

13. Primate Tibiae from the Middle Eocene Shanghuang Fissure-Fillings of Eastern China

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13.1 Introduction

Since this is a volume in celebration of the work of Frederick S. Szalay, we think it is entirely appropriate to open with an appreciation. We gratefully acknowledge

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E.J. Sargis and M. Dagosto (eds.), *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay*, 315–324.
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Dr. Szalay's innovative efforts to bring the study of mammalian postcranial remains to the forefront of evolutionary morphology, a development that has inspired all of our research. MD thanks Dr. Szalay for being a supportive mentor, for instilling a broad and deep understanding of evolutionary biology, for generously allowing a naive graduate student access to important fossil specimens, and for providing the most stimulating environment for research. DLG thanks Dr. Szalay for his many kindnesses

and thoughtful discussions over the years, and celebrates his intuitive ability to demonstrate how postcranial morphology can be used to decipher important evolutionary events in mammalian evolution. KCB acknowledges the intellectual debt he owes to Dr. Szalay, whose comprehensive studies of the systematics, phylogenetic relationships, and functional anatomy of Paleogene primates and other mammals has inspired subsequent generations to continue that legacy. XN and TQ congratulate Dr. Szalay on a long and productive career. Although this essay does not exhibit the breadth and depth typical of Fred's work, it does in its own small way build upon themes evident in his own: the important contribution postcranial remains make to the interpretation of primate and mammalian evolution, systematics, and functional morphology (Szalay et al., 1975, 1987; Szalay, 1977, 1981a, b, 1984, 2007; Szalay and Drawhorn, 1980; Szalay and Lucas, 1993; Szalay and Sargis, 2001).

13.2 The Shanghuang Primates

The joint field expeditions of Carnegie Museum of Natural History and the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences have recovered numerous mammalian fossil remains from fillings in Triassic limestone fissures near the village of Shanghuang, southern Jiangsu province China. Five fissures, labeled A-E have been sampled, and are biostratigraphically correlated with the Irindmanhan and early Sharamurunion Land Mammal Ages approximately 45Ma (Qi et al., 1996). A broad array of mammals has been sampled and described from these localities (Beard et al., 1994; Wang and Dawson, 1994; Qi and Beard, 1996; Qi et al., 1996; Dawson and Wang, 2001). The primates include typically Eocene forms such as adapids, and a single omomyid, *Macrotarsius*, but also the earliest record of a tarsier and a previously unknown group of primates, the Eosimiidae, which are basal anthropoids (Beard et al., 1994, 1996; Ross et al., 1998; Beard, 2002; Kay et al., 2004). The affinities of the latter group have not been without controversy (e.g., Szalay, 2000; Gunnell and Miller, 2001). The discovery of more nearly complete dental remains and postcranial remains have answered some of the early criticism that *Eosimias* is not a primate, and the diversity of postcranial remains demonstrate that not all the primates from Shanghuang fit comfortably under the umbrella of tarsiid or omomyid (Gebo et al., 2001).

The tali and calcanei of several primate groups were described by Gebo and colleagues (Gebo et al., 2000a, b, 2001; Gebo and Dagosto, 2004). The dental remains and tarsal bones suggest the presence of at least five groups of primates, including adapids, an "unnamed haplorhine family" morphologically most similar to omomyids, tarsiids, and two kinds of anthropoids (eosimiids and "new protoanthropoids"). There are several size classes within each group. Here, we describe some less numerous, but still informative limb bone elements.

To clarify the following discussion, readers should note that in this paper we follow the classification given by Gunnell and Rose (2002). The family name Omomyidae refers to lower level taxa included in the Anaptomorphinae, Omomyinae, and Microchoerinae. Tarsiiformes includes the families Omomyidae and Tarsiidae. Following Szalay and Delson (1979), we include both Adapiformes and Lemuriformes in the taxon Strepsirhini, and Tarsiiformes and Anthropoidea (including eosimiids and protoanthropoids) in the taxon Haplorhini. The informal term "prosimian" is used for the group of non-anthropoid primates, e.g., Strepsirhini, Omomyidae, and Tarsiidae.

13.3 Tibiae

Five distal tibiae have been recovered, three from Quarry D and two from Quarry E. The bones are recognized as primate on the basis of the conformation of the articular surfaces for the talus which is unique to Primates among mammals (Dagosto, 1985). Figure 13.1 illustrates once again the point that most of the primate postcranial remains



FIGURE 13.1. Size comparison. From left to right, anterior view of distal tibiae of *Microcebus berthae* (FMNH unnumbered) (~30g); V13020 (fused morph), and V13033 (unfused morph).

TABLE 13.1. Measurements of the distal tibia (mm) in Shanghuang fossils and comparisons to living primates. Measurements were taken with a Reflex microscope. The measurements are illustrated in Figure 13.2, with the exception of measurement 7, which is the mediolateral width across the fused tibiofibula.

Measurement	Shanghuang fused morph		Shanghuang unfused morph			<i>M. berthae</i> (30 g)	<i>M. rufus</i> (50 g)	<i>Galagoidea sp.</i> (70–100g)	<i>T. syrichta</i> (125–150 g)
	V13019	V13020	V13032	V13033	V13034	N = 1	N = 1	N = 4	N = 4
1	0.714	0.84	0.899	1.001	0.864	0.953	0.821	1.799	1.900
2	0.623	0.674	0.629	0.735	0.685	0.653	0.530	1.143	1.334
3	1.223	1.21	1.049	1.011	1.081	1.076	1.197	2.088	2.426
4	1.406	1.399	1.359		1.309	1.810	1.551	2.184	3.256
5	1.468	1.599	2.007	1.911	2.128	2.109	2.231	3.177	3.431
6			1.972		2.122	2.075	2.250	3.256	
7	2.952	3.039							6.499
AP	1.444	1.463	1.721	1.530	1.801	1.688	1.711	2.778	3.320
ML	1.502	1.278	1.417		1.484	1.566	1.537	2.199	3.210
Malleolar rotation	14	11	22	24	24			21	14
AP/ML	96.14	114.97	121.45		121.36	107.8	111.32	126.76	104.0

TABLE 13.2. Shanghuang primate taxa known from dental or postcranial remains. (Data from Beard et al., 1994; Gebo et al., 2001).

	Mass estimated from teeth	Mass estimated from tarsal remains	Number of specimens	Quarries
<i>Adapoides troglodytes</i>	~200–300 g	NA		B, D
<i>Macrotarsius macrorhysis</i>	~1,000 g	NA		D
<i>Tarsius eoacenus</i>	<70 g			A, C, D
<i>Eosimias sinensis</i>	67–137 g			B
Unnamed haplorhines (size class 2)	NA	30–60 g	Calcanei–2 Tali–3	D, E A, D
Tarsiidae (size class 1)	NA	20–30 g	Calcanei–4 Tali–0	D D
(size class 2)		70 g	Calcanei–1 Tali–1	
Eosimiidae (size classes 1–3)	NA	17–75 g	Calcanei–5 Tali–2	C, D D, E
Protoanthropoids (size classes 1–3)	NA	28–80 g	Calcanei–6 Tali–2	A, D, E C

NA = not available

found at Shanghuang come from very small animals (Gebo et al., 2000). We estimate that all of the Shanghuang tibiae belong to primates weighing 50 g or less; in absolute measurements they are as small as or smaller than most individuals of *Microcebus* (30–60 g; Table 13.1). In terms of potential allocations, this immediately rules out the two adapids, which are estimated at 200–400 g on the basis of tooth size, the only currently recognized omomyid, *Macrotarsius*, estimated at 1,000 g, and *Eosimias sinensis*, estimated at 67–137 g (Beard et al., 1994). Considering size alone, the tibiae could belong to the smaller size classes within the “new haplorhine”, tarsiid, or either of the protoanthropoid groups, all of which have representatives within the 20–60 g size range at quarries D and E (Table 13.2).

All of the Shanghuang tibiae described here belong to haplorhine primates as evidenced by the moderate rotation of the anterior part of the medial malleolus (10–24 degrees,

Table 13.1); the flat, laterally facing posterior part of the medial malleolus; and the parallel anterior and posterior edges of the inferior tibial surface which make a relatively square shaped articular surface. These are features typical of tarsiers, omomyids, and anthropoids (Dagosto, 1985; Table 13.3, Figure 13.3). Strepsirhine primates (lemurs, lorises, and adapids) exhibit a very different conformation of the distal tibia with a more strongly rotated medial malleolus (20–40 degrees); no flat laterally facing part of the malleolus; and anterior and posterior edges that diverge laterally making a triangular shaped articular surface for the talus (Dagosto, 1985). That all the tibiae found so far are haplorhine is not surprising given that the vast majority of the tarsal bones are also haplorhine (Gebo et al., 2001). The tibiae, however, clearly represent two different kinds of haplorhine primates, one type in which the tibia is fused to the fibula, and another in which these bones remain separate.

TABLE 13.3. Distribution of tibial character states in primates utilized in Figure 13.3. The filled and diagonal-lined boxes are presumed to be derived conditions; the open boxes, primitive conditions, but the polarity of some of these features (especially 5–7) is not yet certain.? = character state is unknown. For feature 7, anthropoids exhibit all three character states.

Open box	Filled box	Shaded box
1. Lesser degree of rotation of medial malleolus	1. Strong degree of rotation of medial malleolus	
2. Posterolateral surface of medial malleolus flat, laterally facing	2. Posterolateral surface of medial malleolus curved, anteriorly facing	
3. Anterior and posterior edges of distal tibia parallel, rectangular outline	3. Anterior and posterior edges of distal tibia divergent, triangular outline	
4. AP/ML index low	4. AP/ML index high	
5. Tibial and fibular malleoli are parallel	5. Fibular malleolus slopes laterally = talofibular facet on talus slopes laterally	
6. Tibial and fibular malleoli are of equal length	6. Fibular malleolus shorter due to lateral slope	6. Fibular malleolus is shorter than tibial
7. Distal tibiofibular joint synovial	7. Tibia and fibula fused	7. Syndesmosis
8. Medial malleolus long, U-shaped, no strongly marked pit for deltoid ligament	8. Medial malleolus short, rectangular, pit for deltoid ligament	

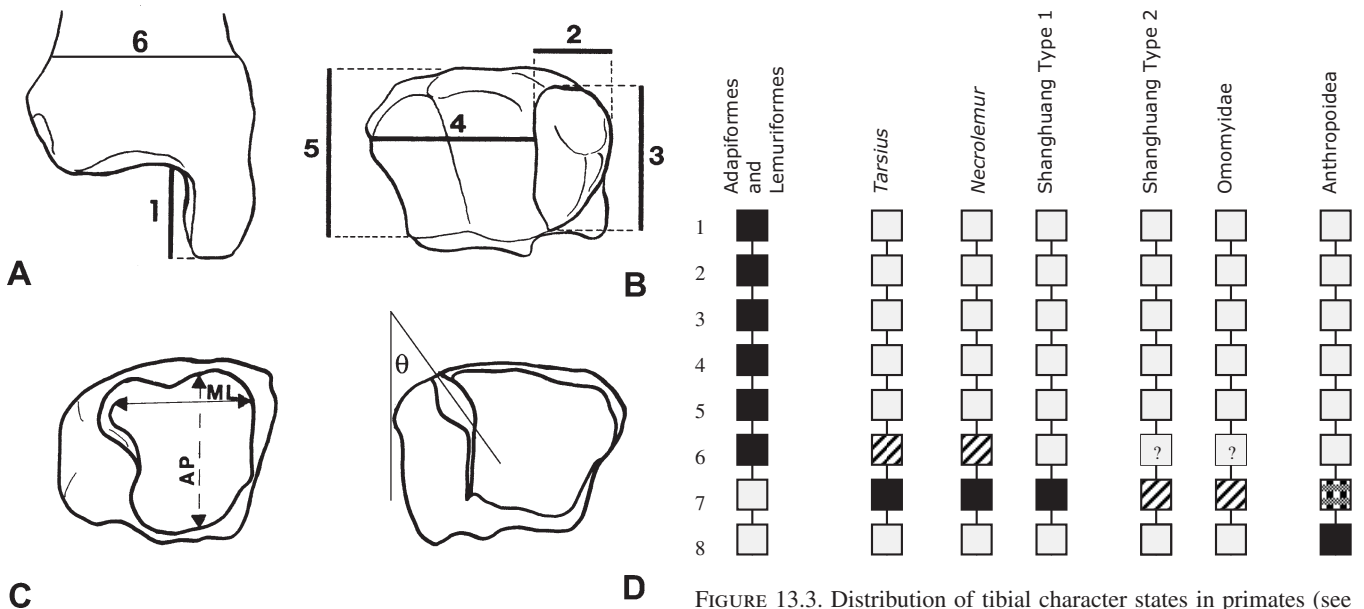


FIGURE 13.3. Distribution of tibial character states in primates (see also Table 13.3). The filled and diagonally lined boxes are presumed to be derived conditions; the open boxes, primitive conditions, but the polarity of some of these features (especially 5–7) is not yet certain.? = character state is unknown. For feature 7, anthropoids exhibit all three character states.

FIGURE 13.2. Measurements of the tibia used in this paper. 1. proximal-distal height of malleolus; 2. mediolateral width of malleolus; 3. Anteroposterior depth of malleolus; 4. width of inferior tibial surface; 5. Anteroposterior depth of tibia; 6. width across the tibia just above the distal epiphysis; AP, anteroposterior depth of tibial facet; ML, mediolateral width of tibial facet; θ , angle of malleolar rotation. A and B, anterior and inferior view of distal tibia after FIGURE 27.8 of Meldrum and Kay (1997). C and D, inferior views of distal tibia in the strepsirhine *Eulemur* (C), and an omomyid (haplorhine) (D), modified from Dagosto (1985) figure 5.

13.3.1 Type 1: Shanghuang Primates With Fused Tibiae-fibulae

Type 1 is represented by two specimens, V13020 (Quarry E) and V13019 (Quarry D) (Figure 13.4). In terms of absolute size these bones are smaller than any measured individual of *Microcebus*, including the 30g *M. berthae* (Table 13.1). The two specimens are similar enough, both in size and

morphology, to belong to the same or very closely related species. In both of these specimens the distal part of the fibula is completely fused to the tibia. V13020 has almost no hint of a suture line. Although the bones are solidly fused in V13019, the suture line is clearly visible. This individual is possibly not fully adult, as the fibular malleolus also exhibits a clear epiphyseal suture line. In the high degree of fusion, these specimens are more similar to *Tarsius* and differ from *Necrolemur*, in which a clearly visible suture line remains, even in adults (Schlosser, 1907; Dagosto, 1985).

As in most primates, there is a small pointed process on the anterior edge of the distal tibia; however, it does not appear to have a smooth surface for articulation with the talus. This

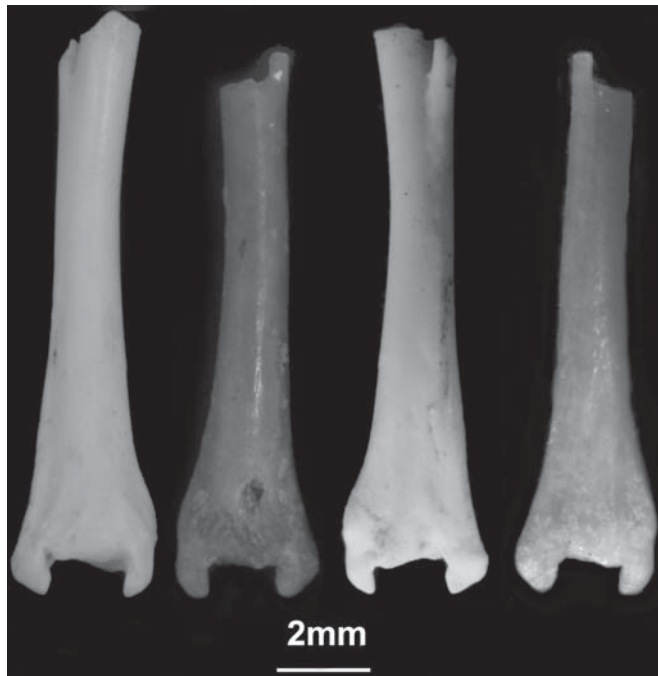


FIGURE 13.4. Anterior (left) and posterior (right) views of fused morph. From left to right, anterior view of V13019, anterior view of V13020, posterior view of V13019 and posterior view of V13020.

differs from most primates, but is a similarity to *Tarsius*, *Necrolemur*, and *Neosaimiri* (Dagosto, 1985; Meldrum and Kay, 1997). The shaft just above the articular surface is compressed anteroposteriorly, as in *Tarsius* and *Necrolemur*. The groove for the tendon of tibilias posterior is shallow and curves around the medial edge of the malleolus, as in *Tarsius*, *Necrolemur*, and the majority of anthropoids. In Bridger Basin omomyids, *Shoshonius* and strepsirhines the groove usually runs more inferiorly (Dagosto, 1985; Ford, 1986; Dagosto et al., 1999).

The ratio of the anteroposterior and mediolateral dimensions of the tibial facet (AP/ML; Table 13.1) is low, as is typical of most haplorhines. The degree of medial malleolar rotation is low (11–14 degrees) like that of *Tarsius*. Like “prosimian” primates, the medial malleolus is fairly long (proximodistally) and U-shaped, and it does not have a particularly well marked pit on its inferior surface (presumably for part of the deltoid ligament (Meldrum and Kay, 1997)). Most anthropoids generally have shorter, wider, more rectangular shaped malleoli, with a marked indentation on the inferior surface for the deltoid ligament, making a stepped shape (Figure 13.5A). *Cebuella*, however, appears to be an exception to this generality, having a malleolus shaped more like that of a prosimian.

Fusion is one obvious similarity of these specimens to *Tarsius* or *Necrolemur*, as is the anteroposterior compression at the distal end of the shaft, and the lack of an articular tibial “stop”. These specimens are also of the appropriate size to belong to *Tarsius eocaenus* and the calcanei and talus

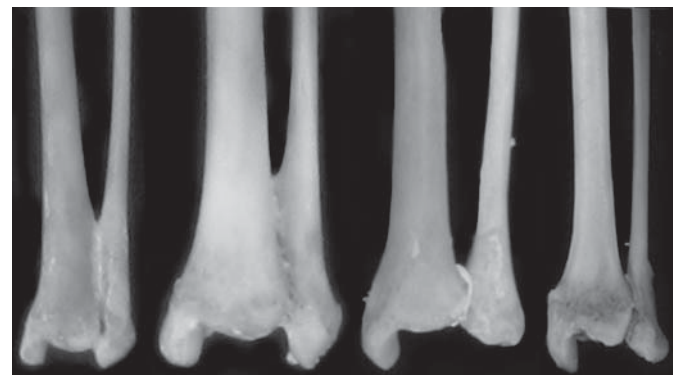
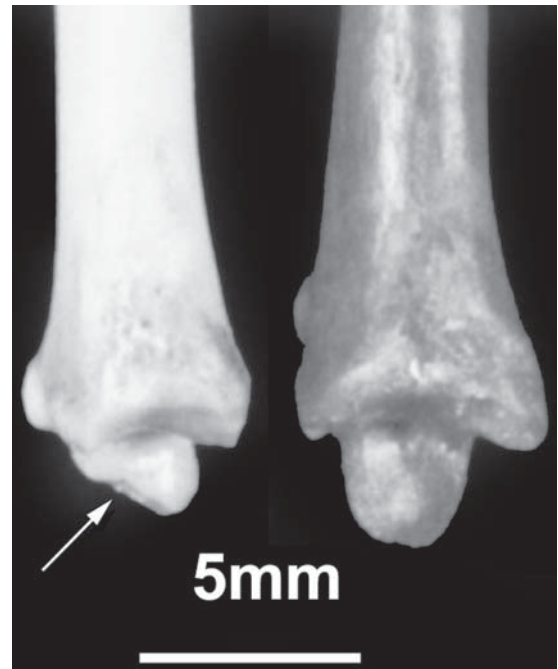


FIGURE 13.5. Differences between anthropoid and strepsirhine distal tibiae. A, lateral view of the tibial malleolus in *Callithrix* (left) and *Galago* (right). Note the shorter, smaller malleolus in the anthropoid. The arrow points to the pit for the deltoid ligament. B, anterior view of tibiofibular mortise in (from left to right) *Cebuella*, *Callithrix*, *Eulemur*, and *Galagoides* (not to scale). Note the symmetrical form of the mortise in the anthropoids due to the proximodistally straight fibular malleolus which extends as far distally as the medial malleolus, contrasted with the asymmetrical form of the mortise in strepsirhines due to the short, laterally flared fibular malleolus.

attributed to the smaller size class of Tarsiidae in Gebo et al. (2001), and thus we provisionally attributed V13020 to this species (Dagosto et al., 1996). There are however, some noteworthy anatomical differences between extant tarsiers and the Shanghuang specimens (Figures 13.6 and 13.7) making other attributions equally possible.

Despite the marked degree of fusion of the bones in the Shanghuang primate, the point of separation of the two bones does not appear to extend as far proximally as in extant tarsiers (Figure 13.6). Although the bones are not complete, we estimate that in the Shanghuang specimens, the bones



FIGURE 13.6. Anterior view of tibiofibula in V13020 (left) with *Tarsius syrichta* (right). The arrows indicate the site of tibiofibular fusion. Scales are 2 mm.

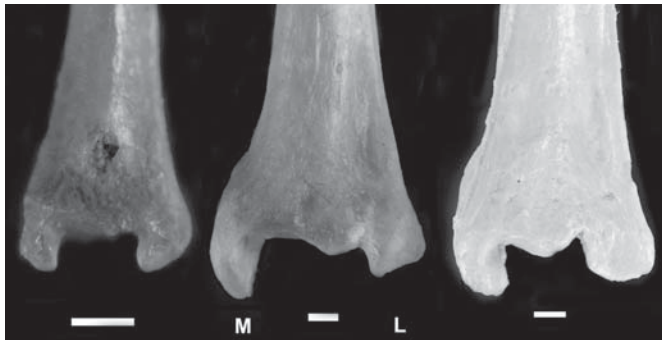


FIGURE 13.7. Anterior view of left tibiofibular mortise of Shanghuang fused morph (V13020; left), *Tarsius syrichta* (middle) and *Necrolemur* (right). M = the medial (tibial) malleolus. L = lateral (fibular) malleolus. Scales are 1 mm. Compare with Figure 13.5B.

were fused for only 40–50% of their length, while in *Tarsius* the comparable figure is 60%. In this feature, the fossils are more similar to *Necrolemur* than *Tarsius* (Schlosser, 1907; Dagosto, 1985). In *Tarsius*, the site where the fibula separates from the tibia occurs about 1 cm above the most distal point of

the cnemial crest, while in the fossils the site is closer to the distal point of the cnemial crest. If one wanted to entertain the hypothesis that the extent of fusion is tarsier-like (e.g., 60% of tibia length) in the Shanghuang specimens, it would follow that the fossil tibiae are relatively short. This would be a different, but still significant difference from *Tarsius*.

In the fused Shanghuang tibiae-fibulae, the tibial malleolus is relatively small, while the fibular malleolus is a much more substantial feature. It is as wide and as long as the medial malleolus, making a symmetrical frame for the talus. This contrasts with *Tarsius*, in which the fibular malleolus, although wide, does not extend as far distally as its medial counterpart (Jouffroy et al., 1984) making an incomplete, asymmetrical frame for the talus (Figure 13.7). *Necrolemur* is similar to *Tarsius*, but has a slightly longer fibular malleolus (Figure 13.7). In these features, V13019 and V13020 differ from *Tarsius* and *Necrolemur* but are similar to small monkeys, especially *Callithrix*, *Cebuella*, *Saimiri*, *Pithecia*, and the fossil anthropoid *Apidium*, all of which likewise have malleoli of equal length (Gregory, 1920; Fleagle and Simons, 1983; Fleagle and Meldrum, 1988; Meldrum and Kay, 1997).

Strepsirhines, even those with closely appressed tibiae and fibulae (e.g., *Microcebus*, *Galago*, *Galagoides*), have a very different profile for the tibiofibular mortise which differs greatly from that of any haplorhine (Figure 13.5B). In contrast to all haplorhines, in strepsirhines the fibular malleolus slopes strongly laterally, matching the slope of the articulating facet on the talus (Gregory, 1920; Beard et al., 1988) so that the mortise is asymmetrical to an even more exaggerated degree and in a different way than in *Tarsius* and *Necrolemur*.

13.3.2 Type 2: Shanghuang Primates With Unfused Tibiafibulae

The other type of tibia is represented by three specimens, two from fissure D (V13032 and V13033), and one from fissure E (V13034). Based on absolute dimensions, these tibiae also belong to primates in the 30–60g size range (Figure 13.1, Table 13.1), and therefore could belong to the smaller size classes of any of the Shanghuang haplorhine groups. The three specimens are similar enough in size and morphology to represent the same or closely related species (Figure 13.8).

Although the fibula was clearly not fused to the tibia, these tibiae all belonged to primates with closely appressed bones having a strong syndesmosis between them. Crests for the anterior and posterior tibiofibular ligaments end just above the joint, and there is no evidence of fibular apposition proximal to this point, as is observed, for example, in *Shoshonius* and *Absarokius* (Covert and Hamrick, 1993; Dagosto et al., 1999). In this, these tibiae are more similar to Bridger Basin omomyids or small anthropoids (Dagosto, 1985; Meldrum and Kay, 1997). The crests for the anterior

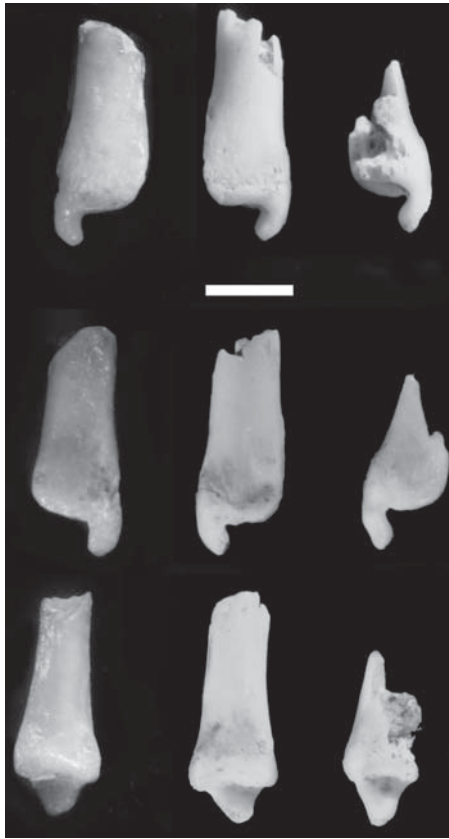


FIGURE 13.8. Comparative views of unfused morph. From left to right V13032, V13033, V13034. Top row, anterior view. Middle row, posterior view. Bottom row, lateral view. Scale is 2 mm.



FIGURE 13.9. Comparison of lateral view of tibia of Shanghuang unfused morph (V13032) and Bridgerian omomyid (USNM 336189). Scales are 1 mm.

and posterior tibiofibular ligaments are not as well developed in the Shanghuang tibiae as they are in Bridger omomyids or *Neosaimiri* (Dagosto, 1985; Meldrum and Kay, 1997).

Like known omomyids, these tibiae appear to lack any distal articular facet for the fibula (Figure 13.9). This contrasts with most anthropoids, which have a small articular facet extending most of the anteroposterior length of the lateral surface of the distalmost aspect of the tibial shaft (Dagosto, 1985; Ford, 1986, 1990), although *Neosaimiri* (*Laventiana*) *annectens* also lacks a clear facet (Meldrum and Kay, 1997), and the facet is small in *Apidium* (Fleagle and Simons, 1983, 1995). It is often, however, extremely difficult to identify the tibial articular facet in *Microcebus*, galagos, and small platyrrhines (e.g., some callitrichids), even though the corresponding facet on the fibula is usually discernible. Therefore, like omomyids with unfused tibiofibulae, the best that can be said about these Shanghuang specimens is that the tibiofibular joint was largely syndesmotiic and any synovial articulation was small, perhaps absent.

In addition to the lack of tibiofibular fusion, this type differs from the previous one in having a longer and narrower tibial articular surface (higher AP/ML ratio; Table 13.1) and greater rotation of the medial malleolus (22–24 degrees).

In these respects, this morph more closely resembles omomyines, anaptomorphines, and anthropoids than tarsiers or *Necrolemur*. The anterior process is not strongly developed in V13032 and V13033, but is more salient in V13034. It does not appear to be faceted. The groove for the tibialis posterior is shallow but runs more inferiorly than medially. The tibial malleolus is relatively long, narrow, and triangular in shape and is without a marked indentation for the deltoid ligament (Figure 13.9).

13.4 Discussion and Summary

Five distal tibiae of haplorhine primates have been recovered from the middle Eocene Shanghuang fissure-fillings. There are two types of tibial morphology represented; in type 1 the tibia is fused to the fibula and in type 2 the bones are separate. Both types exhibit features (lesser degree of malleolar rotation; tibiofibular joint fused or syndesmotiic; restricted mortise shape) which imply that flexion-extension movement between the crus and the tarsus was accompanied by less conjunct rotation than in the majority of strepsirhine primates or larger anthropoids. These characteristics are commonly found among small leaping primates (Hafferl, 1932; Fleagle and Simons, 1983,

TABLE 13.4. An index of medial height of the talus divided by lateral height of the talus. Only a selection of extant primates is shown, but almost all living taxa of strepsirrhines and platyrrhines were measured. In no case did any extant primate have a mean index as high as *Tarsius*.

	Mean	sd	n	Min	Max
Tarsiidae					
<i>Tarsius syrichta</i>	136.0	7.4	7	125.1	146.0
<i>Tarsius bancanus</i>	133.9	12.2	8	111.6	148.6
Omomyidae					
Bridger B omomyid	113.0	5.4	7	103.5	118.4
Bridger C&D omomyid	119.3	6.2	6	112.7	129.1
<i>Tetonius</i> sp.	111.8	3.0	2		
<i>Shoshonius cooperi</i>	89.7		2		
<i>Necrolemur</i> sp.	122.2		1		
Adapidae					
<i>Adapis</i> sp.	110.9		2	107.5	114.3
<i>Leptadapis</i> sp.	95.4		5	90.5	111.3
<i>Notharctus tenebrosus</i>	107.4		2	104.8	110.0
<i>Smilodectes gracilis</i>	111.5	2.5	6	107.4	114.8
Extant primates					
<i>Cebuella pygmaea</i>	105.8	11.6	5	88.2	120.8
<i>Saguinus</i>	114.0	1.1	3	112.8	115.0
<i>Saimiri sciureus</i>	120.6	6.6	15	107.9	130.4
<i>Microcebus murinus</i>	111.0	5.5	15	100.0	122.7
<i>Galago moholi</i>	111.9	3.0	5	108.8	115.6
<i>Eulemur fulvus</i>	118.9	7.1	16	106.6	130.3
Shanghuang primates					
Eosimiid tali	111.2	8.2	6	105.0	126.8
New protoanthropoid	111.0		1		
New haplorhine	86.7		1		

1995; Dagosto, 1985; Fleagle and Meldrum, 1988). In terms of assessing possible phylogenetic affiliations, we first note that it is extremely difficult to distinguish between omomyids (aside from *Necrolemur*) and anthropoids solely on the basis of distal tibial morphology. One salient feature may be the shape of the medial malleolus in lateral view which in anthropoids (with the exception of *Cebuella*) tends to be shorter (at least posteriorly) with a more pronounced indentation for the deltoid ligament. With respect to these features, the shape of the tibial malleolus is more prosimian-like than anthropoid-like in both kinds of Shanghuang tibiae.

Given the fusion of the tibia and fibula exhibited by Type 1, it is reasonable to propose that these tibiae belong to the appropriately sized *Tarsius eocaenus* or an allied species. Regarding the conformation of the tibiofibular mortise (the relative size, distal extent, and degree of sloping of the malleoli), however, the most striking resemblance of the Shanghuang fused morph is to anthropoids, and not to *Tarsius* or *Necrolemur*. However, we cannot say whether the mortise shape exhibited by anthropoids is derived for crown-group anthropoids or primitive for haplorhines (with the *Tarsius-Necrolemur* condition being more derived in the latter case). We do not know the mortise shape of the unfused morph or of omomyids other than *Necrolemur*. The short fibular malleolus of *Tarsius* is likely correlated with the strong asymmetry in height between the medial and lateral sides of its talus. In the majority of primates, the medial side of the talus is taller than the lateral, but

this asymmetry is most exaggerated in *Tarsius* (Table 13.4). If we are correct about the relationship between talar body and mortise asymmetry, the values for omomyid tali (Table 13.4) suggest that they, like anthropoids, did not exhibit the mortise asymmetry seen in *Tarsius* or even the less derived condition seen in *Necrolemur*. This suggests that the symmetrical mortise of omomyids and anthropoids is primitive for haplorhines.

The “equal length-nonasymmetrical” type of mortise shape may even be primitive for euprimates, since the alternate condition of an asymmetrical mortise shared by Lemuriformes and Adapiformes, made by the flare of the lateral malleolus, is almost certainly there to accommodate the flared talofibular facet, a feature considered a derived strepsirrhine apomorphy (Beard et al., 1988; Dagosto and Gebo, 1994). Neither tree shrews (including *Ptilocercus*), nor dermopterans exhibit such an asymmetry of the mortise, nor does it seem to be characteristic of the plesiadapiforms *Ignacius* or micromomyids (Bloch and Boyer, 2007).

If the type 1 Shanghuang tibia does belong to a tarsiid, the differences in mortise morphology suggest that the postcranium of the Shanghuang tarsiids is more different from extant *Tarsius* than are the molars or the skull (Beard et al., 1994; Rossie et al., 2006) and that tibiofibular fusion was attained independently from extant *Tarsius* or *Necrolemur*. Only one talus from Shanghuang has been provisionally allocated to a tarsiid (on the basis of its relatively low and wide talar body and short talar neck) although there are other significant differences between it and extant tarsiers (e.g., talar head shape). This particular talus is too large to be from the same species as the tibiae discussed here (for example, the space between the malleoli in these specimens measures less than 1 mm, and the trochlear width of this talus is 2.13 mm; too large to fit in the mortise). Unfortunately the preservation of this specimen does not permit an assessment of talar asymmetry, but it seems unlikely that it was as exaggerated as in *Tarsius*. Although this actually means that in terms of morphology (but not size), this talus could functionally articulate with the Shanghuang tibiae, it points out again the significant differences between the Shanghuang form and extant tarsiers.

In addition, the dental and postcranial remains of Shanghuang tarsiids are relatively rare compared to the anthropoids or “unnamed haplorhines” (Table 13.2). Therefore, we think it equally likely that this morph belongs to one of the smaller size classes of the better represented Eosimiidae or protoanthropoid group and may provide further evidence of their anthropoid affinities. An eosimiid is the more likely option given that the tarsal morphology of the protoanthropoid group suggests less developed leaping abilities (Gebo et al., 2001). Given the strong degree of tibiofibular apposition in *Apidium*, *Cebuella*, and *Callithrix*, and the fusion (possibly convergent) in *Necrolemur* and *Tarsius*, it is not unreasonable to assume that tibiofibular fusion might occur convergently in other small anthropoids or haplorhines.

The fused tibiofibula from the Fayum region of Egypt that has been referred to *Afrotarsius* (Rasmussen et al., 1998)

actually does not belong to a primate (White and Gebo, 2004). These Shanghuang tibiae, however, might provide evidence of tibiofibular fusion in Eosimiidae, a group that is sometimes linked to *Afrotarsius* (e.g., Ross et al., 1998; Gunnell and Miller, 2001). We stress, however, that (1) these tibiae may very well belong to a haplorhine group other than Eosimiidae; (2) these tibiae are too small to belong to *Eosimias sinensis*; (3) tibiofibular fusion is likely a compliant feature that is closely related to hindlimb function; by itself it is not enough to provide strong support for any potential phylogenetic relationship with *Tarsius*; and (4) the presence of such a derived character in one taxon, even if it proves to be an eosimiid, means only that this particular taxon is unlikely to be *directly ancestral* to anthropoids; it cannot refute an hypothesis that the whole clade is the sister group of crown anthropoids.

The affinities of the unfused morph (Type 2) are also uncertain. The greatest overall phenetic resemblance is to omomyids other than *Necrolemur* (e.g., *Omomys*, *Hemicacodon*, *Shoshonius*, and *Absarokius*). One significant difference from anthropoids may be the absence of an articular facet for the fibula in the unfused Shanghuang morph and omomyids, and the presence of such a facet in almost all anthropoids. Malleolar shape is also more like prosimians than anthropoids. Therefore, attribution to some as yet unrecognized Shanghuang omomyid or the “unnamed haplorhine family” at Shanghuang are both reasonable hypotheses. On the other hand, this morphology is not strikingly different from that of anthropoids and is probably primitive for haplorhines as a whole. Therefore attribution to either of the anthropoid groups is also possible. None of the morphological differences among the tali of the Shanghuang groups makes one attribution more likely than another.

Although we are unable to confidently allocate these bones to any specific group of Shanghuang primates, these tibiae, like the tarsal bones from Shanghuang, demonstrate the diversity of primates that were present at this locality, clearly show that these primates are phylogenetically haplorhine, support the recognition evidenced by the dentitions and tarsal bones of at least two major clades among the haplorhine primates at Shanghuang, and reveal the existence of anthropoid-like morphology among some of these primates.

Acknowledgments. Financial support for this research was provided by grants from the Leakey Foundation, the National Science Foundation (including BCS 9615557 and 0309800), and the Chinese NSF. We thank S. Goodman of the Field Museum of Natural History Chicago for access to uncatalogued *Microcebus* material, the staff of the Mammalogy department at FMNH for access to specimens, and Wang Yuanqing, Li Chuankui, Wang Banyue, Guo Jianwei, and numerous other colleagues at the IVPP for their generous assistance. Two reviewers made very helpful suggestions for improving the manuscript.

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