

The oldest known primate skeleton and early haplorhine evolution

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Reconstructing the earliest phases of primate evolution has been impeded by gaps in the fossil record, so that disagreements persist regarding the palaeobiology and phylogenetic relationships of the earliest primates. Here we report the discovery of a nearly complete and partly articulated skeleton of a primitive haplorhine primate from the early Eocene of China, about 55 million years ago, the oldest fossil primate of this quality ever recovered. Coupled with detailed morphological examination using propagation phase contrast X-ray synchrotron microtomography, our phylogenetic analysis based on total available evidence indicates that this fossil is the most basal known member of the tarsiiform clade. In addition to providing further support for an early dichotomy between the strepsirrhine and haplorhine clades, this new primate further constrains the age of divergence between tarsiiforms and anthropoids. It also strengthens the hypothesis that the earliest primates were probably diurnal, arboreal and primarily insectivorous mammals the size of modern pygmy mouse lemurs.

Primates Linnaeus, 1758
Haplorhini Pocock, 1918
Tarsiiformes Gregory, 1915
Archicebidae fam. nov.
Archicebus achilles gen. et sp. nov.

Etymology. Generic name is derived from arche, Greek for beginning, and cebus, new Latin from Greek, for long-tailed monkey. Specific epithet is from Achilles, in allusion to the very interesting anthropoid-like heel bone (calcaneus) of the type species.

Holotype. IVPP V18618, a partial skeleton preserved as part and counterpart (Fig. 1 and Supplementary Information).

Locality and horizon. The lower part of the lower Eocene Yangxi Formation in Jingzhou area, Hubei Province, China. Bumbanian Asian Land Mammal Age, 55.8–54.8 million years (Myr) ago¹.

Diagnosis. Small haplorhine primate with rounded braincase; short snout; vertically implanted upper canine (C¹); four premolars in each jaw quadrant; long hindlimbs; long feet (especially the metatarsus); and a long tail. Among other basal primates, differs from *Donrussellia*, *Marcgodinotius* and *Asiadapis* in having a single-rooted lower second premolar (P₂), and differs from *Teilhardina belgica*, '*Teilhardina americana*' and '*Teilhardina brandti*' in having a less-reduced P₁. Further differs from *T. belgica* in having relatively shorter and broader distal calcaneus and smaller peroneal tubercle on the first metatarsal. Further differs from '*T. americana*' and '*T. brandti*' in having weaker cingulum and cingulid on upper and lower molars and lacking the *Nannopithecus*-fold. Differs from *Teilhardina asiatica* in having a weaker P₄ metaconid, lower-crowned P₃₋₄, and a more prominent, hook-like mandibular angular process. Differs from *Teilhardina magnoliana* in having stronger mesial and distal cingula on the upper molars and a shorter talonid on P₄.

Description

This new early Eocene primate is a very small animal, with slender limbs and a long tail. The trunk is about 71 mm, the tail is more than 130 mm, and the skull is approximately 25 mm long and 17 mm wide.

Skull

The general shape of the skull is similar to that of *Teilhardina asiatica* and *Tetonius homunculus* (Fig. 2). A postorbital bar is present, but no postorbital septum. Relative to skull length, orbital diameter (7 mm) resembles that of *T. asiatica*², being proportionally smaller than those of most other tarsiiforms, and falling within the range of variation exhibited by extant diurnal primates³ (Supplementary Information). As in other primates, the orbits are significantly convergent. The nasal fossa shows substantial reduction relative to the condition in outgroups. Preorbital snout length (4.7 mm) is short, as in *Tarsius*, *Tetonius*, *Shoshonius* and most anthropoids; in contrast, *Omomys*, *Necrolemur* and most strepsirrhines retain proportionally longer snouts. The left and right upper dental arcades are gently divergent, resembling those of *T. asiatica* and *Rooneyia*. *Tarsius*, *Necrolemur*, *Shoshonius* and other more anatomically derived tarsiiforms have bell-shaped palates, due to the combination of orbital hypertrophy and snout reduction⁴. The dentary is gracile, with a shallow, procumbent and unfused symphysis. The gonial part of the dentary bears a long, hook-like angular process with a very strong pterygoid crest on its medial side.

Dentition

The dentition of *A. achilles* shows a very primitive morphology (Fig. 2), being comparable to that of other phylogenetically basal primates such as *Teilhardina*, *Donrussellia*, *Marcgodinotius* and *Asiadapis*. An isolated lower central incisor, bearing a mesiodistally compressed root and labiolingually compressed (spatulate) and symmetrical crown, is associated with this specimen. C¹ has a vertically implanted root. Its crown projects well below the occlusal plane of the molars. C₁ is not preserved, but its alveolus indicates that this tooth is unreduced. As in other basal primates, there are four premolars in each upper and lower jaw quadrant. P¹⁻² are small, single-cusped and single-rooted teeth. The alveoli for P₁₋₂ suggest that they are small, single-rooted and probably as simple as their upper counterparts. P² and P₂ are present in basal tarsiiforms and anthropoids, in which they

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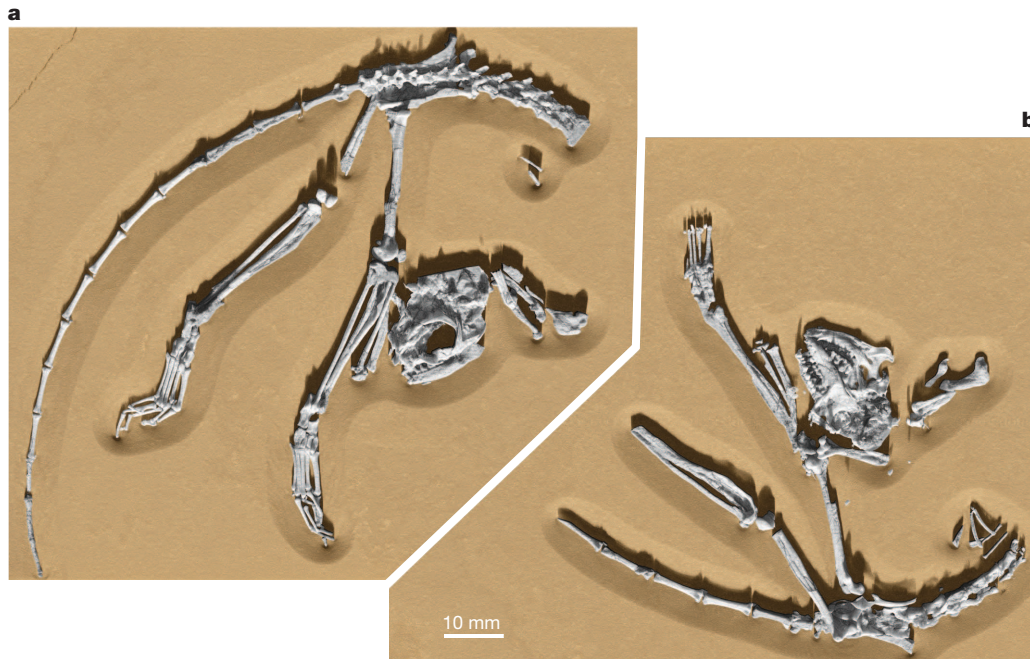


Figure 1 | Three-dimensional reconstruction of the type specimen (IVPP V18618) of *Archicebus achilles*. **a**, Slab-a, dorsal view of the skull, lumbar region and pelvis, laterodorsal view of the tail, posterior view of the left thigh, medial view of the left leg, plantar view of the left foot, lateral view of the right thigh, lateral view of the right leg, and dorsal view of the right foot. **b**, Slab-b, ventral view of the skull, lumbar region and pelvis, anterolateral view of the left

thigh, and posteromedial view of the right thigh. Fossil bones are shown in light grey. Digital casts reconstructed from the preserved impressions are shown in darker grey than the actual bones. The bones yielding the impressions are either preserved on the counterpart or were lost during collection and/or preparation of the specimen.

are small, simple and usually single rooted^{2,5–8}. In contrast, these teeth in haplorhine outgroups such as basal adapiforms are double rooted and only slightly smaller than P³ and P₃ (refs 9–11). P^{3–4} of *A. achilles*

resemble those of *Teilhardina*. The paracones of these teeth are high and sharp, with rounded mesial borders and well-developed distal crests. The protocones of P^{3–4} are large, but mesiodistally shorter than

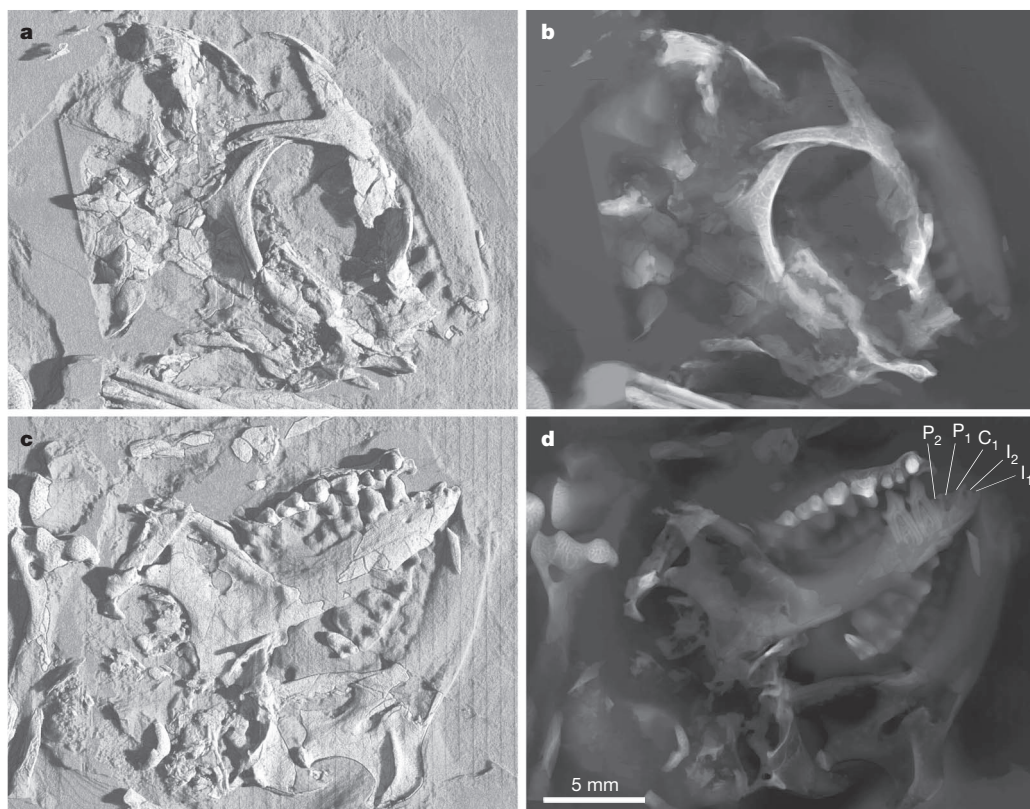


Figure 2 | The head region of *Archicebus achilles*. **a**, Dorsal view of the skull. **b**, Pseudo-radiograph rendering of the dorsal view of the skull. **c**, Ventral view of the skull, lingual view of the left mandible and lateral view of right mandible.

d, Pseudo-radiograph rendering of the ventral view of the skull, lingual view of the left mandible and lateral view of right mandible.

those of *T. asiatica* and *T. belgica*. The trigonids of P_{3-4} bear a single major cusp, and their talonids are short and heel-like. The paraconids of P_{3-4} are low and weak. The metaconid is absent in P_3 and only weakly developed in P_4 , as in *T. magnoliana* and '*Teilhardina brandti*'^{5,12}. The upper molars closely resemble those of *Teilhardina* and other basal tarsiiforms. The distal borders of M^{1-2} are concave, their conules are large, and M^3 is small relative to M^{1-2} . M^{1-2} lack any development of a postprotocingulum or *Nannopithecus*-fold, in contrast to the condition in *Tetonius*, '*T. americana*' and most other anaptomorphine omomyids, being more similar to *T. asiatica* and *T. belgica* in this regard.

Trunk and tail

Only the lumbar region of the trunk is well preserved, showing at least six or possibly seven lumbar vertebrae. The caudal region preserves 18 vertebrae. Considering the gradual reduction of caudal vertebral lengths distally, this new primate may have had over 30 caudal vertebrae in life, making its tail exceedingly long relative to head and trunk length.

Forelimb

The scapula possesses a glenoid fossa that is tear-shaped, and a long coracoid process that almost exceeds the craniocaudal length of the glenoid fossa. The humerus (15.7 mm) is relatively short. The humeral head is oval, projecting slightly above the lesser and greater tuberosities, which are separated by a broad and shallow bicapital groove. This morphology resembles other Palaeogene primates¹³⁻¹⁶. The elbow joint bears a rounded capitulum clearly distinguished from the trochlear joint surface by the zona conoidea, a key feature of primates. A significant capitular tail extends laterally from the capitulum. The trochlea is oblique with a 'downturned' medial rim, a typical feature among early haplorhine primates^{14,17}. In distal view, the distal articular surface is 'waisted', as in anthropoids¹⁶⁻¹⁸. A dorsoepitrochlear fossa is present. This feature is absent in tarsiers but shared by omomyiforms and most basal anthropoids^{16,19}. The entepicondylar foramen is large and located above the medial part of the trochlea, a primitive condition for primates.

The ulna has a short olecranon process, a strong and straight shaft, and a narrow distal end, whereas the radial head has a wide articular circumference and a long and angled radial neck. Relative to the humerus, radial length (estimated as 16.0 mm, brachial index

approximately 102) is unremarkable, except to demonstrate that *A. achilles* does not exhibit the relatively long radius of *Tarsius*. Only impressions of the carpals are preserved. As in other haplorhines, the hamate has a mediolaterally oriented spiral facet for the triquetrum.

Hindlimb

The hindlimbs are almost completely preserved (Figs 1, 3). The ilia are long and narrow, with slightly concave gluteal surfaces. This pelvic shape resembles omomyids, tarsiers and some extant strepsirrhines, but differs from the broader bladed ilia of anthropoids, adapiforms, lemurids and indriids^{16,20-23}. The two iliac crests are slightly divergent and extend cranially over the sacral wing for a short distance. A large inferior iliac spine lies on the cranial side of the acetabulum. The ischium is long, straight and stout, being caudally directed with no significant dorsal projection.

The thigh and lower leg (femur, 27.0 mm; tibia, 30.1 mm; fibula, 29.1 mm) are very long relative to the arm and forearm. The intermembral index (IMI; 55) is equivalent to that of the most specialized extant vertical clinging and leaping primates (for example, tarsiers and galagos), and lower than estimated for *Shoshonius*¹⁴.

The femur is slender, and the femoral head is semi-cylindrical with the proximal articular surface extending onto the femoral neck as in omomyids and extant vertical clinging and leaping primates^{13,14,22}. A large fovea capitis femoris occurs on the medial side of the femoral head. The femoral neck is moderately long (3.7 mm) and forms an angle of 49.7° relative to the femoral shaft. The broad greater trochanter extends above the femoral head. Its lateral border is thick, flaring laterally and being confluent with a triangular-shaped third trochanter distally. The trochanteric fossa is moderately long. The lesser trochanter extends posteromedially and forms an angle of 40.6° relative to the femoral shaft. The proximal part of the femoral shaft is not as anteriorly bowed as in omomyids or microchoerids, resembling anthropoids instead. Distal to the third trochanter, the femoral shaft is straight and robust. The knee is quite tall, with an elevated lateral patellar rim and a long and broad patellar articular facet, additional similarities to frequently leaping primates.

The tibia is quite straight and lacks the marked S-shaped curvature observed in *Shoshonius*¹⁴. The cnemial crest is strong and long, extending distally over half of the total tibial length. The intercondylar eminence of the tibial plateau has two spines, a haplorhine feature²⁴. The crural index (109–113) closely resembles those of leaper-quadrupeds

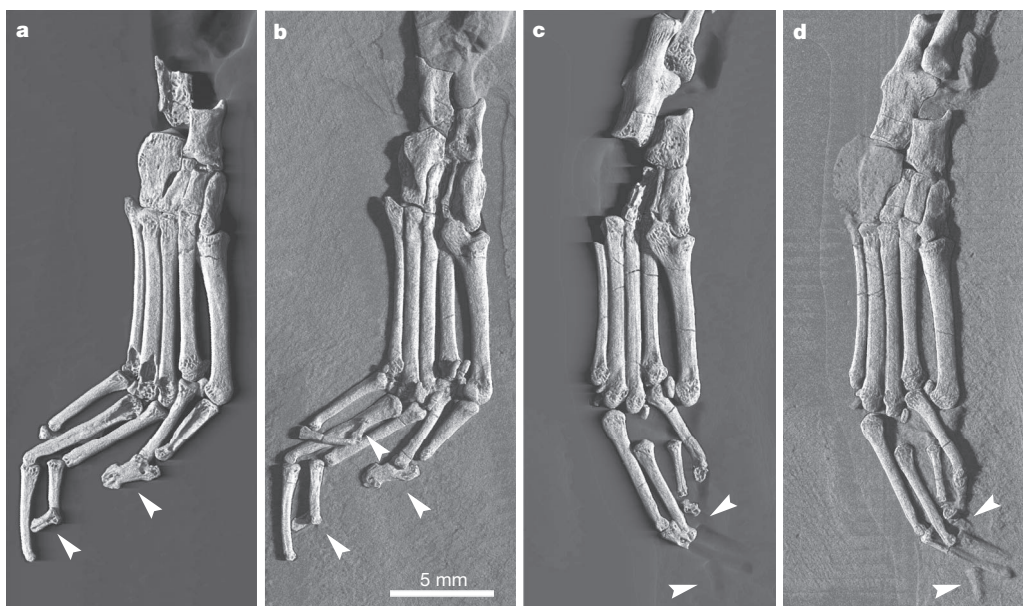


Figure 3 | The foot region of *Archicebus achilles*. **a**, Dorsal view of the left foot (reversed). **b**, Plantar view of the left foot. **c**, Plantar view of the right foot

(reversed). **d**, Dorsal view of the right foot. Arrowheads indicate the scutiform distal phalanges of the big, second, third and fifth toes.

such as *Galagoides* and *Microcebus*, but is higher than that of small vertical clinging and leaping primates¹⁴. The fibula is straight, robust and closely apposed to the tibia for ~36% of the length of the distal shaft. The tibia and fibula are unfused and lack any prominent tibio-fibular scar, in contrast to omomyids. The distal tibia and fibula exhibit a standard haplorhine tibio-fibular mortise, the likely primitive condition for primates. The tibial malleolus is shortened and slightly angled posteriorly, being similar to haplorhines, and in sharp contrast to strepsirrhine primates²⁵.

The foot (Fig. 3, estimated at 33.5 mm long, from the calcaneal tuber to the tip of the fourth digit) is 36.6% of total hindlimb length, a similarity to primates with particularly long metatarsals (for example, callitrichid platyrrhines) but also to primates with a long tarsal region (for example, galagos and tarsiers)²⁶. Relative to body mass, *A. achilles* has a moderately short tarsus, closely similar to those of extant anthropoids; a very long metatarsus, comparable to anthropoids and tupaiids (and different from lemuriforms, adapiforms, or *Tarsius*); and a long phalangeal region, most similar to *Tarsius* (Supplementary Information). This combination of foot proportions is unique among living and fossil primates and their nearest relatives.

The width to length ratio of the calcaneus is 40.2%, a value very close to eosimiids, but higher than other tarsiiforms and lower than platyrrhines and strepsirrhines^{14,22,27–30}. The middle and distal parts of the calcaneus are proportionally wide, the width to length ratio of the posterior facet is high, and the heel is proportionally short relative to posterior calcaneal facet length. These features are very similar to eosimiids and platyrrhines, but differ from other tarsiiforms and strepsirrhines. The distal region of the calcaneus is moderately elongated (52.0% of total calcaneal length), falling in the range of tarsiiforms and eosimiids²⁸. The calcaneocuboid joint is fan-shaped, a primitive primate condition³⁰. The talus is not preserved, but its impression indicates that this bone had a broad head, a long neck and a moderately developed posterior trochlear shelf. These features are present in most tarsiiforms and eosimiids^{14,22,28–30}. The moderately elongated cuboid, navicular and entocuneiform are similar in morphology to those of other tarsiiforms, being only slightly elongated. The navicular-cuboid facet contacts only the ectocuneiform facet of the navicular, a haplorhine characteristic^{13,17,31}.

The first metatarsal-entocuneiform joint is curved, with a narrow joint arc, a similarity shared with other tarsiiforms. However, the curvature of this joint surface is slightly asymmetrical, a similarity to a specimen tentatively referred to an eosimiid or a tarsier³². The peroneal tubercle is moderately long, high and wide, being similar to adapiforms, microchoerids and eosimiids, in contrast to the narrow or pointed peroneal tubercle observed in omomyids or the wide proximal ends of platyrrhines.

The proximal and middle pedal phalanges are long and fairly straight in lateral view. They lack the greater curvature of most primate phalanges. The fourth digit is the longest (ectaxyony), a similarity to tarsiers and lemuriforms, in contrast to third digit elongation (mesaxyony) that characterizes adapiforms and anthropoids. The distal phalanges of the first, third and fifth digits, and a fine impression of the second, are preserved (Fig. 3 and Supplementary Information). All of these distal phalanges are scutiform with dorsoplantarily compressed and expanded distal apical tufts, indicating the presence of flat nails.

Phylogeny

Archicebus achilles possesses a unique mosaic of haplorhine features, some of which resemble anthropoids whereas others resemble tarsiiform primates. For example, in terms of calcaneal shape and metatarsal proportions within the foot, the new taxon recalls anthropoid primates, whereas its skull, dentition and many aspects of its appendicular skeleton resemble tarsiiforms. This combination of anthropoid-like and tarsiiform-like features in a single taxon is unique and unexpected, posing novel possibilities for reconstructing how modern tarsiers and anthropoids evolved their diagnostic characters.

Detailed comparative anatomical research and revised phylogenetic analysis based on an updated, large, combined morphological and molecular character data matrix place *A. achilles* as the most basal member of a monophyletic tarsiiform haplorhine clade (Fig. 4 and Supplementary Information). Anthropoidea is monophyletic and sister group to the tarsiiforms. *Archicebus achilles* therefore helps constrain and push back the age of the split between tarsiiforms and anthropoids, and an early division between strepsirrhine and haplorhine primates^{2,33–35} is supported. Furthermore, adapiforms are more closely related to lemuriforms than to anthropoids or any other haplorhines.

Plesiadapiforms, traditionally regarded as archaic primates^{9,36}, are not even stem primates, corroborating the now common practice of excluding plesiadapiforms from the order Primates^{37–39}.

Adaptive profile

Archicebus achilles (estimated body mass ~20–30 g, Supplementary Information) is as small as the modern pygmy mouse lemur⁴⁰. Its large canines and sharply pointed premolars with well-developed shearing crests suggest a primarily insectivorous diet. The moderately large and convergent orbits of *A. achilles* indicate that the visual system had an important role during ingestion and locomotion, as is the case in modern primates. However, the absence of any marked orbital hypertrophy, which occurs uniformly in extant nocturnal haplorhines, indicates a diurnal activity pattern for *A. achilles* (Supplementary Information). Diurnality has also been suggested for *T. asiatica*, another basal haplorhine primate from Asia².

The postcranium of *A. achilles* shows many hindlimb features associated with frequent leaping, such as a long leg, a semi-cylindrical femoral head with a stout and less oblique femoral neck, a tall knee, and a closely apposed fibula. However, the long coronoid process of

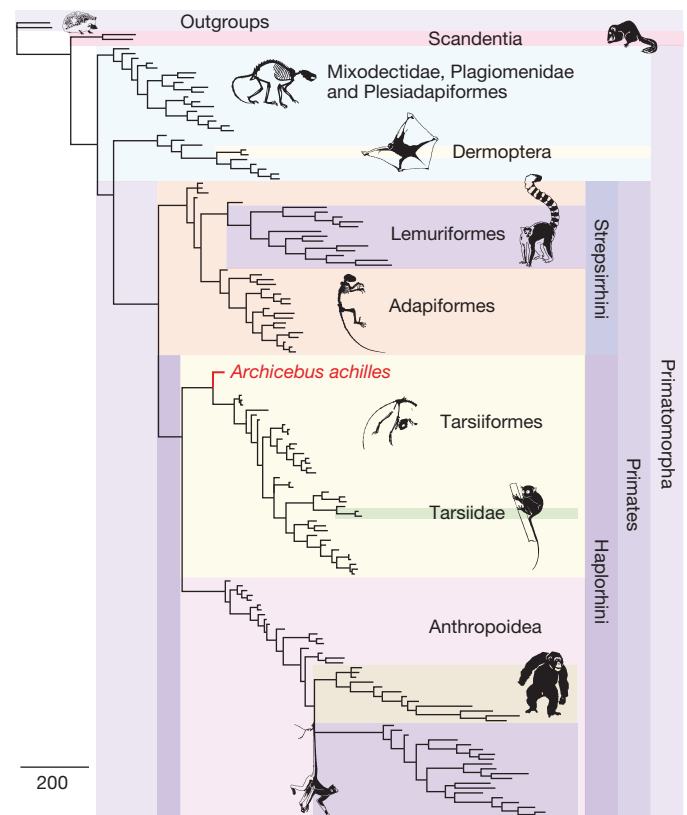


Figure 4 | Summary phylogeny of 157 mammals. Parsimony analysis is based on a data matrix including 1,186 morphological characters and 658 molecular characters of long and short interspersed nuclear elements scored for 119 fossil and 38 living taxa. Topology of extant treeshrews, flying lemurs and primates based on gene supermatrix is used as backbone constraint (Supplementary Information). Scale bar, 200 characters.

the scapula, a moderately rounded humeral head, a long and straight ischium, a high crural index, and the long metatarsal and phalangeal proportions of the foot of *A. achilles* are all linked to more generalized arboreal quadrupedal locomotion (or grasp-leaping), in contrast to the morphology of specialized vertical clinging and leaping primates such as galagids and tarsiers^{14,19,29,41,42}.

A long-standing idea holds that basal members of the major primate radiations are likely to be morphologically very similar to each other^{9,43}. From this perspective, our reconstructed adaptive profile of the remarkably complete and well preserved skeleton of *A. achilles* may well mirror that of other phylogenetically basal primates, including the most basal anthropoids, the most basal haplorhines, and even the last common ancestor of all primates.

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

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Author Contributions X.N. designed the study, analysed the data and wrote the paper. K.C.B., J.M., D.L.G. and M.D. contributed extensively and equally to the work presented in this paper. P.T. performed synchrotron microtomography experiments and edited the manuscript. J.J.F. collected part of the data and edited the manuscript.

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