

in lateral view and lacking serrations; the lower molar having a greatly inflated mesiolingual cusp (a1) and a central basin mesiodistally elongate and deeper distally than mesially; the upper dentition having at least a multi-cusped incisor, probably two premolars and two molars; the distobuccal cusp (A1) the largest in the upper molars; the deep mandible lacking the postdentary trough and Meckelian groove but having a small angular process, a small coronoid process and a mandibular condyle that levels with the tooth row and is dorsoventrally oriented; limbs slim with proportionally short metapodials but long phalanges (Supplementary Information).

Arboroharamiya, as with other mammals, has body hair (preserved as impressions), a single-boned (dentary) mandible that implies a three-boned middle ear, and the digit formula of 2-3-3-3-3. The dentition is differentiated into incisors and multi-rooted premolars and molars, with the canine presumably lost. It differs from other mammals but is similar to allotherians in having two mesiodistally aligned rows of cusps that allow orthal (vertical) and palinal (backward), but not proal (forward) or transverse, jaw movement in mastication.

Arboroharamiya is also similar to other haramiyids in having basined molars with cusps of uneven heights, but differs from them in being larger and having a more inflated a1 and elongate central basin surrounded by more cusps in lower molars. *Arboroharamiya* further resembles multituberculates in having one pair of enlarged lower incisors, a multi-cusped upper incisor, loss of the canine, two upper and lower molars, and the mandibular with a mesially extended masseteric fossa and a condyle positioned low and oriented more vertically than transversely. It differs from the Jurassic multituberculates in having a small angular process and a highly specialized dentition with one lower premolar and two upper premolars and with an occlusal pattern in which the enlarged a1 bites into the basin of the upper molar.

Previously, the only known haramiyid with the mandible and dentition preserved was *Haramiyavia*¹⁰, which was thought to resemble *Morganucodon* and *Kuehneotherium* in having the masseteric fossa un-extended beyond the posterior part of the last molar, the condyle above the level of the teeth, and presence of the postdentary trough^{2,5}. Although *Arboroharamiya* is similar to *Haramiyavia* in having a1 as the largest cusp and the lower molar basin deeper distally than mesially and possessing a gracile postcranial skeleton, it is morphologically more advanced than *Haramiyavia* in lacking the canine and having fewer incisors, premolars and molars. Most importantly, the dentary of *Arboroharamiya* is highly specialized and considerably different from that of *Haramiyavia*, but similar to those of derived multituberculates such as taeniolabidids, in being short and deep and in lacking the postdentary trough, which is one of the characteristics previously used to differentiate haramiyids from multituberculates^{2,5,10}.

Assignment of tooth locus and thus identification of species for most haramiyids are ambiguous because only isolated teeth are preserved¹⁻⁵. The discovery of *Haramiyavia*¹⁰ helped to solve part of the puzzle. However, because the upper premolars of *Haramiyavia* are not preserved, the difference of the upper premolar and molar of haramiyids remains unclear. In light of the new findings from *Arboroharamiya* (Fig. 2 and Supplementary Fig. 3), some haramiyid teeth identified as upper molars^{4,11} are most likely premolars. Similarly, the largest cusp identified as b2 (mesiobuccal) in the lower molar of elutherodontid haramiyids^{2,11-13} is probably a1, and, if so, it would result in a different interpretation of the occlusal pattern in those haramiyids.

The occlusal pattern is a critical feature that was used not only to identify tooth locus and species within haramiyids^{2,4,5}, but more importantly to distinguish Allotheria from other Jurassic mammals that have transverse jaw movement during mastication¹⁴. In Allotheria, the upper and lower molariform teeth have essentially two longitudinal rows of cusps, and the buccal row of the lower molar was considered to bite into the valley between the two rows of the upper molar, involving orthal and/or palinal jaw movement²⁻⁴. The tooth morphology and wear pattern of *Arboroharamiya* confirm the orthal and palinal jaw movements in haramiyids, but nonetheless demonstrate that it is impossible

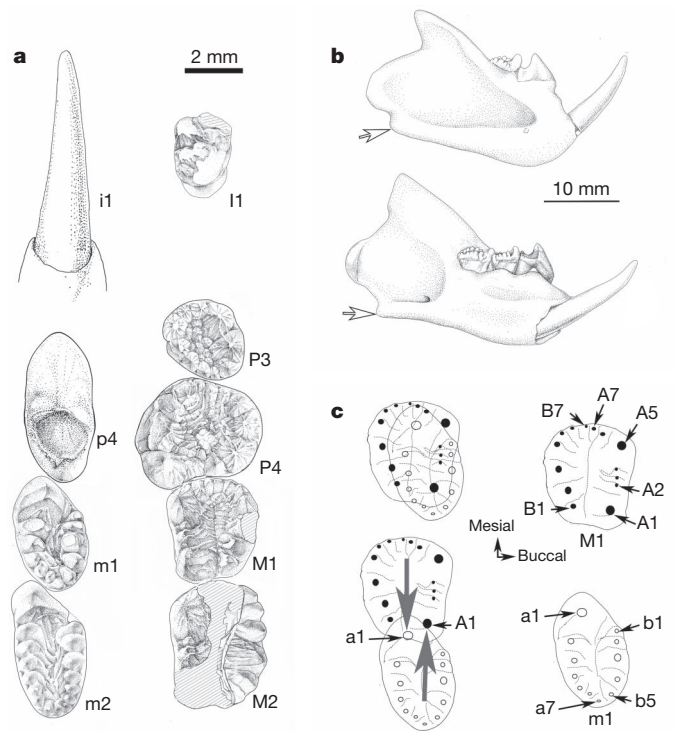


Figure 2 | Teeth, mandibles and tooth occlusal relationships of *Arboroharamiya jenkinsi*. **a**, Occlusal views of right upper and lower incisors (l/i), premolars (P/p) and molars (M/m). Some of the teeth (Supplementary Fig. 3) have been photographically flipped in the stippling drawings. The general shape of p4 is similar to that of *Kermackodon*, one of the earliest known multituberculates⁴, but differs from it in lacking serrations. m1 and m2 are similar in having a high and inflated cusp a1 with cusps decreasing height distally. The distal end of the central basin is closed by cusps. Enamel ridges extend distally from cusps towards the basin, which enhance grinding as A1 of the upper molar ‘moves’ in the valley. The upper premolar differs from molars in being more rounded, with the broad central basin bearing numerous small cusps or crenulations. Upper molars are more mesiodistally elongate and have cusps A1 and A5 the largest and ridges extending mesially. Cusp B3 is the largest in cusp B-row. **b**, Buccal (top) and lingual (bottom) views of the mandible show the anterior extension of the masseteric fossa to the level below p4 and lack of the postdentary trough (Supplementary Fig. 2). The empty arrows point to the angular process. **c**, Line drawings illustrate the cusp numbering of M1 and m1 (right column) following ref. 2 and their relationship in occlusion (upper left). Grey arrows show the relative movements of a1 of m1 and A1 of M1 (bottom left). Tooth identification, measurements and photographs in Supplementary Information.

for the buccal row of the lower molar to bite into the valley of the upper molars. This is because the tall and inflated a1 at the longitudinal axis of m1 and the distally closed central basin in lower molars prevent such an occlusion. The cusp shape and arrangement, wear pattern and occlusal match of M1 and m1 show that, during mastication, a1 of the lower molar must have bit orthally in the basin of the upper molar in the puncture-crushing cycle and then moved palinally within the basin in a grinding cycle (Fig. 2 and Supplementary Figs 3–6). In a reversed symmetry, A1 of the upper molar bit into the central basin of the lower molar and ‘moves’ mesially in the valley of the lower molar. This ‘double engaged’ occlusion prevents both proal and transverse chewing motion; it creates wear in the tooth basin at the distal V-notch and on the buccal side of A1–3, but not the lingual side of M1. It also creates wear on the lingual and buccal sides of a1 in lower molars. This occlusal pattern is unique among mammals and differs from what has been interpreted for both haramiyids and multituberculates^{2,4,10}. The tooth morphology and occlusal pattern suggest that *Arboroharamiya* is probably either granivorous, as proposed for some haramiyids⁴, or omnivorous, as in multituberculates³.

Postcranial features of *Arboroharamiya* show adaptation for an arboreal life. The femur head is not spherical but cylindrical, a derived feature present in omomyines and tarsiers¹⁵. *Arboroharamiya* has relatively short metapodials but long phalanges (Fig. 1 and Supplementary Fig. 7), unique among early Mesozoic mammals but characteristic of animals with prehensile hands and feet for arboreal life, such as arboreal didelphids and cheirogaleid primates¹⁶ (Fig. 3). Even among arboreal mammals *Arboroharamiya* is distinctive in that both manual and pedal phalangeal indices, estimates for degree of prehensility of the hand-foot¹⁷, are clearly higher than those of extant species^{16,18} and extinct scansorial/arboreal species, such as *Eomaia* and *Sinodelphys* (Supplementary Figs 9 and 10). Moreover, the proximal caudal region is relatively long and bears expanded transverse processes. The transitional and longest caudal vertebrae are more distally positioned than those in nonprehensile taxa. These features are functionally related to the hypertrophy of the basal musculature necessary for increased gripping strength indicative of prehensile ability, as in some extant arboreal species^{19,20}. The postcranial morphologies of *Arboroharamiya* suggest a gracile body for arboreal habitat preference.

The phylogenetic relationship of Allotheria remains controversial. It was presumed that haramiyids and multituberculates were not closely related¹⁰, or they formed a clade in which multituberculates are derived

from haramiyids, with the latter being paraphyletic^{2,5,21}. Because of their unique dentition and early occurrences, allotherians were also considered to originate early from other mammals, even before mammaliaformes in the Triassic^{2,4,5,22}. Our phylogenetic analysis supports the view that allotherians form a subgroup of the crown Mammalia^{3,23,24} and that multituberculates are derived from haramiyids^{2,5,21} (Fig. 4). Because *Haramiyavia*¹⁰ and several other haramiyids^{5,10} are from the Upper Triassic (the Norian–Rhaetic), the age for the origin of crown mammals would be in the time range of 228–201.3 Myr²⁵, younger than that estimated in ref. 7 but older than those in other studies^{6,8}. With the ecological diversification recognized in early mammals²⁶, our phylogeny further implies that all major clades and feeding adaptations of mammals had diversified during the Jurassic, coincident with inferred diversifications of major lineages of insects^{27,28} and angiosperms^{29,30}.

Owing to the fragmentary nature of most haramiyids, a thorough phylogenetic analysis of Allotheria remains impractical. However, *Arboroharamiya* demonstrates convincingly that haramiyids had become highly specialized in the Jurassic. It displays several mammalian features and fills some morphological gaps between *Haramiyavia* and multituberculates. Although morphological characteristics support allotherians as a clade, *Arboroharamiya* shows again that homoplasy is a common phenomenon within Mesozoic mammals¹. Some features of *Arboroharamiya*, such as the reduced dentition—shared with advanced multituberculates—and elongated digits—shared with more advanced arboreal mammals—must be convergences. On the other hand, the dentition with multiple

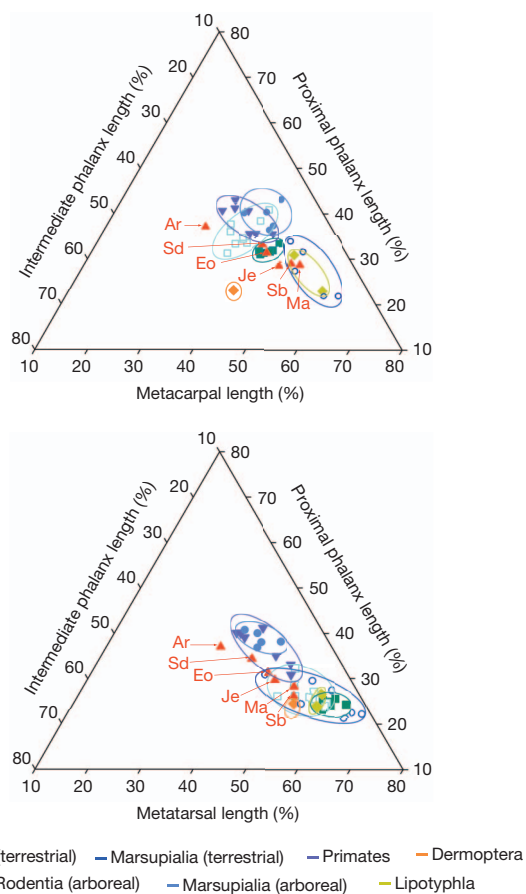


Figure 3 | Ternary diagrams showing intrinsic manual and pedal ray III proportions. Ternary plots showing relative metapodial, proximal and intermediate phalangeal lengths for the third digit ray of the hand and foot. The lengths of the third metapodial, proximal phalanx and intermediate phalanx are shown on their respective axes as a percentage of the combined length of the three segments. Compared to both fossil and extant taxa, *Arboroharamiya jenkinsi* has the intrinsic manual and pedal ray proportions typical of arboreal species in which the proximal and intermediate phalanges are long in respect to the metapodials (Fig. 1 and Supplementary Fig. 7). Abbreviations: Ar, *A. jenkinsi*; Eo, *Eomaia scansoria*; Je, *Jeholodens jenkinsi*; Ma, *Maothierium sinensis*; Sb, *Sinobaatar lingyuanensis*; Sd, *Sinodelphys szalayi*. Measurements and methods in part F of Supplementary Information.

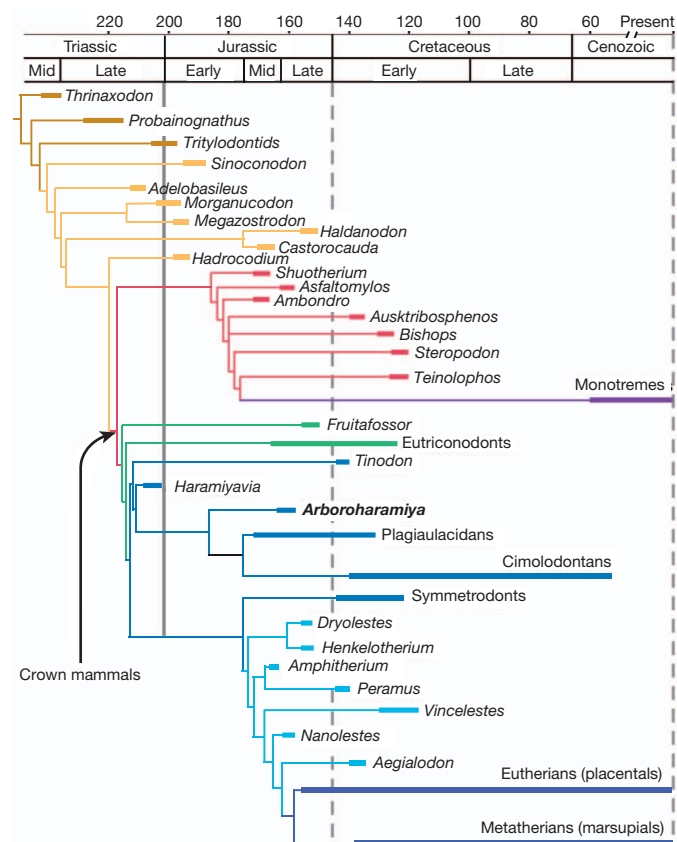


Figure 4 | Relationship of *Arboroharamiya* and geological distributions of major groups of Mesozoic mammals and their relatives. Thin lines represent the phylogenetic relationships and thick lines indicate geological distributions of the taxa. This is a simplified consensus tree (Supplementary Fig. 11) of 12 equally most parsimonious trees of PAUP (Phylogenetic Analysis Using Parsimony and Other Methods, version 4.0b), an analysis of 436 characters and 56 taxa with a focus on Mesozoic non-therian groups (modified from ref. 23; parts G–I in Supplementary Information). Test analyses for alternative hypotheses are in part J of Supplementary Information.

premolars in Jurassic multituberculates has to be considered as reversed from the condition of *Haramiyavia*. Regardless of various phylogenetic scenarios involving allotherians^{2–5,10,21–24}, morphological convergences and/or reversals were common in the early stage of mammalian evolution.

METHODS SUMMARY

Phylogenetic analyses were based on a data matrix consisting of 436 characters and 56 taxa (Supplementary Information), of which 389 characters are parsimony-informative, and were carried out with PAUP (version 4.0b). All characters were unordered and equally weighted, with gaps being treated as 'missing' and multi-state taxa interpreted as polymorphism. Character-states optimized as accelerated transformation (ACCTRAN).

Postcranial elements were measured using a digital caliper from 26 arboreal and non-arboreal extant mammals, except for *Caluromys*. Measurements for *Caluromys* and fossils, except for *Arboroharamiya*, were obtained from the literature. We estimated body mass using dimensions of the first lower molar, and conducted additional estimates based on the ulna, femur and tibia lengths, respectively. Full methods for body mass estimates, digit ray analyses and phylogenetic analyses are provided in Supplementary Information.

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- Sigogneau-Russell, D. Haramiyidae (Mammalia, Allotheria) en provenance du Trias supérieur de Lorraine (France). *Palaeontographica A* **206**, 137–198 (1989).
- Butler, P. M. Review of the early allotherian mammals. *Acta Palaeontol. Pol.* **45**, 317–342 (2000).
- Kielan-Jaworowska, Z., Cifelli, R. & Luo, Z.-X. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure* (Columbia Univ. Press, 2004).
- Butler, P. M. & Hooker, J. J. New teeth of allotherian mammals from the English Bathonian, including the earliest multituberculates. *Acta Palaeontol. Pol.* **50**, 185–207 (2005).
- Hahn, G. & Hahn, R. Evolutionary tendencies and systematic arrangement in the Haramiyida (Mammalia). *Geol. Palaeontol.* **40**, 173–193 (2006).
- Bininda-Emonds, O. R. *et al.* The delayed rise of present-day mammals. *Nature* **446**, 507–512 (2007).
- Meredith, R. W. *et al.* Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on mammal diversification. *Science* **334**, 521–524 (2011).
- O'Leary, M. A. *et al.* The placental mammal ancestor and the post-KPg radiation of placentals. *Science* **339**, 662–667 (2013).
- Sullivan, C. *et al.* The Vertebrates of the Jurassic Daohugou Biota of Northeastern China. *J. Vertebr. Paleontol.* (in the press).
- Jenkins, F. A., Gatesy, S. M., Shubin, N. H. & Amaral, W. W. Haramiyids and Triassic mammalian evolution. *Nature* **385**, 715–718 (1997).
- Averianov, A. O., Lopatin, A. & Krasnolutskii, S. The First Haramiyid (Mammalia, Allotheria) from the Jurassic of Russia. *Dokl. Biol. Sci.* **437**, 103–106 (2011).
- Kermack, K. A., Kermack, D. M., Lees, P. M. & Mills, J. R. New multituberculate-like teeth from the Middle Jurassic of England. *Acta Palaeontol. Pol.* **43**, 581–606 (1998).
- Martin, T., Averianov, A. O. & Pfretzschner, H. U. Mammals from the Late Jurassic Qigu Formation in the southern Junggar Basin, Xinjiang, Northwest China. *Palaeobiodivers. Palaeoenvir.* **90**, 295–319 (2010).
- Crompton, A. & Thomason, J. In *Functional Morphology in Vertebrate Paleontology* (ed. Thomason, J. J.) 55–75 (Cambridge Univ. Press, 1995).
- Dagosto, M. & Schmid, P. Proximal femoral anatomy of omomyiform primates. *J. Hum. Evol.* **30**, 29–56 (1996).
- Lemelin, P. Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. *J. Zool.* **247**, 165–175 (1999).
- Napier, J. *Hands* Ch. 2 26 (Princeton Univ. Press, 1993).
- 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).
- Schmitt, D., Rose, M. D., Turnquist, J. E. & Lemelin, P. Role of the prehensile tail during ateline locomotion: experimental and osteological evidence. *Am. J. Phys. Anthropol.* **126**, 435–446 (2005).
- Youlatos, D. Osteological correlates of tail prehensility in carnivores. *J. Zool.* **259**, 423–430 (2003).
- Hahn, G., Sigogneau-Russell, D. & Wouters, G. New data on Theroteinidae: their relations with Paulchoffatiidae and Haramiyidae. *Geol. Palaeontol.* **23**, 205–215 (1989).
- Simpson, G. G. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**, 1–350 (1945).
- Luo, Z.-X., Chen, P.-J., Li, G. & Chen, M. A new eutriconodont mammal and evolutionary development in early mammals. *Nature* **446**, 288–293 (2007).
- Rowe, T., Rich, T. H., Vickers-Rich, P., Springer, M. & Woodburne, M. O. The oldest platypus and its bearing on divergence timing of the platypus and echidna clades. *Proc. Natl Acad. Sci. USA* **105**, 1238–1242 (2008).
- Ogg, J. G. in *A Geological Time Scale 2012* (eds Gradstein, F. M., Ogg, J. G., Schmitz, M. D. & Ogg, G. M.) 681–730 (Elsevier, 2012).
- Luo, Z.-X. Transformation and diversification in early mammal evolution. *Nature* **450**, 1011–1019 (2007).
- Hunt, T. *et al.* A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* **318**, 1913–1916 (2007).
- Wiegmann, B. M. *et al.* Episodic radiations in the fly tree of life. *Proc. Natl Acad. Sci. USA* **108**, 5690–5695 (2011).
- Magallón, S. A. & Sanderson, M. J. Angiosperm divergence times: the effect of genes, codon positions, and time constraints. *Evolution* **59**, 1653–1670 (2005).
- Smith, S. A., Beaulieu, J. M. & Donoghue, M. J. An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. *Proc. Natl Acad. Sci. USA* **107**, 5897–5902 (2010).

Supplementary Information is available in the online version of the paper.

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