

# The oldest known anthropoid postcranial fossils and the early evolution of higher primates

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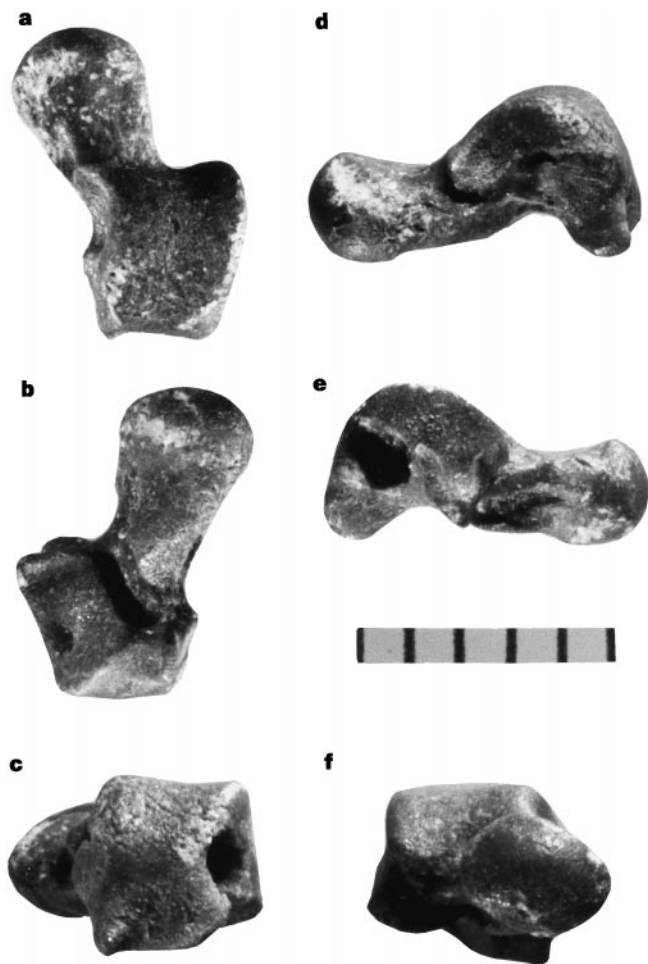
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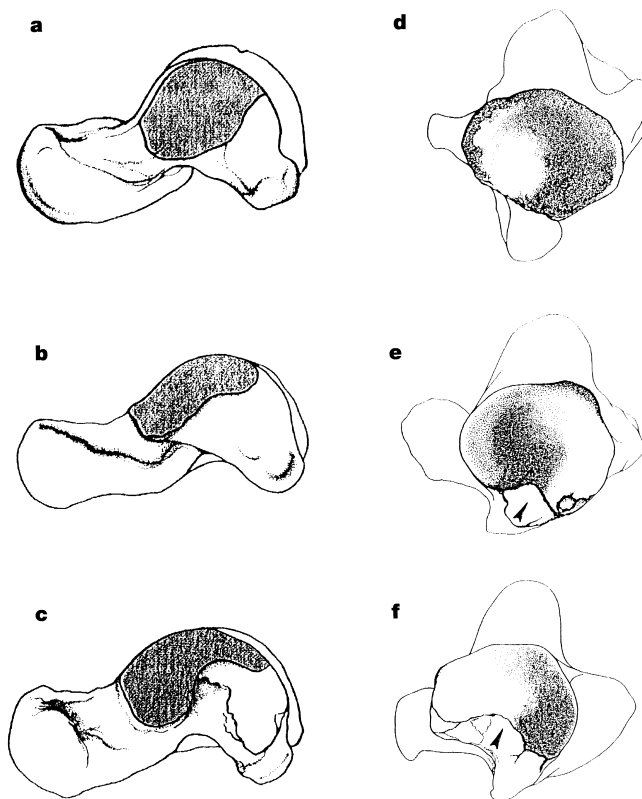
The middle Eocene primate family Eosimiidae, which is known from sites in central and eastern China<sup>1,2</sup> and Myanmar<sup>3</sup>, is central to efforts to reconstruct the origin and early evolution of anthropoid or 'higher' primates (monkeys, apes and humans)<sup>1-6</sup>. Previous knowledge of eosimiid anatomy has been restricted to the dentition<sup>1-3,7</sup> and an isolated petrosal bone<sup>5</sup>, and this limited anatomical information has led to conflicting interpretations of early anthropoid phylogeny<sup>1-6,8,9</sup>. Here we describe foot bones of

*Eosimias* from the same middle Eocene sites in China that yield abundant dental remains of this primate. Tarsals of *Eosimias* show derived anatomical traits that are otherwise restricted to living and fossil anthropoids. These new fossils substantiate the anthropoid status of *Eosimias* and clarify the phylogenetic position of anthropoids with respect to other major primate clades. Early anthropoids possessed a mosaic of primitive and derived traits in their postcranial skeletons, reflecting their derivation from haplorhine ancestors that retained many prosimian-like features.

Primate tarsal bones are highly diagnostic among mammals<sup>10-13</sup>, allowing isolated primate tali and calcanei to be readily identified. Our continuing field studies at Chinese fossil sites have yielded numerous jaws and teeth of eosimiid primates and have led to the recovery of both tali and calcanei that can be referred to *Eosimias* (Fig. 1; see Methods). Overall, the tarsals of *Eosimias* resemble those of omomyids (extinct Eocene primates) and small platyrrhines (South American monkeys) more than those of any other primates. Tali of *Eosimias* preserve three characters that have proved useful in distinguishing the tarsals of strepsirhine and haplorhine primates<sup>14-16</sup>. First, the articular facet for the fibula on the lateral side of the talar body is vertically orientated rather than sloping gently and laterally; second, the groove on the posterior trochlear shelf for the tendon of the flexor muscle (hallucis longus) occurs plantar to the posterior part of the tibiotalar articular surface rather than lateral to it; and third, the posterior trochlear shelf is small rather than large. All of the talar character states present in *Eosimias* resemble those in haplorhines and differ from alternative conditions



**Figure 1** Right *Eosimias* talus (IVPP V11846) from Locality 1, Shanxi Province, China. Views shown are dorsal (a); plantar (b); posterior (c); medial (d); lateral (e) and anterior (f). Scale bar, 5 mm. For talar and calcaneal measurements, see Supplementary Information.



**Figure 2** Medial talar and calcaneocuboid features. a-c, Medial views of haplorhine tali. Shading indicates extent of the medial facet. a, *Hemiacodon*, an Eocene omomyid (YPM 24464, Bridger Basin, Wyoming). b, *Eosimias* (IVPP V11849, Shanghuang, Jiangsu Province, China). c, *Saimiri*, a South American monkey (NIU specimen). d-f, Anterior views of calcaneocuboid joints. d, *Hemiacodon*. e, *Eosimias* (IVPP V11848, Shanghuang, Jiangsu Province, China). f, *Saimiri*. Arrows (e, f) point to the nonarticular wedge on the medioplantar surface of the calcaneocuboid joint. Not to scale.

found in strepsirhines. However, all of these 'haplorhine' character states have been interpreted as primitive for primates<sup>14–16</sup>. Among haplorhines, eosimiid tali retain some features that are more typical of omomyids than anthropoids (including fossil anthropoids from the Fayum, Egypt). These features include (1) a moderate talar neck angle (30°); (2) a moderately high talar body; (3) a shallow trochlea; (4) a small posterior trochlear shelf; and (5) a relatively narrow talar body. The medial facet on the talar body for the tibial malleolus is reduced (Fig. 2), however, a feature that is diagnostic of anthropoid versus prosimian primates<sup>16</sup>. This feature is common in mammals other than primates, and may therefore be interpreted either as a retained primitive character in anthropoids, or as a derived reversal to the primitive condition<sup>15</sup>. Optimization of this character by phylogenetic analysis using parsimony (PAUP) identifies this feature as an anthropoid synapomorphy.

*Eosimias calcanei* can be recognized as belonging to haplorhine primates on the basis of the morphology of the posterior calcaneal facet, which is relatively short and broad, with only a minimal bony distinction between its plantar edge and the supporting bone below it. This morphology is unlike that of adapiform primates, in which the posterior calcaneal facet is ribbon-like (narrow and long), with a well-defined plantar edge. Major primate clades show differential elongation of the anterior or distal part of the calcaneus, which can be quantified by measuring the percentage of total calcaneal length formed by that part of the calcaneus lying distal to the posterior calcaneal facet<sup>17</sup>. *Eosimias calcanei* possess a relatively longer distal segment (45–52% of calcaneal length) than do adapiform primates,

being more similar to the squirrel monkey *Saimiri* (range 43–49%; mean 46%) but shorter than most omomyid primates (range 51–56%) (Fig. 3). The calcaneus of *Eosimias* is moderate in its relative transverse width (calcaneal width-to-length ratio, range 38–45%), being narrower than platyrrhines (range 45–63%) but wider than omomyids (range 30–37%). The calcaneocuboid joint of *Eosimias* is also intermediate between those of Eocene prosimians and anthropoids (Fig. 2). The probably primitive condition for primates, exhibited by notharctids and omomyids, is a broad, flat, fan-shaped surface with a centrally located pivot. In contrast, anthropoids possess a joint surface that resembles a circle with a small nonarticular wedge removed from the medioplantar region and a medially shifted pivot. *Eosimias calcanei* possess a relatively flattened joint resembling that of omomyids and notharctids. However, like anthropoids, the joint is rounded, part of the medioplantar section is nonarticular and the pivot is medially shifted.

The reduction of both the medial talotibial facet and the calcaneocuboid joint surface suggests that there was less stability in sustained habitually inverted foot positions. This implies more frequent use of horizontal foot postures and probably horizontal supports in *Eosimias* than in prosimian primates, a functional attribute shared with anthropoids<sup>16</sup>. In contrast, the primitive features that *Eosimias* shares with omomyids demonstrate its origin from a leaping ancestry.

A phylogenetic analysis<sup>18</sup> of 11 tarsal characters (Fig. 4; see Methods) shows that a sister group relationship between *Eosimias* and a clade including all other anthropoids is the most parsimonious arrangement of taxa. Bootstrap support is weak because this group is supported by only two tarsal synapomorphies. However, this result agrees with previous analyses of dental and gnathic characters<sup>1,2</sup>, and bootstrap support for any other grouping (that is, *Tarsius*-anthropoids, adapiforms-anthropoids, omomyids-anthropoids) is much lower (<5%).

The importance of the *Eosimias* tarsals lies in their unique combination of prosimian-like and anthropoid-like traits. This mosaic of primitive and derived characters in *Eosimias*, a basal member of the anthropoid clade, has substantial implications for understanding anthropoid origins. Because the tarsals of *Eosimias* show numerous features that are typical of haplorhines, but lack the derived traits characteristic of strepsirhines, the oldest known anthropoid postcranial fossils support hypotheses favouring the haplorhine affinities of anthropoids and are inconsistent with hypotheses advocating an adapiform origin for higher primates<sup>8,19–22</sup>. The precise relationship between early anthropoids and other living and fossil haplorhines is still disputed. The main hypotheses are that (1) anthropoids evolved from Eocene omomyids<sup>23</sup>; (2) that anthropoids share more recent common ancestry with living and fossil tarsiers than they do with any other primates<sup>4,6,24–26</sup>; and (3) that anthropoids diverged from other haplorhines early in the Cenozoic, their most likely sister group consisting of a clade including both tarsiers and omomyids<sup>1,2,27,28</sup>. Although we favour the latter phylogeny, we acknowledge that tarsal evidence alone cannot discriminate among these options because omomyid tarsal morphology is probably primitive for all haplorhine primates, and would therefore have characterized any pre-tarsioid haplorhine as well. Nevertheless, the eosimiid tarsals described here serve to bridge the wide morphological gap separating prosimian and anthropoid postcrania, providing further insight into the origins of the anthropoid postcranial skeleton. □

Methods

Allocation

IVPP V11846 is the right talus of a small primate from Locality 1 in the Zhaili Member of the Heti Formation, Yuanqu Basin, central China (Fig. 1). After intensive sampling at this locality, only two primate taxa are known to occur here. The larger of these is *Hoanghoniuss tehlini*, a basal member of the adapiform family Sivaladapidae that weighed roughly 700 g



Figure 3 Dorsal view of haplorhine calcanei. a, *Saimiri* (NIU specimen, a South American monkey). b, *Eosimias* (IVPP V1 1851, Shanghuang, Jiangsu Province, China). c, *Hemicacodon* (AMNH 12046, an Eocene omomyid). Scale bars, 5 mm.

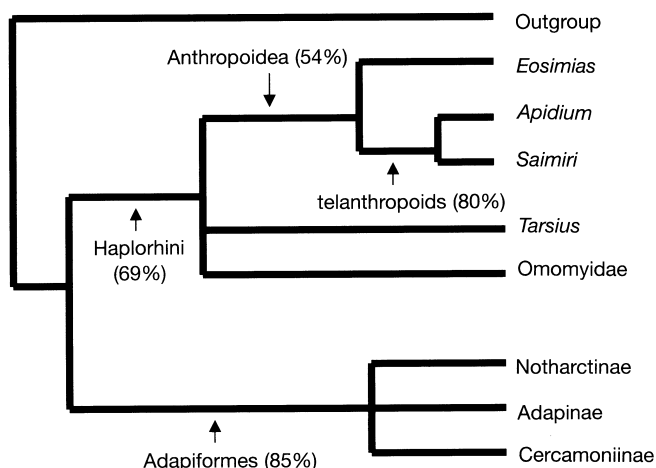


Figure 4 Consensus tree from PAUP analysis. Bootstrap values, given in parentheses, are from 100 replications.

on the basis of regressions of molar area versus body mass in living primates<sup>29</sup>. The smaller primate from this locality is *Eosimias centennicus*, a basal anthropoid that weighed 90–180 g on the basis of similar regressions<sup>2</sup> (all estimates of body mass for eosimiids provided here are ranges of mean estimates derived from multiple regressions). Regressions of talar dimensions versus body mass in living primates<sup>30</sup> show that IVPP V11846 belonged to a primate weighting 90–147 g. Thus, on the basis of size alone, this talus can be confidently allocated to *Eosimias centennicus*. This allocation permits the recognition of additional *Eosimias tali* ( $n = 7$ ) from the Shanghuang fissures. Estimates of body mass for the Shanghuang sample of *Eosimias tali* range from 57 to 118 g, which overlaps the estimated body mass of *Eosimias sinensis* from Shanghuang on the basis of molar regressions (67–137 g). However, several size classes seem to be represented in the Shanghuang sample of tali, and these probably correspond to more than one eosimiid species. Primate calcanei from Shanghuang ( $n = 12$ ) are referred to *Eosimias* on the basis of their functional congruence with the tali from Shanghuang discussed above, as well as their size, provenance and combination of omomyid-like and anthropoid-like traits.

## Phylogenetic analysis

Eleven tarsal characters were subjected to a parsimony analysis using PAUP 4.0 (ref. 18) yielding the nine most parsimonious trees with a consistency index of 0.696. The strict consensus tree is shown in Fig. 4. In all trees, *Eosimias* groups with ‘telanthropoids’<sup>25</sup> (in this case, the clade including *Apidium* and *Saimiri*). The ‘outgroup’ consists of character states known in the most likely outgroups of primates: Scandentia, Dermoptera and Plesiadapiformes; these taxa differ insignificantly in the expression of these traits.

Nodes for telanthropoids, Anthropoidea, Haplorhini and Adapiformes are labelled in Fig. 4; the percentages are bootstrap values from 100 replications. Synapomorphies for Anthropoidea are the shape of the calcaneocuboid joint and a reduced medial talar facet. Synapomorphies for telanthropoids are an increased talar neck angle, an increased talar width and loss of the posterior trochlear shelf. Synapomorphies for Haplorhini are an increased distal length of the calcaneus, a relatively short heel, a steep sided talofibular facet with a lantar lip and a centrally located flexor fibularis groove. Synapomorphies for Adapiformes are a sloping talofibular facet, an increase in the size of the posterior trochlear shelf, a long and narrow posterior astragalocalcaneal facet, an increase in the size of the talotibial facet and an increase in the height of the talar body.

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Supplementary information is available on Nature's Web site (<http://www.nature.com>) or as paper copy from the London editorial offices of Nature.

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# Soil pathogens and spatial patterns of seedling mortality in a temperate tree

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The Janzen–Connell hypothesis<sup>1,2</sup> proposes that host-specific, distance- and/or density-dependent predators and herbivores maintain high tree diversity in tropical forests. Negative feedback between plant and soil communities could be a more effective mechanism promoting species coexistence because soil pathogens can increase rapidly in the presence of their host<sup>3</sup>, causing conditions unfavourable for local conspecific recruitment<sup>4–6</sup>. Here we show that a soil pathogen leads to patterns of seedling mortality in a temperate tree (*Prunus serotina*) as predicted by the Janzen–Connell hypothesis. In the field, the mean distance to parent of seedling cohorts shifted away from maternal trees over a period of 3 years. Seedlings were grown in soil collected 0–5 m or 25–30 m from *Prunus* trees. Sterilization of soil collected beneath trees improved seedling survival relative to unsterilized soil, whereas sterilization of distant soil did not affect survival. *Pythium* spp., isolated from roots of dying seedlings and used to inoculate healthy seedlings, decreased survival by 65% relative to controls. Our results provide the most complete evidence that native pathogens influence tree distributions, as predicted by the Janzen–Connell hypothesis, and suggest that similar ecological mechanisms operate in tropical and temperate forests.

Aggregated spatial distributions of tree species are expected when seed dispersal is highest beneath maternal trees and seedling mortality occurs at random. In contrast, the Janzen–Connell hypothesis predicts that natural enemies will reduce offspring density beneath trees, creating opportunities for heterospecific recruitment. Empirical and theoretical tests of the hypothesis have yielded mixed results<sup>7–16</sup>. This inconsistency has been attributed, in some cases, to predator satiation, whereby seeds or seedlings close to conspecific trees occasionally escape attack<sup>17–19</sup>. Escape is less likely with microbial pathogens that exhibit positive density dependence<sup>20</sup>. Recent studies in temperate communities have suggested that plant–soil feedbacks affect successional dynamics and species diversity<sup>3,4,21–25</sup>. In this study, we investigated whether negative plant–soil feedback was occurring in *Prunus serotina* (black cherry). Black cherry is a mid-successional tree that produces large numbers of bird-dispersed fruits throughout temperate forests