southern mammals by others^{24,25}) in lacking a shelf-like mesial cingulid on the molars, and in having laterally compressed ultimate and penultimate lower premolars without full cusp triangulation; differs from *Ausktribosphenos*, *Bishops* and most stem mammaliaforms in lacking the primitive postdentary trough on the mandible.

Description and comparison

Numerous skeletal apomorphies (evolutionarily derived characters) also distinguish *Eomaia* from currently known eutherians^{3,30–32}, the earliest known metatherians (including marsupials)^{22,23,33–35}, and nontribosphenic therians^{6,7,26,27}. The scapula is slender with a prominent coracoid process on the glenoid and a relatively large acromion process on a tall scapular spine. The clavicle is robust and curved, with its proximal end abutting the lateral process of the clover-shaped manubrium. *Eomaia* differs from the Late Cretaceous eutherians *Asioryctes* and *Zalambdalestes* in having an enlarged and elongate trapezium in the wrist (Fig. 3). The hamate is large, a feature shared probably by all trechnotherians, although not so large as the hypertrophied hamate of marsupials³⁴. The trapezoid and capitata are small, and their proportions to the hamate and trapezium are comparable to the condition in the grasping hands of living scansorial and arboreal mammals^{30,35}. *Eomaia* and other eutherians retain the primitive mammalian condition in which the

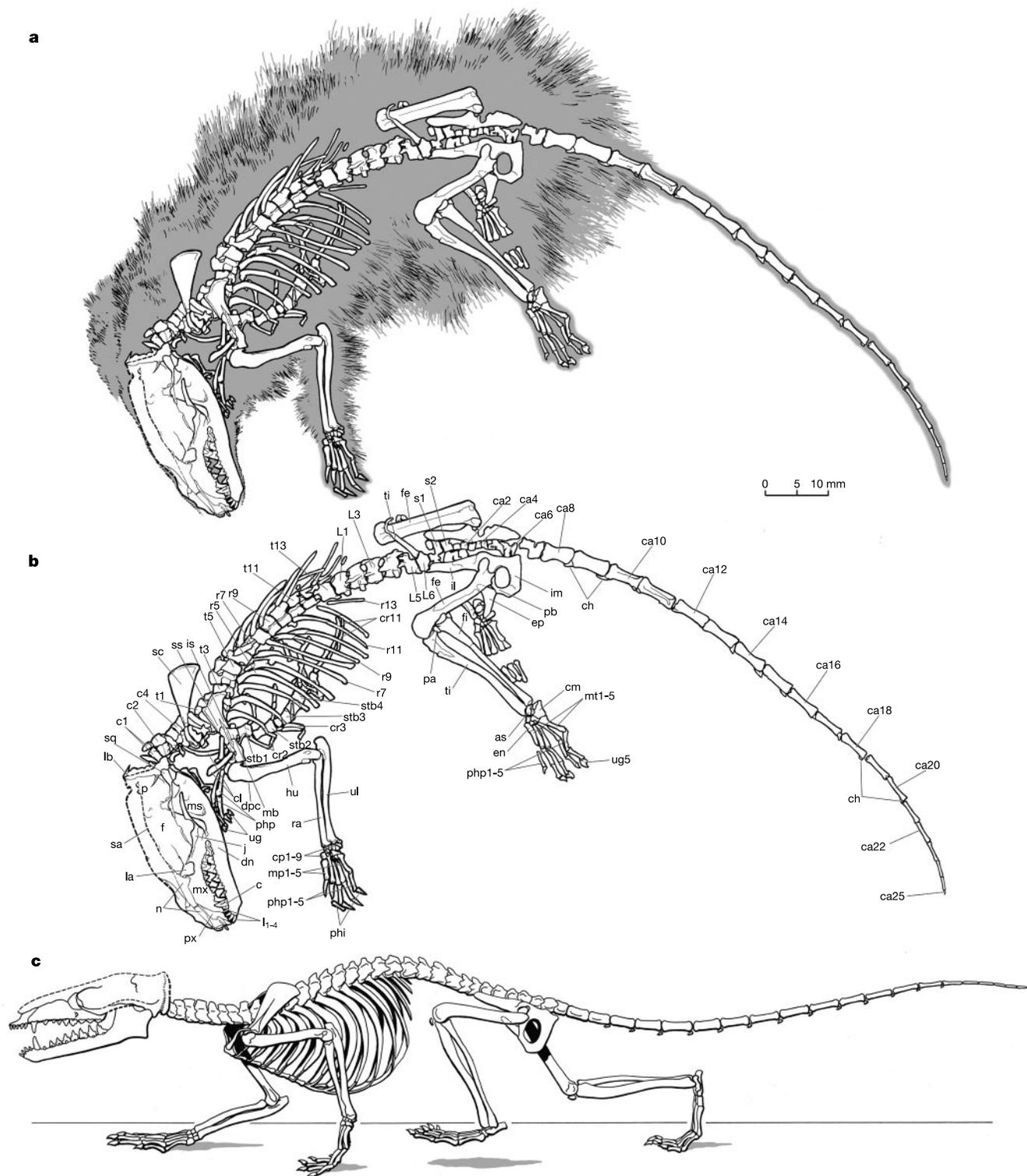


Figure 1 *Eomaia scansoria* (Chinese Academy of Geological Sciences (CAGS) 01-IG-1a, b; holotype). **a**, Fur halo preserved around the skeleton (01-IG-1a, many structures not represented on this slab are preserved on the counter-part 01-IG-1b, not illustrated). **b**, Identification of major skeletal structures of *Eomaia*. **c**, Reconstruction of *Eomaia* as an agile animal, capable of climbing on uneven substrates and branch walking. as, astragalus; c, canine; c1–c7, cervical vertebrae 1–7; ca1–ca25, caudal vertebrae 1–25; ch, chevron (caudal haemal arch); cl, clavicle; cm, calcaneum; cp1–9, carpals 1–9; cr1–11, costal cartilages 1–11; dn, dentary; dpc, deltopectoral crest; en, entocuneiform; ep, epipubis; f, frontal; fe, femur; fi, fibula; hu, humerus; l_{1–4}, lower incisors 1–4; il, ilium;

im, ischium; is, infraspinous fossa of scapula; j, jugal; la, lacrimal; lb, lambdoidal crest; L1–L6, lumbar vertebrae 1–6; mb, manubrium sterni; mp1–5, metacarpals 1–5; ms, masseteric fossa; mt1–mt5, metatarsals 1–5; mx, maxillary; n, nasal; p, parietal; pa, ossified patella; pb, pubis; phi, intermediate phalanges; php1–5, proximal phalanges 1–5; px, premaxillary; ra, radius; r1–r13, thoracic ribs 1–13; s1, s2, sacral vertebrae 1 and 2; sa, sagittal crest; sc, scapula; sq, squamosal; ss, supraspinous fossa of scapula; stb1–5, sternbrae 1–5 (sternbra 5 is the xiphoid); ti, tibia; t1–t13, thoracic vertebrae 1–13; ug1–5, ungual claws 1–5; ul, ulna.

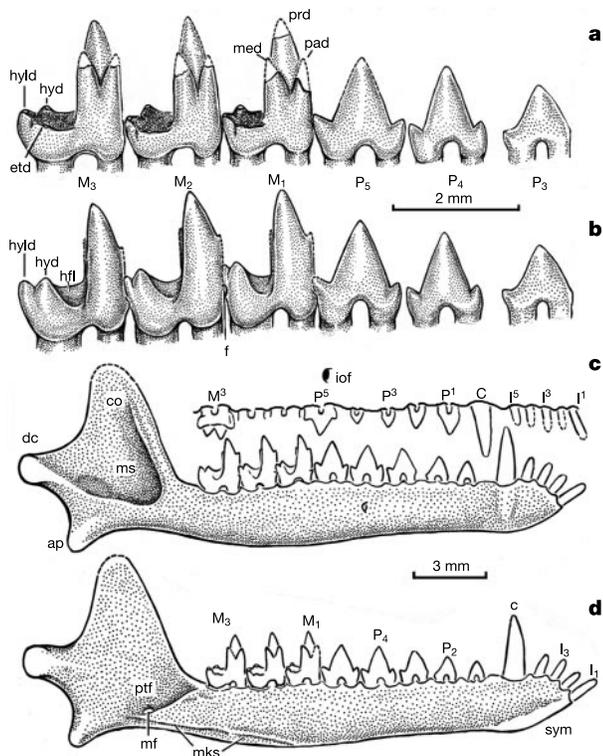


Figure 2 *Eomaia scansoria* dentition and mandible (composite reconstruction). **a**, Lower P₃–M₃ (right, lingual view). **b**, Lower P₃–M₃ (right, labial view). **c**, Upper dentition (incomplete) and mandible (right, lingual view). **d**, Mandible (left, lingual view). ap, angular process; C and c, upper and lower canine; co, coronoid process of mandible; dc, dentary condyle (articular process); etd, entoconid; f, cuspule f (anterolabial cingulid cuspule for interlocking); hfl, hypoflexid; hyd, hypoconid; hyld hypoconulid; I_{1–5} and I^{1–4}, upper and lower incisors; M_{1–3} and M^{1–3}, upper and lower molars; med, metaconid; mf, posterior (internal) foramen of mandibular canal; mks, Meckel's sulcus; ms, masseteric fossa; P_{1–5} and P^{1–5}, upper and lower premolars; pad, paraconid; prd, protoconid; ptf, pterygoid muscle fossa; sym, mandibular symphysis.

scaphoid and the triquetrum are small relative to other carpals, in contrast to the hypertrophied scaphoid and triquetrum in marsupials^{34,35}. Metacarpal 5 is level with the anterior edge of the hamate, a synapomorphy of crown therians, in contrast to the primitive *Zhangheotherium*⁷ and *Jeholodens*⁸, in which the proximal end of metacarpal 5 overhangs and is offset from the hamate (Fig. 3).

The ilium, ischium and pubis are fused. The epipubis is present. Relative to the size of the pelvis and the obturator foramen, the pubic symphysis is much shorter than those of the nontribosphenic therians *Zhangheotherium*, *Henkelotherium*²⁶ and *Vincelestes*²⁷, and early Tertiary metatherians²³. Given the short sacral transverse processes and the deep pelvis, it is likely that the pelvis was narrow at the sacral joint and vertically deep, as in *Zalambdalestes*³¹, *Ukhaatherium*³ and multituberculates^{36,37}, but less like the shallow pelvis of early Tertiary metatherians²³. The patella is present on both hindlimbs, a derived placental feature that is absent in most of the basal metatherians³⁴, and absent in all known skeletons of nontribosphenic trechnotherians, but convergent to multituberculates^{36–38} and monotremes³⁸.

The ankle of *Eomaia* bears strong resemblance to those of Late Cretaceous eutherians^{30–32}. The medial astragalotibial facet is well developed, vertical, and separated by a sharp crest from the lateral astragalotibial facet, a diagnostic eutherian feature. The navicular facet is distinctive from the astragalar neck, and does not extend to the medial side of the neck as in metatherians^{34,35}. The entocuneiform is elongate, and its joint with metatarsal 1 is offset anteriorly

from the joint of the intermediate cuneiform and metatarsal 2 (Fig. 4). The calcaneum is similar to those of *Asioryctes*³⁰, *Ukhaatherium*³² and *Zalambdalestes*^{31,32} in retaining many primitive features of the crown therians^{23,32,34}. The absence of the fibular malleolus is a phylogenetically primitive character, but nonetheless permitting a partial eversion of the foot³⁷.

Hairs are preserved as carbonized filaments and impressions around most of the body, although their traces are thin on the tail (Fig. 1a). The pelage appears to have both guard hairs and a denser layer of underhairs close to the body surface. Fossilized hairs were previously reported in Tertiary placentals and multituberculate mammals³⁹. *Eomaia* adds to the evidence that presence of hairs is a ubiquitous feature of mammals.

Scansorial adaptation

The fore- and hindfeet of *Eomaia* (Figs 4 and 5) show similar phalangeal proportions and curvature to the grasping feet of extant arboreal mammals, such as the didelphid *Caluromys*³⁵, the flying lemur *Cynocephalus*, and arboreal primates^{40,41}. In phalangeal features, *Eomaia* is more similar to arboreal mammals than to such scansorial taxa as the tree shrew and opossum. The proximal manual phalanx is arched dorsally (Fig. 5). Its proximal, ventral surface has a shallow longitudinal groove for the tendon of flexor digitorum profundus. Two protuberances for the fibrous tendon sheaths of the flexor digitorum flank the sides of the phalanx three-quarters of the length towards the distal end, which is partially trochleated. Sesamoid bones are present at both interphalangeal joints. *Eomaia* is similar to the scansorial or fully arboreal archontan eutherians^{40,41} in all these characteristics of the proximal phalanges (Fig. 5). The proportions of the intermediate phalanx to the proximal phalanx differ among terrestrial, scansorial and fully arboreal didelphid marsupials³⁵ and placental carnivores. This ratio in *Eomaia* (Fig. 5f) is intermediate between the fully arboreal *Micoureus* and *Caluromys*, and the scansorial *Didelphis* and the fully terrestrial *Metachirus*³⁵. Pedal digits 4 and 5 are elongate relative to the medial digits (1, 2 and 3). Both proximal and intermediate phalanges of digits 4 and 5 (although not the metatarsals) are longer than their counterparts in digit 3 (Fig. 4), a convergent pattern of many unrelated scansorial and arboreal mammals³⁶, in contrast to terrestrial or cursorial mammals, in which the phalanges in digits 2 and 3 are longer than those in digits 4 and 5 (ref. 36).

Both manual and pedal claws are more similar to those of scansorial mammals^{36,42}, than to fully arboreal taxa⁴². The pedal claws have an arched dorsal margin, a large flexor tubercle, and a small dorsal lip on the proximal articular surface for the extensor insertion. These are identical in lateral profile to those of the dormouse *Glis*, an extant rodent active in low bushes³⁶, and consistent with the claw morphotype of all extant scansorial mammals⁴². The preserved impression of the manual claw lacks the broad and thickened dorsal margin found in *Jeholodens*⁸ and *Zhangheotherium*⁷, so we interpret the claw to be more laterally compressed beyond the articulating margin (Fig. 3) than in the latter taxa. These are typical features of scansorial mammals⁴², such as the tree shrew *Tupaia*^{40,41} and the rodent *Glis glis*³⁶.

Other features of *Eomaia* are also consistent with an arboreal or scansorial adaptation: well-developed scapular acromion and coracoid process plus a tall spine^{23,35}, caudal vertebral column twice the length of the precaudal vertebral column^{26,37}, and elongation of the mid-caudal vertebrae²⁶. These convergences strongly suggest that *Eomaia* was an agile animal with climbing skeletal adaptations, capable of grasping and branch walking, and active both on the ground and in trees or shrubs (for example, like the opossum *Didelphis*, some species of the tree shrew *Tupaia*, and the dormouse *Glis*). We estimate that the holotype of *Eomaia scansoria* had a body mass from 20 to 25 g. For such small mammals, some capacity for climbing is required for moving on uneven substrates even in a terrestrial habitat⁴³; therefore, the anatomical differences between

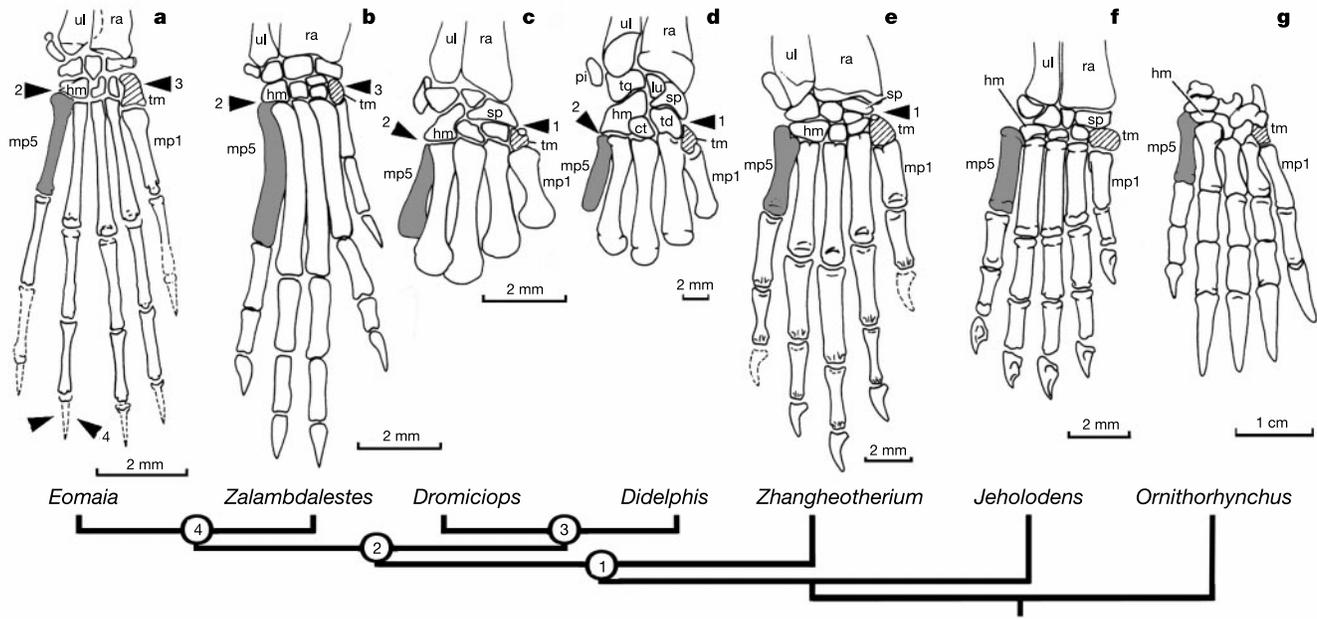


Figure 3 Comparison of forefoot (manus) of *Eomaia scansoria* (dorsal view, right). **a**, Eutherian *Eomaia* (composite reconstruction). **b**, Eutherian *Zalambdalestes*³¹. **c**, Marsupial *Dromiciops*³⁴. **d**, Marsupial *Didelphis*^{30,34}. **e**, Trechnotherian *Zhangheotherium*⁷. **f**, Eutriconodont *Jeholodens*⁸. **g**, Monotreme *Ornithorhynchus*. Apomorphies are as follows. Node 1 (Trechnotheria): enlargement of hamate, elongation of metacarpals, trapezium (hatched) offset from scaphoid (arrow 1; but reversed in eutherians). Node 2 (crown Theria): longitudinal alignment of mp5 (shaded) to hamate

(arrow 2; in contrast to the plesiomorphy of mp5 being offset from hamate; but reversed in some placentals), presence of distal radial malleolus. Node 3 (Marsupialia): hypertrophy of hamate, enlargement of scaphoid and triquetrum³⁴. Node 4 (Eutheria): elongation (longer than wide) of trapezium (hatched) (arrow 3; in contrast to the primitive condition of being wider than long). *Eomaia*: laterally compressed claws (arrow 4). ct, capitata; hm, hamate; lu, lunata; mp1–5, metacarpals 1–5; pi, pisiform; ra, radius; sp, scaphoid; td, trapezoid; tm, trapezium; tq, triquetrum; ul, ulna.

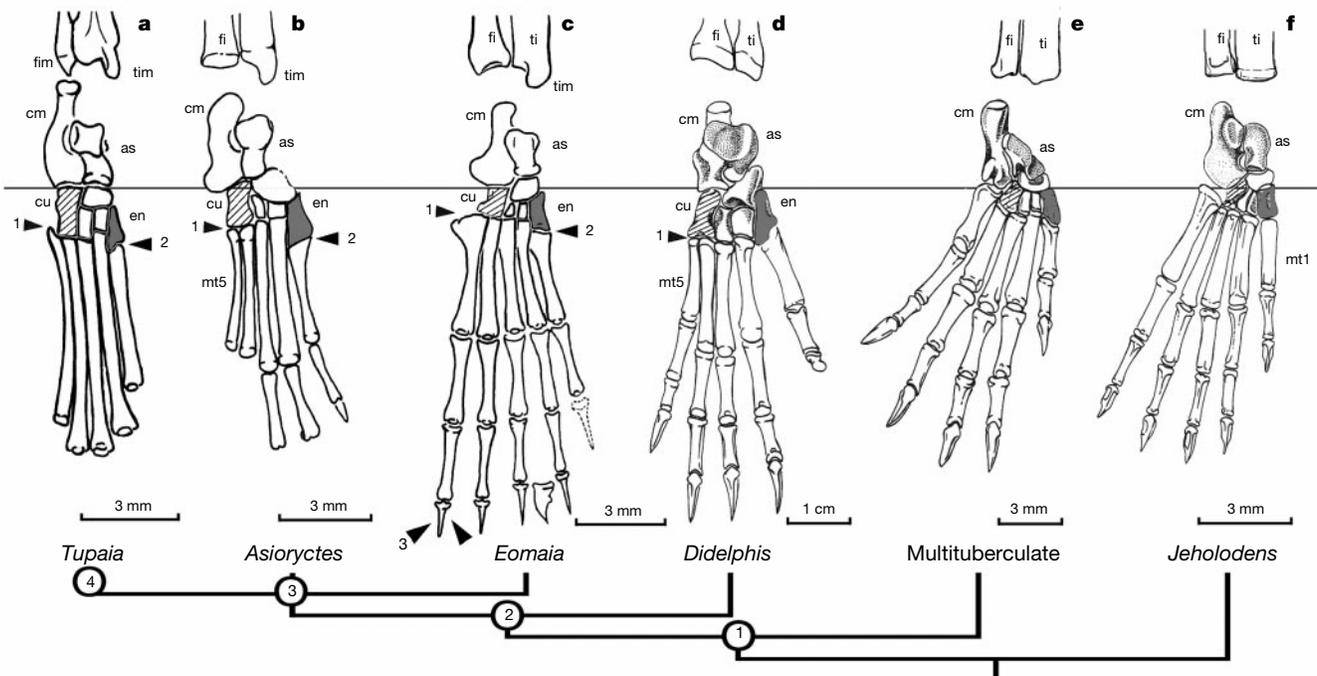


Figure 4 Comparison of hindfoot (pes) of *Eomaia scansoria*. **a**, Placental *Tupaia*³⁰. **b**, Eutherian *Asioryctes*³⁰. **c**, Eutherian *Eomaia* (composite reconstruction). **d**, Marsupial *Didelphis*. **e**, Multituberculata³⁰. **f**, Eutriconodont *Jeholodens*. Apomorphies are as follows. Node 1 (Theriformes³⁹): partial superposition of astragalus and calcaneum, laterally compressed calcaneal tuber. Node 2 (crown Theria): elongation and enlargement of cuboid; distal alignment of cuboid and metatarsal 5 so that the cuboid (hatched) corresponds to both metatarsals 4 and 5 (arrow 1; in contrast to the primitive condition of

mt5 being offset from cuboid). Node 3 (Eutheria): enlarged tibial malleolus; mt1–entocuneiform (shaded) joint offset from the mt2–mesocuneiform joint (arrow 2; in contrast to the primitive condition of the mt1–entocuneiform joint level with the mt2–mesocuneiform joint). Node 4 (Placentalia): fibular malleolus and the complete mortise-tenon upper ankle joint^{32,34}. *Eomaia*: compressed unguis claw (arrow 3). as, astragalus; cm, calcaneum; cu, cuboid; en, entocuneiform; fi, fibula; fim, fibular distal malleolus; mt1–5, metatarsals 1–5; ti, tibia; tim, tibial distal malleolus.

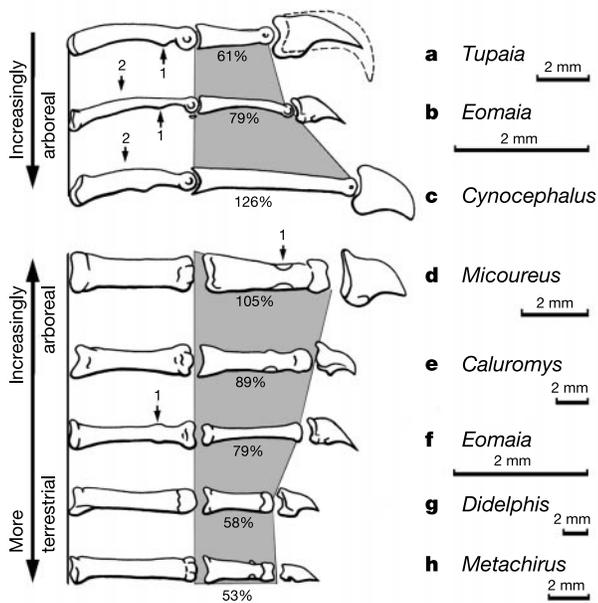


Figure 5 Comparison of manual phalanges and claws of *Eomaia scansoria* to those of scansorial and arboreal placentals (lateral view of digit 3). **a** Tree shrew *Tupaia* (scansorial, after refs 40 and 41). **b**, *Eomaia* (based on CAGS01-IG-1b). **c**, Flying lemur *Cynocephalus* (arboreal, after ref. 40). Comparison to manual phalanges of didelphid marsupials (digit 3; proximal and intermediate phalanges in ventral view; claw in lateral view). **d**, *Micoureus* (fully arboreal, after ref. 35). **e**, *Caluromys* (fully arboreal, after ref. 35). **f**, *Eomaia*. **g**, Opossum *Didelphis* (scansorial, after ref. 35). **h**, *Metachirus* (fully terrestrial, after ref. 35). The proximal phalanges standardized to the same length; percentage represents the length ratio of the intermediate to the proximal phalanges; scale varies among taxa. Arrow 1, protuberance on phalanges for the fibrous tendon sheaths for the flexor digitorum profundus (on the proximal phalanx in eutherians, but on the intermediate phalanx in didelphid marsupials). Arrow 2, dorsal curvature typical of scansorial or arboreal eutherians.

scansoriality and arboreality are not significant^{43,44}. The available evidence is insufficient to determine whether *Eomaia* was scansorial (as in some species of *Tupaia* or *Glis*) or fully arboreal (for example, as the marsupial *Caluromys* and the tupaiid *Ptilocercus*).

Because most basal metatherians are scansorial^{23,34,35}, scansorial skeletal features appear to be primitive for the earliest known eutherians. But the evidence for an ancestral scansorial adaptation for the crown group therians as a whole is less clear, because the successive outgroups to crown therians are either scansorial (for example, *Henkelotherium*²⁶) or terrestrial (for example, *Vincelestes*²⁷ and *Zhangheotherium*⁷).

Phylogenetic relationships

On the basis of 268 characters sampled from all major Mesozoic mammal clades and principal eutherian families of the Cretaceous, *Eomaia* is placed at the root of the eutherian tree with *Murtoilestes* and *Prokennalestes*. Clearly, these three taxa are closer to living placentals than to living marsupials. *Eomaia* is placed in Eutheria (Fig. 6) by numerous apomorphies in the dentition (Fig. 2), the wrist (Fig. 3) and the ankle (Fig. 4). Among eutherians, *Eomaia* is similar to *Prokennalestes* because they have identical features in lower premolars P₄ and P₅^{11,12}, plus identical and unique features of the posterior mandibular foramen on the ventral margin of the pterygoid fossa, with Meckel's sulcus intersecting the margin of the pterygoid fossa posterior to the mandibular foramen (Fig. 2). *Murtoilestes*^{13,14} is similar to *Prokennalestes* in molar characteristics.

Our analysis, including information of *Eomaia*, corroborates several previous hypotheses of relationships among the Late Cretaceous eutherians (Fig. 6a). First, asioryctitherians³ from the Campa-

nian (~75 Myr) of Mongolia form a clade^{3,21} that also includes zalambdalestids. Second, zhelestids from the Coniacian (>85 Myr) of Uzbekistan may be related to ungulatormorphs from the Tertiary of North America^{16,17}. Third, the ungulatormorphs, in a successively more distant order, may be related to the palaeyrctid *Cimolestes* and the leptictid *Gypsonictops* from the Maastrichtian (~70 Myr) of North America, and possibly to the Coniacian eutherian *Daulestes*. Fourth, the North American *Montanalestes*¹⁵ is placed among the basal eutherians, although its position differs in ordered and unordered searches (see Supplementary Information). Our analysis did not include enough extant placental superorders to address

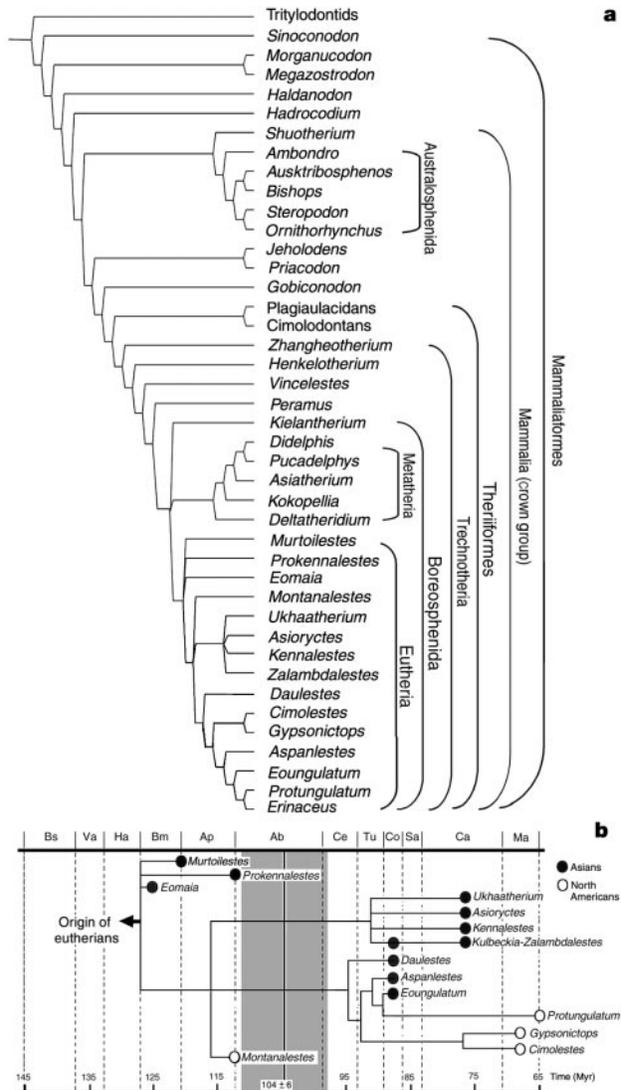


Figure 6 Phylogeny of eutherian *Eomaia scansoria* (**a**) and timing of the earliest evolution of eutherians (**b**). The phylogeny of mammals is based on a strict consensus of 50 equally parsimonious trees (tree length = 919, consistency index = 0.508, retention index = 0.740) from a PAUP analysis (version 4.0b, 1,000 runs of heuristic search, with unordered multistate characters) of 268 dental and skeletal characters that can be scored for the comparative taxa (the topology from searches with some ordered multistate characters is presented in Supplementary Information). The minimal age of *Eomaia* is after ref. 4; the age estimate for *Murtoilestes* is after ref. 13; dating of the Uzbekistan eutherians is after refs 16 and 17; and dating of the Mongolian eutherians is after ref. 45. The earliest molecular estimate^{16,47} of divergence of superordinal placental clades is 104 Myr (also see refs 48 and 49). Cretaceous stages⁵: Ab, Albian; Ap, Aptian; Bm, Barremian; Bs, Berriasian; Ca, Campanian; Ce, Cenomanian; Co, Coniacian; Ha, Hauterivian; Ma, Maastrichtian; Sa, Santonian; Tu, Turonian; Va, Valanginian.

whether some Cretaceous eutherians could be linked to placental superordinal clades, as advocated by some^{16,17}, or these eutherians are extinct lineages unrelated to living placentals, as argued by others^{3,21}.

Earliest eutherian diversification

Because *Eomaia*, *Prokennalestes* and *Murtoilestes* are distinct from each other, and from the three other previously recognized clades of *Montanalestes*, asioryctitherians–zalambdalestids, and zhelestids–ungulatomorphs (Fig. 6), the diversification of some of these clades must have occurred by the first appearance of *Eomaia* (~125 Myr). The second-oldest eutherian, *Murtoilestes*, is near the Barremian–Aptian transition¹³, also consistent with the early diversification of these taxa in the Barremian (~127–121 Myr). *Montanalestes* from the Aptian–Albian of North America is contemporary with (but distinctive from) all Barremian–Albian taxa of Asia, from which it must have split before Aptian–Albian. The ages of these taxa and their basal positions in the eutherian family tree (Fig. 6a) suggest the divergence of such typically Late Cretaceous lineages as asioryctitherians–zalambdalestids and zhelestids–ungulatomorphs (or the divergence of a combination of these clades) was no later than Aptian–Albian (Fig. 6a, tree topology from unordered searches), and could be as early as Barremian (tree topology from ordered searches, see Supplementary Information). Concurrent with their phyletic splitting, these lineages also developed different locomotory specializations that may have facilitated their spread to different niches. *Eomaia* was a scansorial animal in a lake-shore environment^{6–10}. In contrast to *Eomaia*, most (but not all) asioryctitherians were terrestrial^{30,32} in a xeric sand-dune niche⁴⁵. Most ungulatomorphs (including zhelestids), palaeoryctids and leptictids were in a fluvial palaeoenvironment¹⁶, although zalambdalestids with saltatorial locomotion³¹ are known from both the dune-field⁴⁵ and fluvial sediments¹⁶.

Given the earliest eutherian phylogeny (Fig. 6), the dating of *Eomaia* and *Murtoilestes* provides the minimal time for the diversification of stem eutherians at 125 Myr. The molecular dating done most recently shows that the placental superordinal diversification has ranged from 64 to 104 Myr^{46,47}. The earliest minimal quartet estimate (the split of xenarthrans and cetartiodactyls) is 104 Myr (95% confidence interval \pm 6 Myr)^{46,47}. The divergence time of the molecular superordinal clades I (afrotheres) and II (xenarthrans) from III and IV (other placentals) ranges from ~72 to ~112 Myr^{46,47} (at 95% confidence intervals). Although some previous estimates⁴⁸ postulated a 129 ± 18.5 Myr split for xenarthrans, the statistically defensible date for the split of the superordinal placental clades is now reconsidered by the same authors⁴⁹ to be about 112 ± 7 Myr (based on the hystricognaths–sciurognaths split). The minimal divergence time (\geq 125 Myr) of the stem eutherian lineages on the basis of the most recently discovered fossils is consistent with either of the two molecular estimates for divergence of the placental superordinal clades (104 ± 6 Myr^{46,47} or 112 ± 7 Myr by revision⁴⁹ of ref. 48). The time sequence of eutherian diversification (dated by fossils) and the splitting of the extant placental superorders (dated by the molecular clock) are consistent with the phylogenetic sequence in which multiple eutherian stem clades had split (Fig. 6b) well before the radiation of the extant placental superordinal clades. The corroboration of fossils and molecules provides a timetable of the earliest eutherian–placental evolution for calibrating the rates of morphological^{1,2} and molecular^{46–49} evolution.

Previous molecular studies postulated a gap between the putative time of origin of the placental superordinal groups and the then earliest fossil record of stem eutherians (for example, ref. 48). This gap was so large that it conflicted with the preservation likelihood models for eutherians based on empirical assessment of the mammalian fossil records⁵⁰. Discoveries of *Eomaia* and *Murtoilestes*, and the upward revision of molecular dating (for example, refs 46 and 47), have eliminated this putative gap. Whether, or to what extent,

the revised earliest eutherian records (\geq 125 Myr) would be consistent with the recently revised molecular estimates (for example, refs 46–49) can be further tested by the preservation likelihood models⁵⁰. □

Methods

The holotype of *Eomaia scansoria* suffered light diagenetic metamorphism, common for shales of the Yixian Formation. Some bones and all teeth are frail and fractured. However, the impressions of these structures are preserved in excellent detail. Composite restorations of the dentition, manus and pes are based on the outlines by camera lucida tracing; topographic features are based on reversed stereophotos from digital images of the well-preserved impressions. Relationships of *Eomaia* (Fig. 6a) are based on parsimony analysis of all major clades of Mesozoic mammals including the principal families of Cretaceous eutherians, plus the southern tribosphenic mammal *Ausktribosphenos*, considered by some to be eutherian^{28,29}. *Erinaceus* is included here to show that *Ausktribosphenos* and *Bishops* are not related to erinaceids (after refs 24 and 25). A total of 268 dental and skeletal characters was sampled for this analysis. These characters are combined from several recent analyses to resolve relationships of mammaliaforms, southern tribosphenic mammals, eutriconodonts, multituberculates, trechnotherians, stem boreosphenidans, metatherians and eutherians (sources are listed in Supplementary Information).

Received 14 November 2001; accepted 15 March 2002.

- McKenna, M. C. & Bell, S. K. *Classification of Mammals above the Species Level* 1–631 (Columbia Univ. Press, New York, 1997).
- Novacek, M. J. Mammalian phylogeny—shaking the tree. *Nature* **356**, 121–125 (1992).
- Novacek, M. J. *et al.* Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia. *Nature* **389**, 483–486 (1997).
- Swisher, C. C. III, Wang, Y.-Q., Wang, X.-L., Xu, X. & Wang, Y. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* **398**, 58–61 (1999).
- Gradstein, F. M. *et al.* in *Geochronology, Time Scales and Global Stratigraphic Correlation* (eds Berggren, W. A., Kent, D. V., Aubry, M. P. & Hardenbol, J.) 95–126 (Spec. Pub. No. 54, SEPM, Soc. Sed. Geol., Tulsa, Oklahoma, 1995).
- Hu, Y.-M., Wang, Y.-Q., Luo, Z.-X. & Li, C.-K. A new symmetrodont mammal from China and its implications for mammalian evolution. *Nature* **390**, 137–142 (1997).
- Hu, Y.-M., Wang, Y.-Q., Li, C.-K. & Luo, Z.-X. Morphology of dentition and forelimb of *Zhangheotherium*. *Vert. Palasiatic* **38**, 102–125 (1998).
- Ji, Q., Luo, Z.-X. & Ji, S.-A. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature* **398**, 326–330 (1999).
- Wang, Y.-Q., Hu, Y.-M., Meng, J. & Li, C.-K. An ossified Meckel’s cartilage in two Cretaceous mammals and origin of the mammalian middle ear. *Science* **294**, 357–361 (2001).
- Gee, H. (ed.) *Rise of the Dragon—Readings from Nature about the Chinese Fossil Records* 1–262 (Univ. Chicago Press, Chicago, 2001).
- Kielan-Jaworowska, Z. & Dashzeveg, D. Eutherian mammals from the Early Cretaceous of Mongolia. *Zool. Scripta* **18**, 347–355 (1989).
- Sigogneau-Russell, D., Dashzeveg, D. & Russell, D. E. Further data on *Prokennalestes* (Mammalia Eutheria *inc. sed.*) from the Early Cretaceous of Mongolia. *Zool. Scripta* **21**, 205–209 (1992).
- Averianov, A. O. & Skutschas, P. P. A eutherian mammal from the Early Cretaceous of Russia and biostratigraphy of the Asian Early Cretaceous vertebrate assemblages. *Lethaia* **33**, 330–340 (2000).
- Averianov, A. O. & Skutschas, P. P. A new genus of eutherian mammal from the Early Cretaceous of Transbaikalia, Russia. *Acta Palaeontol. Pol.* **46**, 431–436 (2001).
- Cifelli, R. L. Tribosphenic mammal from the North American Early Cretaceous. *Nature* **401**, 363–366 (1999).
- Nessov, L. A., Archibald, J. D. & Kielan-Jaworowska, Z. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. *Bull. Carnegie Mus. Nat. Hist.* **34**, 40–88 (1998).
- Archibald, J. D., Averianov, A. O. & Ekdale, E. G. Late Cretaceous relatives of rabbits, rodents, and other placental mammals. *Nature* **414**, 62–65 (2001).
- Kielan-Jaworowska, Z. Skull structure in *Kennalestes* and *Asioryctes*. *Palaeontol. Pol.* **42**, 25–78 (1981).
- McKenna, M. C., Kielan-Jaworowska, Z. & Meng, J. Earliest eutherian mammal skull from the Late Cretaceous (Coniacian) of Uzbekistan. *Acta Palaeontol. Pol.* **45**, 1–54 (2000).
- Cifelli, R. L. in *Mammal Phylogeny* Vol. 1 (eds Szalay, F. S., Novacek, M. J. & McKenna, M. C.) 205–215 (Springer, New York, 1993).
- Rougier, G. W., Wible, J. R. & Novacek, M. J. Implications of *Deltatheridium* specimens for early marsupial history. *Nature* **396**, 459–463 (1998).
- Cifelli, R. L. & Muizon, C. de. Dentition and jaw of *Kokopellia juddi*, a primitive marsupial or near marsupial from the medial Cretaceous of Utah. *J. Mamm. Evol.* **4**, 241–258 (1997).
- Muizon, C. de. *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiological implications. *Geodiversitas* **20**, 19–142 (1998).
- Luo, Z.-X., Cifelli, R. L. & Kielan-Jaworowska, Z. Dual origin of tribosphenic mammals. *Nature* **409**, 53–57 (2001).
- Luo, Z.-X., Kielan-Jaworowska, Z. & Cifelli, R. L. In quest for a phylogeny of Mesozoic mammals. *Acta Palaeontol. Pol.* **47**, 1–78 (2002).
- Krebs, B. Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. (Eupantotheria, Mammalia) aus dem Oberen Jura von Portugal. *Berliner Geowiss. Abh.* **133**, 1–110 (1991).
- Rougier, G. W. *Vincelestes neuquenianus Bonaparte* (Mammalia, Theria), un primitivo mammifero del Cretacico Inferior de la Cuenca Neuquina. Thesis, Univ. Nac. Buenos Aires (1993).
- Rich, T. H. *et al.* A tribosphenic mammal from the Mesozoic of Australia. *Science* **278**, 1438–1442 (1997).
- Rich, T. H. *et al.* A second tribosphenic mammal from the Mesozoic of Australia. *Records Queen Victoria Mus.* **110**, 1–9 (2001).
- Kielan-Jaworowska, Z. Postcranial skeleton in *Kennalestes* and *Asioryctes*. *Palaeontol. Pol.* **37**, 65–83 (1977).

31. Kielan-Jaworowska, Z. Postcranial skeleton in Zalambdalestidae. *Palaeontol. Pol.* **38**, 3–41 (1978).
32. Horowitz, I. The tarsus of *Ukhaatherium nessovi* (Eutheria Mammalia) from the Late Cretaceous of Mongolia: an appraisal of the evolution of the ankle in basal therians. *J. Vert. Paleontol.* **20**, 547–560 (2000).
33. Szalay, F. S. & Trofimov, B. A. The Mongolian Late Cretaceous *Asiatherium*, and the early phylogeny and paleobiogeography of Metatheria. *J. Vert. Paleontol.* **16**, 474–509 (1996).
34. Szalay, F. S. *Evolutionary History of the Marsupials and an Analysis of Osteological Characters* 1–481 (Cambridge Univ. Press, Cambridge, 1994).
35. Argot, C. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucaldelphis andinus*. *J. Morph.* **247**, 51–79 (2001).
36. Kielan-Jaworowska, Z. & Gambaryan, P. P. Postcranial anatomy and habits of Asian multituberculate mammals. *Fossils Strata* **36**, 1–92 (1994).
37. Krause, D. W. & Jenkins, F. A. Jr The postcranial skeleton of North American multituberculates. *Bull. Mus. Comp. Zool.* **150**, 199–246 (1983).
38. Rowe, T. B. Definition, diagnosis, and origin of Mammalia. *J. Vert. Paleontol.* **8**, 241–264 (1988).
39. Meng, J. & Wyss, A. R. Multituberculate and other mammal hair recovered from Palaeogene excreta. *Nature* **385**, 712–714 (1997).
40. Beard, K. C. in *Primates and Their Relatives in Phylogenetic Perspective* (ed. MacPhee, R. D. E.) 63–90 (Plenum, New York, 1992).
41. Szalay, F. Z. & Lucas, S. G. The postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. *New Mexico Mus. Nat. Hist. Sci. Bull.* **7**, 1–47 (1996).
42. McLeod, N. & Rose, K. D. Inferring locomotory behaviour in Paleogene mammals via eigenshape analysis. *Am. J. Sci.* **293**, 300–355 (1993).
43. Jenkins, F. A. Jr in *Primate Locomotion* (ed. Jenkins, F. A. Jr) 85–116 (Academic, New York, 1974).
44. Schilling, N. & Fischer, M. S. Kinematic analysis of treadmill locomotion of tree shrews, *Tupaia glis* (Scandentia: Tupaiidae). *Z. Saugetierkd.* **64**, 129–153 (1999).
45. Loope, D. B., Dingus, L., Swisher, C. C. III & Minjin, C. Life and death in a Late Cretaceous dunefield, Nemegt Basin Mongolia. *Geology* **26**, 27–30 (1998).
46. Murphy, W. J. *et al.* Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* **294**, 2348–2351 (2001).
47. Eizirik, E., Murphy, W. J. & O'Brien, S. J. Molecular dating and biogeography of early placental mammal radiation. *J. Hered.* **92**, 212–219 (2001).
48. Kumar, S. & Hedges, S. B. A molecular timescale for vertebrate evolution. *Nature* **392**, 917–920 (1998).
49. Hedges, S. B. & Kumar, S. Technical comments: divergence times of eutherian mammals. *Science* **285**, 2031a (1999).
50. Foote, M., Hunter, J. P., Janis, C. M. & Sepkoski, J. Jr Evolutionary and preservational constraints on origins of biologic groups: divergence times of eutherian mammals. *Science* **283**, 1310–1314 (1999).

Supplementary Information accompanies the paper on *Nature's* website (<http://www.nature.com>).

Acknowledgements

We thank K.-Q. Gao, M. Ellison, S.-A. Ji, M. A. Norell and D. Ren for collaborative field work; J. D. Archibald, R. L. Cifelli, Z. Kielan-Jaworowska, M. J. Novacek and G. W. Rougier for sharing ideas on early mammal research; K. C. Beard, M. Fischer, D. Gebo, M. Sánchez-Villagra and F. S. Szalay for discussions on limb anatomy and reconstructing locomotory patterns of fossil mammals; M. R. Dawson and A. Weil for improving the paper; A. Henrici for her skilful preparation; and M. Klingler for illustration of Fig. 1. We received funding from the Ministry of Land Resources of People's Republic of China and National Natural Science Foundation of China (Q.J.), National Science Foundation of USA and National Geographic Society (Z.-X.L.), and the Netting/O'Neil Funds of Carnegie Museum (Z.-X.L. and J.R.W.), and Brackenridge Fellowship of the University of Pittsburgh (J.A.G.).

Competing interests statement

The authors declare that they have no competing financial interests..

Correspondence and requests for materials should be addressed to Z.-X.L. (e-mail: luoz@carnegiemuseums.org).