

Three new Jurassic euharamiyidan species reinforce early divergence of mammals

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The phylogeny of Allotheria, including Multituberculata and Haramiyida, remains unsolved and has generated contentious views on the origin and earliest evolution of mammals. Here we report three new species of a new clade, Euharamiyida, based on six well-preserved fossils from the Jurassic period of China. These fossils reveal many craniodental and postcranial features of euharamiyidans and clarify several ambiguous structures that are currently the topic of debate. Our phylogenetic analyses recognize Euharamiyida as the sister group of Multituberculata, and place Allotheria within the Mammalia. The phylogeny suggests that allotherian mammals evolved from a Late Triassic (approximately 208 million years ago) Haramiyavia-like ancestor and diversified into euharamiyidans and multituberculates with a cosmopolitan distribution, implying homologous acquisition of many craniodental and postcranial features in the two groups. Our findings also favour a Late Triassic origin of mammals in Laurasia and two independent detachment events of the middle ear bones during mammalian evolution.

Mammalia Linnaeus, 1758

Allotheria Marsh, 1880

Euharamiyida (new clade)

Shenshou lui gen. et sp. nov. Bi, Wang, Guan, Sheng and Meng

Etymology. *Shen*, from pinyin of the Chinese word, meaning deity, divinity or cleaver; *shou*, from pinyin of the Chinese word for creature, animal or beast; specific name after Lu Jianhua, the collector of the holotype.

Holotype. A nearly complete skeleton from an adult individual (LDN HMF2001, Lande Museum of Natural History, Tangshan, Hebei Province, China) (Figs 1a and 2d, and Extended Data Figs 1a and 2). Three specimens are referred to as the paratypes (see Supplementary Information, section A).

Paratypes. Three specimens are referred to as the paratypes (see section A of Supplementary Information).

Locality and horizon. The Tiaojishan Formation, Daxishan site of Linglongta, Jianchang County, Liaoning Province, China; the locality was dated as approximately 160 million years ago (within the Oxfordian) (see Supplementary Information, section C, for age constraint).

Diagnosis. Medium-sized euharamiyidan with an estimated body mass of 300 g (Supplementary Information, section D). Dental formula $I^1-C^0-P^2-M^2/I_1-C_0-P_1-M_2$ (I, incisor; C, canine; P, premolar; M, molar; superscript, upper teeth; subscript, lower teeth). The only pair of upper incisors (I^2) are in contact so that a facet is present on the medial side of each tooth; I^2 with two cusps. The mesial upper premolar (P^3) small (not basined) and the ultimate premolar (P^4) not significantly larger than upper molars. Upper molars with two main cusps in the buccal row, separated by a low ridge; three cusps in the lingual one, of which the penultimate cusp (B2) is the largest. P_4 sub-molariform with a main mesiolingual cusp (a1) and a long basined heel with two rows of cusps; M_1 with three cusps in each cusp row, M_2 with four cusps in the lingual and three in the labial row (Fig. 2d; see Supplementary Information, section A, for differential comparisons). The terminology we use to designate cusps in allotherian teeth is as follows: for upper teeth, the buccal (labial or lateral) cusp row is A, lingual row is B, cusps are numbered from the

distal end; lower teeth, the lingual cusp row is a, the buccal row is b (lower case), numbering starts from the mesial (anterior) end.

Eleutherodontidae Kermack *et al.*, 1998

Xianshou gen. nov. Wang, Meng, Bi, Guan and Sheng

Etymology. *Xian*, from pinyin of the Chinese word meaning celestial being or immortal.

Locality and horizon. Same as *Shenshou*.

Diagnosis. Dental formula: $I^2-C^0-P^2-M^2/I_1-C_0-P_1-M_2$; upper and lower molars ovoid in outline, with a shallow central basin. Differ from *Sineleutherus* in having three well-separated cusps of I^2 , non-molariform P_4 with a hypertrophic mesiolingual cusp (a1) and a weakly basined heel. Differ from *Eleutherodon* in the ovoid upper molars by absence of third row of cusps, and lack of cusps and transverse ridges in the central basin. Differ from *Shenshou* and *Arboroharamiya* in having an extra-small I^1 , ovoid upper and lower molars, more distally positioned distobuccal cusp (A1) on P^4 and M^1 ; a hypertrophic mesiolingual cusp (a1) on lower molars (Fig. 2e, f; see Supplementary Information, section A, for differential comparisons, and Extended Data Figs 5 and 6 for additional figures).

Xianshou linglong sp. nov. Wang, Meng, Bi, Guan and Sheng

Etymology. *linglong*, from pinyin of the Chinese word, meaning 'exquisite', and also after the town name Linglongta where the specimen came from.

Holotype. A skeleton preserved on a split slab of laminated siltstone (IVPP V16707A-B, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; Figs 1b and 2e, and Extended Data Figs 1b and 5).

Diagnosis. Estimated body mass of 83 g. I^2 with three cusps; I^3 extremely small and budlike. Upper molars with sharp cusps and stronger and sharper ridges (flutings) than those in *Shenshou* and *X. songae*; M^1 with two main cusps at the mesial and distal end and connected by a low and sharp ridge in each cusp row; an enlarged and more distally extended distobuccal cusp (A1) on P^4 and M^1 ; P_4 enlarged with a hypertrophic mesiolingual cusp (a1) and a small talonid heel; cusp a1 of lower molar procumbent, projecting mesially beyond the crown.

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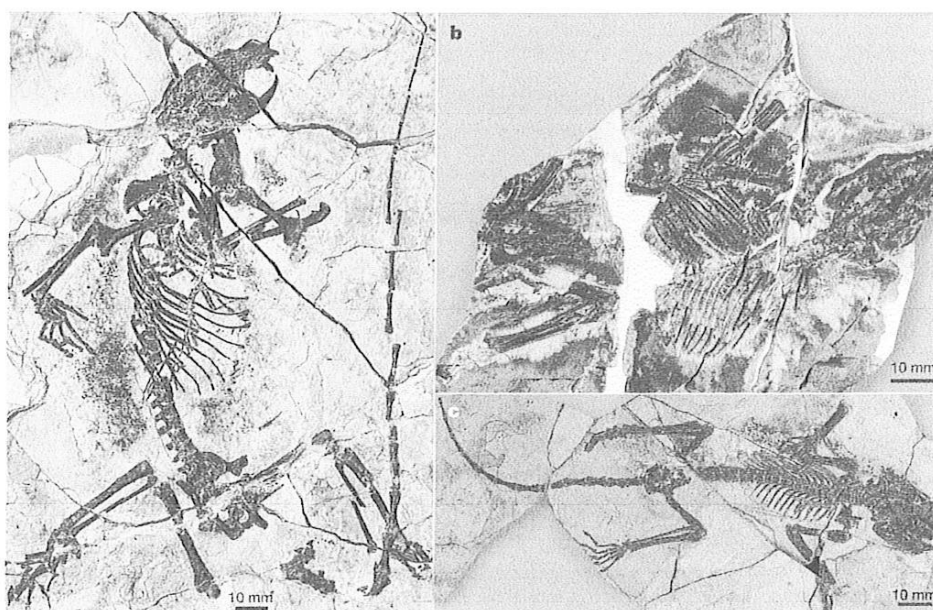


Figure 1 | The holotypes of three euharamiyidan species. **a**, Holotype (LDNHMF2001) of *Shenshou lui*. **b**, Holotype (IVPP V16707A) of *Xianshou linglong*. **c**, Holotype specimen (BMNHC-PM003253) of *Xianshou songae*. See Extended Data Fig. 1 for interpretations of the skeletal features.

Xianshou songae sp. nov. Meng, Guan, Wang, Bi and Sheng

Etymology. The specific name is after Rufeng Song, the collector of the holotype specimen.

Holotype. A skeleton preserved partial skull, mandible, and most of the postcranial skeleton (BMNHC-PM003253, Beijing Natural History Museum, China) (Figs 1c and 2f, and Extended Data Fig. 6).

Diagnosis. A small euharamiyidan with an estimated body mass of 40 g. Differ from *X. linglong* by having significantly smaller body size and in having P^4 more transversely oval, cusp A1 on P^4 and M^1 proportionally smaller and less distally extended. The lingual row of M^1 bears three cusps, of which the middle (B2) is the largest; lower molars anteroposteriorly short with a vertical hypertrophic mesiolingual cusp (a1) and low buccal cusps.

Craniodental features

The general skull shape of the new euharamiyidans is therian-like with a broad basicranial region and a tapered rostrum in dorsal and ventral views (Extended Data Figs 3 and 4) but multituberculate-like in lateral view (Fig. 2a, b). A small septomaxilla is probably present (Extended Data Fig. 2a). The zygomatic arch is slender but fully developed, with the anterior root lateral to P^4 . As reflected by the skull shape, the cranial cavity is more inflated than those of eutriconodontans. The glenoid fossa is anterolateral to the bulging promontorium of the petrosal and anteroposteriorly oriented, and lacks the postglenoid process (Extended Data Figs 4b and 5b). The dentary is similar to that of *Arboroharamiya*¹ and multituberculates in having a distinct diastema between the incisor and premolar, a small coronoid process, a masseteric fossa extending anteriorly to the level of P_4 and a low-positioned mandibular condyle that is

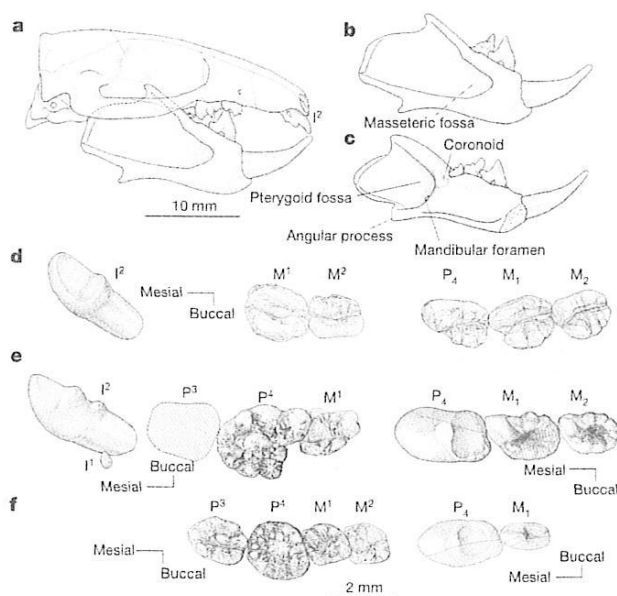


Figure 2 | Teeth, skull and mandibles of euharamiyidans. **a**, Reconstruction of the skull and jaws of *Xianshou linglong* (the small I^1 is on the medial side of the large I^2). **b**, The labial view of the lower jaw of *Xianshou linglong*. **c**, Lingual view of the lower jaw of *Xianshou linglong*. Part of the ascending ramus and coronoid bone have not been preserved and are reconstructed based on *Shenshou lui*. **d**, Right I^1 , I^2 , M^1 , M^2 , and left P_4 - M_2 of *Shenshou lui* in occlusal view. **e**, Left I^1 , I^2 , P^3 , P^4 , M^1 , and P_4 - M_2 of *Xianshou linglong* in occlusal view. Dashed lines represent the alveolus of P^3 . **f**, Right P^3 - M^2 , and P_4 and M_1 of *Xianshou songae* in occlusal view. See text for description of the skull and mandible. Dental formula are $I^{12}-C^0-P^2-M^2/I_1-C_0-P_2-M_2$ (the upper incisor is not preserved in this species). *Shenshou* and *Xianshou* have a multicusped I^2 and a greatly enlarged I_2 that is fully covered with enamel. There is no upper or lower canine. There are one lower and two upper premolars, and two upper and lower molars. Small enamel ridges (flutings) vary in size and density on cheek tooth cusps and basins. Upper premolars are broadly basined with main cusps located peripherally. Lower premolar has an enlarged a1, which is hypertrophic in *Xianshou* and *Arboroharamiya*¹, but there is no serration. Cusp A1 (distobuccal) of the upper premolar and molars is the largest and extends distally. Cusp a1 (mesiolingual) of the lower molars is the largest cusp, extending mesially. The lingual cusps of lower molars bear wear on their lingual sides, indicating that they bit into the central valley of the upper molars in mastication. Molars have a fusiform (spindle-shaped) basin that is closed mesially by a ridge in the upper molars and distally in the lower molars. The ridge can be erased owing to wear so that the central valley becomes confluent in *Shenshou*. Scale bars: **a**-**c**, 10 mm; **d**-**f**, 2 mm. Cusp terminology follows ref. 12. See photographs of teeth in Extended Data Figs 2, 4b, c, 5, 6 and 7a-c.

orientated ventrodorsally. A vestigial coronoid is present on the medial side of the jaw (Extended Data Fig. 2b), posteroventral to M_2 , similar to that of *Arboroharamiya* and the Jurassic multituberculata *Kuehneodon*². A reduced coronoid, usually indicated by a scar on the dentary, is also present in some more advanced mammals, such as *Amphitherium*³ and *Zhangheotherium*⁴. This is in contrast to sizable coronoids that cover the anterior portion of the postdentary unit in primitive mammaliaforms, such as *Morganucodon*⁵ and *Haldanodon*⁶. Unlike multituberculata but similar to *Arboroharamiya*, the dentary has a small angular process that inflects medially.

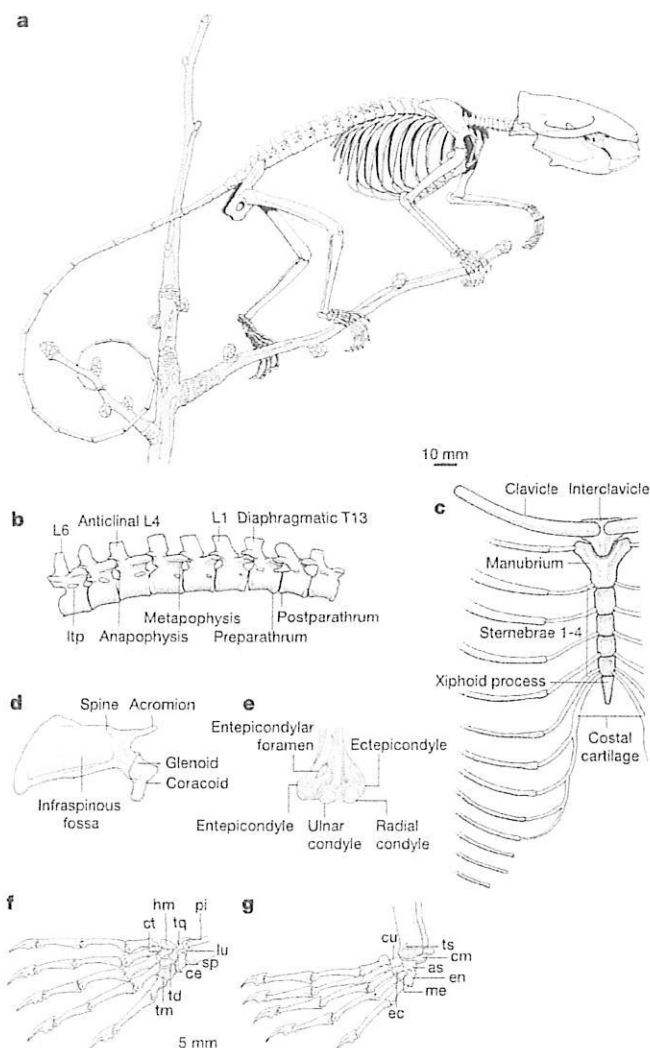
Dentitions are preserved *in situ* in the six specimens (Figs 1 and 2, and Extended Data Figs 1–7), confirming the tooth identification and orientation of *Arboroharamiya*¹ as well as reinterpretation¹ of some previously known euharamiyids^{7–10}. The cusp arrangement and morphology from *Haramiyavia*, *Thomasia*, *Arboroharamiya* and the new species reported here show consistently larger row A cusps (buccal) than row B cusps in upper molars, and larger row a cusps (lingual) than row b cusps in lower molars. In the lower cheek teeth, the mesiolingual cusp (a1) is the largest, whereas the distobuccal one (A1) is the largest in the upper teeth. The lingual lower cusp row bites into the central valley of the upper molars as indicated by wear facets in the upper and lower teeth (Extended Data Fig. 7a–c). These dental features and occlusal patterns should also be applicable to those known only from isolated teeth, such as *Eleutherodon* and *Sineleutherus*. It is also noteworthy that similar tooth cusp morphology and occlusal patterns are present in the upper and lower second molars of some Jurassic multituberculata¹¹, in which

the mesiolingual cusps are the tallest among cusps in the lower molar. The molars with two rows of multiple cusps and their wear patterns, coupled with the morphologies of the lower jaw and the glenoid fossa, convincingly indicate palinal jaw movement during mastication¹².

Postcranial skeleton

Although the vertebral column varies considerably in extant mammals, particularly those from the southern continents¹³, the general or primitive cervical and thoracolumbar counts for therian mammals are conservative¹⁴. The axial skeleton of the new euharamiyids is therian-like in possessing 7 cervical and 19 thoracolumbar vertebrae (13 thoracic and 6 lumbar; Fig. 3). In contrast to the docodontan *Castorocauda*¹⁵, the eutriconodont *Liaconodon* and *Yanoconodon*^{16,17}, and the symmetrodont *Akidolestes*¹⁸, which all have lumbar ribs, euharamiyids (including *Arboroharamiya*) have true lumbar vertebrae that lack ribs but have obliquely oriented facets of the prezygapophysis, elaboration of the transverse process, and the laminapophysis (a mammalian neomorph that split into the anterior metaphysis and posterior anapophysis)¹⁹ (Fig. 3b). These features define a distinct thoracolumbar boundary (Fig. 3a) and, along with fixation of cervical vertebrae²⁰ and well-developed ribcage, are indicative of development of the diaphragm, a unique feature that allows mammals to progressively increase ventilation in adapting to fast movement^{19,20}.

Figure 3 | Skeletal features of euharamiyids. a, Reconstruction of the skeleton of *Shenshou lui*, based in part on *Xianshou linglong* and *Xianshou songae*. b, The vertebral column of *Shenshou lui*. c, The anterior section of the rib cage in *Shenshou lui*. d, The right scapular of *Shenshou lui*. e, The distal end of the humerus in *Shenshou lui*. f, Reconstruction of the hand of *Shenshou lui*, based on LDNHMF2001 and WGMV-001. g, Reconstruction of the foot of euharamiyids, based on *Shenshou lui* (JZT-D061) and *Xianshou songae*. The cervical ribs, present in monotremes and many Mesozoic mammals^{4,17,20,24}, are absent. Similar to therians, such as *Eomaia*³² and *Sinodelphys*²⁷, the first ten thoracic ribs are connected to the ossified manubrium and sternum via costal cartilages and the last three ribs float freely. The capitulum of each rib articulates between two thoracic centra at a ventral position. The last thoracic rib (13th) is identified as the diaphragmatic vertebra because the articular facets of its zygapophyses with the first lumbar are more vertical than horizontal, as in many extant mammals⁴⁹. The anticlinal vertebra is located at lumbar four. The tail consists of 18–22 caudal vertebrae, with the proximal ones bearing expanded transverse processes as in extant prehensile therians⁵⁰. The scapular blade is roughly rectangular and has a large and deep infraspinous fossa but lacks a supraspinous fossa. The clavicle is strap-shaped and slightly curved anteriorly. Its rough proximal end indicates a flexible contact with the depression on the clover-leaf-shaped interclavicle. The distal end of the humerus has a bulbous radial condyle, a relatively smaller spherical ulna condyle, and a prominent entepicondyle. The femur has a hemispherical head with an extensive articular surface but a short neck, the greater trochanter is triangular and does not extend above the head. The distal condyles are small with a shallow patellar groove. The ankles are comparable to those of multituberculata, such as *Kryptobaatar*²⁴, in that the calcaneus has a short and mediolaterally compressed tuber calcanei and are partly superposed by the astragalus. The cuboid is positioned obliquely and has little contact with the calcaneus so that metatarsal V is separated from the calcaneus. The entocuneiform is elongated, and its joint with metatarsal I is offset anteriorly from the joint of the intermediate cuneiform and metatarsal II, similar to that of *Asioryctes* and *Eomaia*³². Metapodials and proximal phalanges possess a well-developed palmar groove for the digital flexor muscle tendon. Metatarsals I and V are short and robust compared to others. The distal ends of proximal and intermediate phalanges are well trochleated. Terminal phalanges are compressed laterally and curved strongly with a sharp tip; each has a massive digital flexor tubercle on the ventral side and a small dorsally extended ridge.



The scapula (Fig. 3d and Extended Data Fig. 7g) is primitively similar to that of *Megazostrodon*, *Haldanodon* and monotremes^{21,22} in that it lacks the supraspinous fossa, but differs from those taxa in that it has a reduced coracoid that is fused to the scapula and forms a small part of the glenoid fossa that faces ventrally. The clavicle (Fig. 3c) is similar to that of multituberculates²³. As in multituberculates the humerus has a slight shaft torsion (approximately 15°)²³, in contrast to a strong proximodistal torsion in cynodonts and other early mammals^{4,24}. The distal end of the humerus is highly comparable to that of multituberculates^{23,24} (Fig. 3e and Extended Data Fig. 7e). In the wrist, the hamate is hypertrophied and the scaphoid and triquetrum are enlarged, as in some extant arboreal marsupials^{25,26} and the scansorial *Sinodelphys*²⁷. Metacarpal V is offset from the hamate and the pisiform is sizable, similar to those of *Zhangheotherium*⁴ (Fig. 3g and Extended Data Fig. 8a).

The epipubic bone, a plesiomorphic feature common in several groups of Mesozoic mammals, including eutherians²⁸, is absent. The pelvis is similar to that of therians in being shallow and differs from the deep pelvis of multituberculates and monotremes in having a reduced pubis and an ischium with a straight dorsal margin and an ischial tuberosity that is slender and less extended dorsoposteriorly²⁴. The ilium is shorter than that of multituberculates. The femur has a short neck, similar to eutriconodonts^{16,29,30}, symmetrodonts^{4,18,31} and more primitive forms^{21,22}, but different from multituberculates, in which the femoral head has a long neck and the greater trochanter projects beyond the head²⁴. There is no parafovea, differing from *Eomaia* and *Jeholodens*^{30,32}. The proximal end of the tibia is roughly symmetrical, contrasting to that of multituberculates³³. The bony extratarsal spur is distinctive and displays different relative sizes in different species reported here. The spur or its os calcis exists in monotremes³⁴ and is common in Mesozoic mammals and their close relatives^{15,35}. As in *Arboroharamiya* and some extant arboreal didelphids and cheirogaleid primates¹, the manus and pes are characterized by relatively short metapodials and long phalanges (Fig. 3f, g and Extended Data Fig. 8). The limb features are collectively indicative of scansorial and/or arboreal adaptation^{1,26,32}.

Phylogenetic relationship

A major unsolved problem in mammalian taxonomy and phylogeny concerns Allotheria (Multituberculata and Haramiyida)^{9,12,33,36–39}, which affects how we view the early evolution of mammals. Most recent studies present contrasting hypotheses that either place allotherians in mammals¹, indicating an explosive model for the origin of mammals in the Late Triassic (approximately 208 million years ago) and a long-fuse model for the origin of therians, or separate them from multituberculates and place them outside mammals⁴⁰, suggesting an explosive model for the origin of the Mammalia in the Middle Jurassic epoch. In light of the new data reported here, we are able to revise characters used in previous studies^{1,11,40}, discuss existing problems relating to *Megaconus* (Supplementary Information, section E), the postdentary trough in 'haramiyidans' (now demonstrated to be a paraphyletic group) (Supplementary Information, section F) and *Hadrocodium* (Supplementary Information, section G) and conduct phylogenetic analyses including the new species (Supplementary Information, sections H–J). The result shown in Fig. 4 (see also Extended Data Fig. 9) is consistent with most recent phylogenetic analyses^{1,11,41,42}, which suggest that the 'haramiyidans' are related to multituberculates to form Allotheria within the Mammalia. This supports a Late Triassic origin of mammals¹. This hypothesis gains support from some Late Triassic 'symmetrodontans', such as *Kuehneotherium* and *Woutersia*, that are considered taxonomically to be members of the trechnotherian mammals^{33,43,44}. Our analyses also recognize a new clade, here named Euharamiyida, that pairs with Multituberculata; this is consistent with the view that previously discovered 'haramiyidans' seem to form a paraphyletic group, from which multituberculates were derived^{12,36,39}. Primitive species traditionally placed in 'haramiyidans', such as *Haramiyavia* and *Thomasia*, form the stem members of allotherians. This resultant topology remains the same whether *Megaconus* was included (Extended Data Fig. 10a) or both *Megaconus* and *Hadrocodium* were

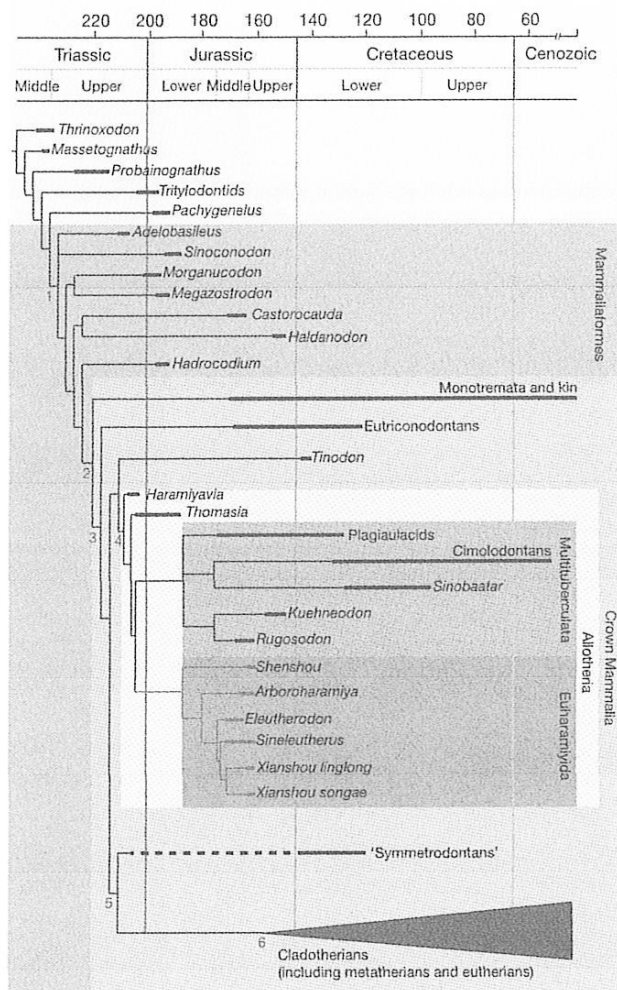


Figure 4 | Phylogeny of mammals with focus on Allotheria. This simplified cladogram is based on the consensus tree (Extended Data Fig. 9) computed from a data matrix with 113 taxa and 495 characters (see Supplementary Information). The dashed line of 'symmetrodontans' indicates occurrences of taxa that existed in the Late Triassic, such as *Kuehneotherium* and *Woutersia*^{33,43}, but are not included in our phylogenetic analyses because of their fragmentary preservation. Tree nodes represent the following clades: (1) Mammaliaformes; (2) Mammalia; (3) unnamed clade consisting of Eutriconodontata, Allotheria and Trechnotheria³³; (4) Allotheria; (5) Trechnotheria; and (6) Cladotheria. Mammaliaformes, Crown Mammalia, Allotheria, Multituberculata and Euharamiyida are also marked as nested colour blocks from the most to the least inclusive group.

excluded (Extended Data Fig. 10b) (see discussions in Supplementary Information, sections E and G).

Character evolution of early mammals

With the discoveries of the new euharamiyidans, it becomes increasingly evident that the cranial and postcranial features of euharamiyidans and multituberculates are similar to each other and to other mammals. However, the fundamental obstacle in interpreting their mammalian affinity remains the fact that the tooth pattern consists of two main rows of multiple cusps that are capable of longitudinal (palinal) chewing function in allotherians^{12,39,45}. If allotherians were placed outside mammals, it is equally difficult to derive the allotherian tooth pattern from other mammaliaformes, such as tritylodontids. Our phylogenetic analyses (Fig. 4) suggest that the primitive allotherian tooth pattern, as represented by *Haramiyavia*, was probably derived by developing an extra cusp row,

or rows, from a triconodont-like tooth pattern or even from a tooth pattern with an initially reversed triangular cusp arrangement. It was noted that in lateral view the teeth of *Haramiyavia* are more similar to those of *Sinoconodon* and *Morganucodon* than to those of multituberculates⁴⁶. We note, however, that the tooth pattern of *Haramiyavia* is also similar to that of *Woutersia*, which co-existed with *Therapsid*, another Late Triassic haramiyid^{36,43}. The tooth morphology and occlusion of euharamiyids indicate that, if the allotherian tooth pattern was derived from a triconodont tooth pattern, the secondary cusp row has to be added on the buccal side in the lower teeth. In the conventional view, however, development of extra cusps on the lingual cingula is common, but buccal cingula are rare on lower molars⁴⁵, although exceptions exist, such as *Hallautherium*⁴⁷. Nonetheless, the orientation of an isolated tooth in early mammals is not always certain, as demonstrated in the case of *Eleutherodontids*¹ (this study). There is no convincing evidence to rule out the possibility that additional cusps could be added on the buccal side of the tooth in early mammals. Better material with teeth *in situ* from each taxon of interest, such as *Woutersia*, is needed to test this hypothesis.

Interpretations of character evolution in early mammals depends on their phylogeny. If 'haramiyids' were separated from multituberculates and placed outside mammals, while multituberculates fell within mammals⁴⁰, then numerous similar craniodental and postcranial features, particularly the molar pattern with two cusp rows and bilateral occlusion, must have evolved independently in 'haramiyids' and multituberculates during different periods of time. In addition, detachment of the postdentary bones from the dentary would have evolved at least four times independently in 'haramiyids', multituberculates, monotremes and therians. However, our phylogeny (Fig. 4 and Extended Data Figs 9 and 10) indicates that Euharamiyida and Multituberculata were probably derived from a *Haramiyavia*-like common ancestor at a minimum oldest age (according to current fossil records; future finds may reveal an earlier ancestor) in the Late Triassic and diversified thereafter during the Jurassic epoch, with known euharamiyids adapting to a scansorial and/or arboreal lifestyle which may explain their rare fossil record. In contrast to interpreting numerous parallelisms in 'haramiyids' and multituberculates⁴⁰, our hypothesis favours homologous acquisition of many similar craniodental and postcranial features in euharamiyids and multituberculates, such as reduction of teeth, enlargement of the lower incisors, possessing only two molars in each side of the upper and lower jaws, and a palinal chewing motion. Moreover, euharamiyids are similar to multituberculates in lacking the postdentary trough and Meckelian groove, indicating the presence of the definitive mammalian middle ear³. If the reinterpretation is correct—that the dentary of *Haramiyavia* has only the Meckelian groove (see Supplementary Information, section F)—then the clade containing Eutriconodonta, Allotheria and Trechnotheria³³ (Fig. 4 and Extended Data Fig. 9) would have evolved from a common ancestor that had a transitional mammalian middle ear¹⁶. This clade and the geological and geographic occurrences of its earliest known members are consistent with accumulating evidence from Gondwana landmasses that shows a cosmopolitan distribution of members in the clade⁴⁸ and suggest a Laurasian origin of mammals. Finally, by reinterpreting *Hadrocodium* as having postdentary bones (see Supplementary Information, section G), our phylogeny suggests that detachment of the postdentary bones evolved twice independently during the early evolution of mammals, once in the clade leading to monotremes and once towards the clade containing Eutriconodonta, Allotheria and Trechnotheria.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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