LETTER

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A Jurassic eutherian mammal and divergence of marsupials and placentals

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Placentals are the most abundant mammals that have diversified into every niche for vertebrates and dominated the world's terrestrial biotas in the Cenozoic. A critical event in mammalian history is the divergence of eutherians, the clade inclusive of all living placentals, from the metatherian–marsupial clade[1–8]. Here we report the discovery of a new eutherian of 160 Myr from the Jurassic of China, which extends the first appearance of the eutherian–placental clade by about 35 Myr from the previous record, reducing and resolving a discrepancy between the previous fossil record and the molecular estimate for the placental–marsupial divergence[9–13]. This mammal has scansorial forelimb features, and provides the ancestral condition for dental and other anatomical features of eutherians.

Class Mammalia
Clade Boreosphenida[14]
Infraclass Eutheria
Order and family incertae sedis
Juramaia sinensis gen. et sp. nov.

Etymology. *Jura*, Jurassic; *maia*, mother, in reference to placental affinities; *sinensis*, of China. The binomial refers to 'Jurassic mother from China'.
Holotype. Beijing Museum of Natural History (BMNH) PM1143 (Fig. 1) is preserved with full dentition, incomplete skull, anterior part of postcranial skeleton and residual soft tissues, such as hairs.
Locality and age. The Daxigou site of Jianchang County of Liaoning Province in the Middle–Late Jurassic Tiaojishan formation. The formation was dated by the SHRIMP U–Pb method on zircon at 164–165 Myr in the neighbouring Ningcheng area[15] and its stratigraphic equivalent dated by the $^{40}Ar/^{39}Ar$ method on sanidines at 160.7 ± 0.4 Myr in the Beipiao area[16] (Supplementary Information).
Diagnosis. I^5–C^1–P^5–M^3/I_4–C_1–P_5–M_3 (Fig. 2), with identical formula as the eutherian *Eomaia*[3] and typical count of five premolars and three molars for Cretaceous eutherians[1]. Molars tribosphenic, with derived eutherian features of distinctive paraconule, incipient metaconule (M2 only), long preprotocrista past the paracone and long postprotocrista past the metacone. The postmetacrista and the extended postprotocrista of an upper molar form two separate ranks of shearing crests that pass the prevallid crest (paracristid) of the succeeding lower molar (Fig. 3). The preparacrista and the preprotocrista form two ranks of shearing crests that pass the postvallid crest (protocristid) of the preceding lower molar. This kind of stepwise or en-echelon shearing is much better developed in *Juramaia* than in most metatherians[17]. Distinct from metatherians in lacking the vertical keel of the paraconid and the hypoconulid shelf[18,19] and in lacking the close approximation of the hypoconulid and the entoconid as in *Sinodelphys*[7] or the twinning of these cusps in other metatherians[6]. Differs from metatherians (except *Sinodelphys*) in lacking the inflected mandibular angle and flat ventral surface of the angle. *Juramaia sinensis* is similar to many eutherians in having the posterior mental foramen of the mandible below the p4–p5 junction, by contrast to metatherians that have the posterior mental foramen below m1. *Juramaia sinensis* is similar to several Cretaceous eutherians in retaining a deciduous dP3 in the middle of the right premolar series[1] but differs from metatherians wherein replacement only occurs at the ultimate premolar position[6,20]. *Juramaia sinensis* differs from all australosphenidans in lacking the continuous mesial cingulid and the wrapping cingulid, and from most australosphenidan and pseudotribosphenidan mammals in lacking the postdentary trough on the mandible[14,21–24]. Among the earliest-known eutherians, *Juramaia sinensis* differs from *Eomaia* in having a two-rooted upper canine[3], and from *Acristatherium* in having different numbers of upper and lower incisors, a larger M3 and absence of

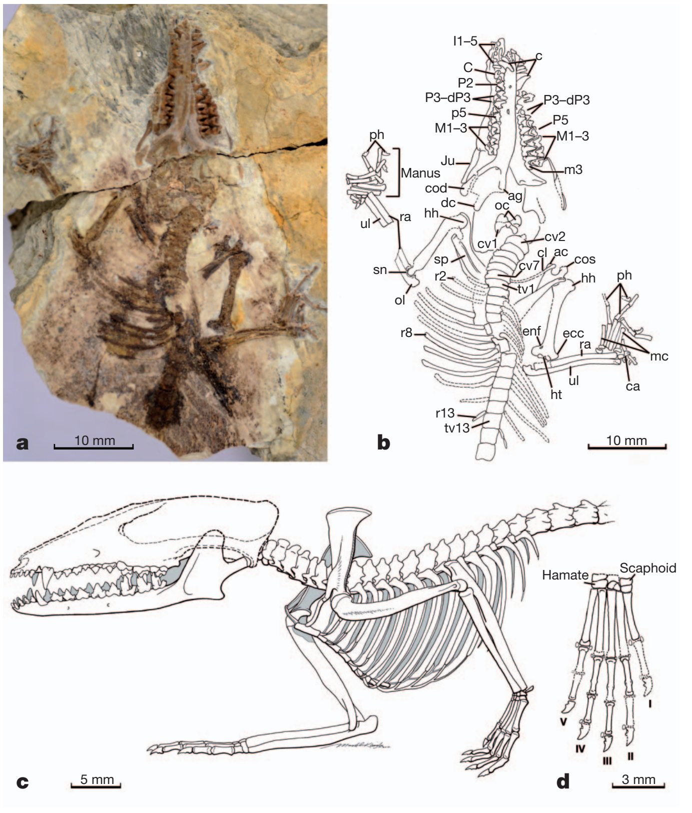

Figure 1 | Holotype specimen of *Juramaia sinensis*, Beijing Museum of Natural History (BMNH) PM1343B. a, b, Specimen photograph and morphological identification. **c**, Restoration of the partly preserved skeleton and skull. **d**, Restoration of hand (ventral view; alignment of incomplete and scattered carpals is conjectural). Abbreviations: ac, acromion (scapula); ag, angular process (dentary); C, c, upper or lower canine; ca, carpals; cl, clavicle; cod, coronoid (dentary); cos, coracoid process (scapula); cv1–7, cervical vertebrae 1–7; dc, dentary condyle; ecc, ectepicondyle; enf, entepicondylar foramen; hh, humeral head; ht, humeral trochlea; I1–5, upper incisors 1–5; Ju, jugal; M, m, upper or lower molar; manus, hand; mc1–5, metacarpals 1–5; oc, occipital condyles; ol, olecranon process; P1–5, upper premolars 1–5; ph, phalanges; r1–13; thoracic ribs 1–13; ra, radius; sn, semilunar notch (ulna); sp., scapular spine; tv1–13, thoracic vertebrae 1–13; ul, ulna.

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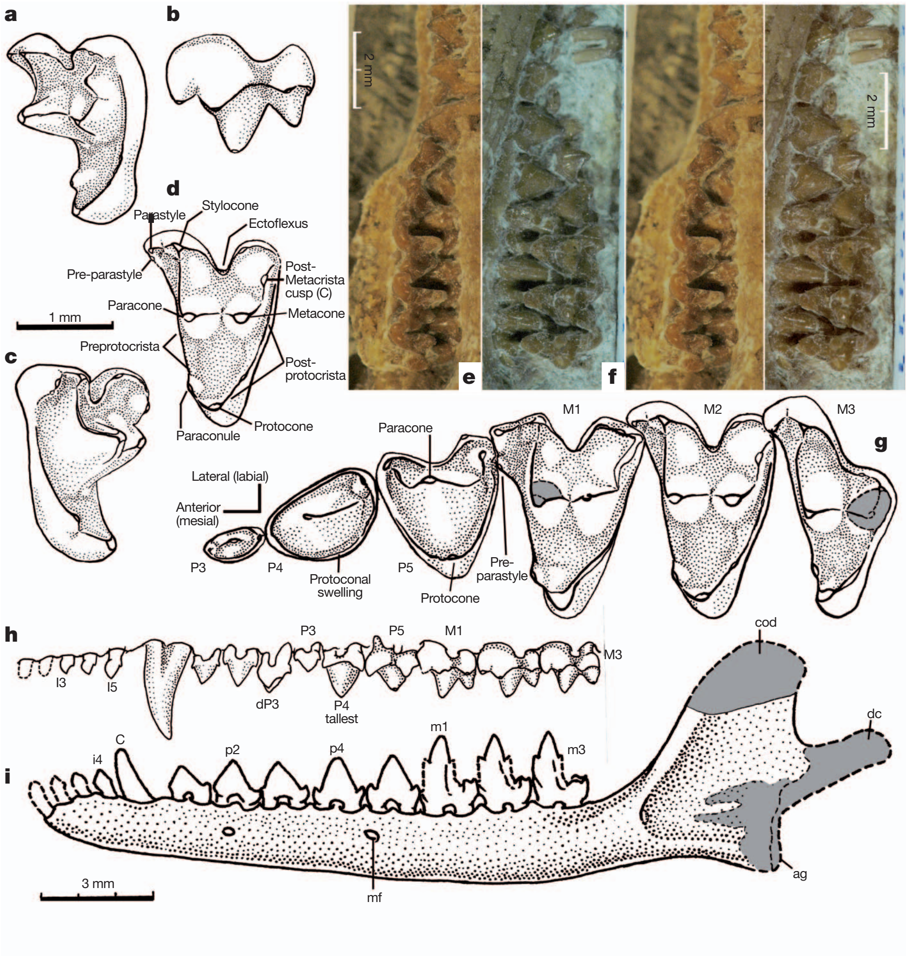

Figure 2 | Dental and mandibular features of *Juramaia sinensis* (BMNH PM1343B). a–d, Right upper M2 in mesial, occlusal, labial and distal views (composite restoration from both the right and the left sides). **e**, Stereo photographs of right premolars and molars. **f,** Stereo photographs of left premolars and molars. **g**, Right P3–M3 in occlusal view. **h**, Left upper dentition restoration in labial view. **i**, Left lower dentition (restoration) and mandible. Grey-shaded areas represent reconstruction from incomplete bone or tooth structure or mould outline in matrix. Abbreviations: ag, angular process; cod, coronoid process of dentary; dc; dentary condyle; M, m, upper and lower molars; mf, mental foramen; P, p, upper and lower premolars; dP3, deciduous P3 *in situ*. Terminology of tribosphenic molar follows Fig. 11.1 of ref. 1.

diastemata between the anterior upper premolars[6]. It differs from *Prokennalestes*, *Murtoilestes* and *Acristatherium* in having a much lower protocone and longer postprotocrista[1,25,26], from all known Early Cretaceous eutherians in a deeper ectoflexus on P5–M2, and from *Montanalestes* in having larger lower premolars 3 and 4. See Supplementary Information for full differential diagnosis and summary of morphological distinction from other Mesozoic mammal groups.

Our study has firmly placed *Juramaia* among the basal-most eutherians, the Mesozoic relatives to the Cenozoic placental mammals (Fig. 3), by phylogenetic analyses of two independent morphological data sets (Supplementary Information). *Juramaia* is more closely related to extant placentals than all metatherians of the Cretaceous including *Sinodelphys* and *Deltatheridium*. In the first parsimony analysis of a comprehensive data set of all Mesozoic mammaliaform clades[24], *Juramaia* and *Montanalestes* form an unresolved polytomy with the *Eomaia*–*Prokennalestes* clade and other eutherians (Fig. 3, left). Placement of *Juramaia* with eutherians is corroborated by analysis of a second and complementary data set of the largest sampling of Cretaceous eutherians[4,5]; *Juramaia* is placed in a more crown-ward position than the Early Cretaceous eutherian *Acristatherium*[5] (Supplementary Information). Our analysis by the mammaliaform data set reaffirms that the autralosphenidan mammals[21] are not eutherians[14]; they represent a separate lineage of Mesozoic mammalian diversity, and are stem taxa to monotremes[1,14], as corroborated by most of the recent independent studies[4,12,22–24].

Juramaia, at an age of 160 Myr (refs 15, 16), establishes a much older geological time for the split of the metatherian–marsupial and the eutherian–placental lineages than previously shown by the fossil record. The previously earliest eutherian record is *Eomaia* and the metatherian record is *Sinodelphys*, both about 125 Myr (refs 3, 7). The next oldest eutherian with a direct geochronological dating is *Acristatherium* at 123 Myr (ref. 5). *Juramaia* extends the first appearance of eutherians from these previous records by about 35 Myr. Because *Juramaia* is unambiguously placed on the placental side of the marsupial–placental divergence, the marsupial–placental divergence must have occurred before *Juramaia*. Therefore this new fossil serves to re-set the minimal age at 160 Myr for the basal-most diversification of marsupials and placentals, the two clades that collectively make up 99.9% of all living mammals and are very important in terrestrial ecosystems, especially after the Cretaceous/Tertiary extinction of non-avian dinosaurs.

Timing of the divergence of marsupials and placentals is critical for calibrating the rates of evolution in therian mammals, especially for molecular evolutionary studies and comparative genomics[2,10,13]. Previously, some molecular time estimates for marsupial and placental divergence postulated significantly older windows for this divergence than the then-oldest fossil records[3,7]. However, these and other previous molecular estimates differed widely. Several were compatible with relatively young placental intraordinal divergences (for example, ref. 10), and just about all showed wide error margins (reviewed by

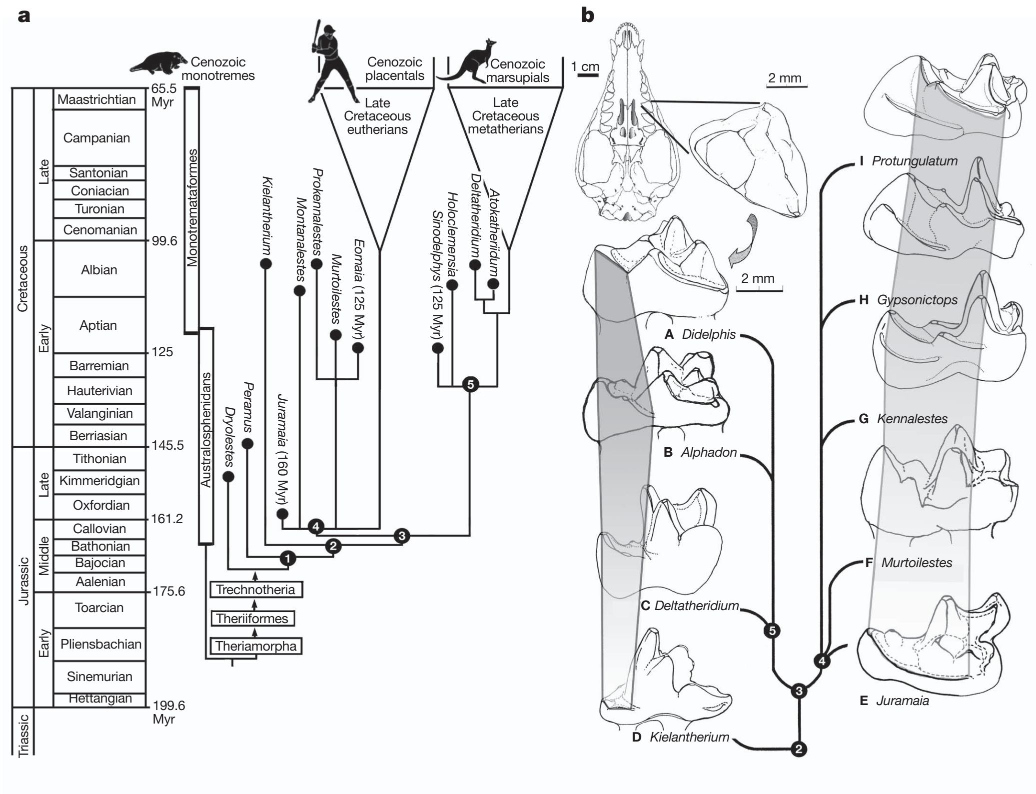

Figure 3 | Time-calibrated phylogeny of the eutherian *Juramaia* among other boreosphenidan mammals, and comparative morphology of some key molar features. a, Basal eutherian and metatherian phylogeny from parsimony analysis of data set of ref. 24 (446 characters of 103 cynodont–mammaliaform clades; based on the strict consensus of 172 equally parsimonious trees (each with treelength 2,243; consistency index 0.373, retention index 0.803) from 1,000 PAUP heuristic runs, without any topology constraints and with all multi-state characters unordered, multi-state taxa interpreted as polymorphism). Placement of *Juramaia* in eutherians is significantly different (*$P<0.050$) from suboptimal hypotheses of *Juramaia* as either a boreosphenidan or a metatherian by Templeton tests. This topology is corroborated by a separate analysis on a different and complementary data set by refs 4, 5 (389 informative characters of 71 eutherian taxa and outgroups), by the strict consensus of 41 equally parsimonious trees, from 1,000 heuristic runs, without topology constraints and 33 multi-state characters ordered, multi-state taxa as polymorphism. Placement of *Juramaia* among basal eutherians is consistent with topologies from constrained search under molecular scaffolding of extant taxa in the main data set of ref. 24 and the complementary data set of refs 4, 5 (details in Supplementary Information). **b**, The increased en-echelon postvallum shearing of upper molars in the earliest eutherians[17], in contrast to metatherians[18] that lack a strongly developed postvallum shearing by metacingulum, except for the Late Cretaceous *Pediomys*[1]. Nodes (1) Cladotheria, (2) Boreosphenida[1,2], (3) crown Theria, (4) Eutheria (including Placentalia), and (5) Metatheria (including Marsupialia).

ref. 13). Regarding the marsupial–placental split, recent molecular rate studies provided estimates of 147.7 ± 5.5 Myr (ref. 11), or 160 Myr (median) with a 95% highest posterior distribution of 143–178 Myr (ref. 12), or a window of 193–186 Myr (ref. 9). This new eutherian fossil age is now similar to the age of placentals at 160 Myr with 95% posterior distribution from 143 to 178 Myr by the latest molecular estimate[12]. The age of *Juramaia* has now set the minimal divergence time by the fossil to coincide with the range of molecular time estimates, serving as a corroboration of the newest fossil record with the molecular clock of evolution. The 160-Myr-old *Juramaia* also has important implications for mammalian evolution as a whole. Eutherian mammals are nested in the more inclusive Mesozoic boreosphenidan clade (Fig. 3, node 1), for which the previously earliest record had been entirely Early Cretaceous[1,27]. The eutherian *Juramaia* requires that the ghost-lineages of boreosphenid and cladotherian mammals would also extend to the Middle Jurassic. Therefore the magnitude of the mammalian faunal turnover from the Early to Middle Jurassic is greater than previously known, and the Early–Middle Jurassic is a critical transition for the appearance of more of the derived mammalian clades[1,2].

Phylogenetically, *Juramaia sinensis* is one of the basal-most eutherians and it is currently the earliest-known eutherian (Fig. 3); therefore, this fossil provides crucial inferences on the ancestral features of all eutherians. *Juramaia* weighed about 15–17 g, and was an insectivore based on tooth morphology. Its long preprotocrista (Fig. 2c, d) and postprotocrista (Fig. 3e) enhance the en-echelon shearing in which more than one crest of the upper molar, arranged in stepwise pattern, shears past the surfaces of the trigonid of the lower molar. This is especially prominent on the posterior face of the upper molar (postvallum) (Fig. 3e–i), an important derived character of eutherians compared with other tribosphenic mammals[17] (Fig. 3).

The forelimb and shoulder girdle of *Juramaia* show several eutherian apomorphies and lack such metatherian features as the supra-scapular notch and the expanded ectepicondylar shelf on the humerus for the supinator muscle[7,28,29]. Its manual phalanges suggest a scansorial adaptation (Fig. 1d). Proximal phalanges of three digits show protuberances of the annular ligament of the digital flexor muscle tendon, suggesting a gripping capability of the hand, common in scansorial extant mammals[3,7]. In the third manual digit, the proximal phalanx is 2.77 mm long, the intermediate phalanx is 2.39 mm and the metacarpal is 4.26 mm. The phalangeal index ((proximal + intermediate phalanges)/metacarpal × 100) (ref. 30) is 121 for *Juramaia*. Most extant mammals with this index value are arboreal. The proximal phalangeal index (proximal/intermediate phalanges × 100) is 65 for *Juramaia*. Extant placental carnivorans, primates and dermopterans with this value also tend to be arborealists, but rodents with this value are all terrestrial[30]. Compared with fossil mammals of the Early Cretaceous Yixian formation, phalangeal indices of *Juramaia* are between *Eomaia scansoria*, a scansorial mammal, and the eutriconodont *Jeholodens jenkinsi*, which is interpreted to be terrestrial[7]. In its habitat preference, *Juramaia* should be similar to the eutherian *Eomaia scansoria*, to the

Cretaceous and Early Cenozoic metatherians[7,28] and to living scansorial or arboreal didelphids[30]. The scansorial habits are also corroborated by the forelimb features, which are indicative of that habitat preference in extant mammals, such as the hypertrophied acromion and the acute posterior angle of the scapula[28].

The earliest-known eutherians *Juramaia* and *Eomaia* and the earliest metatherian *Sinodelphys* are scansorial mammals, and differ from contemporary Mesozoic mammals, most which are terrestrial[1,2]. This suggests that the phylogenetic split of eutherians and metatherians and their earliest evolution are accompanied by major ecomorphological diversification, notably scansorial adaptation, which made it possible for therians to exploit arboreal niches.

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1. Kielan-Jaworowska, Z., Cifelli, R. L. & Luo, Z.-X. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure* (Columbia Univ. Press, 2004).
2. Luo, Z.-X. Transformation and diversification in the early mammalian evolution. *Nature* **450,** 1011–1019 (2007).
3. Ji, Q. *et al.* The earliest known eutherian mammal. *Nature* **416,** 816–822 (2002).
4. Wible, J. R., Rougier, G. W., Novacek, M. J. & Asher, R. J. The eutherian mammal *Maelestes gobiensis* from the Late Cretaceous of Mongolia and the phylogeny of Cretaceous Eutheria. *Bull. Am. Mus. Nat. Hist.* **327,** 1–123 (2009).
5. Hu, Y. M., Meng, J., Li, C.-K. & Wang, Y.-Q. New basal eutherian mammal from the Early Cretaceous Jehol biota, Liaoning, China. *Proc. R. Soc. B* **277,** 229–236 (2010).
6. Rougier, G. W., Wible, J. R. & Novacek, M. J. Implications of *Deltatheridium* specimens for early marsupial history. *Nature* **396,** 459–463 (1998).
7. Luo, Z.-X., Ji, Q., Wible, J. R. & Yuan, C.-X. An Early Cretaceous tribosphenic mammal and metatherian evolution. *Science* **302,** 1934–1940 (2003).
8. Wilson, G. P. & Riedl, J. A. New specimen reveals deltatheroidan affinities of the North American Late Cretaceous mammal *Nanocuris. J. Vertebr. Paleontol.* **30,** 872–884 (2010).
9. van Rheede, T. *et al.* The platypus is in its place: nuclear genes and Indels confirm the sister group relation of monotremes and therians. *Mol. Biol. Evol.* **23,** 587–597 (2006).
10. Kitazoe, Y. *et al.* Robust time estimation reconciles views of the antiquity of placental mammals. *PLoS ONE* **2,** e384 (2007).
11. Bininda-Emonds, O. R. P. *et al.* The delayed rise of present-day mammals. *Nature* **446,** 507–512 (2007).
12. Phillips, M. J., Bennett, T. H. & Lee, M. S. Y. Molecules, morphology, and ecology indicate a recent, amphibious ancestry for echidnas. *Proc. Natl Acad. Sci. USA* **106,** 17089–17094 (2009).
13. Benton, M. J., Donoghue, P. C. J. & Asher, R. J. in *The Timetree of Life* (eds Hedges, S. B. & Kumar S.) 35–86 (Oxford Univ. Press, 2009).
14. Luo, Z.-X., Cifelli, R. C. & Kielan-Jaworowska, Z. Dual origin of tribosphenic mammals. *Nature* **409,** 53–57 (2001).
15. Liu, Y.-Q., Liu, Y.-X., Ji, S.-A. & Yang, Z.-Q. U-Pb zircon age for the Daohugou Biota at Ningcheng of Inner Mongolia and comments on related issues. *Chin. Sci. Bull.* **51,** 2634–2644 (2006).
16. Chang, S.-C., Zhang, H.-C., Renne, P. R. & Fang, F. High-precision 40Ar/39Ar age constraints on the basal Lanqi Formation and its implications for the origin of angiosperm plants. *Earth Planet. Sci. Lett.* **279,** 212–221 (2009).
17. Crompton, A. W. & Kielan-Jaworowska, Z. in *Studies in the Development, Function and Evolution of Teeth* (eds Butler, P. M. & Joysey, K. A.) 249–287 (Academic Press, 1978).
18. Cifelli, R. L. & de Muizon, C. 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).
19. Averianov, A. O., Archibald, J. D. & Ekdale, E. G. New material of the Late Cretaceous deltatheroidan mammal *Sulestes* from Uzbekistan and phylogenetic reassessment of the metatherian eutherian dichotomy. *J. Syst. Palaeontology* **8,** 301–330 (2010).
20. Cifelli, R. L. *et al.* Origin of marsupial pattern of tooth replacement: fossil evidence revealed by high resolution X-ray CT. *Nature* **379,** 715–718 (1996).
21. Rich, T. H. *et al.* Early Cretaceous mammals from Flat Rocks, Victoria, Australia. *Rec. Queen Victoria Mus.* **106,** 1–35 (1999).
22. Martin, T. & Rauhut, O. W. M. Mandible and dentition of *Asfaltomylos patagonicus* (Australosphenida, Mammalia) and the evolution of tribosphenic teeth. *J. Vertebr. Paleontol.* **25,** 414–425 (2005).
23. Rougier, G. W. *et al.* New Jurassic mammals from Patagonia, Argentina: a reappraisal of australosphenidan morphology and interrelationship. *Am. Mus. Novit.* **3566,** 1–54 (2007).
24. Luo, Z.-X., Ji, Q. & Yuan, C.-X. Convergent dental evolution in pseudotribosphenic and tribosphenic mammals. *Nature* **450,** 93–97 (2007).
25. Kielan-Jaworowska, Z. & Dashzeveg, D. Eutherian mammals from the Early Cretaceous of Mongolia. *Zool. Scr.* **18,** 347–355 (1989).
26. 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).
27. Sigogneau-Russell, D., Hooker, J. J. & Ensom, P. C. The oldest tribosphenic mammal from Laurasia (Purbeck Limestone Group, Berriasian, Cretaceous, UK) and its bearing on the 'dual origin' of Tribosphenida. *C. R. Acad. Sci. II* **333,** 141–147 (2001).
28. Argot, C. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *J. Morphol.* **247,** 51–79 (2001).
29. Asher, R. J., Horovitz, I. & Sanchez-Villagra, M. R. First combined cladistic analysis of marsupial mammal interrelationships. *Mol. Phylogenet. Evol.* **33,** 240–250 (2004).
30. Kirk, E. C., Lemelin, P., Hamrick, M. W., Boyer, D. M. & Bloch, J. I. Intrinsic hand proportions of euarchontans and other mammals: Implications for the locomotor behavior of plesiadapiforms. *J. Hum. Evol.* **55,** 278–299 (2008).

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

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