



New primate hind limb elements from the middle Eocene of China

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ABSTRACT

The continued washing, sorting, and identification of middle Eocene (~45 Mya) primates from the Shanghuang fissure-fillings (Jiangsu Province, China) have produced additional hind limb elements. All are isolated elements. The strepsirhine hind limb elements include a first metatarsal and a talus, which are appropriate in size and morphology to pertain to *Adapoides troglodytes*. *Adapoides* is interpreted as a quadrupedal-climbing (nonleaping) primate with similarities to living lorises and the fossil primate *Adapis*. The haplorhine hind limb elements are estimated to span a range of adult body sizes from tiny (17 g) to small (200 g). Included among the new sample of haplorhine hind limb specimens is the smallest primate talus reported thus far. These new postcranial specimens expand our understanding of early haplorhine hind limb anatomy and demonstrate additional similarities between Shanghuang eosimiids and other anthropoids.

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Introduction

The middle Eocene Shanghuang fissure-fillings of Jiangsu Province, China, have produced an astonishingly diverse array of primates (Table 1). These fossils have also provided a rare glimpse of the ecological adaptations that are correlated with very small body size in primates. The five fissures appear to span a relatively short interval of time (likely 1–2 Myr), with Fissure D being slightly older than the rest (Beard et al., 1994; Wang and Dawson, 1994; MacPhee et al., 1995; Qi et al., 1996; Métais et al., 2004). Continued work on the Shanghuang fissure-fillings has produced additional primate postcranial material (Table 2). Here, we describe two new adapiform elements and six new haplorhine specimens from the Shanghuang fissure-fillings.

The new Shanghuang postcranial elements help to document an impressive radiation of primates that inhabited the central coastal region of China during the middle Eocene. At least six families of fossil primates have been identified at the Shanghuang localities, including primitive haplorhine and strepsirhine primates as well as basal anthropoids. Moreover, this fauna has important paleontological implications for European, North American, and African fossil primates (Beard, 1998, 2004; Ni et al., 2005).

Description of adapiform postcranial elements

First metatarsal

The first metatarsal, IVPP V13015 from Fissure A, is a nearly complete right first metatarsal with a small break at the very tip of the peroneal tubercle (Fig. 1). We estimate that this specimen belongs to an individual that weighed 250–300 g on the basis of comparisons with living primates having similarly sized first metatarsals (i.e., *Galago senegalensis*, *Galagoides alleni*, *Euticus matschiei*, and *Loris tardigradus*; Smith and Jungers, 1997). An adapine distal humerus from Shanghuang yields a similar size estimate (200–300 g; Gebo et al., 2007), and previously described adapiform tali and calcanei from Shanghuang have provided body size estimates between 200 and 500 g (Gebo et al., 2001). Body size estimates for these adapine postcranials are similar to those derived from the teeth of *Adapoides troglodytes* (285–343 g). Thus, we believe the V13015 first metatarsal is best allocated to *Adapoides troglodytes*, the smallest adapiform documented at Shanghuang. Other adapiform taxa at Shanghuang are larger than *Adapoides*, but all Shanghuang adapiforms are smaller than the 1 kg or larger body size estimates given for most European adapiforms (i.e., *Adapis*, *Cercamonius*, *Cryptadapis*, *Europolemur*, *Leptadapis*, and *Protoadapis*; Fleagle, 1999). Only *Donrussellia*, *Anchomomys*, and *Microadapis sciureus* (210–600 g; Fleagle, 1999) are comparably sized. Nevertheless, all of the Shanghuang adapiform postcranial bones are substantially larger than the haplorhine elements at this site, with only two exceptions (a haplorhine calcaneus and a distal

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Table 1
Named fossil primates at the Shanghuang fissure-fillings (localities A–D) by Beard et al. (1994)

Shanghuang primates	
Adapidae	Tarsiidae
<i>Adapoides troglodytes</i>	<i>Tarsius eoacaenus</i>
Omomyidae	Eosimiidae
<i>Macrotarsius macrorhysis</i>	<i>Eosimias sinensis</i>

femur; both are estimated within the 200 to 350 g size range). In addition to this size difference, the morphology of the first metatarsal and talus are highly diagnostic, making it easy to distinguish between strepsirhine and haplorhine primates (Beard et al., 1988; Szalay and Dagosto, 1988).

In terms of morphology, the V13015 first metatarsal is most similar to those of adapiform primates, particularly *Adapis* (see Szalay and Dagosto, 1988). V13015 is similar to *Adapis* in relative tubercle width (index A/B; Table 3; Fig. 2), shaft length (E/F), joint surface length (D–C/B), and tubercle lengths (H/F, G/F, F–E/F; Table 3). It differs from *Adapis* primarily in that its peroneal tubercle is longer relative to proximal width (C/D) and the tubercle is taller (H/G). The peroneal tubercle of V13015 is more nearly square in outline compared to the more pointed or tapered shape of *Adapis* and *Leptadapis*. The V13015 tubercle shape more closely resembles that of *Cantius* or *Necrolemur* in terms of its proximal outline. The V13015 proximal joint surface is broad and open with a sellar-shaped surface. This joint surface is flatter and taller in *Adapis*. The V13015 joint surface differs considerably from that of *Hoanghoni*, a sivaladapid adapiform that has two circular depressions (Gebo et al., 1999). The V13015 shaft tapers inward toward the head of the first metatarsal, which is small. The tubercle length/proximal width ratio (C/D) of V13015 is most similar to that of *Hoanghoni*. The peroneal tubercle of V13015 is neither as long nor as prominent as it is in *Necrolemur*, and its proximal joint surface is wider. V13015 also compares well with the loriform *Nycticebus* in several first metatarsal ratios (particularly A/B, E/F, G/F, and F–E/F; Table 3).

Table 2
Shanghuang postcranial elements

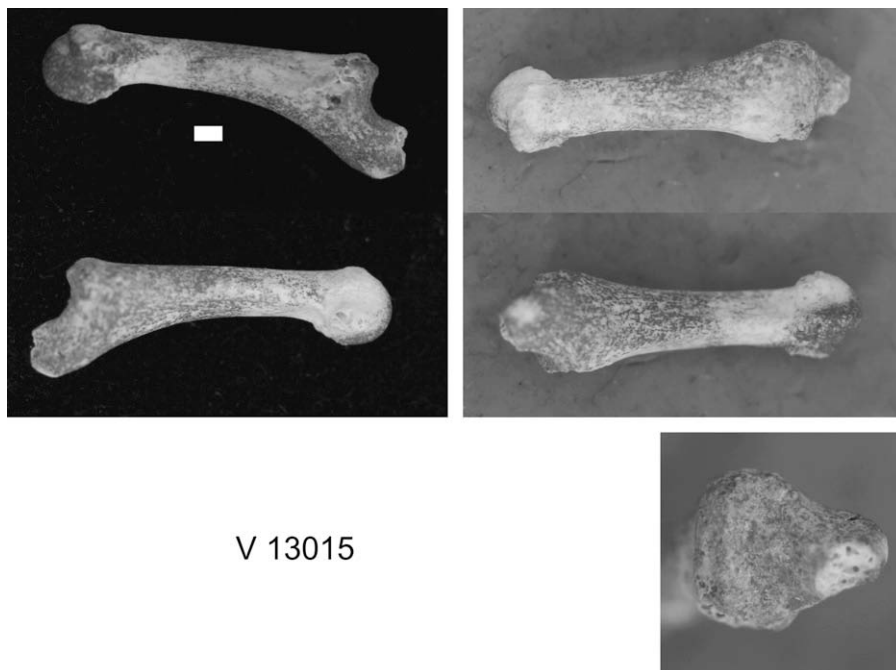
Element	Catalog number	Fissure	Size (g)	Allocation
First metatarsal	V13015	A	250–300	<i>Adapoides troglodytes</i>
Talus	V13016	A	270–530	<i>Adapoides troglodytes</i>
Distal femur	V13017	D	~200	Primitive haplorhine
Innominate	V13032	D	~150	Basal anthropoid
Proximal femur	V13033	E	80–100	Basal anthropoid
Talus	V13034	C	38–42	Primitive haplorhine
Talus	V13035	D	38–41	Primitive haplorhine
Talus	V12323	D	16–18	Primitive haplorhine

A long and robust peroneal tubercle implies a longer lever arm for the peroneus longus muscle insertion. In strepsirhines, long peroneal tubercles are associated with a relatively large peroneus longus muscle (Gebo et al., 2008). Thus, *Adapoides troglodytes* most likely had a forceful peroneus longus muscle coupled with increased mechanical advantage for first metatarsal adduction and opposition, or for eversion (see Boyer et al., 2007). Grasping force would be most critical and advantageous in vertical ascents, making *Adapoides* an excellent and probably frequent climber.

Talus

The IVPP V13016 talus from Fissure A is almost complete and by far the best preserved adapiform talus recovered to date from the Shanghuang fissure-fillings (Fig. 3). However, there is substantial abrasion on the plantar surface of the posterior medial tubercle, some erosion along the outer edges of the medial, lateral, and dorsal surfaces of the talar head, as well as along the dorsal surface of the trochlea. The tip of the lateral fibular facet is broken away as well.

Size estimates for the V13016 talus are 434 g (95% confidence interval = 365–516 g) for talar length (A1), 270 g (confidence interval = 225–325 g) for talar width (A2), and 530 g (confidence interval = 455–619 g) for midtrochlear width (A4, Dagosto and



V 13015

Fig. 1. Comparative views of Shanghuang first metatarsal IVPP V13015. Left: medial (top) and lateral (below); right: dorsal (top), ventral (middle), proximal (bottom). Scale bar = 1 mm.

Table 3

Adapiform first metatarsal measurements (mm) and ratios. A–H represent linear measurements in Fig. 2

	<i>Adapoides troglodytes</i> V13015, n = 1	<i>Adapis parisiensis</i> , n = 1	<i>Hoanghoniuss stehlini</i> V 11845, n = 1	<i>Nycticebus coucang</i> , n = 6
A	1.66	2.5	2.16	2.52
B	3.82	5.47	5.2	5.84
C	2.27	2.5	3.25	2.14
D	4.35	5.75	6.37	5.03
E	11.95	15.88	–	13.31
F	13.34	17.05	–	14.94
G	2.3	2.99	3.3	2.39
H	2.4	2.22	2.85	1.81
A/B	0.43	0.46	0.42	0.43
C/D	0.52	0.43	0.51	0.43
E/F	0.90	0.93	–	0.89
H/G	1.04	0.74	0.86	0.76
H/F	0.18	0.13	–	0.12
D–C/B	0.54	0.59	0.60	0.49
G/F	0.17	0.18	–	0.16
F–E/F	0.10	0.07	–	0.11

Terranova, 1992). Averaged together, the mean size estimate for V13016 is 411.3 g. These estimates compare well with those of the other adapiform tarsals described earlier (211 g, 421 g, and 390–475 g; Gebo et al., 2001). Based on the concordance of dental and postcranial body mass estimates, all of the smaller (<500 g) adapiform tarsals from Shanghuang are best allocated to *Adapoides troglodytes*.

The IVPP V13016 talus has both of the classic strepsirhine talar characters: a laterally sloping talofibular facet and an offset posterior trochlear flexor hallucis longus groove (Dagosto, 1986; Gebo, 1986; Beard et al., 1988). Table 4 (see Fig. 4) lists several comparative measurements and ratios for V13016, *Adapis parisiensis*, and *Nycticebus coucang*. V13016 has a full medial facet for the tibial malleolus that curves well medially distally. This curvature is not as extreme as in lorises (Fig. 5), making *Adapoides* more similar to *Adapis* in this feature. V13016 is similar to *Nycticebus* in talar head angle, neck length (nl/tl and nl/trl), and in talar head width (hw/ht; Table 4). *Adapis* is more similar to *Nycticebus* in talar neck angle, trochlear width (tw/tl), lateral body height (lbh/mtrw and lbh/trl), and midtrochlear width (mtrw/trl) ratios (Table 4). The trochlea is very flat in V13016, extending onto a wide talar neck with trochlear rims that both curve medially. The trochlea in V13016 is much flatter than the well-grooved trochlear surface of living lorises or the slightly grooved surface of *Adapis*. An expanded extension of the trochlear facet onto the talar neck with distal trochlear grooving are features that are characteristic of loriseine tali. Like lorises and *Adapis*, V13016 has a distinctly flattened talar head and body, and a plantarly angled talar head (although not as strongly angled as in living lorises; Dagosto, 1983; Gebo, 1988). The V13016 talus has a small and very short posterior plantar facet

for the calcaneus (posterior calcaneal facet), as is typical for lorises as well. V13016 differs from lorises in that it has a relatively longer talar neck and a very small trochlear shelf, a feature that is lost in lorises and *Adapis*. The lateral trochlear rim is higher in V13016 as it is in *Adapis* and lorises. Overall, V13016, lorises, and *Adapis* all share talar features that are unlike most other primates (e.g., highly angled talar necks or very wide talar heads).

The V13016 adapiform talus compares well to the broken V12307 adapiform talus (Fig. 6) described in Gebo et al. (2001). For example, their body height/midtrochlear width ratios, body height to talar length ratios, midtrochlear width to talar length ratios, and talar head angles are all very similar. The specimens are more divergent in terms of their talar neck angles (32 and 40 degrees), but this is probably within the range of variation for this measure in this taxon. The V12307 talus is smaller (talar width equals 4.2 mm vs. 4.91 mm in V13016), but given the paucity of specimens and the incompleteness of this material, we see no need to recognize separate taxa at present.

Overall, the V13016 talus is morphologically very similar to living lorises. In fact, in terms of talar neck length or trochlear extension onto the neck, this talus is morphologically more similar to extant lorises than *Adapis* is, a fossil primate with otherwise loriseine-like skeletal anatomy (Dagosto, 1983, 1993). Functionally, this talus with its low talar body, long curved neck and body, and flattened talar head and trochlear surface suggests considerable ankle joint mobility. It belongs to a foot adapted for cautious arboreality, being capable of arboreal quadrupedalism and climbing with very flexible foot grasping positions (Grand, 1967; Dagosto, 1983; Gebo, 1988). This ankle is not morphologically oriented toward leaping or forceful propulsion. We infer cautious, fluid, and more cryptic movement patterns akin to loris arboreality with a foot adapted for canopy tangles, lianas, or dense small-branch thickets.

Description of haplorhine postcranial elements

Innominate (os coxa)

A left innominate (IVPP V13032) from Shanghuang Fissure D is broken both proximally and distally, and is missing the entire pubic ramus (Fig. 7). Its absolute length is 16.3 mm. This specimen is smaller than innominates of 200 g primates like *Galago matschiei* or *Galago senegalensis* (Smith and Jungers, 1997). The acetabulum is similar in size to those of larger individuals of *Tarsius syrichta* (126–153 g; Dagosto et al., 2001) but slightly larger than those of *Cebuella pygmaea* (112–160 g; Ford and Davis, 1992). We estimate body size for this specimen to be approximately 150 g.

Most small mammals such as rodents, lagomorphs, lepticids, flying lemurs, and most primitive primates [e.g., galagos, lorises, cheirogaleids, tarsiers, omomyids such as *Hemiacodon*, *Omomys* (Anemone and Covert, 2000), or *Nannopithecus*] have narrow, rod-

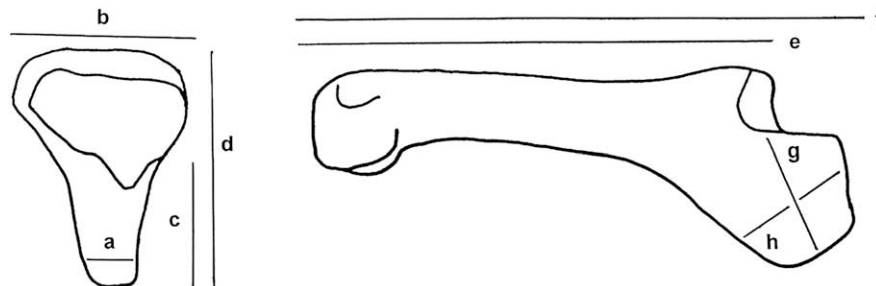


Fig. 2. First metatarsal measurements (A–H; see Table 3).

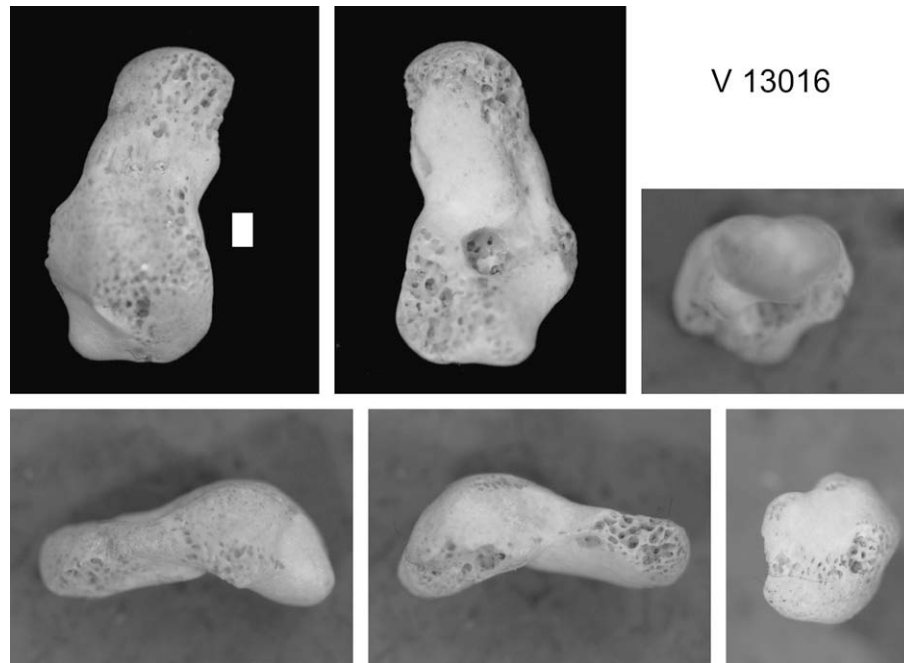


Fig. 3. Comparative views of Shanghuang talus IVPP V13016. Top: dorsal, plantar, and distal views; bottom: lateral, medial, and posterior views. Scale bar = 1 mm.

like ilia. The V13032 os coxa is not rod-like but is wide and rectangular in shape, as is observed among anthropoid primates. Fleagle and Kay (1987) have suggested that the presence of a wide gluteal plane is an anthropoid synapomorphy. Mammals that have been described with rod-shaped ilia all possess expanded cranial regions for this rod-like pelvic structure (Fig. 8). The rod-like shape begins at the base of the ilium, just above the acetabulum. This makes the central part of the ilium narrow and, thus, it has been described as rod-like. In contrast, larger strepsirhines (e.g., lemurs, indriids, and notharctines) possess wider ilia (Fig. 9) but differ from anthropoids in the shape of the ilium. The cranial region of the

ilium is rounded in notharctines and splayed outward in lemurs and indriids. These taxa also possess a narrowing of the ilium after the rectus femoris tubercle and are greatly curved along this edge as it proceeds cranially. In anthropoids, this region is more rectangular in appearance with straighter edges along the edge separating the iliac and gluteal planes (margo acetabuli). Carnivores also possess wider iliac surfaces but with a shorter ilium; they lack a prominent ridge between the iliac and gluteal planes as found in V13032, have different curvatures of alignment for the three pelvic bones, and are generally much larger mammals than the 150 g V13032 specimen. Tree shrews, a small mammal relative to carnivores or lemurs, also have an expanded cranial region of the ilium, and they possess a pelvic structure similar to that of lemurs with a prominent rectus femoris tubercle and great curvature along the edge between the iliac and gluteal planes (the margo acetabuli), but with more laterally splayed ilia. The morphology surrounding the ridge between the iliac and gluteal planes and the shape of the iliac plane in tree shrews also differs from the morphology of anthropoids. After all of these comparisons are made, the V13032 specimen most likely represents an anthropoid primate.

The ilium is divided into three planes: the relatively large and wide dorsal and medial surfaces corresponding to the gluteal and sacral planes, respectively, and the smaller ventral surface being the iliac or frontal plane (Fig. 8). The edges of these planes are separated by a ridge (see Fleagle and Simons, 1979). The edge between the iliac and sacral planes is called margo pubis (Fig. 8). The edge separating the sacral and the gluteal planes is called margo ischiadicus. The edge separating the iliac and gluteal planes is called margo acetabuli. The latter is prominent in anthropoids and in V13032 (Fig. 10). However, it is not as prominent in V13032 as in *Proteopithecus* (DPC 9278), but is more similar to the condition in *Apidium* (Fig. 11; Gebo et al., 1994) that is more pronounced than in extant platyrrhines. The margo acetabuli ridge begins at the dorsal rim of the acetabulum as in *Apidium*, *Proteopithecus*, and many platyrrhines, whereas in notharctines, lemurs, and indriids there is a short gap distal to the formation of this ridge. The V13032 element lacks a prominent anterior inferior iliac spine for the origin of rectus femoris. This spine or tubercle is prominent in notharctine, lemurid, and indriid ilia (see Gregory, 1920) as well as in the rod-like ilia of galagos,

Table 4
Adapiform talar measurements (mm) and ratios. See Fig. 4

Measurements	<i>Adapoides troglodytes</i> V13016, n = 1	<i>Adapis parisiensis</i> , n = 2	<i>Nycticebus coucang</i> , n = 13
Talar length (tl)	9.61	11.5	9.89
Talar width (tw)	4.91	7.75	6.56
Trochlear length (trl)	5.25	7.45	6.38
Midtrochlear width (mtrw)	3.85	4.65	3.85
Head height (hht)	2.25	4.24	3.04
Head width (hw)	3.6	5.49	5.49
Neck length (nl)	4.5	3.75	4.98
Lateral body height (lbh)	3.3	5.45	4.5
Lateral body length (lbl)	6.03	6.88	–
Posterior facet length (pfl)	3.25	6.4	3.74
Posterior facet width (maximum, pfwmax)	2.0	3.52	–
Posterior facet width (minimum, pfwmin)	1.6	2.81	–
Talar neck angle	32°	40.5°	39.6°
Talar head angle	17°	6.5°	19.8°
Ratios			
tw/tl	0.51	0.67	0.66
lbh/mtrw	0.86	1.17	1.17
lbh/trl	0.63	0.73	0.71
nl/tl	0.47	0.33	0.50
nl/trl	0.86	0.50	0.78
hw/hht	1.6	1.29	1.81
hw/mtrw	0.94	1.18	1.42
mtrw/trl	0.73	0.62	0.60

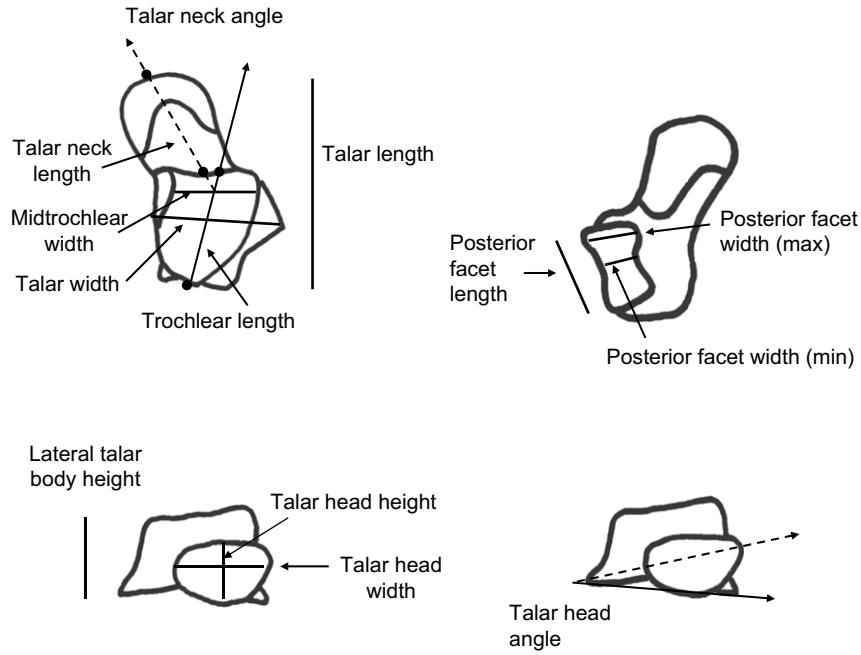


Fig. 4. Talar measurements (see Table 4).

lorises, cheriogaleids, tarsiers, and omomyids. In this feature, V13032 is again similar to *Apidium*, *Proteopithecus*, and platyrrhine primates. The iliac plane is flat in V13032 as it is in anthropoids. In contrast, notharctine, lemurid, and indriid innominates show a depression at the caudal emergence of the iliac plane.

The sacral plane is large, wide, and flat. It has an elevated ridge of bone running craniocaudally along the sacral plane between the ilium and ischium. This craniocaudal ridge is similar to that of *Apidium*. It is not found in notharctine, lemurid, or indriid innominates. The sacral plane of V13032 also lacks the projecting sacral facet commonly found in the ilium of notharctines like *Cantius*, *Smilodectes*, and *Notharctus*.

The ischium, although incomplete, would have been relatively long as in the parapithecoid, *Apidium*, as it also is for many extant and extinct “prosimian” primates. It is not short like those of tarsiers and indriids, and it lacks the large dorsal projection of the ischium associated with vertical clinging and leaping (Fleagle and Anapol, 1992). A longer ischium is often found in leaping primates,

especially quadrupedal ones (Fleagle, 1977; Fleagle and Simons, 1979, 1995; Anemone and Covert, 2000). V13032 lacks an ischial spine, like *Apidium* and platyrrhines. This again contrasts with the prominent spine of lemurids and indriids, and the smaller spine of notharctines. The pubic ramus is also similar in morphology to that of *Apidium* and platyrrhines. It lacks the cranial or upward pubic curvature observed among notharctines.

The dorsal rim of the acetabulum is larger and more buttressed than is the ventral rim. This feature suggests more quadrupedal than leaping movements and is similar to that in anthropoid primates (Schultz, 1969; Fleagle and Simons, 1979, 1995). The acetabulum also has a larger dorsal than ventral facet. The internal morphology of the acetabulum is extremely similar to that of *Apidium* (e.g., DPC 1036). The acetabular internal diameter is 4.25 mm across while the outside rim to rim diameter is 5.18 mm. Following Schultz (1969), the diameter of this acetabulum is 4.73 mm, dorsal breadth, 4.27 mm; ventral breadth, 2.73 mm; medial breadth, 4.05 mm; and acetabular notch (incisura acetabuli), 2.08 mm. The dorsal acetabular facet is

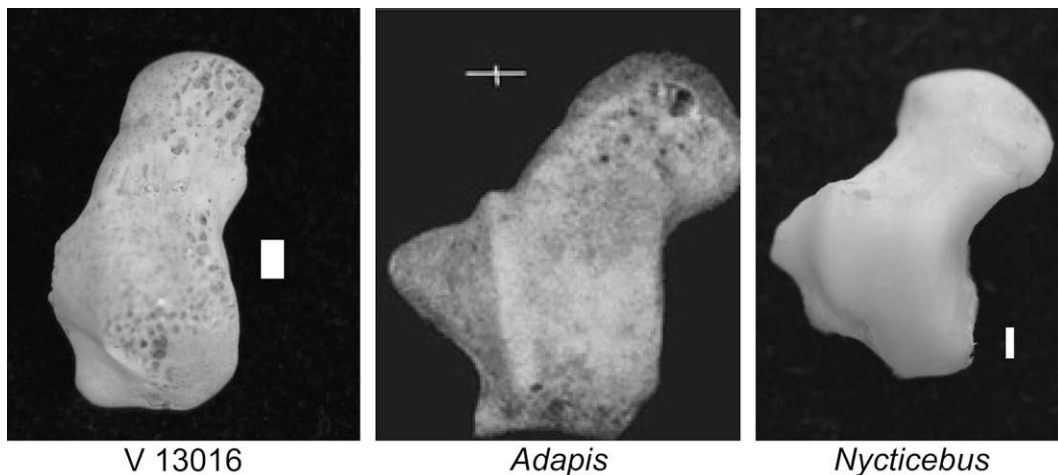


Fig. 5. Comparative dorsal views of left tali of V13016 (left, scale bar = 1 mm), *Adapis parisiensis* (middle, scale = 2 mm), and *Nycticebus coucang* (right, scale bar = 1 mm).

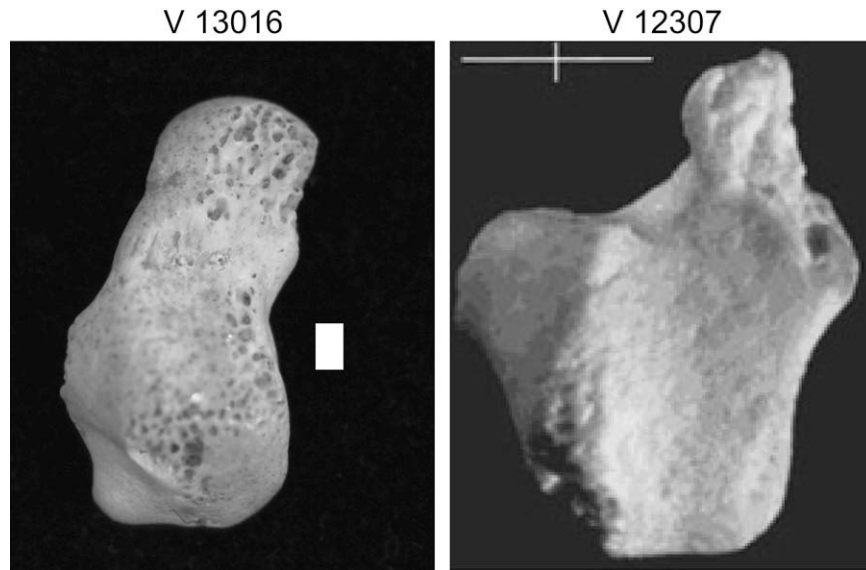


Fig. 6. Shanghuang adapiform tali V13016 (left, scale bar = 1 mm) compared to V12307 (right, scale bar = 2 mm).

2.5 mm wide and 3.0 mm in height. The ventral facet is 2.35 mm wide and 2.69 mm in height. Maximal acetabular depth is 3.08 mm. Using these data, we calculated *Schultz's* (1969) ratios for V13032: acetabular depth/diameter is 59%, incisura/diameter 44%, ventral breadth/dorsal breadth 64%, and diameter/three breadths 43%. The values for the fossil overlap both extant anthropoid and “prosimian” primates, and are thus of no help in making an allocation.

In overall morphology, V13032 is most similar to anthropoid primates (i.e., parapythecids, proteopithecids, and platyrrhines). It does not share any special similarities with tarsiers or omomyids, nor does it compare well with strepsirrhine primates. Based on its morphology, it is most likely allocated to the basal anthropoid taxa found at Shanghuang, either the more common Eosimiidae, or the rarer “Morphology 4” group of more advanced “protoanthropoids” (see Gebo et al., 2001). Given its advanced similarity to parapythecids, proteopithecids, and platyrrhines, the V13032 specimen might be best considered as part of the “Morphology 4” group of

more advanced protoanthropoids. In terms of functional capabilities, the V13032 innominate matches best with arboreal quadrupedal primates, a locomotor interpretation that also applies to basal anthropoid tarsals (Gebo et al., 2001). The body size estimate for V13032 (~150 g) makes it one of the larger basal anthropoids at Shanghuang (Gebo et al., 2001).

Proximal femur

IVVP V13033 is a proximal femur from Shanghuang Fissure E (Fig. 12). It is broken at midshaft and the edges of the greater and lesser trochanters are eroded. There is also breakage posteriorly along the trochanteric ridge and the back of the greater trochanter. The IVVP V13033 proximal femur is smaller than that of tarsiers or the pygmy marmoset (taxa weighing between 100–150 g; Smith and Jungers, 1997). It is larger than all but the largest specimens of *Microcebus* (25–110 g; Rasoloarison et al., 2000). The breadth of the

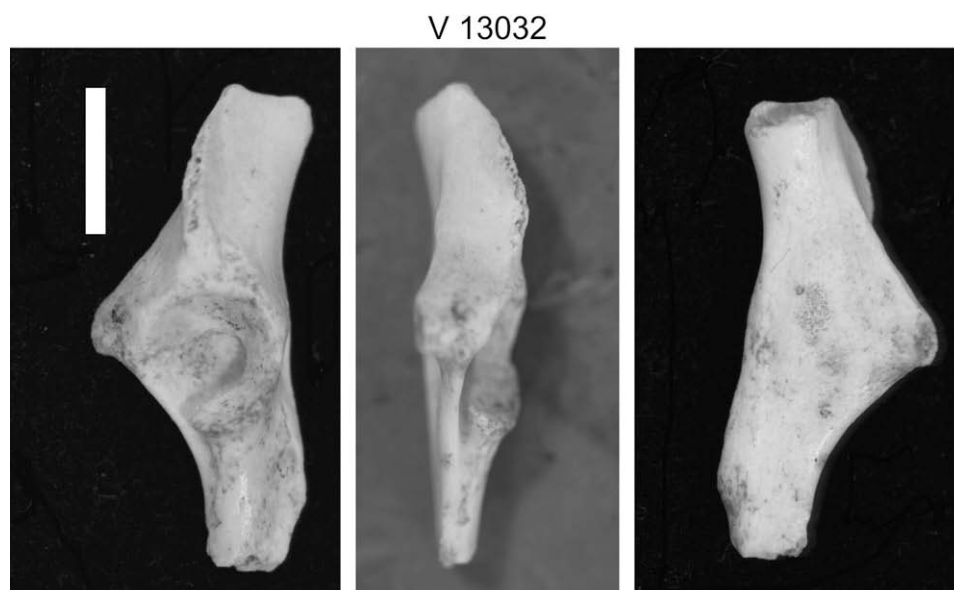


Fig. 7. IVVP V13032 innominate from Shanghuang Fissure D. Left: lateral view (gluteal plane); middle: ventral view (iliac plane); right: medial view (sacral plane). Scale bar = 5 mm.

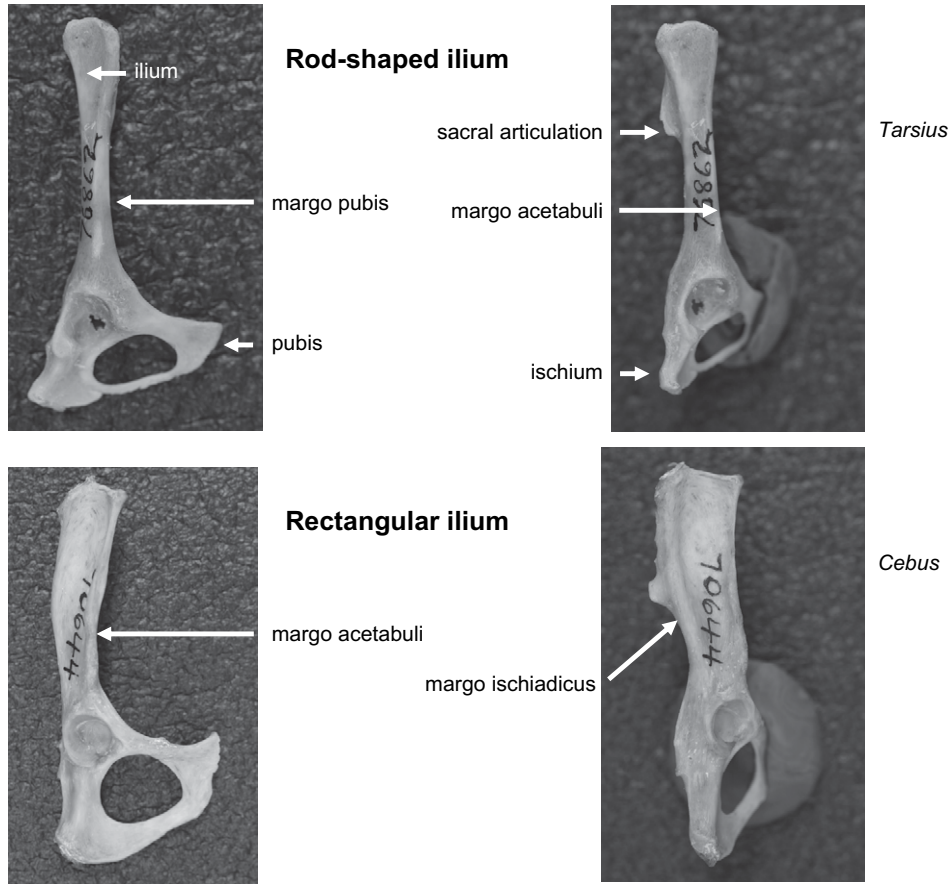


Fig. 8. Two views of a rod-shaped ilium (above: *Tarsius*) versus a wider rectangular ilium (below: *Cebus*).

shaft below the lesser trochanter (2.63 mm) is similar to that of *Shoshonius cooperi* (CM 69755 = 2.59 mm) as is its mediolateral width at the midshaft (2.33 mm for IVPP V13033 vs. 2.46 mm for *Shoshonius*). *Shoshonius cooperi* has been estimated to weigh 60–90 g (Dagosto et al., 1999). Based on these comparisons, we estimate the body size of IVPP V13033 to be between 80–100 g,

outside the range of any adapiform primates at Shanghuang, but consistent with several of the haplorhine groups.

The femoral head extends proximally above the level of the greater trochanter in V13033 (Fig. 12). This morphology is similar to many anthropoid primates, but contrasts with leaping “prosimian” primates, in which the greater trochanter tends to extend

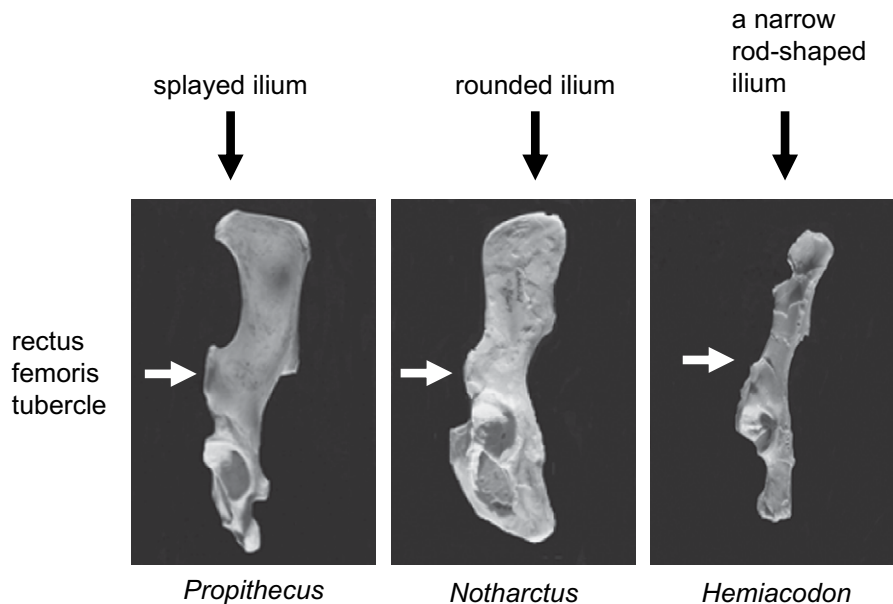


Fig. 9. Comparative images of innominates. *Propithecus verreauxi* (left), *Notharctus tenebrosus* (middle), and *Hemiacodon gracilis* (right).

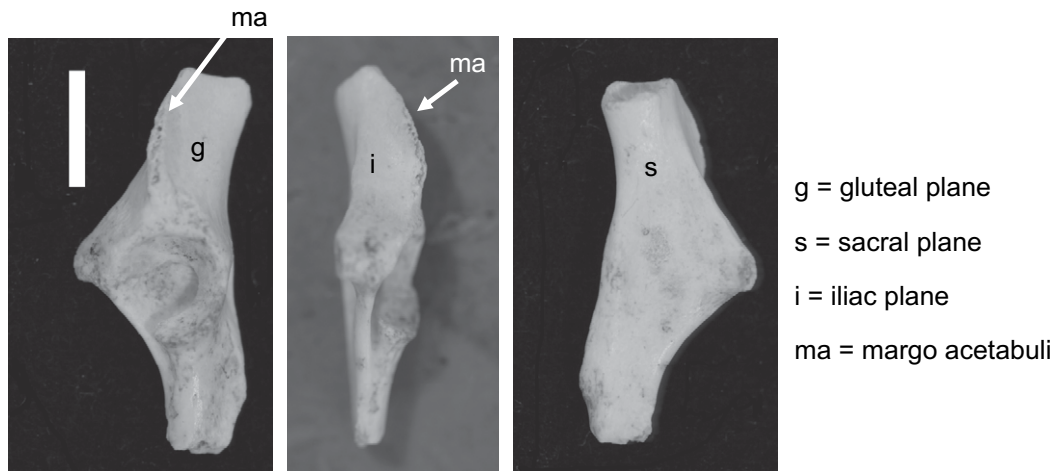


Fig. 10. Three views of V13032 showing its prominent margo acetabuli ridge between the iliac and gluteal planes.

proximally beyond the femoral head. The shape of the femoral head is round, although it flattens along the posterior side and extends onto the femoral neck (Fig. 13). A depression for ligamentum teres is present medially. The femoral head shape of V13033 compares well with the majority of primates; it does not exhibit the cylindrical or semi-cylindrical shape of galagos, tarsiers, or omomyids. The angle of the femoral neck relative to the shaft is 57° , the same as that of *Apidium* and similar to that of many other anthropoids (Dagosto and Schmid, 1996). In contrast, this angle is higher in omomyids and tarsiers, the head being positioned more perpendicular to the shaft (Simpson, 1940; Dagosto and Schmid, 1996; Anemone and Covert, 2000). The femoral neck is long, as in anthropoids and *Necrolemur*, not short, as in omomyids and tarsiers (Dagosto and Schmid, 1996; Anemone and Covert, 2000). Posteriorly, there is no paratrochanteric crest (crista paratrochanterica), a feature present among parapithecids, proteopithecids, and platyrrhines (Ford, 1986; Gebo et al., 1994). This feature is lacking in tarsiers and often absent among omomyids (Dagosto and Schmid, 1996).

V13033 has three trochanters (Fig. 12). The greater trochanter, although broken posterolaterally, appears to be neither as large nor as wide as those of *Apidium phiomense*, *?Proteopithecus* (DPC 7529), and *Necrolemur* sp. (AIZ 9480). The greater trochanter and the proximal shaft are bowed anteriorly in V13033 to a greater degree than in the Fayum specimens or platyrrhines, but not so much as in *Necrolemur*, *Microchoerus*, or omomyids (Dagosto and Schmid, 1996). Strong anterior bowing of the proximal femur is associated with leaping in primates (Walker, 1974; Anemone, 1990; Dagosto and Schmid, 1996). In V13033 the greater trochanter continues onto the proximal shaft as an anterior pillar, a feature also associated with leaping primates (see Dagosto and Schmid, 1996). Both the lesser and third trochanters of V13033 are prominent, a morphological arrangement similar to DPC 7529 (*?Proteopithecus*; Fig. 14). The lesser trochanter is quite large, as it is in specimens from the Fayum and *Microchoerus*; *Necrolemur*, in contrast, has a smaller lesser trochanter. The angle of the lesser trochanter is 42° , a value similar to many anthropoids, including taxa from the Fayum, with the exception of callitrichids (Dagosto and Schmid, 1996). Lesser trochanter angles are lower in omomyids, tarsiers, adapiforms, and lemuriform primates (Dagosto and Schmid, 1996). The third trochanter in V13033 is prominent, being similar in size and development to DPC 7529 (*?Proteopithecus*). This trochanter is absent in *Apidium* and in most extant anthropoids.

There is a long trochanteric fossa and trochanteric ridge that runs distally downward and across to the lesser trochanter in

V13033 (Fig. 12). In *Necrolemur*, *Apidium*, and *?Proteopithecus*, the trochanteric ridge runs straight distally, while it runs obliquely across the shaft in catarrhines (Gebo et al., 1994; Dagosto and Schmid, 1996). A long trochanteric fossa in V13033 is similar to that of parapithecids, proteopithecids, and to *Necrolemur* (Dagosto and Schmid, 1996), but is different than the flattened and more open fossa of platyrrhines, tarsiers, or strepsirrhine primates. The area of the femoral shaft between the lesser and third trochanters posteriorly is buttressed by a bony thickening. This region shows similarities to *Apidium phiomense* (in particular, DPC 2463). Along the medial shaft and distal to the lesser trochanter is a long sulcus. Its position suggests the insertion point for vastus medialis or for one or both of the adductors (adductor longus and adductor magnus).

Comparing the V13033 morphological ratios (Table 5) with those published in Dagosto and Schmid (1996) shows it to possess a lesser trochanter projection (LTB/BSDLT) comparable to both “prosimian” and anthropoid primates, a third trochanter projection (3TB/BSDLT) similar to “prosimian” primates, a long neck and head (N1/BSDLT) like that of lemurids, indriids, cheirogaleids, platyrrhines, and catarrhines, a long neck (N2/BSDLT) that is most similar to lemurids, indriids, and New and Old World monkeys, and a long trochanteric fossa (FL/BSDLT) similar to *Notharctus*, lemurids,

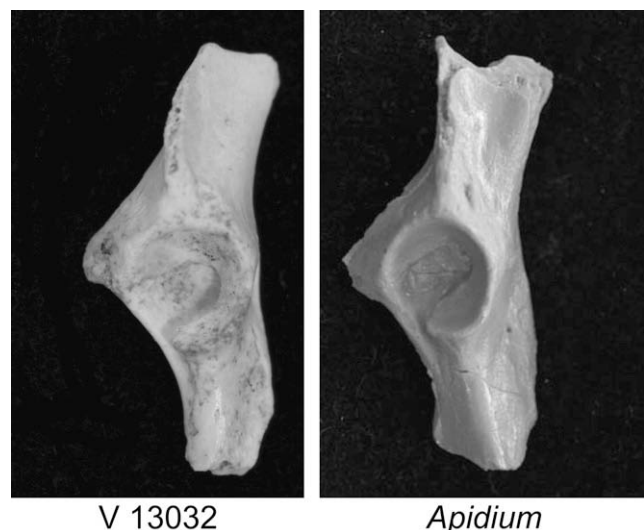


Fig. 11. V13032 (left) compared to *Apidium* (right, DPC 1036, reversed).

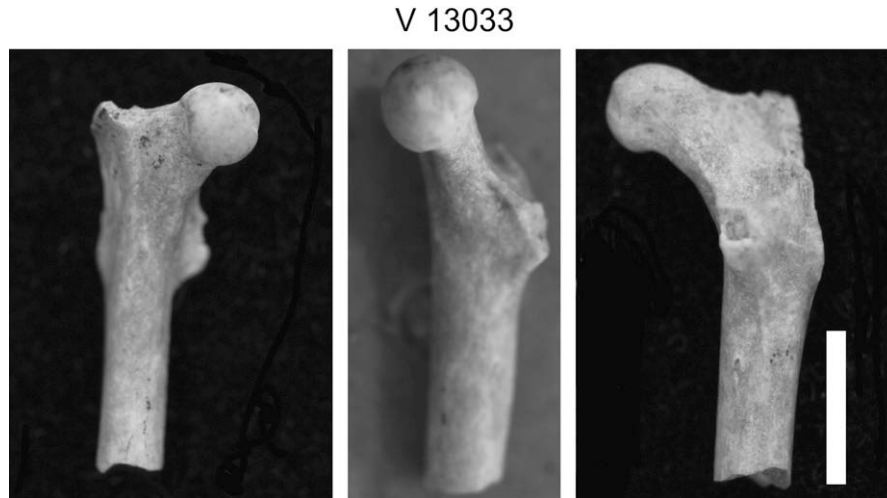


Fig. 12. Anterior, medial, and posterior views of IVPP V13033. Scale bar = 5 mm.

callitrichids, cebids, and *Macaca*. The V13033 femoral ratios are remarkably similar to Fayum anthropoids and *Necrolemur* (Table 5). Dagosto and Schmid (1996) note that a relatively low neck angle and a higher lesser trochanter angle may be derived anthropoid characters. Both are present in V13033.

Overall, the V13033 femur displays morphological similarities to microchoerid and Fayum anthropoid primates (Fig. 14). It is not particularly similar to omomyids, tarsiids, or to platyrrhines, nor does it resemble living or extinct strepsirrhine primates (adapiforms or lemuriforms). Given this overall morphological assessment, the V13033 femur is best allocated to one of the two basal anthropoid groups occurring at Shanghuang, either the more common Eosimiidae, or the rarer “Morphology 4” group of more-advanced anthropoids (see Gebo et al., 2001). The anterior bowing of this femur as well as its prominent third trochanter suggest a frequent quadrupedal leaper. If so, the V13033 femur might be better allocated to the Eosimiidae, a more leaping oriented lineage than the more quadrupedal-climbing “Morphology 4” group, as judged by tarsal morphology (see Gebo et al., 2001). The size estimate of V13033 is well within the tarsal size estimates for either of these basal anthropoid groups.

Distal femur

The IVPP V13017 distal femur is from Shanghuang Fissure D (Fig. 15). It is a large specimen relative to the other postcranial bones from Shanghuang and is much too large to belong to the

same species as the IVPP V13033 proximal femur described above. V13017 compares best in terms of size with galagos like *Galago senegalensis* (199–227 g) or *Galago matschiei* (207–212 g; Smith and Jungers, 1997), and we therefore estimate that it pertains to an animal having an adult body mass of approximately 200 g. A body size of 200 g is much larger than almost all of the haplorhine postcranial specimens known from Shanghuang, with one exception. One calcaneus (V12276) has been estimated to come from a 350 g primate (Gebo et al., 2001). On the other hand, 200 g is at the smallest end of the known size range of Shanghuang adapiforms. The smallest Shanghuang adapiform, *Adapoides troglodytes*, is estimated to weigh between 285–343 g using molar dental dimensions and the all-primate and all-prosimian regression equations developed by Conroy (1987). Moreover, the leaping behavior suggested by the morphology of V13017 precludes this specimen from being associated with *Adapoides*, a primate that likely was primarily quadrupedal. Therefore, the best allocation for the V13017 distal femoral specimen seems to be with the relatively rare large haplorhine primates recovered from the Shanghuang fissures.

V13017 is a distal femur (Figs. 15 and 16) that exhibits features associated with leaping strepsirrhines and tarsiiforms (Napier and Walker, 1967; McArdle, 1981; Anemone, 1990; Dagosto, 1993). The knee is anteroposteriorly tall, with a high lateral patellar rim. Lateral condylar height relative to bicondylar width (1.14) shows V13017 to be similar to a variety of leaping primates (Table 6). Ratio values for *Hemiacodon* (1.16), *Shoshonius* (1.12), *Omomys* (1.11), and *Tarsius* (1.17) are extremely similar to V13017, whereas values for *Microchoerus* (>0.99), *Cantius*, *Smilodectes*, and *Notharctus* (97–99) or *Galago* (1.1) are not significantly different (Dagosto, 1993; Anemone and Covert, 2000). The patellar groove is narrow in V13017 (Fig. 15), like that observed among omomyids and *Apidium*. It is not wide as in tarsiids, microchoerids, notharctines, or platyrrhines. *Apidium* also has a tall knee (1.05 height ratio) with a narrow patellar facet and a deep intercondylar notch (Fleagle and Simons, 1995). Medially, the V13017 specimen has a strong medial epicondylar bulge as in tarsiids and indriids, a feature lacking among omomyids, microchoerids, notharctines, and galagos (Dagosto, 1993). Laterally, there is a prominent popliteal groove. Above this groove is a flattened area for the attachment of the lateral collateral ligament.

Allocation of the V13017 distal femur is difficult given its classic “prosimian” leaping features. This distal femur shows no significant morphological similarities to anthropoids, including *Apidium*, or to

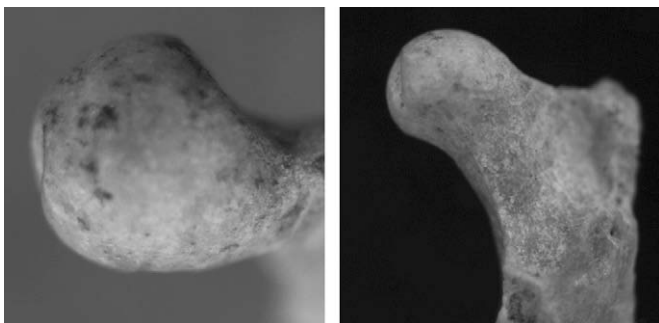


Fig. 13. Femoral head images of IVPP V13033, posterocranial (left) and posterior (right).

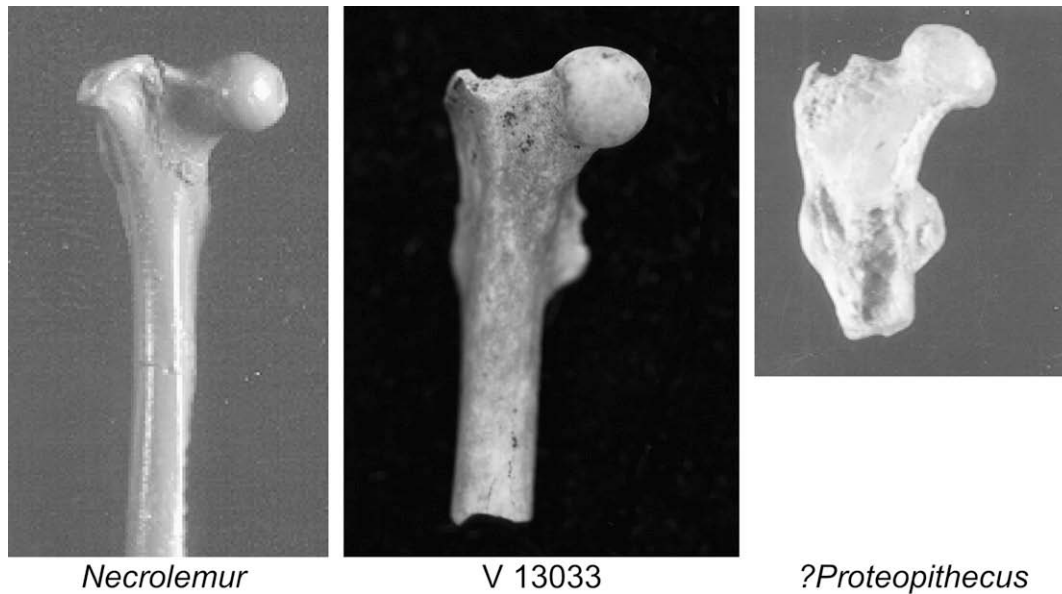


Fig. 14. Proximal femoral comparisons between *Necrolemur* (left), V13033 (center), and DPC 7529 (?*Proteopithecus*; right).

Adapis, a taxon with more flattened knees. Its general proportions are more “prosimian”-like, and it shares a medial epicondylar bulge with tarsiers, and a narrow patellar groove with omomyids and *Apidium*. Although not morphologically unlike notharctine adapiforms or lemuriiforms, it is too small to be allocated to any of the known adapiform taxa at Shanghuang. Our tarsal “Morphology 1” group might best serve as an initial allocation for this distal femur, being morphologically most similar to omomyid primates.

Table 5

Haplorhine femoral measurements (mm) and ratios. Measurements with () designations are from Dagosto and Schmid (1996)

	V13033	DPC 7529 ? <i>Proteopithecus</i>	<i>Apidium</i> <i>phiomense</i> , sp. n = 3	<i>Necrolemur</i>
Femoral head w	2.92	3.8	7.41	3.57
Femoral head ht	3.02	4.3	7.04	3.47
Neck length 1 (N1)	4.93	6.92	10.91	5.01
Neck length 2 (N2)	3.01	4.46	6.2	3.53
Proximal width	6.32	9.83	16.52	7.94
Midshaft a-p depth	2.64	–	6.18	2.94
Midshaft m-l width	2.33	–	6.53	2.9
L to 3rd trochanter	6.86	5.9	–	6.81
Breadth of the lesser trochanter (LTB)	1.72	3.27	4.32	1.71
Height of the lesser trochanter (LTH)	4.3	5.38	10.09	3.98
Breadth of the third trochanter (3TB)	1.05	1.73	–	0.4
Height of the third trochanter (3TH)	4.7	4.57	–	2.16
Length of trochanteric fossa (FL)	3.99	6.18	11.0	6.38
Shaft breadth distal of the trochanters (BSDLT)	2.63	4.26	5.65	2.8
Angle of lesser trochanter (LTA)	42°	40°	39°	47°
Angle of femoral head and neck (NA)	57°	57°	56°	65°
Ratios				
LTB/BSDLT	0.65	0.77	0.77	0.61
3TB/BSDLT	0.40	0.41	–	0.14
N1/BSDLT	1.87	1.62	1.93	1.79
N2/BSDLT	1.14	1.05	1.10	1.26
FL/BSDLT	1.52	1.45	1.42	1.52

Tali

Morph 1. Two new small haplorhine tali have been recovered from the Shanghuang fissure-fillings, one from Fissure C (IVPP V13034) and another from Fissure D (IVPP V13035). In both specimens the talar head is missing, but otherwise they are generally complete. Body size estimates made from midtrochlear width and talar width (Table 7) yield values of 38 and 41 g, respectively, for V13035 (with a 95% confidence interval of 26–59 g). The V13034 specimen is similarly estimated at 42 and 38 g (with a 95% confidence interval between 26 and 62 g). At approximately 40 g, these two tali fall just above the upper size range of *Microcebus berthae*, a pygmy mouse lemur that weighs 30.6 g on average [with a size range between 24.5 and 38 g (Rasoloarison et al., 2000)]. In contrast, talar measurements for these two fossil tali are consistently smaller than the one talus of *Microcebus berthae* we were able to measure (Table 7). Therefore, the body size of the pygmy mouse lemur represents a reasonable approximation for V13034 and V13035.

The steep talofibular facet and midtrochlear position of the flexor fibularis groove demonstrate that these two tali belong to haplorhine primates (Fig. 17; Dagosto, 1986; Gebo, 1986; Beard et al., 1988). In addition, they are too tiny to represent any of the Shanghuang adapiforms. V13034 and V13035 are morphologically most similar to North American omomyid primates with their tall talar bodies, parallel trochlear rims, full medial articular facets for the tibia, and well-grooved trochleae. Both possess an angled posterior trochlear edge similar to that of several omomyid, eosimiid, and platyrrhine tali. V13035 differs from V13034 in its more strongly angled talar neck (Table 7). The talar head is a region that is useful in distinguishing anaptomorphine from omomyine tali. Anaptomorphines, like *Teilhardina*, *Tetonius*, *Arapahovius*, *Anaptomorphus*, *Absarokius*, and *Anemorhysis*, have large talar heads and long necks relative to their proportionally smaller talar bodies. In omomyines, the head and neck proportions relative to the talar body are less extreme. Unfortunately, the talar necks and heads of V13034 and V13035 are broken. The talar body is flatter among anaptomorphines relative to omomyines like *Omomys* and *Hemiacodon*. In this feature, the V13034 and V13035 tali more closely resemble omomyine omomyids like *Omomys* and *Hemiacodon* than anaptomorphines, and also differ from a previously described

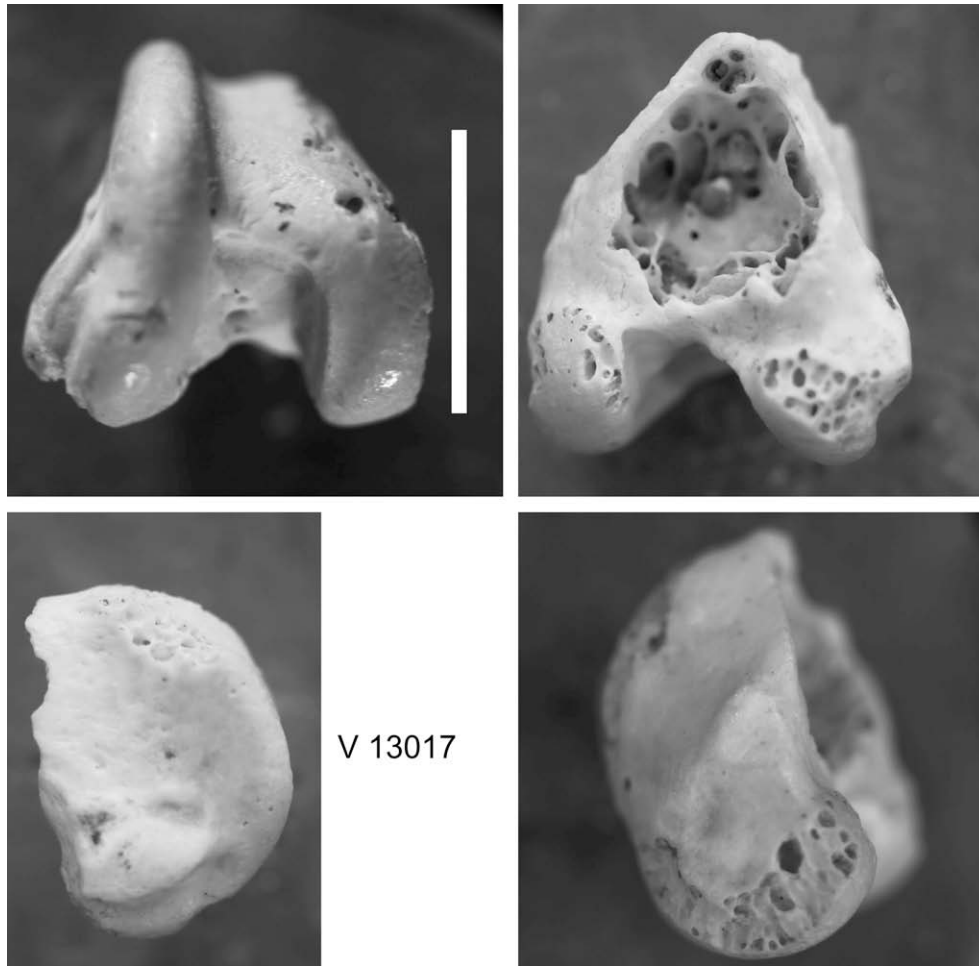


Fig. 15. Anterior and posterior views of V13017 (top; scale bar = 5 mm.); lateral (below left) and medial views (below right).

Shanghuang specimen (V11857) which, like anaptomorphines, has a relatively lower talar body. Both V13034 and V13035 have moderate to slight posterior trochlear shelves, a feature that also resembles anaptomorphine and omomyine omomyids. The posterior trochlear shelf is smaller in omomyines (Rosenberger and Dagosto, 1992) than anaptomorphines, and V13034 and V13035 most resemble omomyines in this feature. Dagosto (1993) has noted that anaptomorphines possess a more rounded medial trochlear rim that extends further distally than the lateral rim relative to the condition in omomyines (Dagosto, 1993).

Omomyines possess sharper trochlear rims (especially the medial rim) and more equal extension of the trochlear rims distally (Dagosto, 1993). In contrast, V13434 and V13035 possess rounded medial rims with a dorsolateral trochlear extension.

We would allocate both specimens (V13034 and V13035) to a species within a single genus. They are very similar to each other in overall talar morphology and size, being distinguished primarily by their talar neck angles. These specimens are similar to our “Morphology 1” tarsal group (Gebo et al., 2001). The new specimens V13034 and V13035 differ, however, from V11857 (Fig. 10 in



Fig. 16. Distal femoral comparisons. Left: *Hemicodon gracilis*, AMNH 12613, reversed from Szalay (1976); middle: V13017; right: *Necrolemur*.

Table 6
Haplorhine distal femoral measurements (mm) and ratios

	V13017	<i>Shoshonius cooperi</i> (CM 69764)	<i>Hemiacodon gracilis</i> (AMNH 12613)	<i>Apidium phiomense</i> (DPC 1030)	<i>Notharctus tenebrosus</i> (AMNH 11478)
Distal bicondylar width (BW)	8.35	5.05	8.1	14.8	16.61
Lateral condyle distal height (LCH)	9.54	5.63	10.15	15.5	17.79
Medial condyle distal height (MCH)	9.2	5.02	8.85	15.2	16.48
Patellar groove width (PG)	2.44	1.58	1.89	4.52	5.62
Medial condyle width (MCW)	2.20	1.71	2.7	4.42	6.02
Lateral condyle width (LCW)	2.73	–	3.16	4.79	5.98
Intercondyle gap width (IG)	3.06	1.43	1.96	3.48	4.75
Ratios					
LCH/BW	1.14	1.12	1.16	1.05	1.07
MCH/BW	1.10	0.99	1.09	1.02	0.99
PG/BW	0.29	0.31	0.24	0.31	0.36
MCW/LCW	0.81	–	0.85	0.92	1.01
IG/BW	0.37	0.28	0.24	0.24	0.29

Gebo et al., 2001). V13034 and V13035 (plus V12297, V12298, and V12299) are more similar to omomyines in talar morphology, whereas V11857 is more anaptomorphine-like. Talar neck angles differ considerably among the Shanghuang omomyine-types, suggesting perhaps an even greater diversity within this morph. Morphology 1 tali at Shanghuang exhibit both of the morphologies observed in North American omomyids.

Morph 2. A tiny new talus, IVPP V12323 from Fissure D (Fig. 18), is smaller than the V13034 and V13535 tali. It is similar in size to the astragali of shrews (see *Crociodura lanosa*, 15 g, Gebo, 2004: his Fig. 2). Talar width and midtrochlear width yield body mass estimates of 18.4 and 16.4 g for V12323 (mean = 17.4 g; the combined 95% confidence interval ranges from 10.2 to 29.6 g). This size range is smaller than that of any living primate but compares well with size estimates made from the smallest Shanghuang calcanei (9.5 and 23.6 g; Gebo et al., 2000). The V12323 talus from Shanghuang is the smallest primate talus ever reported.

In terms of morphology, the V12323 talus differs from any previously described Shanghuang primate morph but shows several phenetic similarities to *Necrolemur*, a microchoerid primate (Fig. 19). The relatively short talar neck and head relative to the talar body are obvious similarities to *Necrolemur* (Table 7), as is its large posterior trochlear shelf. However, the trochlea is not well-grooved as in *Necrolemur* (Godinot and Dagosto, 1983), nor is the talar body as high or as rounded (medial view) as these regions in *Necrolemur* (Fig. 19). This new specimen clearly represents a new talar morph (and species) at the Shanghuang fissures. It could belong to one of the small (4 mm) calcaneal morphs (IVPP V 11847) described in Gebo et al. (2000).

Discussion

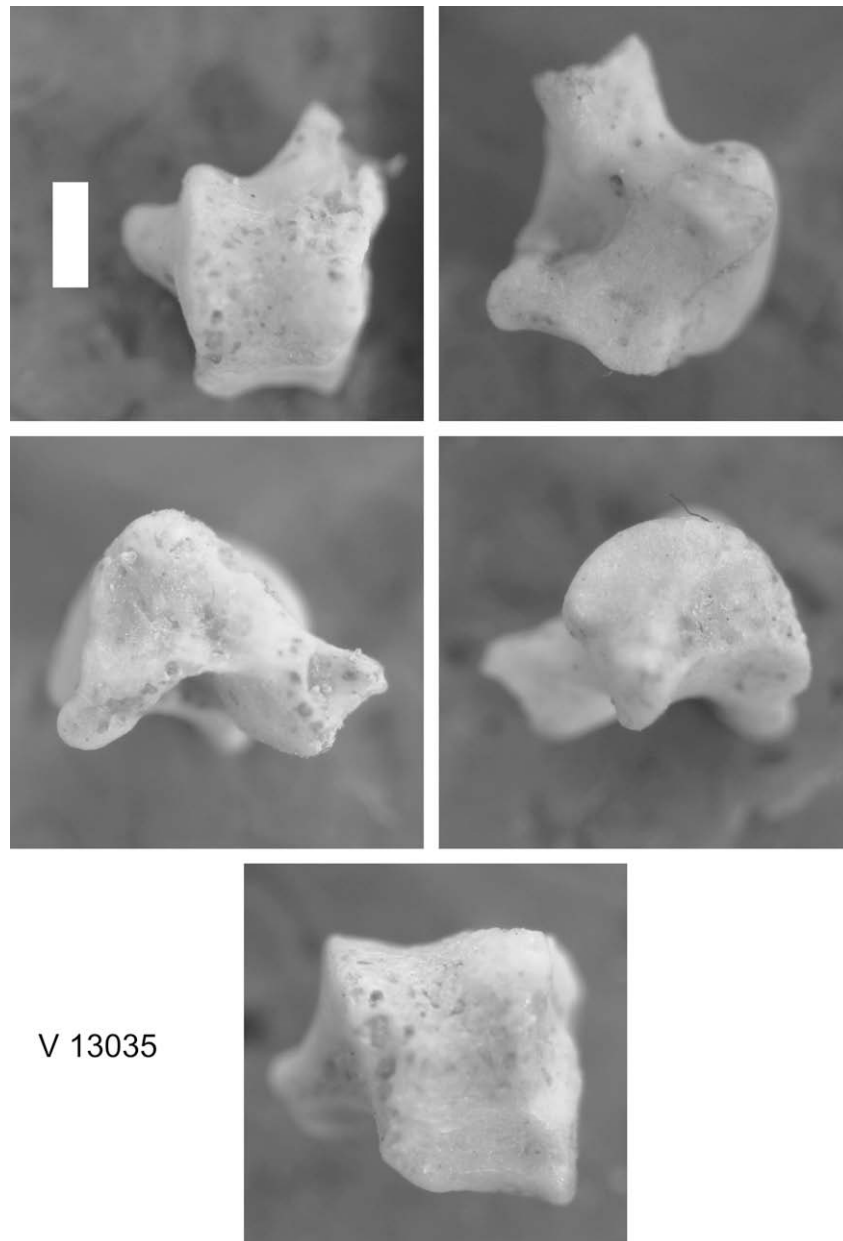
Three new adapine limb elements have been recovered from the Shanghuang fissure-fillings over the last few years. The first, a distal humerus (Fig. 20), exhibits reduced distal humeral and brachial flange widths and a compressed articular region at the elbow (Gebo et al., 2007). All three of these features are morphologically and functionally similar to the Eocene European adapine *Adapis* and to extant lorises. Here, we attribute two additional elements, a first metatarsal and a talus, to *Adapoides troglodytes*. The first metatarsal is morphologically similar to adapiform primates in its peroneal

Table 7
Haplorhine tali measurements (mm). See Table 4 for abbreviations

Measurements	V 13034	V 13035	V 12323	<i>Microcebus berthae</i> , n = 1	<i>Necrolemur</i> sp., n = 1
Midtrochlear width (mtrw)	1.65	1.6	1.25	1.69	2.75
Talar width (tw)	2.35	2.4	1.7	2.59	3.5
Lateral body length (lbl)	2.0	2.1	1.6	2.23	4.0
Lateral body height (lbh)	1.8	1.95	1.2	1.75	2.75
Pcf length (pcf)	1.7	1.7	1.1	1.6	3.6
Pcf minimum width (pcfnw)	0.75	0.65	0.5	0.8	1.35
Pcf maximum width (pcfxw)	1.25	1.10	0.85	1.5	2.5
Trochlear length (trl)	1.9	2.0	1.35	1.8	4.0
Talar neck angle	25°	35°	37°	–	35°
Talar head angle	–	–	15°	–	14°
Talar neck length (nl)	–	–	1.2	2.35	3.05
Talar length (tl)	–	–	2.65	4.47	6.65
Talar head width (hw)	–	–	1.0	1.5	2.55
Talar head height (hht)	–	–	0.85	1.15	2.3
Ratios					
tw/tl	–	–	0.64	0.58	0.53
lbh/mtrw	1.09	1.22	0.96	1.03	1.00
lbh/trl	0.95	0.98	0.89	0.97	0.69
nl/tl	–	–	0.45	0.53	0.46
nl/trl	–	–	0.89	1.3	0.76
nl/mtrw	–	–	0.96	1.39	1.11
hw/hht	–	–	1.18	1.3	1.11
hw/mtrw	–	–	0.8	0.89	0.93
mtrw/trl	0.87	0.80	0.92	0.94	0.69

tubercle morphology although several metric similarities between V13015 and lorises can be recognized (e.g., relative tubercle width, shaft length, tubercle length; Table 3). This metatarsal has a long peroneal tubercle, indicative of a forceful arboreal grasp and good or frequent climbing. Of the three new adapine elements, the talus is the most anatomically similar to lorises in comparison to adapiform primates, including *Adapis*. Functionally, this talus agrees with the other two postcranial elements in that it also indicates a primate adapted for considerable joint mobility. This ankle is not adapted for leaping, nor is it built for rapid quadrupedal movements. Altogether, the postcranial elements attributed to *Adapoides troglodytes* display functional adaptations similar to what we observe in living lorises today (see Grand, 1967). Lorisine locomotion is characterized by their stealthy, strong grasping and flexible movement patterns (Walker, 1969; Charles-Dominique, 1977; Dykyj, 1980; Glassman and Wells, 1984; Gebo, 1987; Demes et al., 1990; Nekaris, 2001). Often this is described as climbing or clambering, but the locomotion of lorises is more complex than such basic descriptions can encompass (Ankel-Simons, 2000; Shapiro and Simons, 2002).

Based on its dentition, *Adapoides* has been linked phylogenetically to the adapine clade of adapiforms (Beard et al., 1994), in contrast to the other Asian Eocene adapiforms (e.g., *Hoan-gonius*, *Rencunius*, and *Guangxilemur*), all of which are sivaladapids (Gingerich et al., 1994; Qi and Beard, 1998). Its teeth are more primitive than those of European adapines. The known postcranial elements described here also show several similarities to European adapines, particularly to *Adapis*. However, the Shanghuang adapiform postcranials are less similar to those of *Leptadapis*, which is the other adapine documented by reasonable postcranial material, and a taxon believed to be closely related to *Adapis* (Godinot, 1998). Since the limb anatomy of *Leptadapis* is more similar to other notharctid adapiforms, it is difficult to accept the limb morphology of *Adapis* or *Adapoides* as primitive for all Adapidae. Thus, the limb morphology of *Adapoides* is almost certainly convergent with both *Adapis* and extant lorises.



V 13035

Fig. 17. D fissure talus, V13035. Top: dorsal (left) and plantar; below top: medial (left) and lateral; lowest view: posterior view. Scale bar = 1 mm.

Six new hind limb elements from Shanghuang Fissures C, D, and E contribute additional postcranial material for two haplorhine clades from Asia. The os coxa and the proximal femur are best allocated to basal anthropoids from Shanghuang. The os coxa possesses a wide gluteal plane, a prominent ridge (the margo acetabuli) that separates the iliac and gluteal planes, and a flat iliac plane. These morphological features are important similarities to anthropoid primates. The V13032 innominate compares best with parapithecids, proteopithecids, and platyrrhines. It lacks the narrow rod-like ilia of other haplorhine primates, including tarsiers or omomyids. In fact, it shares no special similarities with tarsiers or omomyids, nor does it compare favorably with adapiform primates. Functionally, the V13032 innominate would suggest an arboreal quadrupedal primate.

The wide gluteal plane of anthropoids (even the small callitrichines) contrasts with the rod-like ilium of small strepsirhine primates (Tattersall, 1982), tarsiers, and omomyids (Grand

and Lorenz, 1968; Fleagle and Simons, 1995; Anemone and Covert, 2000). Large strepsirhines, like lemurids, indriids, and certain adapiforms, have also expanded the cranial region of the ilium, but in a manner different from the anthropoids. *Lepilemur* and *Daubentonia* have only slightly broader ilia than do smaller strepsirhines. This wide expansion and its mediolateral curvature are related to an increased area of origin and mass of gluteus medius, the largest gluteal muscle among primates (Hill, 1953; Grand, 1968; Schön, 1968; Stern, 1971). Many interpret gluteus medius as a leg retractor and as an abductor of the femur (Berringer et al., 1968; Grand, 1968; Schön, 1968; Howell and Straus, 1971), although Stern (1971) views this muscle as a medial rotator of the thigh (or lateral rotator of the pelvis) and as a hip stabilizer. In contrast, Cortright (1983) notes that the identification of a specific function for gluteus medius across monkeys is especially difficult.

Although body size increase across primates corresponds to an increase in iliac width (an allometric correlation), shape differences

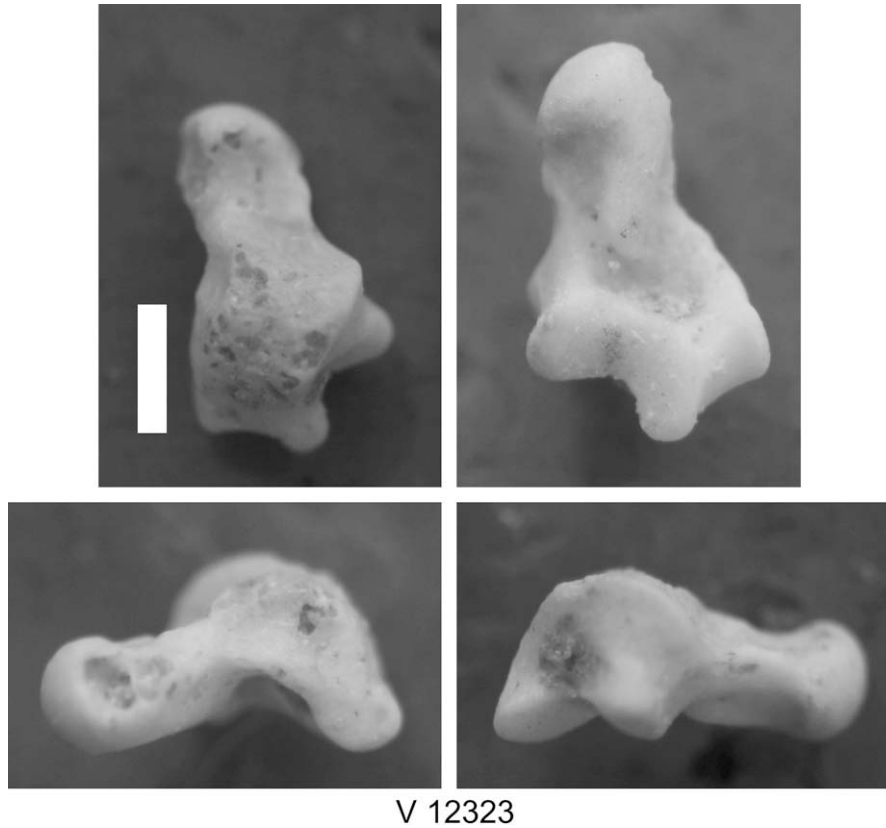


Fig. 18. The new small talus, V12323. Top views: dorsal (left) and plantar; bottom: medial (left) and lateral. Scale bar = 1 mm.

among these lineages hint at other functional possibilities. In contrast to an allometric size trend, the small callitrichines clearly retain the anthropoid condition of a wide ilium. Likewise, large galagos do not possess ilia that are wider than those of their smaller relatives. Lineage-specific iliac shapes seem to hold within taxonomic groups, no matter the size of a species. Whatever its function, a wide and deep gluteal plane is a consistent trait across anthropoids, large or small. This suggests a common functional problem is being addressed by expansion of the ilium. Anthropoid primates are known for their use of quadrupedalism, especially arboreal quadrupedalism. Perhaps hip stability, as noted by Stern (1971), is being addressed. No matter what the ultimate functional explanation, the wide gluteal plane that characterizes all

anthropoid primates is found in the V13032 innominate from the middle Eocene of Shanghuang. This represents the earliest example in the fossil record of an anthropoid-like pelvic anatomy.

The proximal femur, V13033, also shares features with anthropoids: the femoral head extends above the greater trochanter, the femoral neck is long, the angle of the femoral neck and head is high,

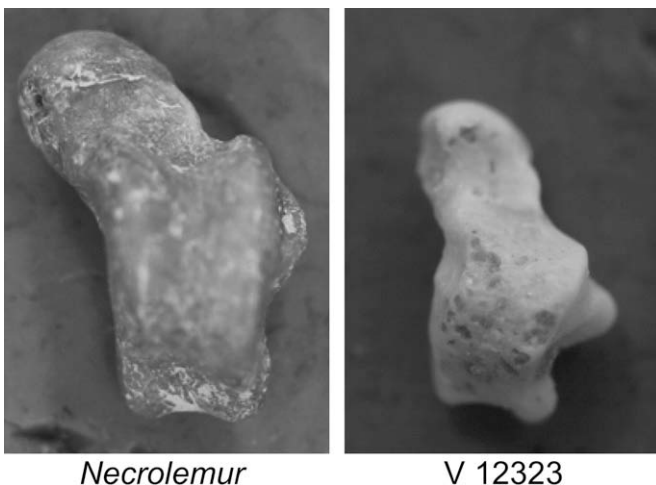


Fig. 19. Dorsal tali comparison. Left: *Necrolemur* (reversed, BFI 876); Right: V12323.

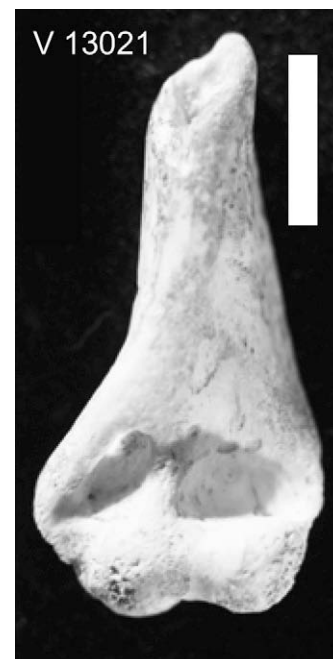


Fig. 20. Distal humerus of *Adapoides troglodytes* (IVPP V13021). Scale bar = 5 mm.

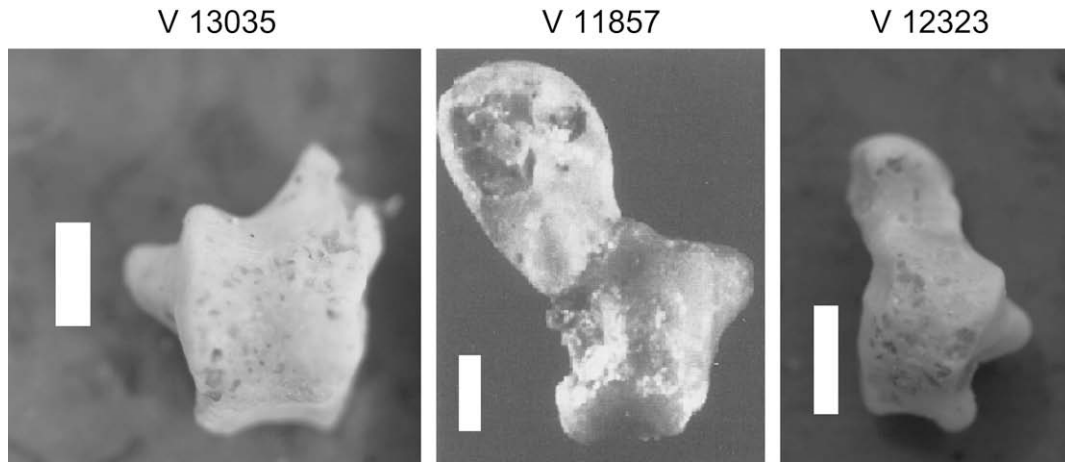


Fig. 21. All three morphs of “Morphology 1” tali: V13035 (left); V 11857 (middle); V12323 (right). Scale bar = 1 mm.

and the lesser trochanter angle is high. Associated with these anthropoid similarities are other femoral features strikingly similar to the microchoerine, *Necrolemur*, especially the anterior bowing of the greater trochanter and its extension as the anterior pillar along the proximal shaft. Unlike most modern anthropoids, this proximal femur has a third trochanter, but such a feature is also seen in proteopithecids. Overall, the V13033 proximal femur shares several morphological similarities to proteopithecoid and microchoerid fossil primates. This combination of anthropoid and microchoerine similarities is unique among basal anthropoids. The anterior bowing and the prominent third trochanter suggest a frequently leaping primate.

In contrast to the os coxa and the proximal femur, the distal femur and the three tali represent more primitive haplorhine primates aligned with the “Morphology 1” tarsal group of Gebo et al. (2001). The distal femur is from a relatively large haplorhine primate weighing approximately 200 g. The functional interpretation of its morphology and its size are most similar to the large distally elongated calcaneus (V12276) previously described from Shanghuang. Both the knee and the calcaneus are very similar to those of omomyid primates, although the distal elongation of this calcaneus (57% of calcaneal length) exceeds that of the majority of omomyid primates (47–55%; with the exception of *Necrolemur*, 65%+) and is more similar to *Microcebus* (61%; Gebo et al., 2001). Both the distal femur with its elevated lateral rim and tall condyles and the elongation of the calcaneus suggest excellent leaping capabilities. In combination, we reconstruct these hind limb elements as belonging to a very omomyid-like, arboreal, frequently leaping primate also capable of climbing and quadrupedalism.

The Shanghuang fissure-fillings demonstrate a wide variety of distinctive morphs of haplorhine primates. Gebo et al. (2001) divided the Shanghuang haplorhine tali into four groups distributed among three distinctive clades. Two of these groups, eosimiids (“Morphology 3”) and an unnamed group designated as “Morphology 4”, have been attributed to basal anthropoids (Gebo et al., 2001). One group (“Morphology 2”) is linked to the Tarsiidae. The third clade, the “Morphology 1” group, was described as omomyid-like basal haplorhines. The additional discoveries described above require a clarification of this group.

The V11857 talus figured in Gebo et al. (2001: their Fig. 10) resembles anaptomorphine omomyids akin to *Teilhardina* and *Tetoniuss*. All share enlarged talar heads with long necks, proportionally smaller talar bodies, and lower talar bodies. V11857 possesses a smaller posterior trochlear shelf relative to *Teilhardina* and *Tetoniuss*. The V11857 talus thus differs in details from the other omomyid-like tali described here. We therefore subdivide the “Morphology 1” tali into several subgroups (see Fig. 21) that mimic

the anatomical distinctions observed among North American anaptomorphine and omomyine omomyids. “Morphology 1A” includes V11857, a primate with more anaptomorphine-like talar anatomy, while “Morphology 1B” is a more omomyine-like group. The V13034 and V13035 tali described above are placed in this group. The tiny talus, V12323, is different, most closely resembling microchoerine primates like *Necrolemur*. It is not very similar to either the Morphology 1A or 1B tali, and therefore we place this morph in Morphology 1C. The V12323 specimen may be the first to document an Asian connection to the European Microchoeridae.

Conclusions

The new postcranial fossils from Shanghuang add important adaptive and phylogenetic characters to the named and unnamed taxa at this middle Eocene locality in Asia. The body elements attributed to *Adapoides* show a loris-like adaptive pattern for this Asian primate, a convergent pattern that will repeat itself in *Adapis* in Europe and again for the later lorisiforms. The haplorhine elements add information in three distinctive ways. First, two elements demonstrate morphological similarities to anthropoid primates and thus contribute directly to the basal anthropoid debate concerning eosimiids. Second, the omomyid-like postcranial elements at Shanghuang are more diverse than initially reported. We suggest three groups that are morphologically similar to haplorhine fossil primates from the Eocene of North America and Europe. All of these morphologies occur at a single Asian locality, however, suggesting an original home continent. Lastly, the tali show just how small Shanghuang haplorhines were, being equivalent or smaller than the pygmy mouse lemur, the smallest living primate. This abundance of tiny primates in several haplorhine clades at Shanghuang provides a unique window into early primate diversity that has been lost in the rainforests of today.

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References

- Anemone, R.L., 1990. The VCL hypothesis revisited: patterns of femoral morphology among quadrupedal and saltatorial prosimian primates. *Am. J. Phys. Anthropol.* 83, 373–393.
- Anemone, R.L., Covert, H.H., 2000. New skeletal remains of *Omomyids* (Primates, Omomyidae): functional morphology of the hindlimb and locomotor behavior of a middle Eocene primate. *J. Hum. Evol.* 38, 607–633.
- Ankel-Simons, F., 2000. *Primate Anatomy*. Academic Press, San Diego.
- Beard, K.C., 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. In: Beard, K.C., Dawson, M. (Eds.), *Dawn of the Age of Mammals in Asia*. *Bull. Carnegie Mus. Nat. Hist.* 34, 5–39.
- Beard, K.C., 2004. The Hunt for the Dawn Monkey. University of California Press, Berkeley.
- Beard, K.C., Dagosto, M., Gebo, D.L., Godinot, M., 1988. Interrelationships among primate higher taxa. *Nature* 331, 712–714.
- Beard, K.C., Qi, T., Dawson, M.R., Wang, B., Li, C., 1994. A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature* 368, 604–609.
- Berringer, O.M., Browning, F.M., Schroeder, C.R., 1968. *An Atlas and Dissection Manual of Rhesus Monkey Anatomy*. Florida State University, Tallahassee.
- Boyer, D.M., Patel, B.A., Larson, S.G., Stern, J.T., 2007. Telemetered electromyography of peroneus longus in *Varecia variegata* and *Eulemur rubriventer*: implications for the functional significance of a large peroneal process. *J. Hum. Evol.* 53, 119–134.
- Charles-Dominique, P., 1977. *Ecology and Behavior of Nocturnal Primates*. Columbia University Press, New York.
- Conroy, G.C., 1987. Problems of body-weight estimation in fossil primates. *Int. J. Primatol.* 8, 115–137.
- Cortright, G.W., 1983. The relative mass of hind limb muscles in anthropoid primates: functional and evolutionary implications. Ph.D. Thesis, University of Chicago, Chicago.
- Dagosto, M., 1983. Postcranium of *Adapis parisiensis* and *Leptadapis magnus* (Adapiformes, Primates). *Folia Primatol.* 41, 49–101.
- Dagosto, M., 1986. The joints of the tarsus in the strepsirrhine primates: functional, adaptive, and evolutionary implications. Ph.D. Dissertation, City University of New York, New York.
- Dagosto, M., 1993. Postcranial anatomy and locomotor behavior in Eocene primates. In: Gebo, D.L. (Ed.), *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois Press, Dekalb, pp. 199–219.
- Dagosto, M., Gebo, D.L., Beard, K.C., 1999. Revision of the Wind River faunas, early Eocene of Central Wyoming. Part 14. Postcranium of *Shoshonius cooperi* (Mammalia, Primates). *Ann. Is Carnegie Mus.* 68 (3), 175–211.
- Dagosto, M., Gebo, D.L., Dolino, C., 2001. Positional behavior and social organization of the Philippine tarsier (*Tarsius syrichta*). *Primates* 42 (3), 233–243.
- Dagosto, M., Schmid, P., 1996. Proximal femoral anatomy of omomyiform primates. *J. Hum. Evol.* 30, 29–56.
- Dagosto, M., Terranova, C.J., 1992. Estimating the body size of Eocene primates: a comparison of results from dental and postcranial variables. *Int. J. Primatol.* 13, 307–344.
- Demes, B., Jungers, W.L., Nieschalk, U., 1990. Size and speed-related aspects of quadrupedal waling in slender and slow lorises. In: Jouffroy, F.K., Stack, M.H., Niemi, C. (Eds.), *Gravity, Posture and Locomotion in Primates*. Il Sedicesimo, Firenze, pp. 175–197.
- Dykjy, D., 1980. Locomotion of the slow loris in a designed substrate context. *Am. J. Phys. Anthropol.* 52, 577–586.
- Fleagle, J.G., 1977. Locomotor behavior and skeletal anatomy of sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yearb. Phys. Anthropol.* 20, 440–453.
- Fleagle, J.G., 1999. *Primate Adaptation and Evolution*, second ed. Academic Press, New York.
- Fleagle, J.G., Anapol, F., 1992. The indriid ischium and the hominid hip. *J. Hum. Evol.* 22, 285–305.
- Fleagle, J.G., Kay, R.F., 1987. The phyletic position of the Parapitheciidae. *J. Hum. Evol.* 16, 483–532.
- Fleagle, J.G., Simons, E.L., 1979. Anatomy of the bony pelvis in parapithecoid primates. *Folia Primatol.* 31, 176–186.
- Fleagle, J.G., Simons, E.L., 1995. Limb skeleton and locomotor adaptations of *Apidium phiomense*, an Oligocene anthropoid from Egypt. *Am. J. Phys. Anthropol.* 97, 235–289.
- Ford, S.M., 1986. Systematics of the New World monkeys. In: Swindler, D.R., Erwin, J. (Eds.), *Comparative Primate Biology*. Alan R. Liss, New York, pp. 73–135.
- Ford, S.M., Davis, L.C., 1992. Systematics and body size: implications for feeding adaptations in New World monkeys. *Am. J. Phys. Anthropol.* 88, 415–468.
- Gebo, D.L., 1986. Anthropoid origins – the foot evidence. *J. Hum. Evol.* 15, 421–430.
- Gebo, D.L., 1987. Locomotor diversity in prosimian primates. *Am. J. Primatol.* 13, 271–281.
- Gebo, D.L., 1988. Foot morphology and locomotor adaptation in Eocene primates. *Folia Primatol.* 50, 3–41.
- Gebo, D.L., 2004. A shrew-sized origin for primates. *Yearb. Phys. Anthropol.* 47, 40–62.
- Gebo, D.L., Dagosto, M., Beard, K.C., Jingwen, W., 1999. A first metatarsal of *Hoanghonius stehlini* from the late middle Eocene of Shanxi Province, China. *J. Hum. Evol.* 37, 801–806.
- Gebo, D.L., Dagosto, M., Beard, K.C., Ni, X., Qi, T., 2007. Primate humeral remains from the Middle Eocene of China. In: Beard, K.C., Luo, Z.-X. (Eds.), *Mammalian Paleontology on a Global Stage: Papers in Honor of Mary R. Dawson*. *Bull. Carnegie Mus. Nat. Hist.* 39, 77–82.
- Gebo, D.L., Dagosto, M., Beard, K.C., Ni, X., Qi, T., 2008. A haplorhine first metatarsal from the middle Eocene of China. In: Fleagle, J.G., Gilbert, C.C. (Eds.), *Elwyn Simons: A Search for Origins*. Springer, pp. 229–242.
- Gebo, D.L., Dagosto, M., Beard, K.C., Qi, T., 2001. Middle Eocene primate tarsals from China: implications for haplorhine evolution. *Am. J. Phys. Anthropol.* 116, 83–117.
- Gebo, D.L., Simons, E.L., Rasmussen, D.T., Dagosto, M., 1994. Eocene anthropoid postcrania from the Fayum, Egypt. In: Fleagle, J.G., Kay, R.F. (Eds.), *Anthropoid Origins*. Plenum Press, New York, pp. 203–233.
- Gebo, D.L., Dagosto, M., Beard, K.C., Tao, Q., 2000. The smallest primates. *J. Hum. Evol.* 38, 585–594.
- Gingerich, P.D., Holroyd, P.A., Ciochon, R.L., 1994. *Rencunius zhoui*, new primate from the late middle Eocene of Henan, China, and a comparison with some early Anthropoidea. In: Fleagle, J.G., Kay, R.F. (Eds.), *Anthropoid Origins*. Plenum Press, New York, pp. 163–177.
- Godinot, M., 1998. A summary of adapiform systematics and phylogeny. *Folia Primatol.* 69, 218–249.
- Godinot, M., Dagosto, M., 1983. The astragalus of *Necrolemur* (Primates, Microchoerinae). *J. Paleontol.* 57 (6), 1321–1324.
- Glassman, D.M., Wells, J.P., 1984. Positional and activity behavior in a captive slow loris: a quantitative assessment. *Am. J. Primatol.* 7, 121–132.
- Grand, T., 1967. The functional anatomy of the ankle and foot of the slow loris (*Nycticebus coucang*). *Am. J. Phys. Anthropol.* 28, 168–182.
- Grand, T.L., 1968. The functional anatomy of the lower limb of the howler monkey (*Alouatta caraya*). *Am. J. Phys. Anthropol.* 28, 163–182.
- Grand, T., Lorenz, R., 1968. Functional analysis of the hip joint in *Tarsius bancanus* (Horsfield, 1821) and *Tarsius syrichta* (Linnaeus, 1758). *Folia Primatol.* 9, 161–181.
- Gregory, W.K., 1920. On the structure and relations of *Notharctus*, an American Eocene primate. *Mem. Am. Mus. Nat. Hist.* 3, 49–243.
- Hill, W.C.O., 1953. *Primates – Comparative Anatomy and Taxonomy*. Strepsirhini, vol. 1. Edinburgh University Press, Edinburgh.
- Howell, A.B., Straus, W.L., 1971. The muscular system. In: Hartmann, C.G., Straus, W.L. (Eds.), *The Anatomy of the Rhesus Monkey*. Hafner Publishing Company, New York, pp. 89–175.
- MacPhee, R.D.E., Beard, K.C., Qi, T., 1995. Significance of primate petrosal from middle Eocene fissure-fillings at Shanghaung, Jiangsu Province, People's Republic of China. *J. Hum. Evol.* 29, 501–514.
- McArdle, J.E., 1981. Functional morphology of the hip and thigh of the Lorisiformes. *Contrib. Primatol.* 17, 1–132.
- Métais, G., Guo, J., Beard, K.C., 2004. A new small dichobunid artiodactyls from Shanghaung (middle Eocene, eastern China): implications for the early evolution of protoselenodonts in Asia. *Bull. Carnegie Mus. Nat. Hist.* 36, 177–197.
- Napier, J.R., Walker, A.C., 1967. Vertical clinging and leaping – a newly recognized category of locomotor behavior of primates. *Folia Primatol.* 6, 204–219.
- Nekaris, K.A.L., 2001. Activity budget and positional behavior of the Mysore slender loris (*Loris tardigradus hydekkerianus*): implications for slow climbing locomotion. *Folia Primatol.* 72, 228–241.
- Ni, X., Hu, Y., Wang, Y., Li, C., 2005. A clue to the Asian origin of euprimates. *Anthropol. Sci.* 113, 3–9.
- Qi, T., Beard, K.C., 1998. Late Eocene sivaladapid primate from Guangxi Zhuang Autonomous Region, People's Republic of China. *J. Hum. Evol.* 35, 211–220.
- Qi, T., Beard, K.C., Wang, B., Dawson, M.R., Guo, J., Li, C., 1996. The Shanghaung mammalian fauna, Middle Eocene of Jiangsu: history of discovery and significance. *Vert. Palasiatica* 34, 202–214.
- Rasoloarison, R.M., Goodman, S.M., Ganzhorn, J.U., 2000. Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *Int. J. Primatol.* 21, 961–1019.
- Rosenberger, A.L., Dagosto, M., 1992. New craniodental and postcranial evidence of fossil tarsiiiformes. In: Matano, S., Tuttle, R.H., Ishida, H., Goodman, M. (Eds.), *Topics in Primatology*, vol. 3. University of Kyoto Press, Kyoto, pp. 37–51.
- Schön, M.A., 1968. *The Muscular System of the Red Howling Monkey*. Bulletin 273. US National Museum, Smithsonian Institution Press, Washington, D.C., 1–185.
- Schultz, A.H., 1969. Observations on the acetabulum of primates. *Folia Primatol.* 11, 181–199.
- Shapiro, L.J., Simons, C.V.M., 2002. Functional aspects of strepsirrhine lumbar vertebral bodies and spinous processes. *J. Hum. Evol.* 42, 753–783.
- Simpson, G.G., 1940. Studies of the earliest primates. *Bull. Am. Mus. Nat. Hist.* 77, 185–212.
- Smith, R.J., Jungers, W.L., 1997. Body mass in comparative primatology. *J. Hum. Evol.* 32, 523–560.
- Stern, J.T., 1971. Functional myology of the hip and thigh of cebid monkeys and its implications for the evolution of erect posture. *Bibliotheca Primatologica* 14, 1–318.
- Szalay, F.S., 1976. Systematics of the Omomyidae (Tarsiiformes, Primates): taxonomy, phylogeny, and adaptations. *Bull. Am. Mus. Nat. Hist.* 156 (3), 1–449.
- Szalay, F.S., Dagosto, M., 1988. Evolution of hallucial grasping in the primates. *J. Hum. Evol.* 17, 1–33.
- Tattersall, I., 1982. *The Primates of Madagascar*. Columbia University Press, New York.
- Walker, A.C., 1969. The locomotion of the lorises, with special reference to the pottos. *East Afr. Wildl. J.* 7, 1–5.
- Walker, A.C., 1974. Locomotor adaptation in past and present prosimian primates. In: Jenkins, F.A. (Ed.), *Primate Locomotion*. Academic Press, New York, pp. 349–381.
- Wang, B., Dawson, M., 1994. A primitive cricetid (Mammalia: Rodentia) from the middle Eocene of Jiangsu Province, China. *Ann. Carnegie Mus. Nat. Hist.* 63, 239–256.