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Early Eocene lagomorph (Mammalia) from Western India and the early diversification of Lagomorpha

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We report the oldest known record of Lagomorpha, based on distinctive, small ankle bones (calcaneus and talus) from Early Eocene deposits (Middle Ypresian equivalent, *ca* 53 Myr ago) of Gujarat, west-central India. The fossils predate the oldest previously known crown lagomorphs by several million years and extend the record of lagomorphs on the Indian subcontinent by 35 Myr. The bones show a mosaic of derived cursorial adaptations found in gracile Leporidae (rabbits and hares) and primitive traits characteristic of extant Ochotonidae (pikas) and more robust leporids. Together with gracile and robust calcanei from the Middle Eocene of Shanghuang, China, also reported here, the Indian fossils suggest that diversification within crown Lagomorpha and possibly divergence of the family Leporidae were already underway in the Early Eocene.

Keywords: Lagomorpha; Leporidae; Early Eocene; India; Shanghuang; China

1. INTRODUCTION

Considerable evidence points to Asia as the centre of origin of the mammalian superordinal clade Glires, which includes the extant orders Rodentia and Lagomorpha. Most primitive Glires and their closest relatives were either endemic to Asia or common there during their initial radiations (Beard 1998; Meng & Wyss 2005; Missiaen *et al.* 2006). The early record of Lagomorpha and its extinct sister group, Mimotonidae (together composing the Duplicidentata), has significantly improved over the last two decades, particularly as a result of fossil discoveries in central and eastern Asia. Although the broad distribution of basal members of some mammalian orders (e.g. Primates, Artiodactyla, Perissodactyla) makes their place of origin ambiguous, the restriction of the oldest duplicidentates to Asia is considered strong evidence that they originated in that part of the world (McKenna 1982). Until now, the oldest known Lagomorpha came from the Late Early or Early Middle Eocene of central Asia (Russell & Zhai 1987; Shevyreva 1995; Averianov & Lopatin 2005; Lopatin & Averianov 2006; Li *et al.* 2007), and both fossil and molecular evidence suggested that the dichotomy of the order into the extant families Ochotonidae (pikas) and Leporidae (rabbits and hares) did not occur until the Late Eocene (McKenna 1982; Douzery *et al.* 2003; Asher *et al.* 2005). Here, we describe lagomorph fossils from India that are older than any previously reported and provide evidence that the two extant families may already have diverged by the Early

Eocene, in agreement with one recent molecular study (Springer *et al.* 2003).

The oldest definitive lagomorphs previously reported come from central Asian strata of Late Early or Early Middle Eocene age (Arshantan and Irindmanhan Land Mammal Ages = Lutetian and possibly the latest Ypresian). They comprise two lagomorph dental taxa and lagomorph tarsals presumably referable to one of them from Andarak II in Kyrgyzstan (Averianov 1991; Shevyreva 1995; Averianov & Lopatin 2005; Lopatin & Averianov 2006), and a new basal lagomorph, *Dawsonolagus*, from the Arshanto Formation of Inner Mongolia known from craniodental fossils and ankle bones (Li *et al.* 2007). By later in the Middle Eocene, a diversity of lagomorphs is known from China (Tong 1997; Meng *et al.* 2005). However, lagomorphs are practically unknown in the fossil record of southeast Asia, and none are known from Eocene strata in Pakistan, India, Thailand or Myanmar. Until now, the oldest lagomorphs from the Indian subcontinent dated from the Miocene (Flynn *et al.* 1997; Barry *et al.* 2002; Winkler *et al.* 2007); they consist of a small number of fragmentary Late Miocene leporids (*ca* 7.0–7.8 Myr ago) and a single Early Miocene ochotonid molar (*ca* 18 Myr ago).

We report here the oldest known record of Lagomorpha, from the Early Eocene Cambay Shale (Middle Ypresian equivalent) of Gujarat, west-central India. The fossils were found in continental clays at the Vastan lignite mine, northeast of Mumbai. They come from a layer approximately 15 m below the occurrence of the foraminiferan *Nummulites burdigalensis burdigalensis*, a marker of Shallow Benthic Zone 10 and planktonic zone 6b (Serra-Kiel *et al.* 1998; Sahni *et al.* 2006), which are dated at *ca* 53 Myr ago (Berggren & Aubry 1998;

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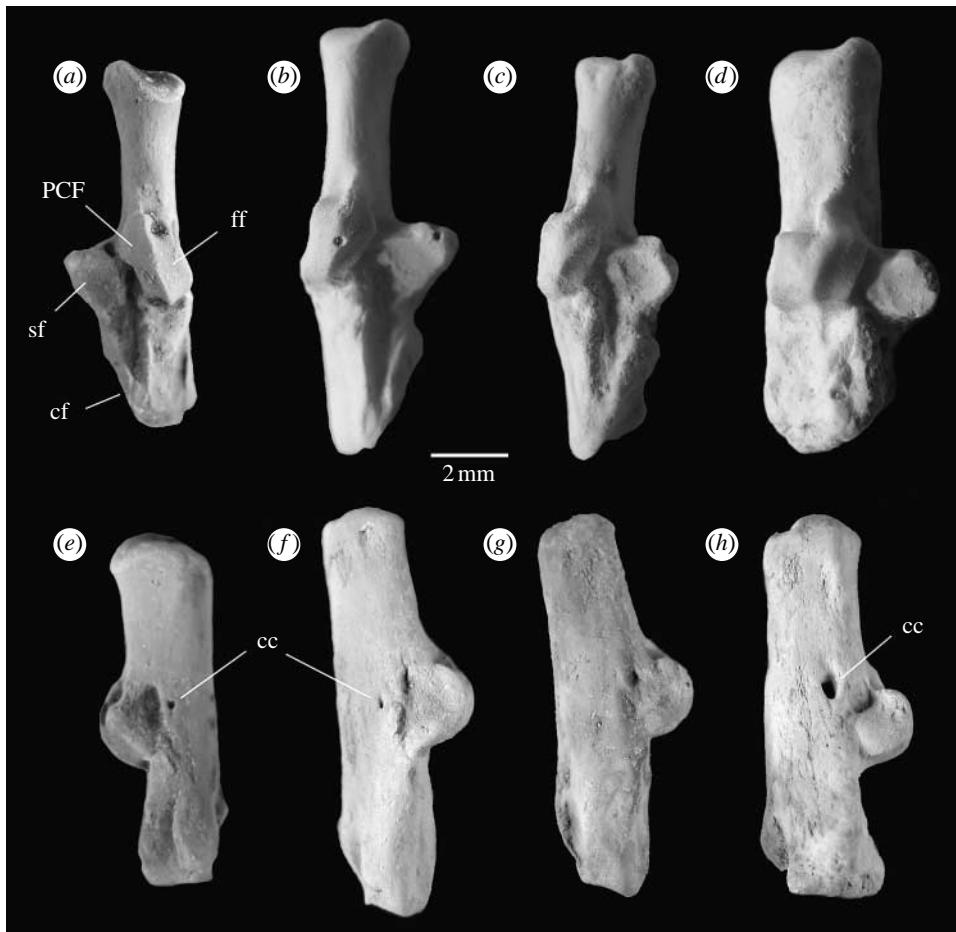


Figure 1. Calcanei of Eocene lagomorphs in (a–d) dorsal and (e–h) lateral views. Garhwal University, Srinagar, India (GU), and Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China (IVPP). (a,e) Left calcaneus, GU/RSR/VAS 711 from Early Eocene Vastan mine, India; (b–d, f–h) right calcanei from Middle Eocene of Shanghuang, China, IVPP 15537, 15538, 15539, respectively. ff, fibular facet; sf, sustentacular facet; PCF, posterior calcaneal facet; cf, cuboid facet, cc, calcaneal canal.

Luterbacher *et al.* 2004); consequently, they predate the oldest lagomorphs previously reported by several million years.

2. MATERIAL AND METHODS

The Vastan fossils consist of ankle bones, the calcaneus and talus (figures 1 and 2), which are comparable in size to those of the extant pika *Ochotona*. Also described here are three calcanei and a talus from the Middle Eocene of Shanghuang, China. They are compared to an extant sample including representatives of both living families: eight species in six genera of Leporidae and two species of the single extant genus *Ochotona* (see electronic supplementary material, table 1). The comparative sample was not intended to be comprehensive, but rather to reflect the range of variation in size and shape of the calcaneus and talus in extant lagomorphs. The six genera of extant leporids span the size range of the family and include taxa that possess tarsals which range from gracile to robust. Living ochotonids are much more homogeneous in size and tarsal morphology. Several factors limited the sample size. Skeletons are typically much less numerous in collections than skulls, and tarsal bones are sometimes lacking. Even when present, tarsals of small mammals are often inaccessible in museum skeletons, either left in skins or in articulation. The latter circumstance prevented two measurements in *Brachylagus* and in one *Romerolagus* specimen.

Skeletons of three of the genera, *Romerolagus*, *Brachylagus* and *Nesolagus*, are particularly rare in collections.

Linear measurements of the fossil tarsals and the extant sample of ochotonids ($n=9$) and leporids ($n=17$) are provided in the electronic supplementary material, table 1. Larger specimens were measured with digital calipers under a binocular microscope and smaller specimens with an ocular micrometer fitted to the lens of the binocular microscope. Owing to the disparate size between many leporids and ochotonids, measurements were scaled by the length of each element, yielding relative linear measurements for comparisons among taxa.

Phylogenetic analyses were run using PAUP v. 4.0b10 (Swofford 2002), based on the matrix published by Asher *et al.* (2005) supplemented with characters from the fossils reported here (electronic supplementary material, table 2). Character definitions are identical to theirs except for character 211 that was returned to the original definition of Meng *et al.* (2003). The resulting morphological data matrix of 71 taxa and 228 characters is included in the electronic supplementary material, NEXUS file. We used a heuristic search with random addition sequence for 50 replicates. All characters were considered unordered.

Principal components analysis (PCA) was used as a data reduction technique to demonstrate the position of the fossil specimens relative to the range of variation in extant lagomorphs. Specimens with missing data were excluded.

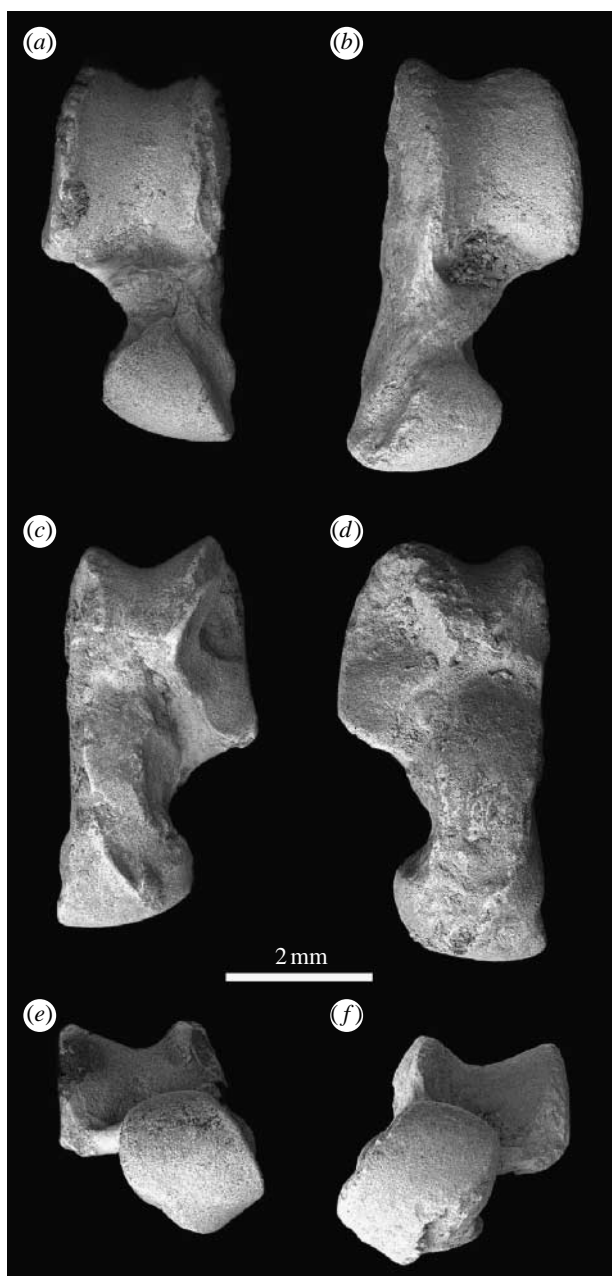


Figure 2. Tali of Eocene lagomorphs in (a,b) dorsal, (c,d) ventral and (e,f) distal views. (a,c,e) Right talus from Vastan mine, India (GU/RSR/VAS 712); (b,d,f) left talus from Shanghuang, China (IVPP 15540).

Data were evaluated for skewness, kurtosis, sampling adequacy and sphericity. Because the fossil tarsals were not associated *in situ*, separate analyses were conducted for calcaneus and talus. Non-parametric two-tailed Mann–Whitney *U*-statistics were used to test for significant differences in univariate shape measurements between the extant samples, and a conservative Bonferroni multiple comparisons adjustment was applied.

3. RESULTS AND DISCUSSION

The Vastan calcaneus and talus (figures 1 and 2) are highly diagnostic at the ordinal level and show derived features characteristic of gracile leporids combined with primitive traits typical of more robust leporids and *Ochotona*. The Vastan tarsals are anatomically very similar to the previously unreported gracile lagomorph tarsals from

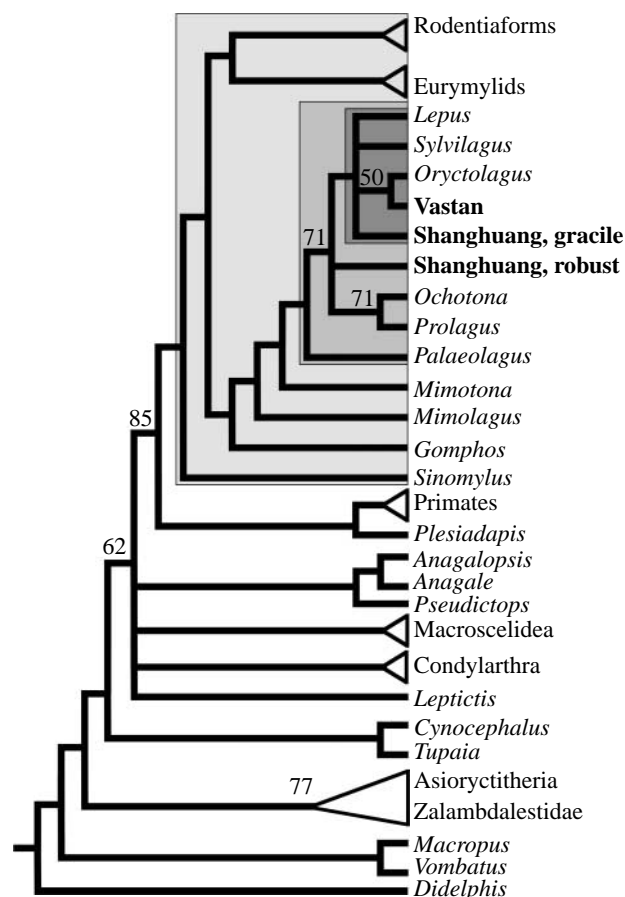


Figure 3. Majority rule consensus tree of 1820 most parsimonious trees (MPTs) recovered by PAUP v. 4.0b10, rooted using three marsupial taxa as an outgroup. Numbers left of clades show the percentage of MPTs in which the clade occurs when this percentage is lower than 100%. Tree length, 1402 steps; CI, 0.2482; RI, 0.6941. Light grey shading indicates the position of Glires, intermediate grey shading shows Lagomorpha and dark grey shading shows Leporidae. Characters used in the analysis are listed in the electronic supplementary material, table 2.

Middle Eocene fissures at Shanghuang, China, as well as to the tarsals from Andarak II in Kyrgyzstan (Averianov 1991), whereas they are more slender and more derived than the tarsals of *Dawsonolagus* from Inner Mongolia (Li *et al.* 2007).

The calcaneus of lagomorphs is distinctive in retaining a well-developed, wide fibular facet on the calcaneus and a longer, medially facing posterior calcaneal facet (PCF = ectal facet), the distal half of which is aligned with the sustentacular facet. The presence of a fibular facet has sometimes been considered a primitive trait, a polarity possibly supported by its presence in the Early Eocene eurymylid simplicidentate *Rhombomylus* (Meng *et al.* 2003) as well as in Palaeocene *Pseudictops* (Sulimski 1968) and arctostylopids (Missiaen *et al.* 2006), both arguably related to Glires. However, absence of calcaneo-fibular contact in other Glires (*viz.* Rodentia and Mimotonidae; Meng *et al.* 2004; Asher *et al.* 2005; Meng & Wyss 2005) as well as Anagalidae and Zalambdalestidae (Li & Ting 1985) suggests that contact in lagomorphs is secondarily derived (Szalay 1985; Li *et al.* 1987). A distal talocalcaneal facet in addition to the sustentacular facet, and a sharply angled medially facing cuboid facet, is also characteristic of lagomorph calcanei.

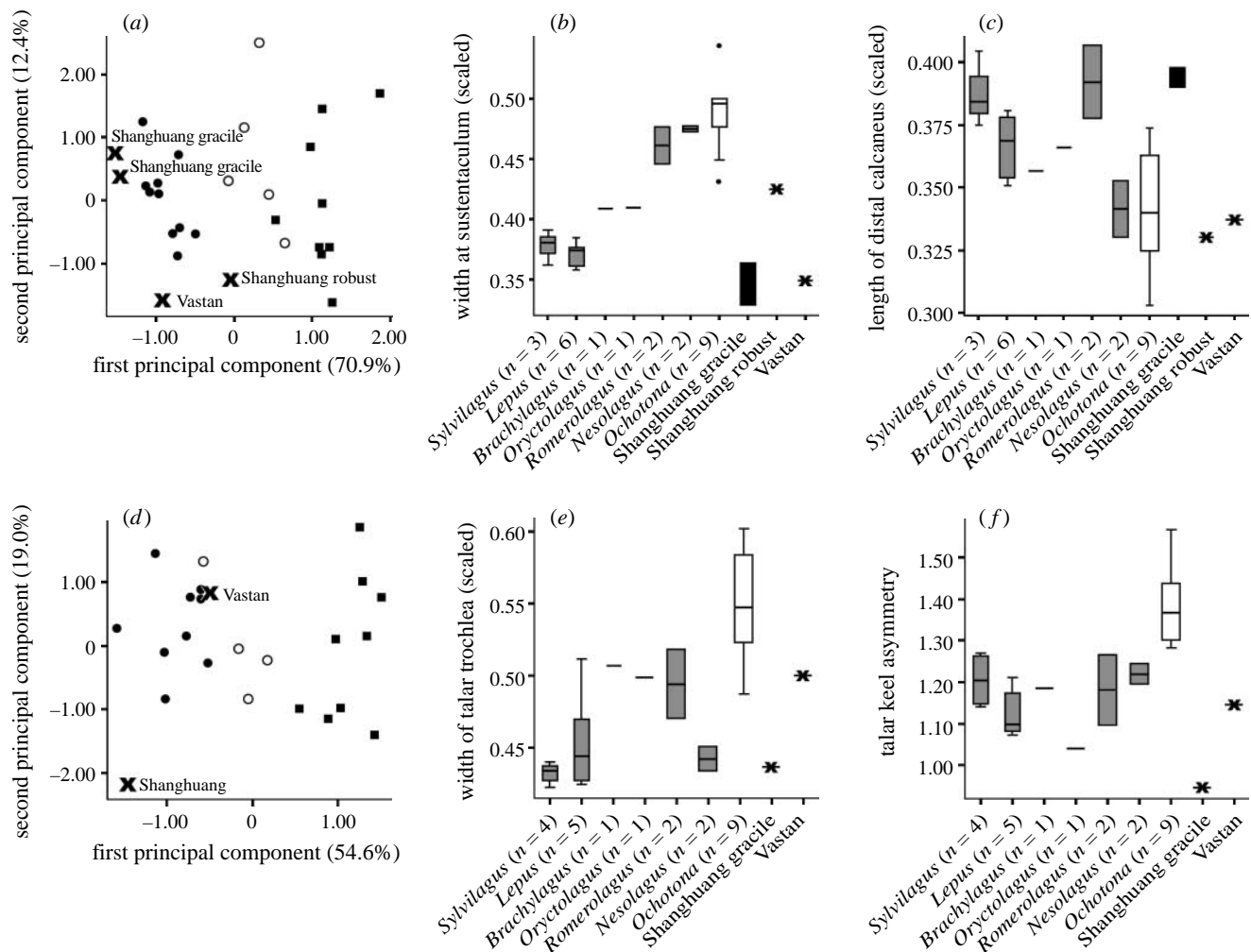


Figure 4. Statistical analyses of scaled shape measures for Vastan and Shanghuang tarsals compared to extant lagomorphs (SPSS for Windows, v. 15.0.1). (a,d) PCA based on all measures of calcaneus and talus; graphs show first two principal components and the amount of variation explained by each component (filled circles, gracile leporids; open circles, robust leporids; filled squares, ochotonids; labelled crosses, fossil specimens). (b,c,e,f), Univariate distributions of selected scaled measurements by genus (filled boxes, Leporidae; open boxes, Ochotonidae; black boxes and crosses, fossil specimens). Boxplots indicate median and quartile values, with outliers (more than 1.5 times interquartile range) indicated by isolated dots. (b) Calcaneal width at the sustentaculum, (c) calcaneal distal elongation, (e) talar width, (f) trochlear asymmetry (lateral/medial keel lengths). See also electronic supplementary material, figures S1–S14.

The talus of extant lagomorphs has a deeply grooved, asymmetrical trochlea with the lateral keel longer and higher than the medial and a moderately long to very long neck. The head (navicular facet) is subcylindrical about a transverse axis and in line with the trochlear groove.

A unique feature of lagomorphs is the calcaneal canal that passes diagonally through the bone, entering on the lateral side just inferior or proximal to the fibular facet and emerging just distal to the sustentacular facet and proximal to the cuboid facet (Bleefeld & Bock 2002). The canal is larger in Ochotonidae than in Leporidae, in which it is occasionally absent. Bleefeld & Bock observed that the canal also was large in all fossil lagomorphs then known, hence they interpreted the smaller size in leporids to be a derived state within lagomorphs. The canal appears to transmit a small lymphatic or blood vessel into the distal part of the foot (Bleefeld & Bock 2002; K. D. Rose 2007, personal observation), but otherwise its significance is poorly understood.

Ochotona (the only extant ochotonid) is much smaller than the well-known leporids *Lepus* and *Sylvilagus* and differs in having relatively shorter and more robust

calcanei and tali, a relatively longer and wider fibular facet, a relatively wider and more asymmetrical talar trochlea (lateral keel much longer than medial keel) and a wider and dorsoventrally flatter talar head (electronic supplementary material, table 1 and figures S1–S14). Additionally, *Ochotona* has a continuous, convex PCF that allows proximodistal translation of the talus on the calcaneus. *Lepus* and *Sylvilagus* have more slender and distally longer calcanei and tali, a more nearly symmetrical talar trochlea, a narrow navicular facet on the talar head that tapers dorsally and a specialized PCF separated into distinct proximal and distal faces offset at a sharp angle. The latter morphology prevents proximodistal excursion of the talus while increasing stability of the ankle and promoting crurotalar flexion–extension. These distinctions represent extremes of lagomorph tarsal anatomy but do not always distinguish the two families. Some leporids (e.g. *Nesolagus*) have more robust tarsals proportionally similar to those of ochotonids, and some ochotonids were more cursorial than *Ochotona* (e.g. a leporid-like PCF is present in Neogene *Prolagus*; Dawson 1969); though no known ochotonid evolved such gracile, elongate tarsals as

in *Sylvilagus*. Outgroup comparison (to mimotonids; Meng *et al.* 2004; Asher *et al.* 2005) suggests that more robust tarsals lacking distal elongation and a talus with a moderately wide, asymmetrical trochlea are morphotypic for Lagomorpha.

The importance of tarsal and postcranial morphology for the relationships of Glires has been shown before in phylogenetic analyses (Meng *et al.* 2003; Asher *et al.* 2005). The addition of the Vastan and Shanghuang tarsal characters to these analyses clearly allies them with lagomorphs, and not with any other group (figure 3). They are distinctively lagomorph like in the morphology and position of all three talocalcaneal articular surfaces, the prominent fibular facet and the strongly oblique distal calcaneal articular surface for the cuboid. Within Lagomorpha, PCAs of scaled calcaneal and talar dimensions place the Vastan and Shanghuang tarsals within or on the periphery of the leporid cluster, distinct from ochotonids (figure 4a,d; see also electronic supplementary material). The Vastan calcaneus resembles that of *Sylvilagus* and several other leporids in its gracile, elongate form, but is statistically inseparable from *Ochotona* and the tarsally robust leporid *Nesolagus* in its shorter distal calcaneal length (figure 4b,c; electronic supplementary material, figures S3–S6). The PCF is convex with only the faintest hint of a ridge separating it into proximal and distal parts, in this feature resembling *Ochotona* more than leporids. The fibular facet is slightly narrower than that in extant lagomorphs. The calcaneal canal is very small, the proximal opening leporid like in size and position and the probable distal opening just inferior to the proximal cuboid facet. Distally there is a distinct peroneal process (less salient than in *Ochotona*) and a prominent plantar tubercle. The talus is like that of *Sylvilagus* in being distally elongate, having a relatively deep trochlea with the lateral keel only slightly longer than the medial, and having a narrow, vertically oriented talonavicular articulation; but it is intermediate in relative trochlear width (figure 4e,f; electronic supplementary material, figures S9–S14). Unlike extant lagomorphs, however, the talar head is slightly offset (medially) relative to the trochlear groove. Distal talar and calcaneal proportions suggest that, as in other primitive lagomorphs, the calcaneus did not extend farther distally than the astragalus, contrary to the condition in extant leporids. The Vastan tarsals thus share several derived traits with Leporidae, but in other traits they are more primitive than extant leporids.

The Vastan tarsals are slightly more primitive than the gracile lagomorph calcanei and talus from Shanghuang (IVPP 15537, 15538, 15540; figures 1b,c,f,g and 2b,d,f). The gracile Shanghuang calcanei are distally longer and within the range for extant leporids examined (figure 4c). The PCF in the Shanghuang calcanei shows incipient separation into proximal and distal surfaces, but the two surfaces are not nearly as distinct as in extant leporids. The calcaneal canal is vestigial in IVPP 15537 but absent in IVPP 15538. A third Shanghuang calcaneus is more robust, shorter distally and has a well-developed calcaneal canal (IVPP 15539, figure 1d,h), in these features closely approximating *Ochotona* and *Nesolagus*. Its fibular facet is wider and shorter than that in the other Shanghuang calcanei, within the range of extant leporids (electronic supplementary material, figures S7 and S8). The PCF is also wider but similar in being incipiently separated into

two facets. The Shanghuang talus (figure 2b,d,f) differs from the Vastan talus in having a narrower, nearly symmetrical trochlea (figure 4e,f). It probably represents the same taxon as the gracile calcanei. As in the Vastan talus (but unlike extant lagomorphs), the trochlear axis passes lateral to the head. Also contrary to other lagomorphs, the lateral keel is slightly shorter than the medial keel. Lagomorph tarsals from Andarak II (Averianov 1991) resemble the gracile tarsals from Vastan and Shanghuang.

4. CONCLUSIONS

The fossil tarsals described here illustrate mosaic evolution of specialized tarsal traits in basal lagomorphs. Previous fossil and molecular evidence suggested that the extant lagomorph clades Ochotonidae and Leporidae diverged in the Late Eocene (McKenna 1982; Douzery *et al.* 2003; Asher *et al.* 2005); but the Shanghuang fossils show that gracile and robust tarsal adaptations similar to those of both families were present in the Middle Eocene. More significantly, the Early Eocene Vastan tarsals show not only diagnostic lagomorph features but also some gracile adaptations seen today only in leporids. These derived traits evident in the Vastan tarsals imply that functional diversification within Lagomorpha, and possibly the dichotomy between the two families, had already begun by the Early Eocene.

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