Volume 58, Issue 2, February 2010 ISSN 0047-2484

Journal of Human Evolution

JOURNAL OF HUMAN EVOLUTION

A hominoid distal tibia from the Miocene of Pakistan

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ARTICLE INFO

ABSTRACT

A distal tibia, YGSP 1656, from the early Late Miocene portion of the Chinji Formation in Pakistan is described. The fossil is 11.4 million years old and is one of only six postcranial elements now assigned to *Sivapithecus indicus*. Aspects of the articular surface are cercopithecoid-like, suggesting some pronograde locomotor activities. However, YGSP 1656 possesses an anteroposteriorly compressed metaphysis and a mediolaterally thick medial malleolus, ape-like features functionally related to orthograde body postures and vertical climbing. YGSP 1656 lacks specializations found in the ankle of terrestrial cercopithecoids and thus *Sivapithecus* may have been primarily arboreal. Nevertheless, the morphology of this tibia is unique, consistent with other interpretations of *Sivapithecus* postcranial functional morphology that suggest the locomotion of this ape lacks a modern analog. Based on the limited postcranial remains from *S. indicus*, we hypothesize that this taxon exhibited substantial body size dimorphism.

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Introduction

This report focuses on the description of a recently recognized distal tibia, YGSP 1656, assignable to *Sivapithecus indicus*, from locality Y076 in the early Late Miocene of the Chinji Formation of the Siwalik Group in the Potwar Plateau, Pakistan (Pilbeam et al., 1979; Flynn et al., 1990; Kappelman et al., 1991). Two other hominoid specimens have been recovered from locality Y076: an undescribed right M[3], YGSP 31557, and a left humeral shaft with distal epiphysis, YGSP 30730 (Pilbeam et al., 1990).

There are almost 38,000 mammalian fossils from the Potwar Plateau in the collections made in collaboration with the Geological Survey of Pakistan (GSP) and the Pakistan Museum of Natural History (PMNH). There are at least a dozen primate species recognized in our collections (Lydekker, 1879,1884; Pilgrim, 1910,1932; Lewis, 1933; Simons and Pilbeam, 1965; Gingerich and Sahni, 1979; Jacobs, 1981; MacPhee and Jacobs, 1986; Kelley, 1988; Flynn and Morgan, 2005); 75% of the primate fossils represent the hominoid *Sivapithecus*, within which Kelley (2005a) has tentatively identified three species. *Sivapithecus parvada* is found only at locality Y311 in the Nagri Formation (Kelley, 1988; Scott et al., 1999), dated at 10.1 Ma (Barry et al., 2002). *Sivapithecus indicus* and *S. sivalensis* are probable time-successive, ancestor-descendant species (Kelley, 2005a) exhibiting relatively minor differences in molar size and proportions, the former sampled from the Chinji Formation

between 12.8 Ma and 11.4 Ma (Kappelman et al., 1991; Behrensmeyer et al., 1995; Willis and Behrensmeyer, 1995; Ogg and Smith, 2004), the latter from the Dhok Pathan Formation between 9.3 and 8.5 Ma (Barry et al., 2002; Nelson, 2007). Alternatively, *S. indicus* and *S. sivalensis* may not differ enough to be considered separate species (Kelley, 2005b). A few indeterminate specimens, either *S. indicus* or *S. sivalensis*, are sampled from the poorly fossiliferous intervening Nagri Formation.

The Harvard-GSP project has collected 22 *Sivapithecus indicus* specimens from the Chinji Formation, ranging in age between 12.8 Ma and 11.4 Ma. YGSP 1656, the first tibia recovered from the Potwar Plateau, is one of only six postcranial specimens from the Chinji Formation assignable to *S. indicus* (Raza et al., 1983; Rose, 1984,1989,1993; Pilbeam et al., 1990; Madar et al., 2002; see Table 4). Previously described postcranial remains of all three *Sivapithecus* species have been characterized as representing a generalized arboreal, predominantly pronograde quadruped, capable of some antipronograde or orthograde behaviors, including vertical climbing (see Rose, 1993; Madar et al., 2002). Both dental (Kelley, 2005a,b) and postcranial specimens (at least of *S. parvada*; Kelley, 1988) imply considerable size dimorphism.

Locality Y076 is classified as a simple floodplain channel with mixed lithologies (Behrensmeyer et al., 2005). The locality measures >50 m across and is approximately 5 m thick. Fossils derive from lenses of conglomerate and interbedded sand and red silty sand. More than 1500 fossil specimens have been cataloged from this locality, representing over 56 mammalian species from 10 orders. The fauna of Y076 is similar in taxonomic composition and

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relative abundance to many other Chinji localities, with the addition of more rare taxa reflecting the high fossil productivity of this locality. Suids, anthracotheres, giraffids, bovids, tragulids, rhinocerotids, and proboscideans dominate the large mammal fauna while cricetids and rhizomyids are the most diverse and abundant small mammals (Flynn et al., 1995; Morgan et al., 1995). Dated to 11.4 Ma by correlations to the paleomagnetic timescale (Kappelman et al., 1991; Ogg and Smith, 2004), Y076 predates the first appearance of hipparionines in this sequence at 10.8 Ma (Pilbeam et al., 1996).

Materials and methods

We compared YGSP 1656 to distal tibiae of adult wild-shot anthropoid primates (Table 1), studied at the Cleveland Museum of Natural History, Harvard Museum of Comparative Zoology, American Museum of Natural History, National Museum of Natural History, Yale Peabody Museum, and Field Museum (Chicago). The platyrrhine taxa were chosen to test hypotheses that *Sivapithecus* may have moved like a modern howler or capuchin monkey (Rose, 1983,1989). Fossil tibiae from the Miocene were studied at the National Museum of Kenya and the Uganda National Museum. A high quality research cast of the *Hispanopithecus laietanus* tibia IPS-18800 (courtesy of S. Moyà-Solà) was measured at the Harvard Peabody Museum of Archaeology and Ethnology (PMAE).

Six measurements were taken on the articular surface of the distal tibia: the maximum mediolateral width of the anterior, posterior, and midpoint aspects of the articular surface, and the maximum anteroposterior length of the most medial, lateral, and midpoint aspects of the articular surface (Fig. 2). Measurement error, assessed by repeating these measures on 40 specimens a month after the original measurements were taken, was within 5%. The geometric mean (GM) of these six measures was calculated by taking the product of all six and then the (1/6)th root of the product. Each raw measure was then divided by the GM, following the size-adjustment protocol established by Darroch and Mosimann (1985). This approach has been used in previous paleoanthropological studies including a study of the primate ankle (Seiffert and Simons, 2001) and a study on *Sivapithecus* postcranial remains (Madar et al., 2002).

The mediolateral width of the tibial metaphysis was measured as the maximum mediolateral dimension taken at the point when the medial malleolus begins to curve medially, just superior to the distal articular surface, so as to not include the medial malleolus in the measurement. The anteroposterior dimension was the maximum dimension perpendicular to the mediolateral width. The thickness of the medial malleolus was taken at the midpoint of the malleolus at its most superior junction with the articular surface of

the distal tibia. The thickness of the malleolus is reported here relative to the anteroposterior length of the medial malleolus, which was measured as the maximum anteroposterior length perpendicular to the medial malleolar width. The relative thickness of the medial malleolus is measured to assess loading of the joint in inversion, an important joint motion during orthograde climbing bouts in hominoids (Wunderlich, 1999; DeSilva, 2008). The similarity between YGSP 1656 and extant taxa was statistically evaluated using a single observation with the mean test (Sokal and Rohlf, 1995: 228–229).

A non-stepwise discriminant function analysis was performed on the size-adjusted measures of the distal tibia using SPSS 16.0. Included in this analysis were the dimensions of the metaphysis, the six dimensions of the articular surface of the distal tibia and also three dimensions of the medial malleolus: the maximum anteroposterior length, maximum mediolateral width, and maximum superoinferior height. The GM of these eleven measurements was calculated and each raw value divided by the GM and entered into the discriminant function. The fossil tibiae from the Miocene were entered as separate groups.

Description

YGSP 1656 is the distal $\sim$30 mm of a well preserved, male-*Nasalis*-sized left tibia which we assign to *Sivapithecus indicus*; its epiphysis has a maximum mediolateral width of 24.1 mm and an anteroposterior length of 18.6 mm (Fig. 1). The tibia was found in January of 1975, prepared and identified in April of 2007, and is currently curated at the PMAE, on loan from the PMNH.

YGSP 1656 possesses a mediolaterally broad (21.9 mm) and anteroposteriorly compressed (15.3 mm) metaphysis (Fig. 1). The tibial shaft, as exposed in cross section, is pear shaped, with its mediolateral axis parallel to the epiphyseal surface. At the break, the cortical bone is exposed allowing the thickness to be estimated: 4.5 mm lateral, 2.7 mm medial, 2.4 mm posterior, 2.9 mm anterior. The medial surface of the shaft is flat. The anterior and posterior surfaces are convex and taper laterally to a sharp interosseous crest, which anchored the anterior tibiofibular ligament. This crest divides $\sim$12 mm superior to the articular surface to form a triangular fibular notch, its anterior margin being sharp and posterior margin very gently rounded, terminating in a projection for the posterior tibiofibular and the transverse tibiofibular ligaments. The slightly concave distal margin of the notch is $\sim$10 mm long anteroposteriorly. There is a very small facet for the fibula located in the most anterior and inferior aspect of this notch. Inferiorly the anterior rim of the distal tibia has a very slightly projecting lip of bone; posteriorly, the tibial edge is essentially flat. There is a small

Table 1
Distal tibial measurements[a]

Species/Specimen	n	Metaphyseal dimensions		Articular surface of distal tibia						Medial Malleolus		
		Mediolateral	Anteroposterior	AP Lateral	AP Midpoint	AP Medial	ML Anterior	ML Midpoint	ML Posterior	SI	AP	ML
YGSP 1656	1	21.9	15.3	15.8	13.0	12.5	16.9	14.0	12.7	9.1	13.7	8.7
Pan troglodytes	49	30.6 ± 3.1	21.8 ± 1.8	19.2 ± 1.6	20.8 ± 1.9	18.7 ± 1.7	27.3 ± 2.1	21.4 ± 1.5	17.7 ± 1.7	13.3 ± 1.4	18.7 ± 1.7	13.5 ± 1.3
Gorilla gorilla gorilla	44	44.1 ± 7.0	28.0 ± 4.6	24.7 ± 3.1	27.7 ± 3.7	26.4 ± 3.3	38.7 ± 4.5	29.0 ± 3.8	21.6 ± 3.3	15.0 ± 2.2	26.9 ± 3.6	18.4 ± 2.6
Pongo pygmaeus	35	26.5 ± 4.3	16.0 ± 2.9	17.1 ± 2.3	20.0 ± 2.5	15.2 ± 2.7	24.7 ± 3.4	21.4 ± 2.8	18.2 ± 2.6	8.1 ± 1.4	15.0 ± 2.1	12.0 ± 1.6
Hylobates lar	40	12.2 ± 1.2	10.5 ± 0.8	9.4 ± 0.8	10.3 ± 0.6	8.9 ± 0.6	11.3 ± 0.7	9.2 ± 0.8	7.4 ± 0.6	6.0 ± 0.6	9.3 ± 0.7	5.6 ± 0.5
Symphalangus syndactylus	12	15.5 ± 1.2	10.3 ± 1.0	10.7 ± 0.9	11.5 ± 0.9	9.1 ± 0.6	13.4 ± 0.9	10.5 ± 0.4	9.4 ± 1.0	6.9 ± 0.5	9.3 ± 0.7	7.1 ± 0.7
Papio spp.	35	19.7 ± 2.6	16.8 ± 2.2	14.5 ± 2.2	15.7 ± 2.0	13.8 ± 2.4	17.8 ± 2.2	15.6 ± 2.0	13.7 ± 1.7	10.2 ± 1.3	15.6 ± 1.8	7.6 ± 1.0
Mandrillus sphinx	12	18.6 ± 2.6	16.1 ± 2.3	12.8 ± 2.1	14.4 ± 2.0	12.0 ± 1.9	16.7 ± 2.6	14.2 ± 2.0	13.3 ± 2.6	9.3 ± 1.1	13.3 ± 1.6	7.3 ± 1.3
Nasalis larvatus	37	18.0 ± 2.6	14.8 ± 2.0	12.0 ± 1.4	14.6 ± 1.5	12.6 ± 1.3	15.4 ± 1.5	13.6 ± 1.5	11.6 ± 1.4	7.9 ± 1.1	12.6 ± 1.5	6.6 ± 1.0
Alouatta palliata	30	13.5 ± 1.3	8.8 ± 0.9	8.7 ± 0.8	9.7 ± 0.8	7.4 ± 0.8	12.4 ± 1.1	10.4 ± 1.2	9.3 ± 1.1	5.3 ± 1.0	7.1 ± 0.7	6.0 ± 0.6
Cebus capucinus	20	9.6 ± 0.7	7.6 ± 0.5	7.6 ± 0.7	8.4 ± 0.8	7.2 ± 0.7	9.0 ± 0.7	8.9 ± 0.8	7.9 ± 0.7	5.3 ± 0.8	7.3 ± 0.7	3.7 ± 0.3

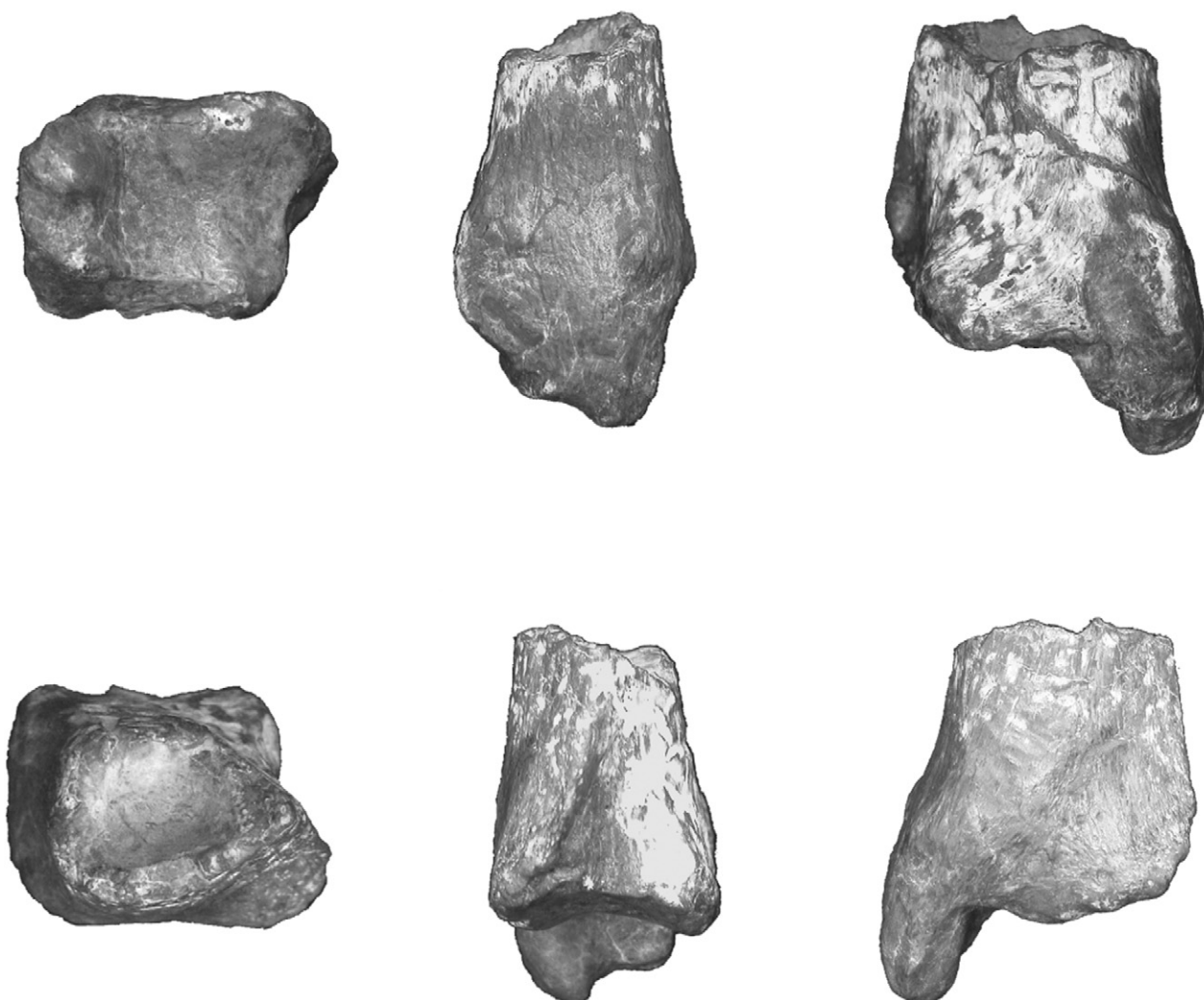[a] All measurements reported as mean ± 1 standard deviation.

Fig. 1. *Sivapithecus indicus* distal tibia YGSP 1656 in (top left to right) inferior, medial, and posterior view and (bottom left to right) superior, lateral, and anterior view. Scale bar = 1 cm.

stop facet along the anterior rim that measures 3.9 mm mediolaterally and 3.3 mm superoinferiorly.

The malleolus is robust, 13.7 mm anteroposteriorly, 8.7 mm mediolaterally, and 9.1 mm superoinferiorly; it projects more anteriorly than posteriorly and possesses a moderately developed intercollicular groove for the attachment of the posterior tibiotalar ligament. Its articular anterolateral surface is continuous with the lateral surface of the malleolus and with the trochlear surface, and is delimited by a marked anterior crest which is continuous with the crest at the anterior margin of the medial half of the trochlear surface. Posteriorly, the groove for the tibialis posterior runs inferiorly from the tibial shaft onto the posterior half of the malleolus and is demarcated by clear margins on either side, especially medially; it is 4 mm wide and slightly less than 1 mm deep. Lateral to the malleolar groove, there is a slight indentation demarcating the path of the flexor hallucis longus tendon.

The trochlear surface is trapezoid shaped, with a wider anterior aspect (16.9 mm) and a narrower posterior surface (12.7 mm). The medial half of the trochlear surface is perpendicular to the tibial long axis, while the lateral part slopes superolaterally at an angle of 27.5 degrees relative to the articular surface of the medial portion, producing an inferior talar facet angle of 102.5 degrees relative to

the long axis of the tibia. The medial and lateral parts of the joint surface are separated by a gently rounded median keel that equally divides the medial and lateral surfaces. The keel is more strongly projecting anteriorly and tapers posteriorly.

Comparative anatomy and functional interpretation

The morphology of YGSP 1656 suggests that *S. indicus* had a mobile ankle, adapted for generalized pronograde arboreal quadrupedalism and some ape-like, antipronograde positional behaviors such as vertical climbing.

Using a single observation with the mean test (Sokal and Rohlf, 1995: 228–229), the shape of the metaphysis of YGSP 1656 (Fig. 3) is most similar to the morphology found in modern chimpanzees ($t = 0.20$, $p = 0.85$), siamangs ($t = 0.66$, $p = 0.53$), and gorillas ($t = 1.23$, $p = 0.23$). The shape is quite unlike the square morphology of the metaphysis in baboons ($t = 2.99$, $p = 0.005$) and *Nasalis* ($t = 2.29$, $p = 0.03$). This ape-like anteroposteriorly compressed metaphysis of YGSP 1656 would have facilitated a wide range of motion at the ankle joint, in contrast to a cercopithecoid-like anteroposteriorly broad metaphysis, in which the anterior lip of the distal tibia reaches the neck of the talus at the more reduced angle of dorsiflexion of only 15–25° (Hirasaki et al., 1993; DeSilva,
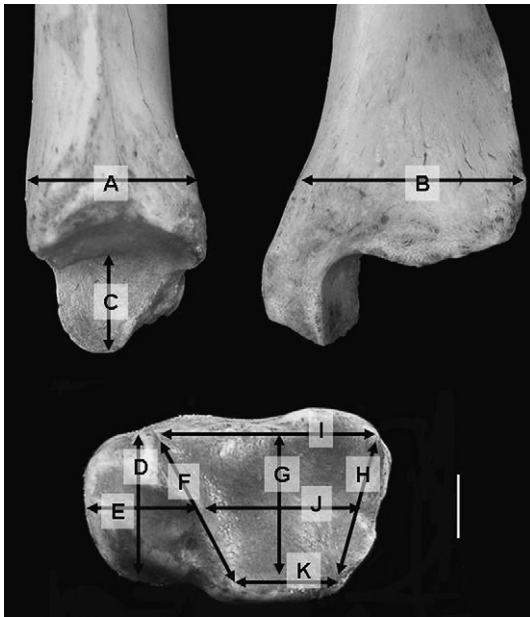
Fig. 2. Measurements taken in this study illustrated on a chimpanzee (*Pan troglodytes*) distal tibia (PMAE 22-2-50/60353.0) in lateral (upper left), anterior (upper right), and inferior (bottom) views (scale bar = 1 cm). The measurements taken are as follows: A: Anteroposterior (AP) length of metaphysis; B: Mediolateral (ML) width of metaphysis; C: Superoinferior (SI) height of medial malleolus; D: AP length of medial malleolus; E: ML width of medial malleolus; F: AP length of medial articular surface; G: AP length of midpoint of articular surface; H: AP length of lateral articular surface; I: ML width of anterior articular surface; J: ML width of midpoint of articular surface; K: ML width of posterior articular surface. Copyright 2009 President and Fellows of Harvard College.

2008). Additionally, the mediolaterally wide metaphysis of YGSP 1656 implies loading of the ankle joint in positions outside of the parasagittal plane and therefore suggests a greater range of foot and ankle mobility than is present in modern cercopithecoids.
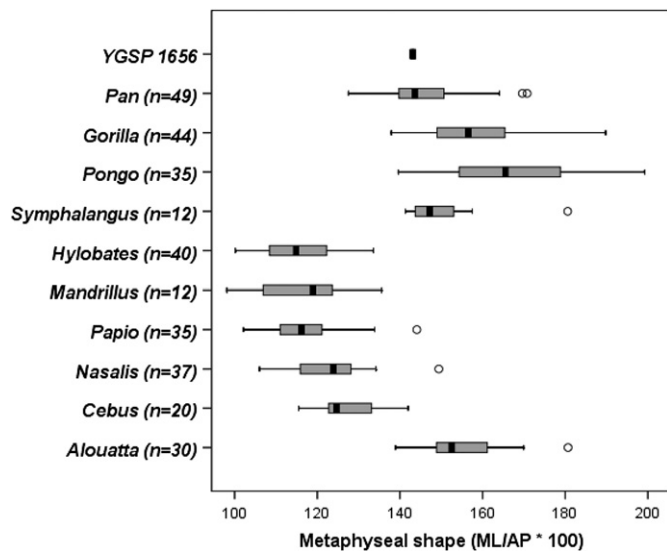
Cercopithecoids possess a bulbous medial malleous, which articulates with a cup-shaped cotylar fossa of the talus and is thought to stabilize the medial ankle joint during rapid flexion and extension (Harrison, 1989). YGSP 1656 does not have this morphology, and instead possesses a flatter, more ape-like medial malleolus. Terrestrial cercopithecoids have a strongly keeled talar facet, which stabilizes the ankle joint in the parasagittal plane (Harrison, 1989). The YGSP 1656 tibia has a more gently sloped keel, suggestive of increased foot and ankle mobility, perhaps in an arboreal environment.

The pronounced anterior interosseous crest on YGSP 1656 indicates mobility between the tibia and the fibula during positions of ankle dorsiflexion, which is a characteristic of apes rather than cercopithecoids (Barnett and Napier, 1953). Furthermore, because the flexor hallucis longus muscle originates on the fibula, increased fibular mobility suggests a strong hallucial grasping capacity in *Sivapithecus*. YGSP 1656 possesses a noticeable groove just lateral to the medial malleolus for the tendon of flexor hallucis longus, implying an important role of this muscle in the foot of *Sivapithecus*. This anatomy and functional interpretation is consistent with an analysis of a robust terminal hallucial phalanx from *S. parvada* (Madar et al., 2002), and the robust *S. sivalensis* hallux, YGSP 14046 (Pilbeam et al., 1980). However, the relatively small fibular facet on the YGSP 1656 tibia may indicate slightly less mobility at the tibiofibular joint than is found in modern hominoids.

The mediolateral thickness of the malleolus in YGSP 1656 (Fig. 4) is more similar to the average medial malleolus thickness in *Hylobates* ($t = 0.67$, $t = 0.51$) and *Gorilla* ($t = 0.92$, $p = 0.36$) than to the distinctly different morphology of the medial malleolus in both *Nasalis* ($t = 2.55$, $p = 0.02$) and *Papio* ($t = 3.91$, $p < 0.001$). This thickness suggests that *Sivapithecus* loaded its foot in positions of inversion and climbed in a more hominoid-like than cercopithecoid-like manner. During climbing bouts, modern hominoids load the medial side of the foot, whereas cercopithecoids load the lateral aspect of the foot (Wunderlich, 1999). A skeletal correlate of medial midfoot loading and foot inversion is reflected at the ankle joint in the form of a mediolaterally thick medial malleolus (Fig. 4), as is seen in the YGSP 1656 tibia. YGSP 1656 also has a strong lateral tilt to the
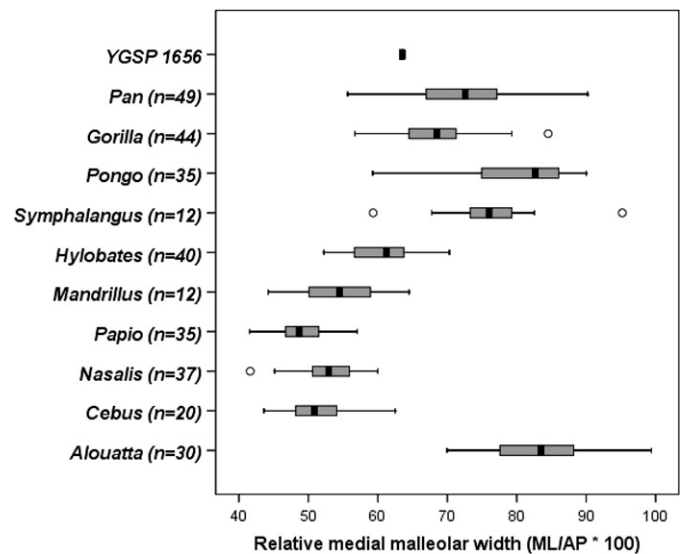

Fig. 3. Dimensions of the tibial metaphysis in YGSP 1656 compared to modern anthropoid primates. The *Hylobates*, cercopithecoids, and *Cebus* have square-shaped metaphyses whereas those of *Symphalangus*, the great apes, and *Alouatta* are more rectangular. This cross-sectional shape in the apes and ateline monkeys increases the possible range of dorsiflexion in the ankle and also implies mediolateral loading of the ankle joint. YGSP 1656 is quite unlike the cercopithecoids and instead has a shape closest to the modern African apes and *Symphalangus*. Figures 3–5 show the medial (black bar), interquartile range (box), and overall range (whiskers) of the data. Outliers, defined as 1.5 times the interquartile range, are shown as circles.

Fig. 4. Relative thickness of the tibial medial malleolus in YGSP 1656 compared to modern anthropoid primates. The hominoids and *Alouatta* have relatively thick medial malleoli, suggesting loading of the ankle joint in positions of inversion. Cercopithecoid monkeys and *Cebus* have significantly thinner medial malleoli. YGSP 1656 has malleolar morphology most like *Hylobates* and *Gorilla* suggesting that *Sivapithecus* loaded its ankle more like a modern ape than a modern cercopithecoid.

distal tibia, which is more characteristic of arboreal catarrhines like *Nasalis* than terrestrial catarrhines like *Papio*. This morphology places the foot in a more inverted position as in the arboreal cercopithecoids, whereas the morphology of the terrestrial cercopithecoids places the tibia closer to a parasagittal plane (Meldrum, 1991). The attachment for the posterior tibiotalar ligament (PTTL) on YGSP 1656 is unlike that found on *Pongo* tibiae which have little or no attachment, and unlike the terrestrial cercopithecoids, which have a significantly more excavated region for this ligament (DeSilva, 2008, 2009). The PTTL attachment is similar to that found in the hylobatids, African apes, and the arboreal cercopithecoids. This morphology may indicate that the PTTL helped to stabilize the ankle during extreme dorsiflexion in *Sivapithecus*.

The anterior aspect of the tibial plafond is mediolaterally broad in hominoids (Fig. 5). This morphology is functionally linked to loading the talocrural joint in extreme dorsiflexion, an important joint motion during orthograde vertical climbing in most hominoids (DeSilva, 2008, 2009). In contrast, cercopithecoids have a mediolaterally shortened anterior aspect of the distal tibia. The distribution of bone on the inferior aspect of YGSP 1656 is unlike the condition found in modern great apes, *Symphalangus*, or platyrrhine monkeys, and is instead most similar to *Hylobates* ($t = 0.18$, $p = 0.86$) and cercopithecoids ($t = 0.40$, $p = 0.69$).

Because the anterior aspect of the articular surface is not mediolaterally broad, *S. indicus* probably did not engage in orthograde vertical climbing bouts as often as do modern great apes. Instead, the morphology of the articular surface of the YGSP 1656 tibia suggests that *Sivapithecus* loaded its ankle in positions of both dorsiflexion and plantarflexion, reflecting a varied positional and locomotor repertoire. The articular surface of YGSP 1656 is suggestive of a generalized locomotor strategy in *Sivapithecus*, including arboreal quadrupedalism and other pronograde positional behaviors, but the thick medial malleolus and anteroposteriorly compressed metaphysis are consistent with antipronograde behaviors common to all apes, such as vertical climbing, clambering, and bridging.
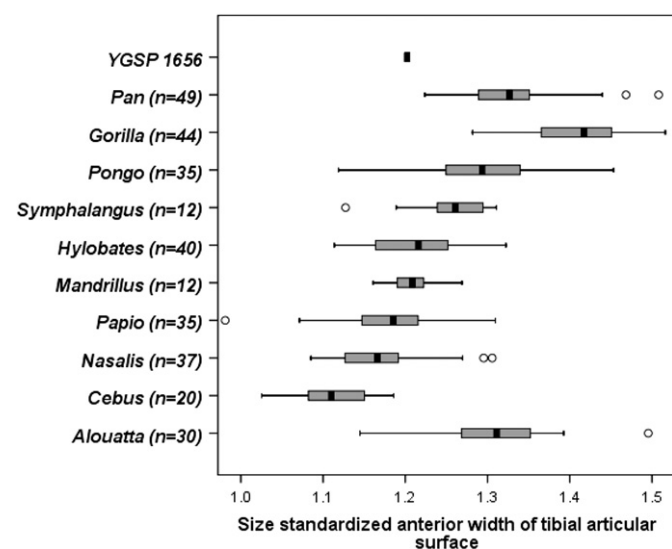

Fig. 5. Size-standardized width of the anterior aspect of the distal tibial articular surface in YGSP 1656 compared to modern anthropoid primates. The great apes and atelines have mediolaterally wide anterior aspects of the distal tibia resulting in a trapezoid-shaped articular surface. Cercopithecoids and *Hylobates* tend to have a square-shaped articular surface. YGSP 1656 falls between these two extremes, with an articular morphology similar to that found in modern gibbons, though not unlike some cercopithecoid monkeys.

Multivariate analysis

Figure 6 and Tables 2 and 3 summarize the results of a multivariate analysis of YGSP 1656 and a suite of extant and fossil primates. Along function 1, YGSP 1656 is in the general morphospace between the great apes (to the right) and the cercopithecoids (to the left), and is within the lower limits of *Pan* and *Symphalangus*, and the upper limits of *Cebus* and *Nasalis*. Function 2 has less resolving power. Although YGSP 1656 clusters primarily with *Hylobates* and *Pan*, it falls within the range of variation found in *Papio*, *Mandrillus*, *Symphalangus*, *Gorilla*, and *Pongo*. Based on Mahalanobis Distances (Table 3), the probabilities of group membership are highest in *Pan* (p = 0.51), and *Symphalangus* p = 0.46). For all other taxa, the probability of group membership is ≤0.02. Hypotheses that locomotion in *Sivapithecus* may have been similar to that found in modern platyrrhines *Cebus* and *Alouatta* (Rose, 1983, 1989) are not supported by this analysis of the *S. indicus* ankle. The ankle of *Sivapithecus* is also strikingly different from that of *Pongo*. All of the other Miocene catarrhine distal tibiae included in this analysis cluster with the cercopithecoids and *Hylobates* (but not *Symphalangus*) with the exception of the *Proconsul major* tibia NAP I'58 (Rafferty et al., 1995) and the *Hispanopithecus laietanus* tibia from the IPS-18800 skeleton (Moyà-Solà and Köhler, 1996), both of which are more like modern apes. A thorough comparative analysis of Miocene catarrhine distal tibiae appears elsewhere (DeSilva, 2008, in prep).

Discussion

This *S. indicus* distal tibia provides the first evidence for the functional morphology of the ankle joint in this Middle and Late
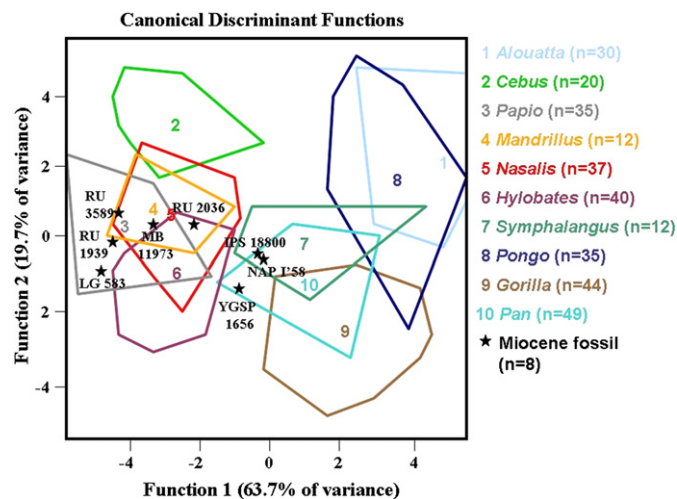

Fig. 6. Plot of scores on Functions 1 and 2 of a canonical discriminant analysis, with convex shapes showing ranges of modern taxa. This graph should be read in conjunction with Table 2. The first discriminant function explains 63.7% of the variance and is dominated by the mediolateral width of the medial malleolus and the mediolateral width of the anterior aspect of the distal tibial articular surface (Table 2). Along this function, there is a continuum from the cercopithecoids and *Cebus* to the large bodied orthograde hominoids and *Alouatta*. The second discriminant function explains 19.7% of the variance and is dominated by the mediolaterally elongated posterior and midpoint dimensions of the tibial articular surface (Table 2). Based on Mahalanobis Distances, YGSP 1656 is most like *Pan* and *Symphalangus*. Miocene catarrhine tibia are from *Proconsul major* (NAP I'58), *P. nyanzae* (KNM-RU 1939), *P. heseloni* (KNM-RU 2036, KNM-RU 3589), *Dendropithecus* or *P. africanus* (KNM-LG 583), *Victoriapithecus macinnesi* (KNM-MB 11973), and *Hispanopithecus laietanus* (IPS 18800). Most Miocene catarrhine tibiae are cercopithecoid-like, except for those belonging to *P. major* and *H. laietanus*, both of which are *Pan*-like. Species identification of fossil tibiae from Harrison (1989), Rafferty et al. (1995), and Moyà-Solà and Köhler (1996).

Table 2
Structure matrix for discriminant function analysis[a]

Variable	Function (% of variance)[b]		
	1 (63.7%)	2 (19.7%)	3 (7.4%)
Metaphyseal width (ML)	0.282	−0.270	0.109
Metaphyseal length (AP)	0.348	−0.170	−0.012
Malleolar width (ML)	**0.482**	−0.353	−0.240
Malleolar height (SI)	0.297	−0.025	**−0.557**
Malleolar length (AP)	−0.393	−0.341	**0.553**
Articular anterior width (ML)	**0.455**	−0.223	0.174
Articular midpoint width (ML)	0.220	**0.474**	0.357
Articular posterior width (ML)	0.113	**−0.704**	−0.059
Articular lateral length (AP)	−0.049	0.147	−0.145
Articular medial length (AP)	−0.160	−0.205	0.339
Articular midpoint length (AP)	−0.029	0.328	0.185

[a] Pooled within-group correlations between variables and first three discriminant functions.
[b] The largest two correlations.

Miocene hominoid. As with other aspects of *Sivapithecus* post-cranial anatomy, the combination of features present on YGSP 1656 is unlike any modern anthropoid and suggests a generalized loco-motor repertoire without a close modern analog.

For nearly every measure, the shape of this fossil is located in the morphospace between the extant hominoids and cercopithecoids. Of the modern species, YGSP 1656 is most similar to *Pan troglodytes* and *Symphalangus syndactylus* based on Mahalanobis Distances (Table 3). However, this does not imply that *Sivapithecus* used its feet precisely like a chimpanzee or siamang, and unlike these modern taxa there is little evidence from the forelimb that *S. indicus* was capable of significant suspensory behaviors (Pilbeam et al., 1990; Madar et al., 2002). Instead, the foot of *Sivapithecus* was probably adapted for pronograde positions of arboreal quadru-pedalism, and mobile foot positions during orthograde climbing and bridging. Finally, the morphology of YGSP 1656 suggests that *Sivapithecus* was adapted for arboreality. Although this analysis does not rule out the possibility that *Sivapithecus* also used terrestrial substrates, it is consistent with other functional analyses that suggest *Sivapithecus* was primarily an arboreal ape (Rose, 1984, 1989; Madar et al., 2002). YGSP 1656 is most similar to tibiae of the arboreally adapted apes *Pan* and *Symphalangus*, and more closely resembles those of the primarily arboreal *Nasalis* than the more terrestrial *Papio*, particularly in regards to ligament attachments and bony joint stability.

The results of the functional analysis of the distal tibia reported here are consistent with functional interpretations of *S. indicus* based on previous descriptions of a navicular, lateral cuneiform, and calcaneus from the Chinji Formation (Table 4). From the navicular (YGSP 46459), the *S. indicus* foot was reconstructed as one that could produce a powerful grip and load the foot in positions of

inversion (Madar et al., 2002). This capacity would enable *Sivapi-thecus* to navigate large diameter substrates both in pronograde and orthograde positions. Additionally, a lateral cuneiform (YGSP 17118) is most similar to that found in modern chimpanzees and is functionally consistent with arboreal quadrupedalism and climbing (Rose, 1984). The calcaneus from the Chinji Formation (YGSP 28230) has been reconstructed as one belonging to a foot capable of strong grasping, well adapted for arboreal climbing and quadru-pedal locomotion (Rose, 1989). The humerus (YGSP 30730) and capitate (YGSP 17119) are interpreted as representing a generalized arboreal quadruped, capable of palmigrade quadrupedalism, climbing, and some suspension (Raza et al., 1983; Pilbeam et al., 1990). Based on these data from the forelimb, foot, and ankle, *S. indicus* can be reconstructed as a hominoid with a mosaic loco-motor repertoire that combines arboreal quadrupedalism with antipronograde activities such as vertical climbing, clambering, and bridging. Postcranial remains of *S. parvada* and *S. sivalensis* indicate a very similar repertoire (see Pilbeam et al., 1980; Madar et al., 2002). It remains of interest that in some facial features *S. sivalensis* resembles *Pongo*, whereas postcranially all three *Sivapithecus* species differ from all extant apes, and in particular from *Pongo*.

The reconstruction of *Sivapithecus* as an arboreally adapted ape is consistent with habitat reconstruction based on carbon isotope data and ecomorphological studies of bovid lower limbs (Scott et al., 1999). Stable carbon isotope values ($\delta^{13}C$) from 11 mammalian herbivore species average -11.4 ± 0.9 ‰ ($n = 14$) and indicate pure C_3 vegetation. $\delta^{13}C$ values of paleosol carbonates at this strati-graphic level range between -9.3 and -10.7 ‰ ($n = 5$; Quade and Cerling, 1995), implying plant biomass values near -24 to -27 ‰, consistent with C_3 forest habitats (Cerling et al., 2004). The eco-morphological inferences of Scott et al. (1999), including seven bovid specimens from Y076, also suggest predominantly forested habitats at this locality. Two *S. indicus* teeth yield $\delta^{13}C$ values of -11.9 and -11.7 ‰, again indicating forest, although not entirely closed canopy forest (Nelson, 2007). The arboreal adaptations of the *Sivapithecus* ankle are thus compatible with a forested habitat (although we recognize that semi-terrestrial primates can be found in modern equatorial forests).

Finally, this distal tibia allows us to better estimate body mass dimorphism in *S. indicus*. Based on qualitative assessments of YGSP 1656 (Table 4), this individual was between 16–24 kg, roughly the size of a male *Nasalis larvatus*. The humerus, YGSP 30730, also from the Y076 locality, is from an individual with a similar estimated body mass (Table 4). The *Sivapithecus* M³ from Y076, YGSP 31557, has a molar occlusal area (length × breadth) around 110 mm², which would make it one of the smallest inferred female *S. indicus* (Kelley, 2005a). Although it is tempting to suggest that these three specimens may belong to the same individual, given the complex nature of this locality it is not possible to associate any of these

Table 3
Mahalanobis distance matrix from discriminant function analysis[a]

	Alouatta	Cebus	Papio	Mandrillus	Nasalis	Hylobates	Symphalangus	Pongo	Gorilla	Pan
Alouatta	–									
Cebus	40.1	–								
Papio	62.7	22.4	–							
Mandrillus	47.4	24.4	*14.2	–						
Nasalis	51.7	*19.6	*17.7	*18.2	–					
Hylobates	51.2	30.4	21.1	20.7	*18.6	–				
Symphalangus	19.9	35.9	35.4	32.6	30.8	28.6	–			
Pongo	*16.2	52.6	63.2	63.2	59.0	61.0	27.8	–		
Gorilla	28.3	58.0	43.7	50.7	36.6	36.6	29.5	29.8	–	
Pan	21.4	36.5	26.8	29.8	28.7	25.4	*16.4	28.6	*17.6	–
YGSP 1656	49.2	43.2	28.5	35.3	30.2	22.4	*10.8	63.2	33.1	*10.2

[a] Probabilities of group membership >0.05 signified with *

Table 4
Sivapithecus indicus postcranial specimens and body weight estimates[a]

Specimen number	Locality, Age (Ma)	Element	Qualitative estimate (kg)
YGSP 1656	Y076, 11.4	Left distal tibia	Most similar in size to male *Nasalis larvatus,* MCZ 41563, recorded body weight 21 kg.
YGSP 30730	Y076, 11.4	Left humerus	Most similar in size to male *Papio doguera neumani (Papio anubis)*, MCZ 8304. (Larger than largest male *Nasalis larvatus* at MCZ) Size estimate is ∼24 kg.[b]
YGSP 17118	Y495, 11.6	Left ectocuneiform	Most similar in size to small male *Pan troglodytes troglodytes*, MCZ 20041. Much larger than *Papio* and *Nasalis* males. Size estimate is ∼45–50 kg.[c]
YGSP 28230	Y499, 12.1	Partial right calcaneus	Most similar in size to male *Nasalis larvatus*, MCZ 41557, recorded body weight 20 kg.
YGSP 46459	Y499, 12.1	Left navicular	Intermediate in size between two male *Nasalis larvatus*, MCZ 37328, recorded body weight 19 kg, and MCZ 41563, recorded body weight 21 kg. Size estimate is ∼20 kg.
YGSP 17119	Y500, 12.1	Right capitate	Slightly smaller than both female and male *Pan paniscus,* MCZ 38019 and MCZ 38018. Much larger than *Papio* and *Nasalis* males. Size estimate is ∼30–40 kg.[c]

[a] We made qualitative body mass assessments, comparing individual elements to homologs in living species, or in some cases, specimens of known body weight. Given that *Sivapithecus* is inferred to be a pronograde quadruped, capable of some ortho-grade postures and locomotion, for comparisons we concentrated on pronograde quadrupedal cercopithecoids, particularly *Nasalis* and *Papio*, and species of *Pan*.

[b] The MCZ specimen was collected in Kenya. Size estimate based on live wild weight of 24.2 +/− 2.4 kg for male *Papio anubis* from Kenya as reported by Smuts (1985).

[c] Jungers and Susman (1984) provide average weight and weight ranges for *Pan paniscus* (female 33.2 kg, 27–38 kg; male 45 kg, 37–61 kg) and *Pan troglodytes troglo-dytes* (female 33.4 kg, 42.3–50 kg; male 40.9 kg, 50–70 kg). YGSP 17119 is difficult to match to a living primate because its morphology is unlike any living primate.

hominoid remains with one another. The *S. indicus* navicular (YGSP 46459) and calcaneus (YGSP 29230) yield similar body size esti-mates (Table 4). The ectocuneiform (YGSP 17118) and capitate (YGSP 17119) are from larger individuals, estimated at between 30 and 50 kg in mass. There are now six postcranial body weight estimates for *S. indicus.* Four cluster between 20 and 24 kg, the other two are between 30 and 50 kg. (We are more confident about the 45–50 kg estimate for the YGSP 17118 ectocuneiform than the 30–40 kg estimate for the YGSP 17119 capitate. See notes to Table 4). We interpret this distribution as implying a high degree of body mass dimorphism; Kelley (1988) inferred similar dimorphism for *S. parvada.* Thus the presumed males were between the size of an average male and female chimpanzee, whereas the females were about the size of an average male *Nasalis* or *Papio*. This degree of body size dimorphism, in which the males are around twice as large as the females, is comparable to that found in extant primates such as *Nasalis larvatus*, *Papio hamadryas*, *Pongo pygmaeus*, and *Gorilla gorilla* (Smith and Jungers, 1997; Delson et al., 2000).

Conclusions

YGSP 1656 is the first tibial fragment known from the Miocene genus *Sivapithecus*. The functional morphology of this bone is consistent with interpretations of other postcranial remains of *Sivapithecus*, indicating that it was primarily arboreal and had a varied locomotor repertoire consisting of both pronograde quadrupedalism and occasional antipronograde activities such as vertical climbing. YGSP 1656 is probably that of a female about the size of a modern male *Nasalis*, giving further support to the hypothesis of considerable body size dimorphism in *Sivapithecus*.

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