VERTICAL CLIMBING ADAPTATIONS IN THE ANTHROPOID ANKLE AND MIDFOOT: IMPLICATIONS FOR LOCOMOTION IN MIOCENE CATARRHINES AND PLIO-PLEISTOCENE HOMININS.

by

Jeremy M. DeSilva

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Doctoral Committee:

Associate Professor Laura M. MacLatchy, Chair
Professor Daniel C. Fisher
Professor John C. Mitani
Professor Milford H. Wolpoff
Research Scientist William J. Sanders

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ABSTRACT

Vertical climbing has featured prominently in hypotheses of both early hominoid evolution and the origins of hominin bipedalism. Although the kinematics of vertical climbing has been studied for the shoulder, elbow, hip and knee joints, the talocrural joint, or ankle, has not received nearly as much attention. Yet, the ankle is a critical region for determining how the foot will be positioned against a vertical substrate and the morphology of this joint may be specifically adapted for vertical climbing in those species that practice this form of locomotion. This dissertation attempts to improve our understanding of the kinematics of the talocrural joint during vertical climbing bouts in hominoids and to use these data to isolate skeletal correlates of vertical climbing in extant primates. Results from these analyses are used to interpret the functional morphology of the talocrural joint in early Miocene catarrhines and Plio-Pleistocene hominins to assess whether vertical climbing was a significant component of their locomotion.

Kinematic data were collected on wild chimpanzees at the Ngogo study site in Kibale National Park. Vertical climbing kinematics in wild chimpanzees are consistent with biomechanical models that suggest climbing animals keep themselves close to the substrate to reduce the moment at their lower limb joints. In part, this is accomplished by extreme dorsiflexion at the talocrural joint in wild chimpanzees. Analyses of 63 video stills taken in lateral view find that chimpanzees dorsiflex at the ankle approximately 45˚.

Flexion at the ankle during vertical climbing is accompanied by foot inversion and abduction. These joint positions keep the climbing chimpanzee close to the vertical substrate, thus reducing climbing costs associated with the muscular activity needed to counter downward forces acting on a large climbing ape. Similar degrees of dorsiflexion were observed on captive gorillas and orangutans and are known from published studies on gibbons and two ateline primates, *Ateles* and *Lagothrix*. Thus, in addition to vertical climbing quite often in the wild, hominoids and atelines appear to vertical climb in a kinematically similar manner. This is in contrast to cercopithecoid monkeys. Cercopithecoids rarely vertically climb, though when they do engage in this behavior, it is kinematically different from that practiced by hominoids and atelines. Data from the literature and ankle flexion calculated from video of climbing bouts in wild baboons and geladas in this study find that cercopithecoid monkeys do not experience extreme dorsiflexion at the ankle, and instead dorsiflex in the midfoot region during climbing. Based on the frequency and unique kinematics of vertical climbing at the talocrural joint in hominoids and atelines, it is predicted that these primates have skeletal morphologies adapted to frequent loading of the ankle in positions of dorsiflexion, inversion, and abduction. Specific predictions are based on data from the orthopaedic literature and kinetic work on climbing primates.

I test the hypothesis that hominoids and some atelines have an ankle morphology specifically adapted for bouts of vertical climbing using linear and angular measurements taken on 379 tibiae and 224 tali from adult wild primates. Skeletal correlates of abduction do not differentiate among the primates studied. However, vertically climbing primates have unique skeletal morphologies functionally related to loading of the talocrural joint in dorsiflexion and inversion. Relative to cercopithecoids, hominoids and ateline primates have a mediolaterally wide anterior surface of the distal tibia, adapted for efficiently distributing the forces through the ankle during positions of extreme dorsiflexion. In addition, the great apes and ateline primates have an anteroposteriorly reduced tibial metaphysis, which may allow for an increased range of dorsiflexion. Finally, hominoids and atelines have significantly mediolaterally thicker medial malleoli than the cercopithecoids monkeys, consistent with kinetic data demonstrating medial loading of the midfoot during vertical climbing. Interestingly, few measures of the distal tibia and talus functionally related to dorsiflexion, inversion, or abduction differentiate arboreal and terrestrial cercopithecoids suggesting that whether they are in an arboreal or terrestrial situation, cercopithecoids have conserved ankle kinematics.

These data are used to interpret the morphology of catarrhine distal tibiae and tali from the early Miocene in order to assess whether any taxa possessed hominoid-like vertical climbing adaptations. Most tibiae and tali are either cercopithecoid-like or have no modern analogue. However, the large tibia from Napak, Uganda assigned to *Proconsul major* has a mediolaterally expanded anterior surface of the talar surface, a mediolaterally wide medial malleolus, and a mediolaterally expanded tibial metaphysis. These three features are functionally related to loading of the ankle in dorsiflexion and inversion and differentiate hominoids and atelines from cercopithecoids. It is thus unlikely that *P. major* was simply a scaled-up version of *P. nyanzae* and may instead demonstrate the role that body size can have on postcranial anatomy in arboreal catarrhine primates. There is also evidence from the talus that the unusual catarrhine *Rangwapithecus* may have engaged in extremes of dorsiflexion.

In addition, skeletal correlates of vertical climbing in hominoids and atelines are used to test the hypothesis that any Plio-Pleistocene hominins were adapted for bouts of hominoid-like vertical climbing. Linear and angular measurements were taken on the distal tibiae and tali of African apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla gorilla*, *Gorilla gorilla beringei*) and modern humans. African apes differ from modern humans in the features functionally related to vertical climbing. None of the fifteen known hominin distal tibiae from 4.12 million to 1.6 million years ago possessed a mediolaterally expanded anterior rim of the articular surface for the talus. These hominins were thus poorly adapted for loading of the ankle in positions of extreme dorsiflexion and probably did not engage in ape-like vertical climbing. In fact, it is hypothesized that adaptations for bipedality in the talocrural joint result in a morphology maladapted for vertical climbing. In addition, coronal views of digitally sectioned fossil distal tibiae reveal that the perpendicular orientation of the ankle relative to the long axis of the tibia had evolved by 4.12 million years ago and would have hindered foot positions needed in vertical climbing bouts. This dissertation also introduces a technique by which isolated tali can be used to assess whether the tibia was perpendicularly oriented over the foot, and therefore whether the individual also possessed a valgus knee. This technique, by which the general morphology of the entire lower limb can be estimated from isolated tali will be quite useful for interpreting the morphology and locomotion in early hominins.

Because dorsiflexion is such an important foot motion for bringing the primate close to the tree during vertical climbing, inhibitors of dorsiflexion are hypothesized to be poorly developed in nonhuman hominoids and atelines. The posterior tibiotalar ligament

(PTTL), which originates in the intercollicular groove in the medial malleolus, is an important dorsiflexion restrictor in the human ankle. Tests of the biomechanical properties of this ligament in baboons using an Instron tensiometer demonstrate that the ligament is structurally similar in humans and a non-human primate, and thus skeletal correlates can be used to reasonably assess ligament size, strength, and function. Hominoids and atelines have a weakly developed intercollicular groove and the attachment of the PTTL is close to the ankle axis of rotation, limiting the ligament’s role to an ankle stabilizer. In contrast, the intercollicular groove in terrestrial cercopithecoids and modern humans is significantly larger and positioned away from the axis of rotation, changing the role of the PTTL to one that restricts dorsiflexion. Implications for the early Miocene catarrhines and Plio-Pleistocene hominin fossil record are consistent with other aspects of talocrural functional morphology.

Despite the functional similarities between modern humans and fossil hominins, there are important differences as well. Many fossil hominin tali have a deeply keeled trochlear groove that some have suggested is related to an obliquely oriented tibia and thus an inverted set to the foot. Instead, it is argued that these hominins have not yet evolved an anterior talofibular ligament. The tubercle for this ligament is absent in early forms, but present on later Plio-Pleistocene hominin tali. The presence of the ligament may have increased in frequency as selection favored a hominin talocrural joint that was flatter as a result of increased body size and activity in *Homo erectus*. Thus, differences in morphology do not always mean differences in function.

Finally, the hypothesis that hominins may have compensated for reduced talocrural dorsiflexion by flexing at the midfoot is tested. The anatomical location of the

midtarsal break is reassessed using data from radiographs, dissections, EMG studies, and kinematic analysis of captive primates. Though the calcaneocuboid joint is an important region for establishing midfoot stability, the majority of midfoot flexion during the midtarsal break actually occurs between the cuboid and the lateral metatarsals. The metatarsal facets on the cuboid and the bases of the 4th and 5th metatarsals are significantly more curved on African apes than on modern humans or fossil hominins. These data suggest that midfoot stability, perhaps in the form of a longitudinal arch, was present by 3.2 million years ago. It is thus unlikely that hominins vertically climbed by flexing at the midfoot as modern cercopithecoids do. In addition, the presence of a longitudinal arch would have restricted midfoot grasping and severely compromised arboreality.

CHAPTER 1

Introduction

This dissertation uses kinematic data collected on wild chimpanzees to isolate skeletal correlates of vertical climbing in the talocrural joint. These results are then applied to the fossil record to assess whether the ankles of any Miocene catarrhines or Plio-Pleistocene hominins were adapted for ape-like bouts of vertical climbing.

Vertical climbing, defined as the ascension of a tree that is angled greater than 45° relative to the ground, is a locomotion frequently performed by all of the extant large-bodied apes[1] and some ateline primates (Hunt, 1996; Gebo, 1996; Isler, 2005). Although cercopithecoid monkeys climb, they prefer to scramble up acutely inclined branches rather than ascend large-diameter vertical substrates in the wild (Hunt, 1992; Gebo, 1995). In experimental settings, there are data suggesting that cercopithecoids vertically climb in a kinematically different manner than extant apes and atelines (Hirasaki *et al.*, 1993; 2000; Isler, 2002; 2004; 2005), though hominoid and cercopithecoid climbing kinematics have never been directly compared. However, it is unclear whether vertical climbing is a hominoid synapomorphy, or a behavior that evolved in parallel during the Miocene. Furthermore, although vertical climbing is not an important part of the locomotor repertoire of modern humans, the question of whether early hominins vertically climbed is still a subject of intense debate in the paleoanthropological

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[1] Throughout this dissertation, the word “ape” will be used to describe all non-human hominoids.

literature. Studies of vertical climbing kinematics have focused primarily on the knee, hip, elbow, and shoulder joints (Isler, 2003); however, because of its importance in positioning the foot against the vertical substrate, the talocrural joint, or ankle, may also be an important skeletal element for identifying correlates of vertical climbing. This dissertation uses a multi-faceted approach to test the hypothesis that non-human hominoids and some atelines possess an ankle morphology specifically adapted for bouts of vertically climbing.

The talocrural joint, or ankle, is formed between the distal tibia, fibula, and talus. Although some refer to this joint as the upper ankle, and the subtalar joint as the lower ankle, proper anatomical terminology defines the talocrural joint as the only "ankle." The ankle is, for the most part, a simple hinge joint with motion at the talocrural joint primarily restricted to dorsiflexion and plantarflexion, although the shape of the joint in humans permits some rotation and version as well (Barnett and Napier, 1952; Scott and Winter, 1991; Michelson and Helgemo, 1995; Hamel *et al*., 2004). Motions other than plantarflexion and dorsiflexion are in part a result of the morphology of the talus, which has been referred to as a "badly mounted wheel" (Rasmussen *et al*., 1983). During dorsiflexion, the tibia internally rotates, the talus externally rotates, and the foot is in an abducted position. During plantarflexion, the tibia externally rotates, the talus internally rotates and the foot is in an adducted position (Scott and Winter, 1991; Michelson and Helgemo, 1995). The axis of rotation of the ankle runs roughly through the medial and lateral malleoli, which are slightly offset from one another in both the coronal plane and the transverse planes (Inman, 1976).

The ankle also contains a structurally complex array of ligaments that function primarily to stabilize the bony connections between the talus and the long bones of the lower leg. The distal tibia and fibula are attached to one another via the anterior and posterior tibiofibular ligaments. Three distinct ligaments, the anterior talofibular, calcaneofibular, and posterior talofibular ligaments, support the lateral side of the ankle joint by anchoring the fibula to the talus and calcaneus. The medial side of the joint is supported by the thick and strong deltoid ligament which connects the medial malleolus of the tibia to the talus, navicular, and calcaneus (Sarrafian, 1993; Leardini et al., 2000). Ligaments can stabilize a joint and/or restrict joint motion depending on their size, strength, and insertion relative to the joint axis of rotation (Alexander and Bennett, 1987). Skeletal correlates of the presence, size, and function of the ligaments of the primate ankle can help reconstruct whether the ankle of extinct Miocene catarrhines and Plio-Pleistocene hominins were capable of the joint positions important during vertical climbing.

It is not clear from the current literature on climbing kinematics, however, precisely what the talocrural joint does during vertical climbing bouts in hominoids, particularly in the great apes. Based on principles of biomechanics, a vertically climbing ape would reduce its climbing costs by pulling itself closer to the tree (Cartmill, 1972; Cartmill, 1985; Autumn et al., 2006). During climbing, the ape experiences a downward acting torque, which is the product of the force of gravity, the mass of the animal, and the distance between the tree and the center of mass. This torque must be balanced by muscular activity that prevents the animal from falling. The force of gravity and the mass of the ape cannot be changed during a climbing bout; however, the animal can reduce the moment arm acting on the center of mass by pulling that mass closer to the tree, thereby reducing the muscular forces necessary to prevent falls. Close proximity between a climbing animal and the vertical substrate has been observed in a wide range of animals from geckos and squirrels to climbing black bears. However, unlike these other animals, hominoids do not possess large grasping claws or sticky finger pads and must instead reduce their distance from the vertical substrate by flexing, abducting, and inverting their lower limb joints.

Data on climbing kinematics in wild chimpanzees is presented in Chapter 2. The hypothesis presented above that apes pull themselves close to a tree via joint flexion is tested at the talocrural joint using data collected on vertical climbing bouts in wild chimpanzees at the Ngogo study site in Kibale National Park, Uganda. These are the first data on climbing kinematics for any wild hominoid species. These results are compared to kinematic data from the literature and from climbing bouts of wild and captive cercopithecoids to examine whether predictable differences exist in the talocrural joints of cercopithecoids and apes.

Results in Chapter 2 indicate that wild chimpanzees engage in extreme dorsiflexion, accompanied by foot abduction and inversion when climbing. These observations are used to make specific predictions about how the morphology of the distal tibia and talus of a vertical climber should differ from a non-vertical climbing primate.

These predictions are tested in Chapter 3 using linear and angular measurements on the talocrural joint in 14 different extant anthropoid species. The hypothesis that there are differences in the talocrural morphology of those species engaging in frequent bouts of vertical climbing (apes and atelines), and those rarely climbing vertical substrates (cercopithecoids, *Cebus*) is tested. Specifically, I examine whether the talocrural joint of vertical climbers is better adapted for the extreme positions of dorsiflexion, accompanying inversion, and abduction observed in wild chimpanzees. Principles of functional morphology are applied in this chapter, including assumptions that the range of motion at a joint in a living animal can be reconstructed from the articular geometry of isolated skeletal elements and that increased area of an articular surface is an adaptation for reducing stress experienced during joint loading. Results from these comparisons are applied to the fossil record of early Miocene catarrhines to assess whether chimpanzee-like vertical climbing may have been a component of the locomotor repertoire of, for example, early purported hominoid species.

In Chapter 4, the contentious hypothesis that early hominins may have been adapted for vertical climbing is tested using data from the talocrural joint. The hypothesis that differences exist in the talocrural joint morphology of African apes and modern humans is tested using linear and angular measurements of the distal tibiae and tali of adult wild chimpanzees and gorillas and three populations of modern humans. These data are compared to 30 fossil hominin tibiae and tali from 4.12 to 1.53 million years ago. There is a tendency to regard differences from the modern human condition as evidence that early hominins behaved more like our African ape cousins. In this chapter, it is expected that hominin tali and distal tibia will not be precisely like modern human ankles and will often fall in the morphological range between the modern African ape and modern human talocrural joint. Reasons for these differences include variations in body size and obstetrics, and mosaic patterns of evolutionary change in the hominin foot and ankle. Instead of simply asking whether fossil hominin tibiae and tali differ from the modern human morphology, I investigate whether fossil hominins differ from modern humans in a functionally meaningful manner and in a way that would allow them to practice ape-like vertical climbing. In addition, my concern is not whether a hominin taxon occasionally climbed a tree, but whether the total morphological pattern inferred from the anatomy of the talocrural joint is consistent with both bipedalism *and* frequent climbing as has been suggested (e.g. Susman et al., 1984; Preuschoft and Witte, 1991).

Extreme dorsiflexion is theoretically important for bringing the animal close to a tree during vertical climbing; an assertion supported by kinematic data on wild chimpanzees (Chapter 2). Therefore, it is important to recognize and identify not only how dorsiflexion can be enhanced but also how it can be inhibited. Chapter 5 of this dissertation examines the evolution of the posterior tibiotalar ligament (PTTL), which is a significant restrictor of extreme dorsiflexion in modern humans. In this chapter, I test whether this ligament has the same biomechanical properties in a non-human primate (*Papio anubis*). If so, then skeletal correlates of the size of the PTTL can be used to infer strength. Similarly, the role of a ligament as either a joint stabilizer or restrictor of motion is primarily a function of the region of origin and insertion relative to the axis of rotation of the joint it crosses. It is hypothesized therefore that primates with limited ankle dorsiflexion (*Homo* and cercopithecoids) will possess a PTTL that inserts farther from the axis of rotation.

Chapter 6 addresses the question of why ankles of modern humans are quite susceptible to sprains of the anterior talofibular ligament. It begins by asking whether tilting of the talus away from the tibia is a means by which vertically climbing apes augment their range of inversion. During dorsiflexion, the natural version movement of the talus is eversion. Yet, during vertical climbing, the great apes are able to put their foot in positions of inversion while dorsiflexed. This motion is most likely to occur primarily at the subtalar and transverse tarsal joints. However, based on human studies, it is reasonable to suggest that inversion can occur at the talocrural joint in the form of "talar tilting" (Cox and Hewes, 1979). Inversion, or talar tilting at the talocrural joint, is resisted partially by the anterior talofibular ligament (Cass and Settles, 1994; Leardini et al., 2000; Hinterman, 2002). It is hypothesized that the anterior talofibular ligaments should differ between humans and vertically climbing apes and that these differences are related to inversion at the ankle.

Chapters 3-6 apply an ape model to hypotheses of climbing in early Miocene catarrhines and Plio-Pleistocene hominins. This model suggests that extreme dorsiflexion at the talocrural joint, inversion, and abduction are essential joint movements for vertical climbing. In Chapter 2 it is shown that cercopithecoids, though infrequent vertical climbers, utilize a slightly different kinematic strategy and do not flex at the ankle, but do so instead at the midfoot. Chapter 7 addresses the possibility that dorsiflexion in the midfoot region, often called the "midtarsal break", may be an alternative means by which a primate can pull its body close to a tree during vertical climbing bouts. It is unclear *where* midfoot flexion occurs anatomically, with some suggesting the calcaneocuboid joint and others the cuboid-metatarsal joint. This study employs radiographs, dissections, EMG analysis, and kinematics of terrestrial walking in captive primates to test these alternative hypotheses regarding the location of the midtarsal break. Skeletal correlates of midfoot mobility are then measured and applied to the hominin fossil record to assess whether our early ancestors had a mobile midfoot and could vertically climb in a cercopithecoid-like manner.

CHAPTER 2

Kinematics of the talocrural joint during vertical climbing bouts in wild chimpanzees.

Abstract

Vertical climbing, a behavior frequently performed by extant apes and atelines, has figured prominently in hypotheses of locomotor evolution in the hominoids and hominins. It has even been proposed that vertical climbing pre-adapted hominins for bipedality. However, whether any known Pliocene hominins or Miocene catarrhines engaged in significant amounts of vertical climbing is still a subject of debate. Previous work on vertical climbing kinematics has focused on the upper limb, hip and knee joints, with less attention paid to the ankle joint. This study focused specifically on the kinematics of the talocrural joint. Video data were collected from 166 separate climbing bouts by wild chimpanzees at Ngogo, Kibale National Park, Uganda. Chimpanzees engage in extreme dorsiflexion at the talocrural joint during single stance phase of climbing, flexing the ankle approximately 45˚. This helps bring the ape closer to the tree thus reducing the torque at the ankle, knee, and hip and increasing the efficiency of climbing. The foot is also placed in a position of abduction and inversion during vertical climbing bouts. Similar climbing strategy was observed during vertical climbing in captive orangutans and gorillas, but is quite distinct from the climbing approach used by cercopithecoids. Furthermore, the range of dorsiflexion achieved by chimpanzees during vertical climbing exceeds the dorsiflexion possible in the human ankle without severe

injury. These data are useful for identifying bony morphology in the talocrural joint adapted for vertical climbing and assessing whether ape-like vertical climbing was part of the locomotor repertoire in any known Miocene catarrhines and Plio-Pleistocene hominins.

Introduction

Apes are large-bodied fruit eaters well adapted for orthograde and suspensory positional behaviors in an arboreal environment (Young, 2003; MacLatchy, 2004; Pilbeam and Young, 2004). Locomotion, including vertical climbing, has featured prominently in hypotheses of hominoid evolution, and the identification of hominoid synapomorphies (Avis, 1962; Temerin and Cant, 1983; Hunt, 1991; Gebo, 1996; Doran, 1996; MacLatchy, 2004; Isler, 2005; Thorpe and Crompton, 2006). Based on behavioral observations of modern apes, Hunt (1991) suggested that arm hanging and vertical climbing are the most important ape locomotor adaptations. However, he noted that while apes vertically climb more often than monkeys, only arm hanging is kinematically unique to the apes and thus a true hominoid synapomorphy (Hunt, 1991). However, Thorpe and Crompton (2006) collected data on orangutans suggesting that general orthogrady, and not suspensory behavior per se, is the unique ape locomotor adaptation. Doran (1996) supported earlier work by Fleagle (1976) that quadramanous climbing distinguishes the apes from other catarrhines. More specifically, it has been argued that vertical climbing is a distinct ape locomotion and may have been practiced by the last common ancestor of the hominoids (Isler, 2003; Isler and Thorpe, 2003; Isler, 2005). These hypotheses have often been based on data from captive primates or qualitative assessments of locomotion in the wild. More data on comparative kinematics of climbing in wild primates are necessary to determine the extent to which apes vertically climb.

In addition to its importance in hominoid evolution, vertical climbing has also featured prominently in hypotheses of hominin evolution and the origins of bipedalism (Fleagle et al., 1981; Senut, 1988). EMG studies provide evidence that vertical climbing preadapted hominins for bipedality. EMG activity patterns of hip and thigh musculature (Stern, 1971; Vangor, 1977; Vangor and Wells, 1983), gluteal muscles (Stern and Susman, 1981), and brachial muscles (Tuttle and Basmajian, 1974) demonstrate that the muscles active during bipedal movement are more often active during vertical climbing than during quadrupedal walking. Kinematic data on extension of the hip and knee also suggests that vertical climbing would preadapt a primate for bipedality more than quadrupedal walking would (Yamazaki et al., 1983; Yamazaki and Ishida, 1984; Payne, 2001). An arboreal origin for bipedalism has recently been suggested using orangutans as a model for a prebipedal hominin (Crompton et al., 2003; Thorpe et al., 2007). These hypotheses suggest that orthograde scrambling and hand assisted bipedalism practiced by modern orangutans serve as preadaptations for bipedality (Crompton et al., 2003). Thorpe et al. (2007) found that hand assisted bipedality occurred most often in wild orangutans during feeding bouts in a small branch environment. Using orangutan locomotion as a model, these authors suggest that the kinematics of bipedalism, such as an extended hindlimb, may have evolved in a terminal branch setting. This hypothesis is supported by biomechanical data of bipedal walking in orangutans in which the kinematics of the hip and knee better adapt these Asian apes for bipedalism than the African apes (Payne, 2001). However, evidence from the hindfoot (Gebo, 1996) and the wrist (Richmond et al., 2001) indicate that bipedalism may have been preceded by a terrestrial, rather than arboreal, phase. These workers recognize the importance of vertical climbing, but argue that the last common ancestor would have employed knuckle-walking while moving between food patches, much like modern chimpanzees do. Tuttle (1974) was the first to propose that knuckle-walking may be a morphological compromise for an ape adapted for vertical climbing and suspensory behavior that moves terrestrially between food patches.

Testing these models with the fossil record has been hampered by relatively few postcranial remains of the earliest hominins. However, even for hominins well represented in the fossil record, like *Australopithecus afarensis*, interpretations have yielded mixed results. Some argue that adaptations for bipedalism restrict arboreality and that early hominins could not engage in much arboreal locomotion once bipedalism evolved (Lovejoy, 1978; Latimer et al., 1987; Latimer and Lovejoy, 1990a; Latimer and Lovejoy, 1990b; Latimer and Lovejoy, 1990; Latimer, 1991; Lovejoy, 2005a; Lovejoy, 2005b; Lovejoy, 2007; Sawyer and Lovejoy, 2008). In contrast, others find abundant evidence for climbing in the postcrania of australopithecine fossils (Prost, 1980; Stern and Susman, 1983; Susman and Stern, 1984; Preuschoft and Witte, 1991; Heinrich et al., 1993; Deloison, 2003; Alemseged et al., 2006). Richmond et al. (2001, p. 100) noted the importance of kinematic studies in interpreting fossil remains and contributing to this debate, writing “It is critical that we understand the biomechanics and functional anatomy involved in knuckle-walking, climbing, bipedalism, and other forms of locomotion so that reliable interpretations of fossils are possible.”

Arboreal behavior in apes and cercopithecoids

Many studies have attempted to quantify the amount of vertical climbing and arboreal activity engaged in by wild apes and cercopithecoids (Table 2.1). However, these data have been variously reported as a % of total activity, % of arboreal activity or a % of total locomotor activity and thus are not always directly comparable (Hunt, 2004). Furthermore, the term "climbing" has been used in some studies to encompass any arboreal ascent, whereas other studies separate climbing from the more specific "vertical" climbing using Hunt's definition that limits vertical ascents to those on substrates angled at greater than 45° from the horizontal (Hunt, 1996). An attempt to standardize the results found that vertical climbing composed these percentages of total locomotor budget: gibbon 15.5%, siamang 32.2%, orangutan 20.6%, bonobo 50.4% (arboreal budget only), chimpanzee 6.5%, mountain gorilla <1%, lowland gorilla 19.7%, and baboon 0.7% (Hunt, 2004). Hunt (2004) regarded the gibbon, siamang, orangutan, and lowland gorilla values as estimates and the chimpanzee, mountain gorilla, and baboon values as reliable. The data on the amount of climbing and vertical climbing practiced by extant primates will be further reviewed below.

Apes are arboreal climbers (Table 2.1). The siamang (*Syndactylus symphalangus*) dedicates 37% of its total travel to climbing (Fleagle, 1976), though this study did not differentiate between climbing and vertical climbing specifically. The agile gibbon (*Hylobates agilis*) has been observed to spend 14% of its total locomotor activity climbing (Gittins, 1983). Female orangutans are almost exclusively arboreal though male orangutans will regularly come to the ground to travel between food resources (MacKinnon, 1974; Rodman and Mitani, 1987). Three separate studies of wild orangutans (*Pongo pygmaeus*) have obtained relatively consistent results of the total travel expenditure spent climbing. Orangutans have been found to vertically climb 9-13% (Sugardjito and van Hooff, 1986), 18% (Cant, 1987), and 16% (Thorpe and Crompton, 2006) of their total locomotion.

Table 2.1 Frequency of vertical climbing in extant anthropoids.

Species	Source	Vertical Climbing Frequency	Criteria
Pan troglodytes	Doran, 1993	11%	Of total locomotion
Pan troglodytes	Hunt, 1989; 1992	5.5%	Of total locomotion
Pongo pygmaeus	Cant, 1987	18%	Of total travel
Pongo pygmaeus	Sugardjito & van Hooff, 1986	9-13%	Of total locomotion
Pongo pygmaeus	Thorpe & Crompton, 2006	16%	Of total locomotion
Gorilla gorilla gorilla	Remis, 1995	48%	Of arboreal travel
Gorilla gorilla beringei	Watts & Tuttle, 1985	1.6%	Of daily activity
Hylobates agilis	Gittins, 1983	14%	Of total locomotion
Symphalangus syndactylus	Fleagle, 1977	37% climbing (not specifically vertical)	Of total travel
Papio anubis	Hunt, 1989	0.4-1.2%	Of arboreal activity
Papio anubis	Rose, 1977	0.2%	Of adult daily activity
Lagothrix lagotricha	Cant et al., 2001	3.7%	Of total locomotion
Ateles belzebuth	Cant et al., 2001	4.2%	Of total locomotion
Alouatta seniculus	Guillot et al., submitted	6.0%	Of total locomotion

The African apes are more terrestrial than the Asian apes, but they too spend a considerable amount of their total travel in an arboreal environment. Doran (1996) has argued that climbing is second only to terrestrial quadrupedalism in terms of the most frequently used locomotor behaviors in the African great apes. Hunt (1989; 1992) found that chimpanzees at Gombe and Mahale (*Pan troglodytes schweinfurthii*) spent 5.5% of their total locomotor budget vertically climbing; whereas Doran (1993) found that chimpanzees in the Tai forest (*Pan troglodytes verus*) spend 11% of their total locomotor activities vertically climbing. Interestingly, female chimpanzees climb more often than male chimpanzees at Gombe and Mahale, but there appear to be no sex differences in climbing frequency among the chimpanzees in the Tai forest (Doran, 1993a, Doran, 1993b, Doran and Hunt, 1994). Chimpanzees climb primarily to obtain arboreal food resources. Hunt (1998) found that 70% of the total time chimpanzees at the Mahale and Gombe study sites spend in trees, they are foraging for food. Bonobos (*Pan paniscus*) were originally considered to be almost exclusively arboreal (Susman, 1984); however, these bonobos were not habituated to human presence and the amount of time they spent in trees could not be accurately assessed (Mitani, pers. comm.). Kano (1983) found that the bonobos at Yalosidi in the present day Congo travel terrestrially between food sources, much like chimpanzees. Lowland gorillas (*Gorilla gorilla gorilla*) spend 48% of their arboreal travel time climbing (Remis, 1995). Remis (1995) has even suggested that female gorillas are as arboreal as chimpanzees. Most of the food resources consumed by lowland gorillas are arboreal, and gorillas will typically build night nests in trees (Tutin, 1996). In contrast, mountain gorillas (*Gorilla gorilla beringei*) are considerably more terrestrial than lowland gorillas, though they do spend 2.9% of their total daily activity budget in trees, of which 56% of the time is spent climbing (Tuttle and Watts, 1985). This difference in arboreality between the two gorilla species is at least partially a function of ecological differences, with few trees growing 10,000 feet above sea level in the Virunga Mountains.

Relative to what is known about wild apes, the locomotion of wild cercopithecoids is less understood. There is considerable variation in cercopithecoid use of landscapes, from the mostly terrestrial patas monkey (*Erythrocebus patas*) to the mostly arboreal proboscis monkey (*Nasalis larvatus*) (Fleagle, 1999). Because this current study focuses on wild chimpanzees, the locomotion of a cercopithecoid monkey that moves both terrestrially and arboreally would provide a valuable comparison. The few data that exist on wild baboons are relevant in this context. Baboons spend a limited amount of their activity budget climbing (Hunt, 2004). Rose (1977) found that olive baboons (*Papio anubis*) spend less than 1% of their total daily activity budget climbing, and this is done primarily during play bouts (54.2%) and mostly by infants. Adult baboons climbed only 0.2% of their total daily activity budget (Rose, 1977). Similarly, Hunt (1989) found that baboons rarely climbed vertically, recording climbing in only 0.4-1.2% of their total arboreal activity. Hunt (1992) also noted that while chimpanzees at Gombe and Mahale vertically climb, baboons ascend similar vertical substrates by leaping and walking up angled branches. A similar climbing strategy has been observed in wild black and white colobus monkeys (*Colobus guereza*), red colobus monkeys (*Procolobus badius*), grey-cheeked mangabeys (*Lophocebus albigena*), and red-tailed monkeys (*Cercopithecus ascanius*) (all personal observations in Kibale National Park).

In contrast to Old World cercopithecoid monkeys, many New World ateline primates vertically climb, though not quite as often as apes do. Cant et al. (2001) found that vertical climbing comprised 3.7% of total locomotion in *Lagothrix lagotricha* and 4.2% of total locomotion in *Ateles belzebuth*. The howler monkey (*Alouatta*) spends 6% of its total locomotor activity vertically climbing (Guillot et al., in press).

Comparative vertical climbing kinematics

Prior research has not made it clear whether apes and cercopithecoids vertically climb in a kinematically distinct manner. A study of chimpanzees and baboons in the Gombe and Mahale National Parks of Tanzania suggested that although chimpanzees climb more often than baboons, they do so in a kinematically similar manner (Hunt, 1991). This was suggested despite observations that baboons either pulse climb or leap up angled branches of a tree; behaviors rarely performed by chimpanzees (Hunt, 1989). Gebo (1996) suggested that vertical climbing in apes may be kinematically different than in monkeys, but noted presently available data cannot be used to resolve this important question.

No study has directly compared the vertical climbing kinematics of non-human hominoids and cercopithecoids. However, the two groups have been indirectly compared via observations of atelines. Kinematic data indicate that captive Japanese macaques (*Macaca fuscata*) vertically climb in a different way than do spider monkeys (*Ateles geoffroyi*) (Hirasaki et al., 1993; Hirasaki et al., 2000). Spider monkeys exhibit greater extension at the hip and knee, and greater flexion at the ankle than macaques (Hirasaki et al., 1993). Additionally, force plate data produced during vertical climbing bouts indicate that in *Ateles*, the hindlimb forces are greater than the forelimb forces whereas in *Macaca*, they are approximately the same (Hirasaki, et al., 1993).

Additional work on vertical climbing in captive and semi-wild primates found that the kinematics of vertical climbing in ateline primates is quite similar to the kinematics of vertical climbing in apes. Isler (2002; 2003; 2004; 2005) compared vertical climbing kinematics in bonobos (*Pan paniscus*), lowland gorillas (*Gorilla gorilla gorilla*), gibbons (*Hylobates lar*), orangutans (*Pongo pygmaeus*), spider monkeys (*Ateles* *belzebuth*), and woolly monkeys (*Lagothrix lagotricha*). These studies found that the kinematics of climbing are quite similar in apes and atelines. Unlike cercopithecoids, the apes and atelines had an extended hip during the push-off phase of vertical climbing (Isler, 2003; Isler, 2004; Isler, 2005). Despite the similarities in climbing kinematics, important differences also exist. *Pongo* exhibited the greatest flexion at the hip, but less at the knee than African apes or atelines (Isler, 2003). Although African apes and atelines climbed in a kinematically similar fashion (Isler, 2003; Isler, 2004), the former positioned themselves closer to the vertical substrate through flexion at the elbow and the knee than did the latter (Isler, 2003). Bonobos (*Pan paniscus*) vertically climbed in a faster, more efficient manner than gorillas (Isler, 2002), and bonobos exhibited greater knee flexion than *Gorilla* (Isler, 2003; Isler, 2005). Interestingly, it was observed that a juvenile *Gorilla* and juvenile *Pongo* and the smaller-bodied *Hylobates* positioned themselves farther from the vertical substrate than the adult great apes, perhaps because their smaller mass results in a smaller moment at the joints of the lower limb (Isler, 2003; Isler, 2005). Nevertheless, the results of these studies suggest that the kinematics of vertical climbing in apes and atelines fundamentally differ from that observed in cercopithecoids. Because of the kinematic similarities between apes and atelines (Isler 2003, 2004, 2005) and because *Ateles* has been shown to vertically climb in a kinematically distinct manner from *Macaca* (Hirasaki et al., 2003; Hirasaki et al., 2000), there is reason to suspect that apes and cercopithecoids may vertically climb in a kinematically different way (contra Hunt, 1989; 1991; 1992).

Data from the literature thus suggests two important differences between apes and atelines, and the cercopithecoid monkeys. 1.) Apes and atelines vertically climb more often than cercopithecoids in the wild; and 2.) apes and atelines may vertically climb in a kinematically different manner than cercopithecoids. Whether these conclusions can be generalized is unclear because prior kinematic data have been collected primarily on captive primates usually ascending rope-like vertical substrates.

Several studies have examined the biomechanics of vertical climbing of vertebrates in general (Preuschoft, 1970; Cartmill, 1972; Bock and Winkler, 1978; Cartmill, 1985; Preuschoft et al., 1992; Autumn et al., 2006). Preuschoft et al. (1992) stated that the “energetically most expensive motion is ascending trees” because the animal has to propel itself directly against the downward force of gravity. Because the downward force due to gravity is directly proportional to the mass of the animal, climbing in large bodied-apes presents a particularly difficult challenge and thus climbing adaptations are likely to evolve to reduce these costs.

A free body diagram modeling the forces imposed on a vertically climbing ape demonstrates that several factors can influence the efficiency of climbing (Figure 2.1). The moment produced by the climbing ape is a function of the acceleration due to gravity, the mass of the animal, and the distance the animal is from the tree. This moment, termed the “overturning moment” by Autumn et al. (2006) can best be conceptualized if one imagines that the chimpanzee in Figure 2.1 lets go of the tree with his hand and begins to fall backwards. This overturning moment must be balanced by a stabilizing moment at both the foot and the hand. The balancing moment is a product of the vertical force of the foot operating at a horizontal distance which is approximately the diameter of the vertical substrate and the horizontal force of the foot operating at the distance between the hand and the ipsilateral foot (Cartmill, 1972). Thus, the relationship

Figure 2.1. Free-body diagram of forces on chimpanzee during vertical climbing.

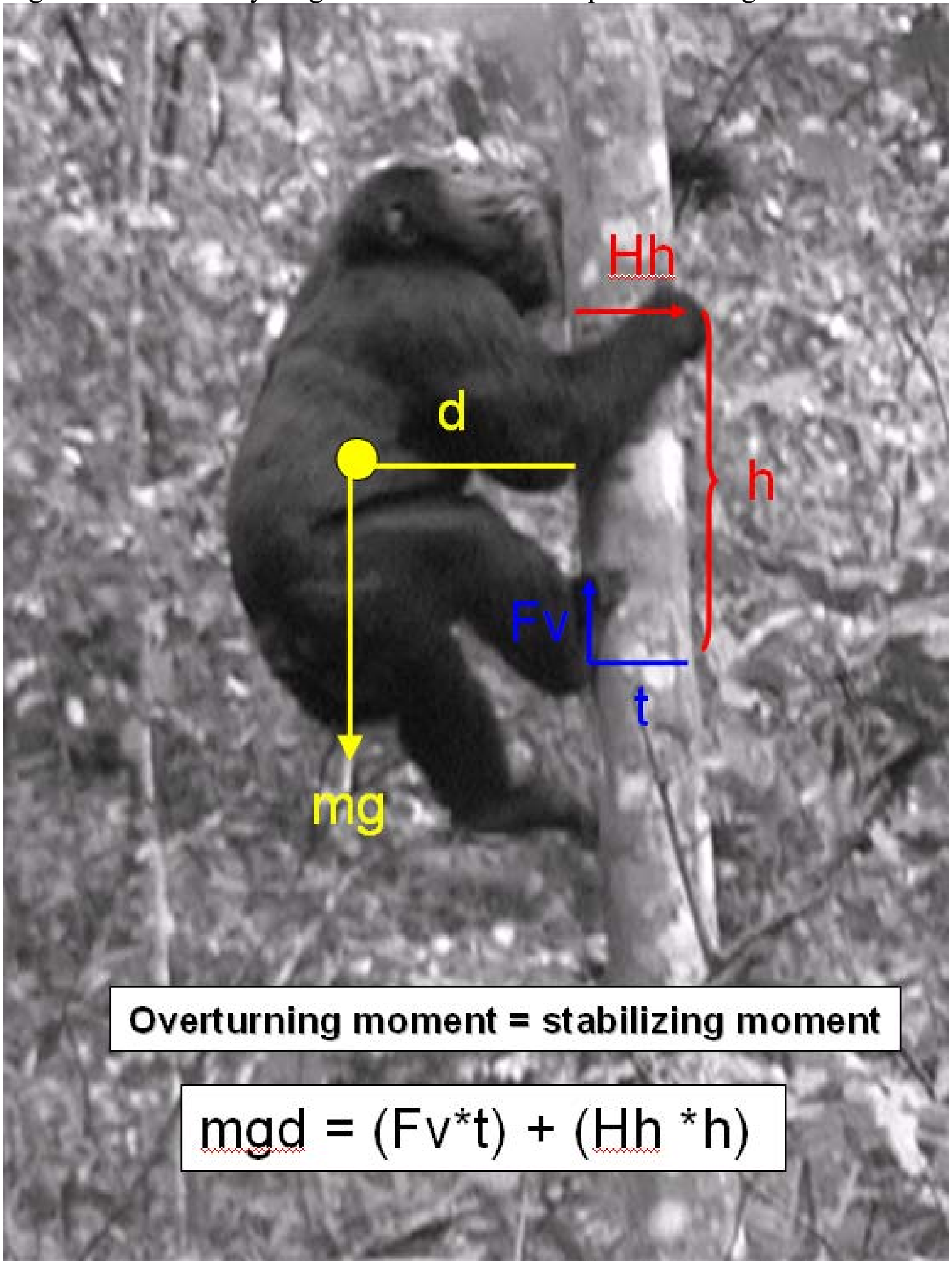


Figure 2.1. Biomechanics of vertical climbing (simplified from Cartmill, 1972; Cartmill, 1985; Autumn et al., 2006). A moment that is a function of the mass of the chimpanzee (m), the force of gravity (g), and the distance that the chimpanzee is from the tree (d) is countered by a vertical force applied by the grasping foot (Fv) acting at a distance that the foot is from the fulcrum (t), plus a horizontal force (Hh) applied by the hand acting at a distance between the grasping hand and the foot (h). Dorsiflexion at the ankle pulls the ape closer to the tree thus reducing its overturning moment, and reducing the force necessary to counteract this moment.

between the mass of the animal (m), the force due to gravity (g), the distance the center of mass is from the tree (d), the horizontal force produced by the foot (Fh), the vertical force produced by the foot (Fv), the distance between the hand and the foot (h), and the diameter of the tree (t) is:

$$mgd = Fhh + Fvt$$

However, because the forces must also balance, the horizontal force produced by the hand is equal and opposite to the horizontal force produced by the foot. Thus, when the horizontal force of the hand (Hh) is substituted into the above equation, the relationship between the variables is:

$$mgd = Hhh + Fvt$$

The force necessary to stabilize the climbing animal can be reduced if the distance between the grasping hands and feet is increased. This relationship may help explain why long arms are considered to be an adaptation for climbing in the apes by reducing the forces necessary to hold onto the vertical substrate (Cartmill, 1985), and why a strong upper limb has been identified as a climbing adaptation in extant and extinct hominoids (Cartmill, 1985; Isler, 2003). The moment is also balanced by the force produced by the foot and thus a grasping foot is a critical adaptation for vertical climbing in the apes (Preuschoft, 1970; Cartmill, 1985; Latimer and Lovejoy, 1990). On the left hand side of the equation, acceleration due to gravity is a constant, as is, for the purpose of this exercise, the mass of the animal. Therefore, the moment attempting to overturn the animal can be reduced by reducing the distance that the climbing ape is from the tree. This can be achieved by having short legs abducted and flexed at the hip, flexed at the knee and ankle, and inverted in the midfoot region. Several studies on the biomechanics of vertical climbing have emphasized the importance of minimizing the distance between the center of mass of the animal and the vertical substrate (Preuschoft, 1970; Cartmill, 1972; Cartmill, 1985; Preuschoft et al., 1992). Experimentally, limb flexion has been shown to be as a vertical climbing strategy employed by gecko lizards (Autumn et al., 2006). Furthermore, work on captive apes has found that during vertical climbing larger bodied adult apes pull their bodies closer to the vertical substrate than juvenile apes or the small-bodied gibbons, presumably to reduce the costs associated with climbing (Isler, 2005). It is hypothesized in this study that dorsiflexion of the talocrural joint in non-human hominoids is one of a suite of adaptations (also including hip abduction, hip and knee flexion, and foot inversion) to reduce the force of the overturning moment arm during bouts of vertical climbing.

This study examined the kinematics of the talocrural joint during vertical climbing bouts in wild chimpanzees to test the following hypotheses:

1. As has been shown for the hip and the knee (Isler, 2003; Isler, 2005), large bodied apes help reduce their climbing costs by pulling their bodies close to the substrate. It is hypothesized that that flexion at the talocrural joint also contributes to reducing the distance between the climbing ape and the vertical substrate.
2. Data tentatively suggest that the kinematics of climbing fundamentally differ between apes and cercopithecoids, though this has never been assessed at the ankle. This study tests the null hypothesis that there are no differences in the kinematics of the talocrural joint between vertically climbing apes and cercopithecoids.

Materials and Methods

Observations of wild chimpanzees of the Ngogo community in the Kibale National Park, Uganda were made during three weeks in June 2006 and July-August 2007. The Kibale National Park is located in western Uganda, east of the Rwenzori Mountains. The Ngogo study site is in the north-central portion of the park, approximately 1400 meters above sea level. At this elevation, the forest comprises a combination of lowland and montane rainforest, consisting of primarily undisturbed old growth forest with a continuous 25-30 meter high canopy. The Ngogo community of common chimpanzees (*Pan troglodytes schweinfurthii*) is exceptionally large, with approximately 150 individuals. The unusual size of the community facilitates finding and following chimpanzees daily.

Chimpanzees were followed for a period of three weeks and filmed opportunistically when vertical climbing. Observations were made primarily on adult males, though some juveniles and females were studied as well. Chimpanzee vertical climbing was filmed as the animal made its ascent from the forest floor to the highest height achieved in the forest canopy. Video data was collected with a Canon GL2 hand-held digital video recorder. The distance between the video camera and climbing chimpanzee varied because climbing episodes were filmed in real time as they occurred. The distance between the observer and climbing chimpanzee was typically between 5 and 10 meters. Attempts were made to film chimpanzees in lateral view as they ascended the tree. The individual identity of the climber was usually known, though there are cases in which the climber could only be identified by age and sex. Additionally, the circumference of the tree was measured at breast height. If the chimpanzee used one vertical substrate to access food resources in another tree, efforts were made to measure the circumference and diameter at breast height of both trees. In total, 166 separate climbing bouts were filmed and tree circumferences obtained.

Video data was downloaded and the usability of the video was assessed using the program Windows MovieMaker. Frames of vertical climbing were viewed individually with a temporal resolution of 70 msec. Several criteria were applied to identify video that could be used to assess dorsiflexion at the talocrural joint within a reasonably accurate range.

First, the animal had to be in lateral view to estimate dorsiflexion at the talocrural joint. Dorsiflexion at the talocrural joint was always assessed as the maximum angle achieved by the ankle nearest to the observer. Video in which the opposite hip or shoulder of the chimpanzee could be easily seen or was completely obscured by the tree during climbing were eliminated. Only video in which the far hip and shoulder were obscured by the near hip and shoulder were considered lateral.

Second, videos of lateral views had to be captured within 10 meters from the ground. This requirement was established by testing the effect of height on angle measurement on a University of Michigan building. Window corners of 90˚ angles were filmed from different heights at a distance of 10 meters. The corner angle of windows filmed less than 10 m above the ground could be accurately measured to within 5˚ of 90˚. The angle of window corners higher than 10m from the ground had errors greater than 5˚. Thus, video in which the first few steps of ascent were captured in lateral view could be analyzed. This proved difficult as there was a considerable amount of ground cover at

Ngogo. Thus, the video stills that met the above criteria generally were taken from chimpanzees that were approximately 2-5 meters off the ground at a distance of approximately 5-10 meters. Of the 166 videos obtained from vertically climbing chimpanzees, 63 met the above criteria and were measured.

Video stills of the initial steps of the 63 chimpanzees vertically climbing taken in lateral view were imported into the program Image J. The angle tool was used to measure the angle of dorsiflexion at the talocrural joint. This was taken by drawing a straight line from the knee to the heel, and another straight line from the heel through the metatarsophalangeal joint of the 5th metatarsal. The angle was then subtracted from 90˚ to make it comparable to results from the literature. The knee to heel line was drawn as an approximate bisection of the tibia, whereas the long axis of the foot followed the skin/hair line which runs along the lateral side of the foot (Figure 2.2). Confidence in these lines to approximate dorsiflexion in the ankle was based on dissections of the lower limb of a chimpanzee at the Harvard Museum of Comparative Zoology, and manual manipulation and measurement of live chimpanzee lower limbs performed during veterinary procedures on an adult male and an adult female at the Detroit Zoo in which the location of the knee, ankle, and heel were assessed. Dorsiflexion angles of the same video stills measured a month apart suggest that maximum measurement error is ± 5˚. When measurements were taken to the nearest 5˚, error was reduced to zero.

Foot inversion associated with vertical climbing was assessed qualitatively from both lateral and posterior views of climbing from all 166 vertical climbing bouts captured on film. Abduction was estimated by measuring the angle between the foot and the tibia

Figure 2.2. Method of estimating dorsiflexion at talocrural joint in vertically climbing wild chimpanzee.

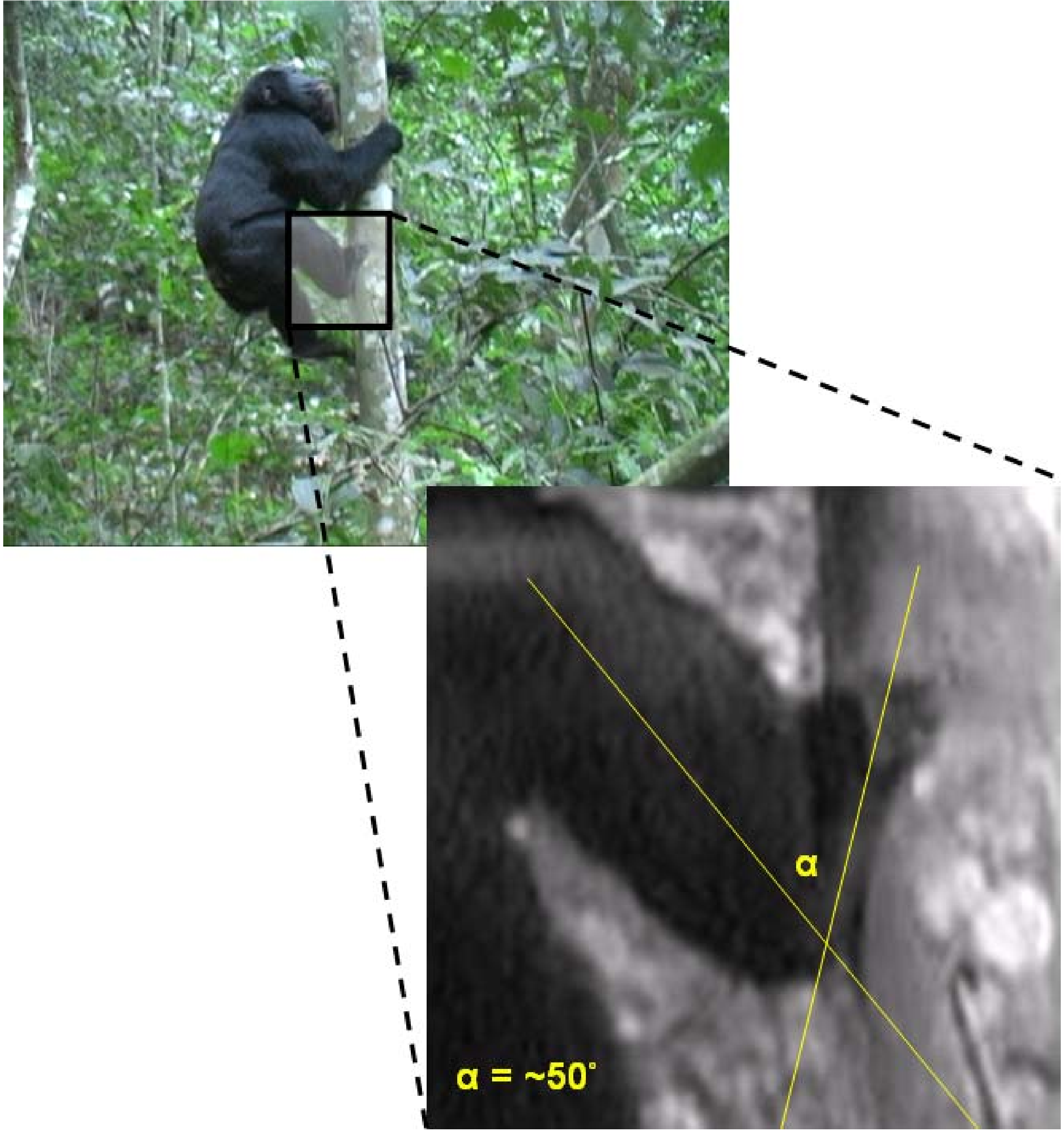


Figure 2.2. Video stills in which the vertically climbing chimpanzee is in lateral view and <10 meters from the ground were captured (see text for more details). In this example, a male chimpanzee is experiencing maximum dorsiflexion of the right foot during push-off of the opposite foot. To estimate the degree of dorsiflexion, the ankle region is enlarged, a line is drawn down the long axis of the tibia and along the hair-skin line of the lateral aspect of the foot. The angle measured is then subtracted from 90˚ so that high angles indicate extreme dorsiflexion whereas low angles represent little ankle dorsiflexion.

Figure 2.3. Method for approximating foot abduction during vertical climbing bouts in wild chimpanzees.

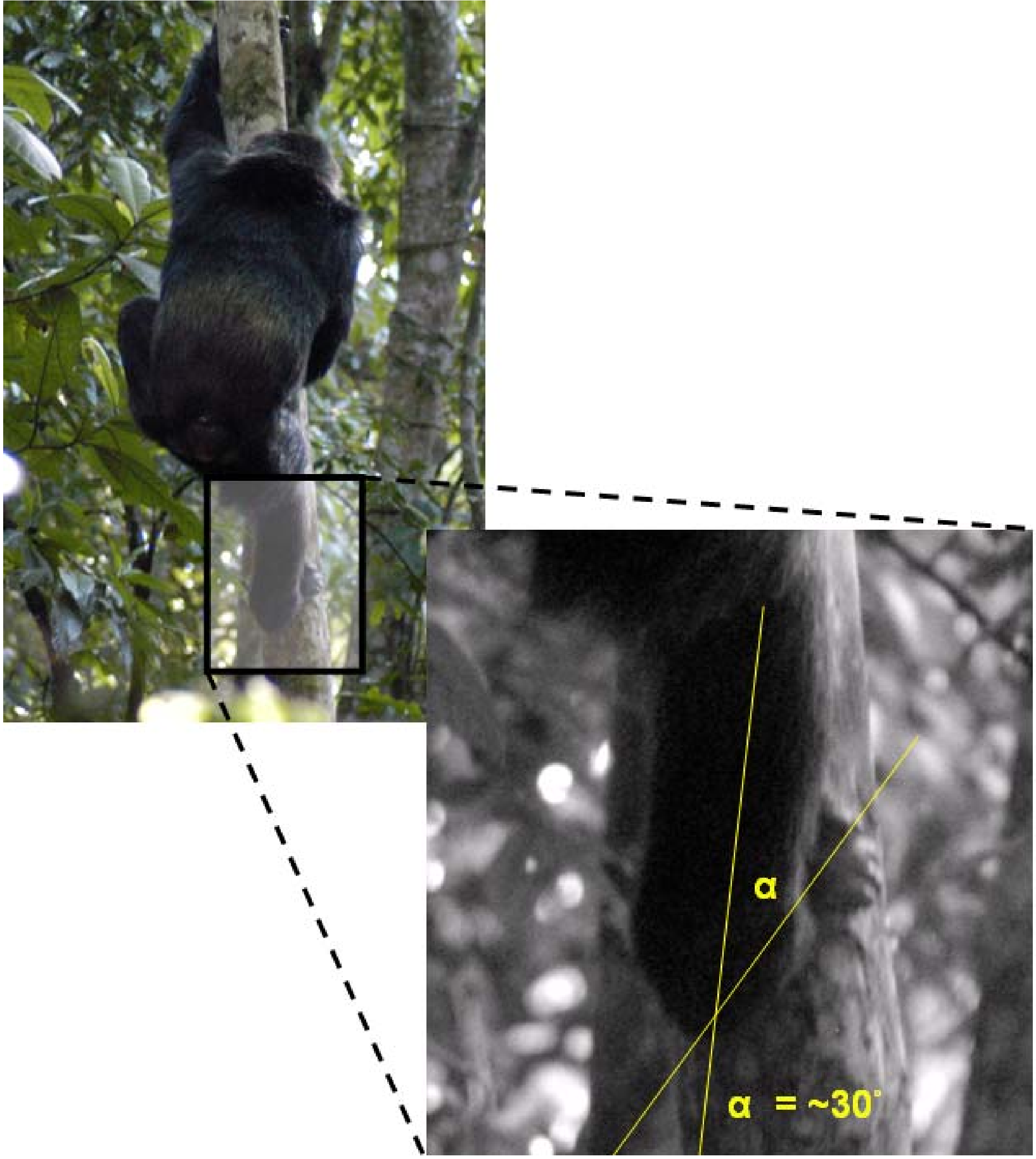


Figure 2.3. Video stills in which the vertically climbing chimpanzee is in posterior view and <10 meters from the ground were captured (see text for more details). In this example, which is taken from a photograph and not used in this study except to illustrate this measurement, a male chimpanzee is abducting the right foot during a vertical climbing bout. To estimate the degree of abduction, a straight line is drawn down the long axis of the tibia, and another line bisects the abducted foot. The angle measured between these two lines is the approximate amount of foot abduction.

while observing vertical climbs in posterior view (Figure 2.3). Of the 166 vertical climbs filmed, only 27 were taken in posterior view, defined as film in which the medial aspect of the arm or leg, and the anterior aspect of the torso is not in view.

Comparative kinematic data were obtained in the same manner as described above from additional video data captured on both wild and captive primates. To assess whether the results obtained from filming chimpanzees in the wild were comparable to other great apes, film was taken of gorillas, and orangutans in a more controlled captive setting at the Toledo Zoo. The gorillas consisted of a mixed group of adolescent and adult males and females (n=8) in an indoor habitat containing vertically oriented ropes with a diameter of approximately 5 cm. Eight gorilla climbing bouts fit the criteria described for the wild chimpanzees above. Additionally, film was taken of a family of orangutans consisting of an adult male, female, and juvenile, and nine vertical climbing bouts met the established criteria described above and had ankle angles that could be quantified.

To assess whether the results obtained were comparable to cercopithecoid monkeys, video of wild chacma baboons (*Papio ursinus*) in the Moremi Game Reserve in the Okavango Delta in Botswana and wild geladas (*Theropithecus gelada*) in the Simiens Mountains National Park were provided by Jacinta Beeher and Thore Bergman of the University of Michigan. Vertical climbing bouts of geladas (n=2) and baboons (n=1) were in lateral view and able to be quantified. Additionally, video was taken and analyzed of a single vertical climbing bout in a captive Allen’s swamp monkeys (*Allenopithecus nigroviridis*) at the Toledo Zoo. Because few climbing bouts were captured on video, the results of the kinematic analysis of these cercopithecoids should be considered preliminary.

Results

Vertical climbing bouts were filmed in 137 adult males, 25 adult females, and 4 juvenile chimpanzees. Forty-seven different individuals (10 female, 37 male) were filmed. Chimpanzee dorsiflexion at the talocrural joint during vertical climbing bouts was measured on 63 vertical climbing bouts from a minimum of 30 different individual chimpanzees (5 female, 25 male). Maximum dorsiflexion at the talocrural joint during vertical climbing averages 45.5˚ ± 7.1˚ with a range of 31.7˚ to 57.7˚. When measurements were taken to the nearest 5˚, the average was 45˚ ± 5˚ with a range of 30˚ to 60˚. There were no difference in dorsiflexion measured between climbing males and females (t=0.39, df=51, p=0.70). Maximum dorsiflexion occurred during lift-off of the opposite hand and foot for each chimpanzee. Thus, maximum dorsiflexion occurred when the weight of the animal was being supported by a single foot and the ipsilateral hand. Maximum dorsiflexion occurred prior to any contribution to flexion from midfoot flexion (see discussion). Midfoot flexion only occurred during the initial push-off phase of climbing.

Abduction of the foot quantified from 27 separate vertical climbing episodes from 23 adult males and four adult females. The abduction angle was approximately 28.8˚ ± 6.6˚.

The average diameter of tree climbed was 13.9 cm ± 7.7 cm (Figure 2.4). Seventy-seven percent of climbs were performed on trees between 10-25 cm, whereas only 9% were on trees less than 10 cm, and 14% on trees greater than 25 cm. There were no differences found between the diameter of tree climbed by adult males and those climbed by adult females (t=0.735, df=162, p=0.46).

There were differences, however, in the diameter of tree climbed during June of 2006 and July-August of 2007 (t=2.51, df=162, p=0.01). In June 2006, the average tree diameter climbed was 15.6 cm ± 7.2 cm whereas in July-August of 2007 the average tree diameter was 12.6 cm ± 8.0 cm. In June 2006, *Uvariopsis congensis* was fruiting and chimpanzees were preferentially climbing this tree. In July-August 2007, *U. congensis* was not fruiting, and the chimpanzees were often climbing lianas to obtain fruit from large-diameter *Ficus* and *Chrysophyllum* trees. There were 16 cases measured in July-August 2007 in which the chimpanzees climbed smaller diameter trees or lianas (9.2 cm ± 5.2 cm) to get into large diameter ones (50.9 cm ± 10.7 cm). When climbing bouts using lianas (n=10) are removed from the July-August 2007 data, the difference between the years measured is reduced (t=1.95, df=152, p=0.05).

Observations of gorillas, and orangutans at the Toledo Zoo demonstrate that similar ranges of dorsiflexion are employed by climbing apes ascending ~5 cm vertical ropes in captivity. Gorillas (n=8) flexed to approximately 50.6˚ ± 11.4˚, and orangutans (n=9) 44.7˚ ± 8.5˚. Ascent of a vertical rope substrate was performed in a kinematically different manner in the cercopithecoid *Allenopithecus*, however. Flexion occured primarily in the midfoot region, and dorsiflexion at the talocrural joint was measured to only 25˚.

Limited data from video taken on wild cercopithecoids yield similar results as those obtained on *Allenopithecus*. Geladas (*Theropithecus gelada*) have little opportunity to climb as their habitat in the Ethiopian highlands contains very few trees. However, video of two vertical ascents by an adult and an infant gelada suggested that these primates choose to leap up alternatively angled branches during climbing and appear to flex at the midfoot rather than at the talocrural joint when they do climb substrates angled >45˚. Talocrural flexion was 20˚ for the adult, and 22˚ for the infant.

Figure 2.4. Vertically climbing in wild *Papio ursinus* (left), and *Pan troglodytes* (right).

Figure 2.4. Comparative kinematics of vertical climbing in a cercopithecoid (*Papio ursinus*) on the left and a hominoid (*Pan troglodytes*) on the right, both in lateral view. Both primates were in the same stage of climbing with maximum dorsiflexion of the left ankle, push-off of the right foot, grasping of the substrate with the left hand and the beginning of a vertical reach with the right hand. Notice the difference in flexion at the left ankle between the chimpanzee and the baboon. Notice too the differences in flexion at the hip and knee.

This climbing approach is also apparent from video data of chacma baboons (*Papio ursinus*). When ascending a small diameter tree, the baboons leap up alternatively angled branches. However, they will also engage in vertical climbing, though the primary amount of dorsiflexion is located at the midfoot rather than at the ankle (Figure 2.4). Talocrural flexion was estimated to be only 15˚. When ascending a large diameter tree, the baboons practice a kinematically distinct approach. They splay their legs laterally and pull themselves up the tree in a pulse-like manner (Figure 2.5). Dorsiflexion at the ankle appears to be limited when this approach is utilized, though not possible to quantify with the methods employed in this study.

Figure 2.5. Pulse vertical climbing in wild chacma baboon (*Papio ursinus*).

Figure 2.5. Pulse climbing in a wild baboon (*Papio ursinus*) in the Moremi Game Reserve in the Okavango Delta in Botswana. There are 70 msec between each frame.

Discussion

These are the first data reported on the kinematics of vertical climbing in wild chimpanzees. Observations from 63 vertical climbing bouts demonstrate that wild chimpanzees dorsiflex approximately 45˚ during their vertical ascent. This is an extreme range of motion, potentially unique to the non-human hominoids and some ateline primates among the anthropoids. The acute amount of dorsiflexion documented here may represent a specific adaptation to facilitate vertical climbing.

A review of reported dorsiflexion achieved at the talocrural joint during walking in modern humans found angles ranging from 8.3˚ to 25.7˚ (Rome, 1996). This review reported that many factors can effect this measurement, including the instrument used, age of the subject, and the position of the calcaneus. Siegler et al. (1988) attempted to decouple the contributions of the talocrural and subtalar joints to dorsiflexion and found that of the 25˚ of maximum dorsiflexion achieved in humans during walking, about 20˚ occurred at the talocrural joint. A similar result was obtained by Lundberg et al. (1989)

who found that 23˚ of the maximum 30˚ of dorsiflexion achieved by walking humans happens at the talocrural joint. Lundberg (1989) also found that because of the proximal attachment of the gastrocnemius to the distal femur, bending at the knee allows for a greater degree of dorsiflexion.

Although there is variation in the degree of dorsiflexion achieved during walking in humans, two studies have concurred that the human talocrural joint fails at approximately 45˚ of flexion (Begeman and Prasad, 1990; Parenteau et al., 1998). Sixteen lower limbs from cadavers could be dorsiflexed to about 20˚ before resistance from the Achilles tendon and the deltoid ligament became apparent (Begeman and Prasad, 1990). During impact to simulate a car accident, 11 of the 16 ankles dorsiflexed less than 45˚ and did not sustain injury while 5 of the 16 dorsiflexed greater than 45˚ and all sustained severe injury including rupture of the deltoid ligament and malleolar fractures (Begeman and Prasad, 1990). A study of thirty-two lower limbs of cadavers loading to failure found that the talocrural joint failed at an average of 44˚ ± 10.9˚ (Parenteau et al., 1998). The most common injuries included lateral malleolar fractures and failure of the calcaneofibular ligament (Parenteau et al., 1998). Though human newborns are capable of approximately 45˚ of dorsiflexion (Bernhardt, 1988), the adult ankle fails at that angle.

Like humans, cercopithecoid monkeys exhibit only moderate flexion at the talocrural joint during walking. For example, Vervet monkeys (*Cercopithecus aethiops*) were found to dorsiflex approximately 15˚ during quadrupedal walking (Vilensky and Gankiewicz, 1990). Apes have a greater range of dorsiflexion during walking than that measured in either humans or cercopithecoids. Bonobos (*Pan paniscus*) flex at the ankle an average of 37.4˚ during quadrupedal walking (D'Août et al., 2002). However, some of this flexion is achieved at the midfoot and when foot flexion is taken into consideration, flexion at the talocrural joint alone ranges from 26˚-29˚. Many studies have reported foot dorsiflexion during bipedal walking in the apes. Chimpanzees (*Pan troglodytes*) dorsiflex at the ankle approximately 25˚ (Jenkins, 1972); orangutans (*Pongo pygmaeus*) flex up to 40˚ during bipedal walking (Payne, 2001); gibbons dorsiflex about 20˚ during bipedalism (Yamazaki and Ishida, 1984). Because these apes do not walk bipedally very often in the wild, kinematic data on bipedally walking apes is useful in assessing joint capability, rather than what is commonly practiced.

Few comparative data exist on the degree of dorsiflexion achieved by vertically climbing primates (Table 2.2). Hirasaki et al. (1993) reported that the ankle is flexed to a different degree in vertically climbing spider monkeys (*Ateles geoffroyi*) than that measured in macaques (*Macaca fuscata*). Spider monkeys dorsiflex an average of 32.7˚ during vertical climbing whereas macaques only dorsiflex 15.1˚-25.1˚ when they vertically climb in captivity (Hirasaki et al., 1993). These data on macaques are consistent with what was observed in this study on cercopithecoids. Preliminary data reported here suggest that during vertical climbing bouts in cercopithecoids, the majority of flexion occurs at the midfoot rather than at the talocrural joint (Figures 2.4 and 2.6). Like spider monkeys, gibbons have been found to experience a greater degree of dorsiflexion during vertical climbing than that found in cercopithecoids, achieving approximately 40˚ (Yamazaki and Ishida, 1984). This result of 40˚ is consistent with dorsiflexion achieved during vertical climbing in captive bonobos, lowland gorillas, and orangutans (Isler, personal communication), and parallels the results obtained in this study on wild chimpanzees and captive gorillas and orangutans. These data on the

Table 2.2. Maximimum degree of ankle dorsiflexion during vertical climbing in anthropoids.

Species	Wild/Captive	N	Dorsiflexion during vertical climbing	Source
Pan troglodytes	Wild	63	45.5˚ ± 7.1˚	This study
Gorilla gorilla gorilla	Captive	8	50.6˚ ± 11.4˚	This study
Pongo pygmaeus	Captive	9	44.7˚ ± 8.5˚	This study
Hylobates lar	Captive	-	~40˚	Yamazaki and Ishida, 1984
Papio ursinus	Wild	1	~15˚	This study
Theropithecus gelada	Wild	2	~21˚ ± 1.4˚	This study
Allenopithecus nigroviridis	Captive	1	~25˚	This study
Macaca fuscata	Captive	30	15.1˚ ± 7.5˚; 16.5˚ ± 7.6˚; 25.1˚ ± 9.4˚	Hirasaki et al., 1993
Ateles geoffroyi	Captive	10	32.7˚ ± 4.6˚	Hirasaki et al., 1993

Figure 2.6. Comparative kinematics of climbing in the ankle of a hominoid (left) and cercopithecoid (right).

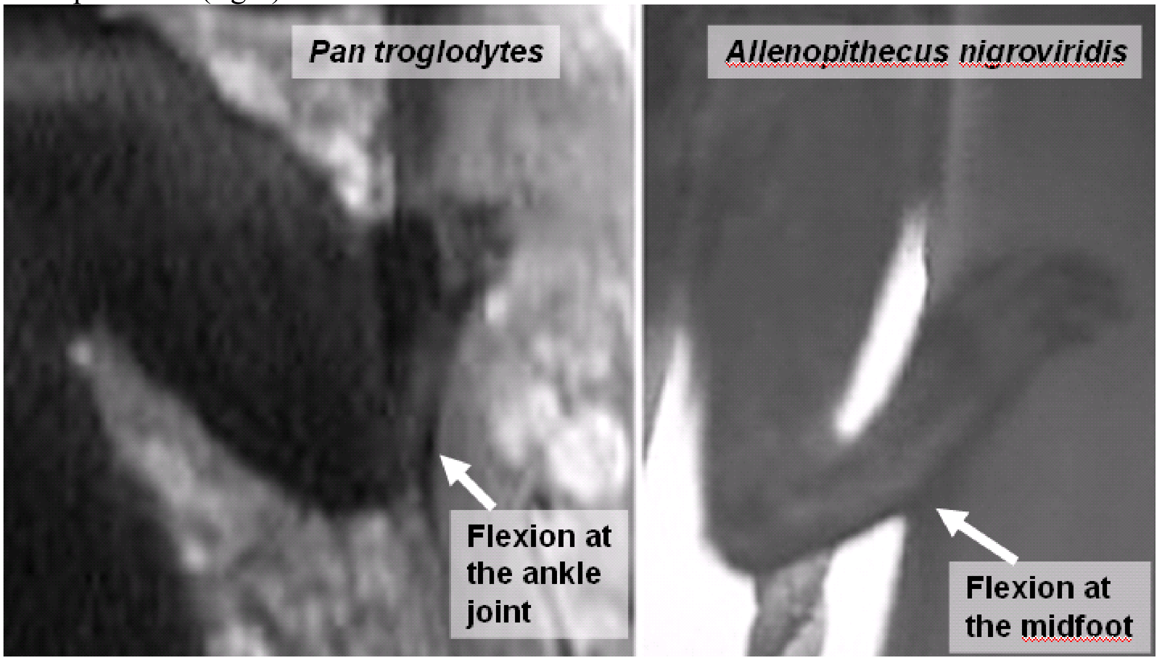


Figure 2.6. Comparative kinematics of vertical climbing in the foot and ankle of a chimpanzee (left) and the cercopithecoid *Allenopithecus* (right). The ape on the left flexes approximately 45˚ at the ankle to bring itself closer to the vertical substrate. Alternatively, monkeys have reduced ankle dorsiflexion (~20˚) and compensate by flexing at the midfoot.

talocrural joint are consistent with other studies that have found kinematic convergence between apes and atelines during vertical climbing (Isler, 2003; Isler, 2004).

Ascending a large body directly against the pull of gravity is energetically expensive (Preuschoft et al., 1992). In addition, because a fall from the heights achieved by climbing apes could be fatal (Goodall, 1986; Carter et al., 2008), adaptations are likely to evolve to ensure that apes efficiently navigate their arboreal environment (Cartmill, 1985; Preuschoft et al., 1992; Pontzer and Wrangham, 2004). One of these adaptations may be extreme flexion at the talocrural joint. As discussed in the introduction, during vertical climbing, there is a force produced by the pull of gravity that is proportional to the mass of the animal and the distance that the animal is from the tree. A climbing ape cannot change its own mass during climbing, and thus adaptations that allow the animal to be closer to the vertical substrate will reduce the downward force acting on the animal and the costs of climbing. Keeping the body close to the substrate in order to reduce the forces on the climbing animal is a vertical climbing adaptation that has been noted elsewhere (Preuschoft, 1970; Preuschoft et al., 1972; Cartmill, 1972; Cartmill, 1985; Autumn et al., 2006). It has been suggested that the abducted, short lower limb of the great apes helps reduce the climbing moment by pulling them closer to the tree. Here, I suggest that extreme dorsiflexion at the talocrural joint is an additional adaptation that reduces climbing costs.

Interestingly, the Ngogo chimpanzees climbed trees of a limited diameter compared to the large range of trees found in the Kibale National Park (Figure 2.7). A survey of 578 trees from 20 species found that the Ngogo study area consists of trees with an average diameter of 108.64 cm ± 84.7 cm, ranging from a minimum of 8.2 cm

Figure 2.7. Size of trees climbed by chimpanzees compared to the size of trees available to climb in Kibale National Park.

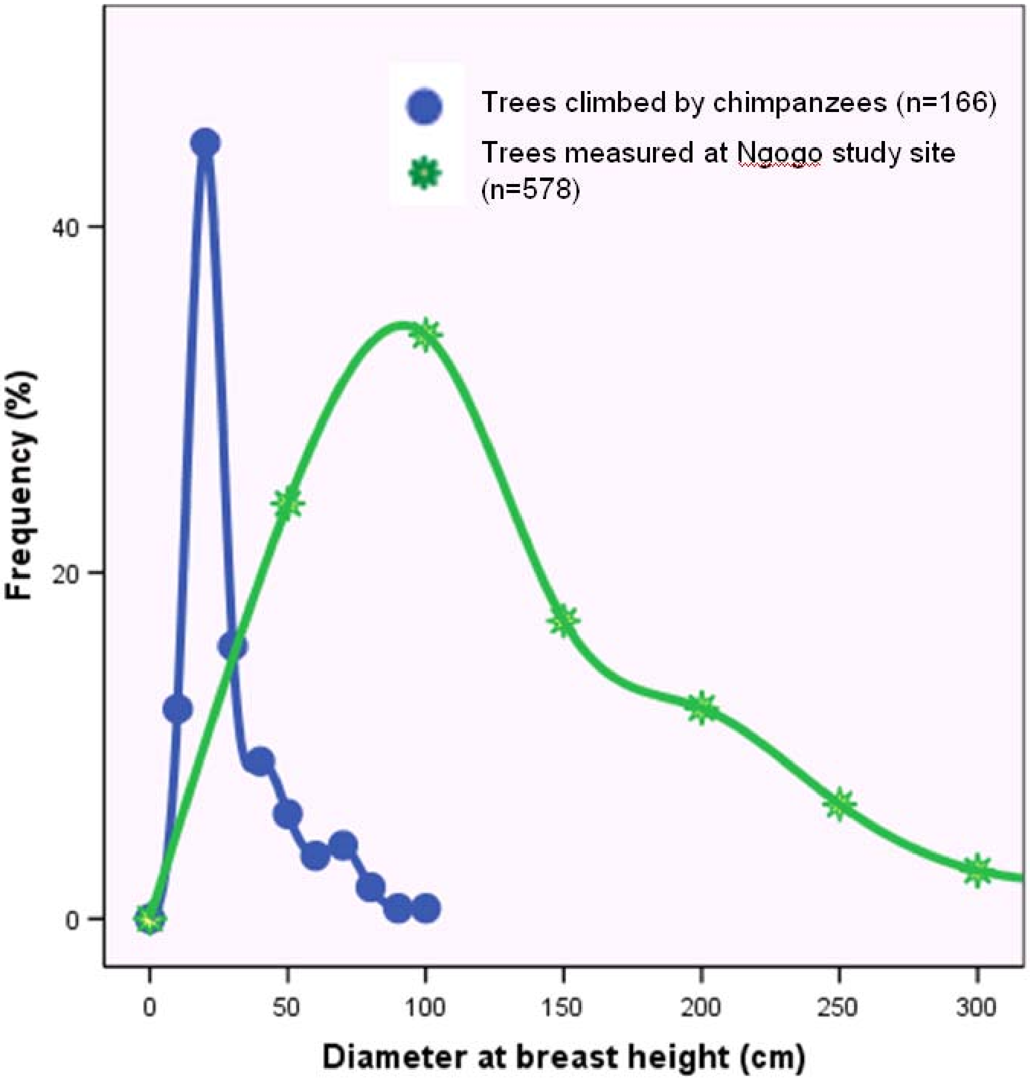


Figure 2.7. Chimpanzees climb a very specific range of tree diameters of 13.9 cm ± 7.7 cm. A histogram of the frequency of tree diameters climbed by chimpanzees are illustrated by the blue circles. These data are compared to the size of trees actually in the Kibale Forest, the frequency of which are illustrated by the green stars. Almost 80% of chimpanzee climbs are on trees with a diameter at breast height of 10-25 cm. Chimpanzees may favor trees with a diameter small enough to fully grasp with the divergent hallux and lateral digits of their feet. Data provided by Jeremiah Lwanga and John Mitani.

(*Uvariopsis congensis*) to 680 cm (*Ficus mucuso*) (Lwanga, personal communication).

The average tree diameter of the 166 trees vertically climbed by chimpanzees was 13.9

cm ± 7.7 cm. Thus, chimpanzees preferentially climb trees with smaller diameters than the majority of trees available to them (two sample Kolmogorov-Smirnov test, $z = 7.293$, $p<0.0001$). Climbing these trees may allow the chimpanzee to obtain a prehensile grip around the substrate and maximize the vertical force produced by the foot. Larger diameter trees may prohibit a prehensile grip, and thus would be more difficult, and more dangerous, to climb. This hypothesis is consistent with data on wild lowland gorillas which have a larger span between the abducted hallux and the lateral four digits and climb larger trees that are between 48.5 cm and 66 cm (Remis, 1999).

However, the results obtained in this study also suggest that wild chimpanzees are capable of climbing more variable vertical substrates than has been previously reported. Chimpanzees at the Gombe Stream and Mahale Mountains National Parks climb trees that have a diameter of 2-10 cm 85% of the time (Hunt, 1992). In this study, the chimpanzees of the Ngogo community climbed trees 2-10 cm in diameter only 9% of the time. The choice of climbing specific diameter trees may be season and forest dependent.

Evidence presented here suggests that there may be two distinct kinematic strategies in the foot and ankle during vertical climbing bouts in anthropoid primates. The first, practiced by cercopithecoids, maintains a less flexed talocrural joint while flexing the midfoot to pull the monkey close to the tree. The second, practiced by *Ateles* (Hirasaki et al., 1993) and apes (Yamazaki and Ishida, 1984; Isler, pers. comm., this study), involves flexion at the talocrural joint to pull the animal's body close to the vertical substrate. These different models of climbing result in specific predictions for how the ankle and foot anatomy of cercopithecoids, apes and atelines should differ.

These predictions are detailed in the following chapters (Chapters 3-5), and thus will be only briefly discussed here.

Dorsiflexion in humans is restricted by the Achilles tendon (Costa et al., 2006), and by the posterior fibers of the deltoid ligament (Rasmussen et al., 1983; Siegler et al., 1988). The absence of a prominent Achilles tendon in chimpanzees is a likely source of the extremes of dorsiflexion achieved by vertically climbing chimpanzees. Likewise, one might posit a smaller or weaker posterior tibiotalar ligament in vertically climbing apes. The distal tibia of humans and Old World monkeys, in contrast, are predicted to have a large area of attachment for the posterior tibiotalar ligament, which would restrict extreme dorsiflexion at the talocrural joint (Chapter 5).

Loading the talocrural joint in a position of dorsiflexion, inversion and abduction yields specific predictions regarding skeletal adaptations of that joint. Human cadaver studies have demonstrated that loading of the talocrural joint during dorsiflexion shifts the load anteriorly (Corazza et al., 2005), while loading of the joint during foot inversion shifts the load medially (Calhoun et al., 1994). Thus, it is hypothesized that skeletal correlates of ape-like vertical climbing would include an expansion of the anterior surface of the distal tibia and talus, and an enlarged medial malleolus of the distal tibia.

This study suggests that the range of motion and loading environment of the talocrural joint during vertical climbing differs substantially between apes and cercopithecoids. A comparative study of this joint may therefore yield important skeletal and ligamentous information regarding adaptations for vertical climbing. Functionally significant skeletal correlates of talocrural dorsiflexion, if supported by further study, will help interpret the locomotor capacity of Miocene catarrhines and Plio-Pleistocene hominins, and help test whether any of these early apes or early hominins were adapted to vertically climb like a modern chimpanzee.

Conclusion

These are the first kinematic data on vertical climbing in wild chimpanzees. These data demonstrate that chimpanzees pull themselves close to the vertical substrate during vertical climbing in part via extreme dorsiflexion at the talocrural joint. This magnitude of dorsifleixion, 45˚, is not possible in the human ankle without severe injury. Limited data on vertical climbing in wild and captive cercopithecoids, in contrast, suggest that they pull themselves close to the substrate by flexing the midfoot, rather than dorsiflexing the ankle. These data support the hypothesis that apes and cercopithecoids vertically climb in a kinematically distinct manner. Skeletal correlates of vertical climbing in the talocrural joint may provide insight into locomotor repertoire of Miocene catarrhines and early hominins.

CHAPTER 3

Vertical climbing adaptations in the anthropoid talocrural joint: Implications for early Miocene catarrhine locomotion.

Abstract

Extant apes and ateline primates vertically climb more often than cercopithecoid monkeys, and in a kinematically different manner. At the ankle joint, apes and atelines use extreme dorsiflexion, combined with foot inversion and abduction, to keep their bodies close to the substrate while vertically climbing, whereas cercopithecoids flex primarily at the midfoot. Thus, the ankle of vertical climbing apes and atelines is hypothesized to be well-adapted to a unique loading environment able to withstand the forces incurred during extremes of dorsiflexion, inversion, and abduction. Linear and angular measurements were taken on 379 tibiae and 224 tali of wild-collected adult anthropoid primates from the genera *Pan*, *Gorilla*, *Pongo*, *Hylobates*, *Symphalangus*, *Papio*, *Mandrillus*, *Macaca*, *Theropithecus*, *Nasalis*, *Cebus*, *Ateles*, *Alouatta* and *Lagothrix*. Skeletal correlates of vertical climbing in ape and ateline ankles include an expansion of the anterior aspect of the tibia, a thickened medial malleolus of the tibia, and a mediolaterally expanded tibial metaphysis. A study of 10 tibia and 26 tali from Miocene deposits in Kenya and Uganda finds little evidence for vertical climbing adaptations in the ankles of Miocene catarrhines, including the earliest hominoids. Instead, most specimens are cercopithecoid-like, or have no modern analogue. There is, however, evidence from the tali of *Rangwapithecus* and *Simiolus* that they may have

engaged in extremes of dorsiflexion at the ankle and loaded the medial side of the foot during climbing bouts. Additionally, the *Proconsul major* distal tibia from Napak, Uganda is not simply a scaled up version of smaller *Proconsul* tibiae, but rather has a distinct morphology suggestive of some vertical climbing in this large bodied hominoid. These data suggest that there may have been more locomotor diversity in the early Miocene than has been proposed.

Introduction

The ankle, or talocrural joint, is formed between the tibia, fibula, and talus. Though often characterized as a simple hinge joint because motion is primarily restricted to dorsiflexion and plantarflexion, subtle morphological differences among primate species in the shape of the talus and distal tibial facet can result in abduction/adduction and inversion/eversion at the talocrural joint as well. Attempts have been made by many workers to link these skeletal differences to locomotor constraints in extant primates in order to interpret the functional morphology of fossil anthropoid ankle bones (Conroy, 1976; Fleagle, 1977; Harrison, 1982; Conroy and Rose, 1983; Fleagle and Simons, 1983; Dagosto, 1985; Langdon, 1986; Gebo and Simons, 1987; Dagosto, 1988; Fleagle and Meldrum, 1988; Ford, 1988; Strasser, 1988; Harrison, 1989; Seiffert and Simons, 2001). Though skeletal correlates of leaping, arboreal quadrupedalism, and terrestrial quadrupedalism at the talocrural joint have all been investigated, ankle morphology adapted for vertical climbing has not yet been systematically assessed in the anthropoid ankle. Predictions of skeletal correlates of vertical climbing in the talocrural joint are derived from kinematic analysis of ankle during vertical climbing bouts in wild and captive apes (Chapter 2). This study tests whether the talocrural joint differs among apes, cercopithecoids, and atelines in ways functionally related to joint mobility and loading in positions of dorsiflexion, abduction, and inversion known to be important during vertical climbing.

The vast majority of primates share unique features of the ankle functionally related to hallucial grasping and arboreality (Lewis, 1980; Dagosto, 1985; Gebo, 1993). These features include an unfused, mobile fibula important for hallucial grasping while moving along uneven arboreal substrates (Barnett and Napier, 1953; Fleagle and Simons, 1983), and evidence for a prominent flexor hallucis longus (Conroy and Rose, 1983; Gebo et al., 2000). In addition, while most mammals have a prolonged medial aspect of the talocrural joint, primates have an elongated lateral aspect, which puts the foot in a position of abduction during dorsiflexion (Dagosto, 1985; Strasser, 1988; Gebo, 1993). This morphology has been described as a primate synapomorphy (Dagosto, 1985), and functionally linked to arboreality (Gebo, 1993).

Within this general morphological framework, variation in the morphology of the distal tibia, fibula, and talus has been functionally linked to primate leaping, and arboreal and terrestrial quadrupedalism. Both leaping primates and quadrupedal cercopithecoids possess a deeply concave talar surface and corresponding keel on the distal tibia (Gebo and Simons, 1987) which stabilizes the joint in the parasagittal plane (Harrison, 1989). This morphology is a primitive feature of the mammalian ankle (Dagosto, 1985). However, there are important functional differences in the ankle between leaping and generalized quadrupedal primates. In comparing sympatric leaf monkeys in Malaysia, Fleagle (1977) found that the leaper *Presbytis melalophos* possessed a talar trochlea with an equal height to the lateral and medial rims. This is in contrast to the arboreal quadruped *Presbytis obscura* which has a higher lateral rim. This asymmetry between the lateral and medial heights of the talar rims is common in all cercopithecoids (Harrison, 1982; Strasser, 1988; Gebo, 1993) and has been argued to be an adaptation for foot stabilization during walking and running (Langdon, 1986), because talar asymmetry would limit foot abduction thus keeping the foot stable in a parasagittal plane (Gebo, 1993). Dagosto (1988) has also proposed that the high trochlear rims in primate tali prevent inversion at the talocrural joint, shifting that motion to the subtalar and transverse tarsal joints.

Differences between leapers and arboreal quadrupeds have also been studied in the platyrrhine ankle (Fleagle and Meldrum, 1988). Compared with the arboreal quadruped *Chiroptes*, the leaping New World Monkey *Pithecia* has an anteroposteriorly narrow distal tibia, and an extension of the facet for the distal tibia onto the neck of the talus, morphologies both consistent with extreme dorsiflexion. In addition, *Pithecia* possesses strong ligamentous connections between the distal tibia and fibula, and a relatively thin, laterally flat medial malleolus consistent with the reduced role of hallucial grasping and motion limited to dorsiflexion and plantarflexion.

Fewer attempts have been made to interpret differences in ankle morphology among cercopithecoids and non-human hominoids and the results have been conflicting. For example, the cotylar fossa, a small facet on the medial aspect of the talus for the medial malleolus has been characterized in the following three ways: Deeply cupped in cercopithecoids but shallow in platyrrhines and apes (Le Gros Clark and Leakey, 1951; Harrison, 1982), cupped in both cercopithecoids and apes (Dagosto, 1985), cupped in cercopithecoids and gibbons but not great apes (Fleagle, 1983; Rose, 1994). Furthermore, the function of this morphology is not clear. It has been suggested to be an adaptation for climbing (Gebo and Simons, 1987), an adaptation for joint stability during dorsiflexion not related to arboreality at all (Lewis, 1980; Harrison, 1982), or a variable feature not functionally informative (Ford, 1988). These differing interpretations are in part the result of qualitative assessments of a highly variable feature that may have no functional significance.

Another uncertain morphological feature perhaps more relevant to the issue of vertical climbing is the presence of a wedge-shaped talar trochlea and corresponding mediolateral expansion of the anterior aspect of the distal tibia relative to the posterior rim. Conroy (1976) found little variation in talar wedging among primates; Langdon (1986) argued that the African ape and ateline talus is more strongly wedged than the tali of cercopithecoids or Asian apes; Harrison (1982) suggested that this morphology discriminated apes and cercopithecoids. In addition to different patterns of talar wedging, there are different functional interpretations. A wedged talus has been argued to provide stability for the talocrural joint during dorsiflexion (Gomberg, 1981; Rose, 1983; Langdon, 1986) and correspondingly permits greater abduction and adduction in plantarflexion (Rose, 1993). However, in humans, who have a moderately wedged talus, there is no evidence for greater talocrural laxity in plantarflexion than in dorsiflexion (Barnett and Napier, 1952; Close, 1956; Inman, 1976; Morris, 1977; Bremer, 1985; Pereira et al., 1996) and thus there are problems with the interpretation that wedging promotes mobility in plantarflexion and stability in dorsiflexion, as others have noted (Conroy, 1976). While some have suggested that the function of talar wedging is unclear

(McCrossin, 1994), others have argued that wedging is a by-product of the conical nature of the primate talus (Inman, 1976).

Many have observed that relative to cercopithecoids, apes possess a more robust medial malleolus (Harrison, 1982; Harrison, 1989), and a more mediolaterally broad distal tibia (Harrison, 1989; Rose, 1993; McCrossin, 1994). In addition, it has been noted that some features of the ape tarsal region can also be found in New World atelines, and may be functionally related to climbing (Gebo, 1989). However, the functional significance of the hominoid talocrural joint has yet to be systematically explored. Many of the comparative studies that have been attempted on the primate ankle have involved multivariate canonical analyses that provide few functional insights (Day and Wood, 1969; Oxnard, 1972; Wood, 1973; Lisowski et al., 1976).

Prior research on the primate ankle has been combined with studies on the rest of the postcranial skeleton to interpret the functional anatomy of early Miocene catarrhines. The locomotion of these early catarrhines is an area of great interest to paleoanthropologists in part because extant hominoids and cercopithecoids move in such different ways and possess unique postcranial anatomies (Harrison, 1987; Pilbeam and Pilbeam, 1996; Young, 2003; MacLatchy, 2004). Understanding how Miocene catarrhines moved will help establish the pattern of locomotor evolution in both the hominoid and cercopithecoid clades, and perhaps reveal the role that locomotion may have played in the divergence of hominoids and cercopithecoids from the last common catarrhine ancestor. Despite the evidence for taxonomic diversity in the early Miocene, there is little evidence for locomotor diversity (Fleagle, 1999). Instead, many of the early Miocene taxa have been reconstructed as generalized arboreal quadrupeds (Rose, 1993;

Rose, 1994). The best known Miocene hominoid *Proconsul* is reconstructed as an above branch, perhaps slow-moving, pronograde quadruped (Walker and Pickford, 1983; Rose, 1983; Rose, 1993; Rose, 1994; Walker, 1997). Similar locomotion has been reconstructed for *Afropithecus*, and *Limnopithecus* (Rose, 1993; Fleagle, 1999). There is some evidence that *Turkanapithecus* may have been capable of more forelimb suspension than *Proconsul* (Rose, 1993), and the small-bodied *Dendropithecus* and *Simiolus* are also reconstructed as possessing more suspensory abilities than *Proconsul* (Rose, 1992; Rose, 1993). In addition, the 20.6 million year old ape *Morotopithecus* is reconstructed as an orthograde, suspensory animal with adaptations for vertical climbing (Sanders and Bodenbender, 1994; Gebo et al., 1997; MacLatchy et al., 2000; MacLatchy, 2004). While the elongated forelimbs and long pedal digits of the 14-15 million year old KNM-BG 35250 *Nacholapithecus* skeleton suggest that this ape was capable of more orthogrady and vertical climbing than *Proconsul* (Rose, 1996; Ishida et al., 2004), the scapula and clavicle are more indicative of colobine-like locomotion in an arboreal habitat (Senut et al., 2004). Moreover, the long, *Proconsul*-like lumbar region of KNM-BG 35250 (Ishida et al., 2004), suggests that *Nacholapithecus* was not as well adapted to frequent orthograde postures as extant apes. The 15 million year-old hominoid *Kenyapithecus* is also a generalized quadruped that may have been more terrestrial than these other Miocene taxa (McCrossin and Benefit, 1997).

Few studies have commented on the locomotion of two Miocene apes, *Proconsul major* and *Rangwapithecus gordoni*. The distal tibia of *P. major* has been described as morphologically similar to other *Proconsul* tibiae (Rafferty et al., 1995). However, some have suggested greater climbing capacity in this species of *Proconsul* than the others based on the morphology of a fragmentary ulna (Nengo and Rae, 1992), the morphology of the calcaneocuboid joint (Gebo, 1989), and femora (Gommery et al., 1988; Gommery et al., 2002). In addition, the medial cuneiforms potentially of *Rangwapithecus* from the Miocene site of Songhor appear to possess a morphology adapted for arboreal climbing (Nengo and Rae, 1992). The talus BMNH 26903, perhaps attributable to *Rangwapithecus*, clusters with hominoids in a multivariate study, though no functional inferences were made (Seiffert and Simons, 2001). The functional morphology of these two apes has not been reconstructed primarily because of a lack of postcranial material that can be definitively assigned to them.

Interpretations of the hominoid fossil record, both behaviorally and phylogenetically, are contingent on the identification of skeletal correlates of locomotor behaviors currently practiced by the living apes. These include orthograde postures, suspensory behaviors, quadramanous climbing, and vertical climbing. Studies on modern ape locomotion have hypothesized the importance and potential uniqueness of each of these forms of locomotion. Based on data from wild siamangs (*Symphalangus syndactylus*), Fleagle (1976) suggested that apes are quadramanous climbers. More recently, observations of wild chimpanzees at Mahale and Gombe made by Hunt (1991) suggested that the key hominoid locomotor adaptation was arm-hanging postures and suspensory locomotion. In contrast, Thorpe and Crompton (2006) found that wild orangutans use arm-hanging postures and suspensory locomotion less often than previously thought, and suggested instead that general orthogrady, rather than strict arm-hanging, was an ape synapomorphy. Building on the suggestion by Doran (1996) that general climbing differentiated the apes from other anthropoids, Isler and Thorpe (2003) and Isler (2003) have argued that an increased frequency of vertical climbing and the unique kinematics of climbing performed by hominoids unites this group to the exclusion of the cercopithecoids.

This study focuses specifically on vertical climbing. Although apes vertically climb more frequently than cercopithecoid monkeys (Chapter 2), some have argued that they do so in a kinematically identical manner (Hunt, 1989; Hunt, 1992). This hypothesis has been disputed by observations made of captive and semi-wild primates (Isler, 2003; Isler, 2005). Interestingly, ateline primates *Ateles* and *Lagothrix* have converged with apes and not only vertically climb as frequently as extant apes, but in a kinematically similar manner (Hirasaki et al., 1993; Isler, 2003; Isler, 2004). As reported in Chapter 2, one of the kinematically unique approaches taken by vertically climbing apes and atelines involves extreme dorsiflexion at the ankle. Extreme dorsiflexion may not be an approach used by cercopithecoid monkeys in the rare occasions that they ascend a vertical substrate. Instead, cercopithecoid monkeys may flex primarily at the midfoot region (Chapter 2). Inversion and adduction are also important motions during vertical climbing, though it is not clear if apes and atelines have a greater range of these motions than cercopithecoids during vertical climbing bouts. All three motions- dorsiflexion, inversion and adduction- at the ankle help bring the vertically climbing ape or ateline closer to the vertical substrate, thus reducing torque at the hip, knee, and ankle produced by the weight of the climbing primate acting at a distance from the tree. Thus, data from wild and captive studies are strongly suggestive that during vertical climbing bouts, apes and atelines load their ankles in a different manner than cercopithecoid monkeys do.

If apes and atelines vertically climb more often than do cercopithecoids and do so by loading their ankles differently than cercopithecoids, then I predict that the skeletal morphology of the distal tibia and talus of apes and atelines will differ from cercopithecoids in ways that are functionally related to an increased range of dorsiflexion, inversion, and adduction. In addition, I hypothesize that the ankles of apes and atelines will be well adapted to withstand forces incurred on a joint loaded in these foot positions. Specific skeletal predictions are outlined in detail below and in the materials and methods section.

Studies of human cadavers have found that during dorsiflexion, the contact point between the tibia and the talus shifts anteriorly (Driscoll et al., 1994; Corazza et al., 2005). Vertically climbing primates experience extremes of foot dorsiflexion during climbing bouts, and therefore it is hypothesized that they will produce a loading environment at the talocrural joint with high anterior forces. Because stress is equal to force divided by a given surface area, increased bone in the anterior aspect of the talocrural joint would help reduce the stress in this region despite the high forces being incurred. Thus, it is predicted that vertically climbing apes and atelines will have relatively broader anterior aspects of the distal tibia and talus than the cercopithecoids.

Inversion at the talocrural joint in the human ankle shifts the contact point medially on the articular surface and onto the medial malleolus (Calhoun et al., 1994; Kura et al., 1998). In addition, detailed kinetic work on the primate foot has shown that the force on the foot shifts medially when chimpanzees climb a vertical pole; however, the force remains in a lateral position in pole climbing cercopithecoids (Wunderlich, 1999). It is therefore hypothesized that vertically climbing apes and perhaps atelines will produce a loading environment at the talocrural joint with high medial forces. Again, because stress is equal to force divided by a given surface area, increased size of the medial aspect of the talocrural joint would help reduce the stress in this region despite the high forces being incurred. Thus, it is predicted that vertically climbing primates will have more robust medial malleoli and a flattened medial side to the talus.

Because vertical climbing has been hypothesized to be a unique non-human hominoid locomotion (Isler and Thorpe, 2003; Isler, 2003), the identification of vertical climbing adaptations in the postcranial bones of early Miocene catarrhines has important ramifications for hypotheses of hominoid evolution and catarrhine phylogenetics. This study applies behavioral data of vertical climbing frequency of wild primates with kinematic data on the talocrural joint in primates to make specific predictions about how the talocrural joint should differ between vertically climbing apes and atelines, and the cercopithecoid primates.

I hypothesize that the ankle joint will differ in vertically climbing apes and atelines from cercopithecoid primates in ways that are functionally related to extreme dorsiflexion, inversion, and abduction. Data are collected on specific morphologies of the ankle that have been hypothesized to be adaptive based on the biomechanics of vertical climbing described above. Two-dimensional linear and angular measurements are taken on the distal tibiae and tali of 14 different genera of anthropoid primates. These measurements quantify the geometry of the articular surface of the distal tibia, the robustness of the medial malleolus, and the range of abduction possible at the talocrural joint. Specific measurements and their functional rationale are detailed in the material and methods section. Results are then applied to the early hominoid fossil record to examine whether any Miocene hominoids or generalized catarrhines had an ankle morphology adapted for frequent vertical climbing in the same kinematic way that modern apes and atelines do.

Materials and methods

The right distal tibia and talus of adult wild-shot primates were studied at the Cleveland Museum of Natural History, Harvard Museum of Comparative Zoology, American Museum of Natural History (New York), National Museum of Natural History (Washington D.C.), Yale Peabody Museum, and Field Museum (Chicago). Primate taxa studied include: African apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla gorilla*, *Gorilla gorilla beringei*), Asian apes (*Pongo pygmaeus*, *Hylobates lar*, *Symphalangus syndactylus*), atelines (*Ateles* spp., *Alouatta palliata*, *Lagothrix lagotricha*, *Brachyteles arachnoides*), *Cebus capucinus*, and the cercopithecoids (*Nasalis larvatus*, *Macaca fascicularis*, *Macaca nemestrina*, *Mandrillus sphinx*, *Theropithecus gelada*, and *Papio* spp.). The numbers of tibia and tali, and the sexes of the specimens are listed in Tables 3.1 and 3.2. Based on data from the literature (Rose, 1977; Fleagle, 1999; Ankel-Simmons, 2000), cercopithecoids were grouped into a terrestrial category composed of *Papio*, *Mandrillus*, *Theropithecus*, and *Macaca nemestrina*, and a more arboreal cercopithecoid category composed of *Nasalis* and *Macaca fascicularis*.

Fossil tibia and tali from the Miocene (Tables 3.3 and 3.4) were studied at the Kenya National Museum in Nairobi, and the Uganda National Museum in Kampala. High quality research casts of the tibia KNM-MV 2 and tali BMNH M26309, RUD 27, and GSP 10875 were provided by the Harvard Peabody Museum. All linear measurements on

Table 3.1. Extant anthropoid tibiae measured in this study.

Family	Species	Male	Female	Sex unknown	Total
Hominoid	*Pan troglodytes*	18	20	10	48
	Pan paniscus	2	1	1	4
	Gorilla gorilla gorilla	23	19	2	44
	Gorilla gorilla beringei	15	6	1	22
	Pongo pygmaeus	12	19	5	36
	Hylobates lar	19	20	1	40
	Symphalangus syndactylus	2	5	1	8
Cercopithecoid	*Papio* spp.	18	5	12	35
	Mandrillus sphinx	3	4	3	10
	Theropithecus gelada	3	2	0	5
	Macaca fascicularis	3	2	0	5
	Macaca nemestrina	4	2	0	6
	Nasalis larvatus	18	19	0	37
Platyrrhine	*Alouatta palliata*	11	7	2	20
	Ateles spp.	12	8	3	23
	Brachyteles arachnoides	0	0	1	1
	Lagothrix lagotricha	8	5	3	16
	Cebus capucinus	10	9	0	19

Table 3.2. Extant anthropoid tali measured in this study.

Family	Species	Male	Female	Sex unknown	Total
Hominoid	*Pan troglodytes*	19	22	10	51
	Pan paniscus	2	1	1	4
	Gorilla gorilla gorilla	23	19	3	45
	Gorilla gorilla beringei	10	3	0	13
	Pongo pygmaeus	12	18	7	37
	Hylobates lar	17	17	2	36
	Symphalangus syndactylus	4	3	1	8
Cercopithecoid	*Papio spp.*	13	3	8	24
	Mandrillus sphinx	2	2	3	7
	Theropithecus gelada	2	1	0	3
	Macaca fascicularis	2	1	0	3
	Macaca nemestrina	0	1	0	1
	Nasalis larvatus	15	8	12	35
Platyrrhine	*Alouatta palliata*	0	0	2	2
	Ateles spp.	8	7	1	16
	Lagothrix lagotricha	7	3	0	10
	Cebus capucinus	5	3	0	8

fossil and extant tibiae and tali were made with digital calipers. Significance was assessed for all measures in this study using a Tukey honestly significantly different (HSD) *post hoc* test after first performing a one-way analysis of variance (ANOVA test). The Tukey test was chosen over a Fisher's least significant difference (LSD) for planned comparison test even though planned comparisons were hypothesized *a priori* because in cases where more than three pairs of comparisons are made, the HSD test decreases the probability of committing Type I errors more than the LSD test (Day and Quinn, 1989). Furthermore, although the focus of the study was limited to vertical climbing adaptations, other differences in morphology between different primate groups is of *post hoc* interest because these primates engage in other locomotor activities than vertical climbing.

Table 3.3. Fossil catarrhine tibiae measured in this study.

Accession number	Geological age	Family	Taxon	Body mass estimate (kg)[*]
NAP I'58	19.5[1,2]	Hominoid	*Proconsul major*[3,5]	77.5
BUMP 99	19.5[1,2]	Catarrhine	*?*	6.3
BUMP 764	19.5[1,2]	Catarrhine	*?*	2.6
KNM-LG 583	19.5[4]	Hominoid? Catarrhine?	*?P. africanus*[5] *?Dendropithecus macinnesi*[3]	7.6
KNM-MV 2	19.5[4]	Catarrhine	*Micropithecus clarki*[5]	8.0
KNM-ER 1939	17.8[6]	Hominoid	*P. nyanzae*[3, 7]	29.4
KNM-RU 3589	17.8[6]	Hominoid	*P. heseloni*[3]	9.0
KNM-RU 2036	17.8[6]	Hominoid	*P. heseloni*[3]	11.1
KNM-BG 35250	~15[8]	Hominoid	*Nacholapithecus kerioi*[9]	9.7 (distorted)
KNM-MB 11973	14-15[10]	Cercopithecoid	*Victoriapithecus macinnesi*[11]	2.1
KNM-ER 40443	1.9-2.1[12, 13]	Cercopithecoid	*Theropithecus oswaldi*[13]	38.5
KNM-ER 3823	1.9-2.1[12, 13]	Cercopithecoid	*T. oswaldi* [13]	21.8
KNM-WT 16875	1.4-2.1[13]	Cercopithecoid	*T. oswaldi* [13]	29.4
KNM-WT 16755	1.4-2.1[13]	Cercopithecoid	*T. oswaldi* [13]	15.0
KNM-ER 3877	1.9-2.1[12, 13]	Cercopithecoid	*T. oswaldi* [13]	23.4
KNM-ER 5474	1.9-2.1[12, 13]	Cercopithecoid	*T. oswaldi* [13]	31.8
KNM-ER 597	1.9-2.1[12, 13]	Cercopithecoid	*T. oswaldi* [13]	27.1
KNM-ER 866	1.9-2.1[12, 13]	Cercopithecoid	*T. oswaldi* [13]	57.9
KNM-ER 5491	1.9-2.1[12, 13]	Cercopithecoid	*T. oswaldi* [13]	38.5
KNM-OG 1109	>0.74[13]	Cercopithecoid	*T. oswaldi* [13]	27.6

[1]Bishop, 1969; [2]MacLatchy et al., 2006; [3]Rafferty et al., 1995; [4]Pickford and Andrews, 1981; [5]Harrison, 1982; [6]Drake et al., 1988; [7]Le Gros Clark, 1952; [8]Sawada et al., 1998; [9]Ishida et al., 1999; [10]Feibel and Brown, 1991; [11]Harrison, 1989; [12]Feibel et al., 1989; [13]Krentz, 1993.

[*]Body mass estimates based on equations provided in Rafferty et al., 1995.

Table 3.4. Fossil catarrhine tali measured in this study

Accession number	Geological age	Family	Taxon	Body mass estimate[*]
KNM-SO 389	19.5[3]	Hominoid	*Proconsul major*[1,2,4,5]	49.4
KNM-SO 1402	19.5[3]	Catarrhine	*Rangwapithecus gordoni*?[5]	12.5
KNM-SO 1705	19.5[3]	Catarrhine	*P. africanus*[5]	16.6
KNM-SO 966	19.5[3]	Catarrhine	*R. gordoni*[4,5]	12.5
KNM-SO 968	19.5[3]	Catarrhine	*R. gordoni*[4,5]	9.5
KNM-CA 1305	19.5[3]	Catarrhine	*Micropithecus clarki*[4] *Dendropithecus macinnesi*[5]	6.1
KNM-SO 967	19.5[3]	Catarrhine	*M. clarki*[4,5]	5.6
KNM-SO 392	19.5[3]	Catarrhine	*Limnopithecus evansi*[4] *M. clarki*[5]	3.0
KNM-LG 621	19.5[3]	Catarrhine	*Limnopithecus legetet*[4,5] *D. macinnesi?*[5]	5.1
KNM-SO 478	19.5[3]	Catarrhine	*M. clarki*[4,5]	6.5
BMNH M26309	19.5[3]	Catarrhine	*R. gordoni*[4,5]	7.1
KNM-RU 1743	17.8[6]	Hominoid	*P. nyanzae*[4,5]	41.5
KNM-RU 1744	17.8[6]	Hominoid	*P. heseloni*[4,5]	7.9
KNM-RU 1745	17.8[6]	Hominoid	*P. heseloni*[4,5]	10.0
KNM-RU 1748	17.8[6]	Catarrhine	*D. macinnesi?* [4,5]	7.3
KNM-RU 1896	17.8[6]	Hominoid	*P. nyanzae*[2, 4, 5, 7]	37.9
KNM-RU 2036	17.8[6]	Hominoid	*P. heseloni*[5,21]	10.2
KNM-RU 3105	17.8[6]	Hominoid	*P. nyanzae*[5]	20.7
KNM-RU 5940	17.8[6]	Hominoid	*P. nyanzae*	36.2
KNM-RU 5872	17.8[6]	Hominoid	*P. nyanzae*[5]	~40 kg (Walker and Pickford, 1983)
KNM-RU 5945	17.8[6]	Catarrhine	*Nyanzapithecus vancouveringi?* *D. macinnesi?*	10.8
KNM-RU 1663	17.8[6]	Catarrhine	*D. macinnesi?*[4,5]	7.5
KNM-WK 18120	16-18[8]	Hominoid	*Afropithecus turkanensis*[8,9]	25.4
KNM-WK 17171	16-18[10]	Catarrhine	*Simiolus enjiessi*[10,11]	4.3
KNM-BG 35250	15[12]	Hominoid	*Nacholapithecus kerioi*[13]	22.8

KNM-MB 9422	14-15[14]	Cercopithecoid	*Victoriapithecus macinnesi*[15]	4.0
RUD 27	~10.0[17]	Hominoid	*Dryopithecus brancoi?*[16] *Anapithecus hernyaki?*[17]	17.0
GSP 10785	~8.0[18]	Hominoid	*Sivapithecus indicus*[18]	10.8
KNM-ER 745	1.4-1.6[19, 20]	Cercopithecoid	*Theropithecus oswaldi*	44.7
BK II/OLD 1957/1050	1.15-1.7[19, 20]	Cercopithecoid	*T. oswaldi*	50.8

[1]MacInnes, 1943; [2]Pilbeam, 1969; [3]Pickford and Andrews, 1981; [4]Harrison, 1982; [5]Langdon, 1986; [6]Drake et al., 1988; [7]Le Gros Clark, 1952; [8]Leakey and Leakey, 1986; [9]Leakey et al., 1988; [10]Leakey and Leakey, 1987; [11]Rose et al., 1992; [12]Sawada et al., 1998; [13]Ishida et al., 1999; [14]Feibel and Brown, 1991; [15]Harrison, 1989; [16]Morbeck, 1983; [17]Kordos and Begun, 2001; [18]Pilbeam et al., 1980; [19]Feibel et al., 1989; [20]Krentz, 1993; [21]Walker et al., 1993

Note: Specimens referred to as *P. africanus* at Kisingire sites (Harrison, 1982; Langdon, 1986) were later reassigned to *P. heseloni* (Walker et al., 1993) and are assigned as such. *P. africanus* talus only at Songhor.
[*]Body mass estimates based on equations provided in Rafferty et al., 1995.

All ankle morphology of extant anthropoids was quantified to assess features related to the three types of movement that typified vertically climbing wild chimpanzees (Chapter 2): dorsiflexion, abduction, and inversion.

Dorsiflexion

Four separate analyses were undertaken on the tibia and talus to assess both the capacity for extreme dorsiflexion, and to test whether loading occurs in the joint during periods of extreme dorsiflexion.

DISTAL TIBIA

1.) Six measures were taken on the articular surface of the distal tibia: the maximum mediolateral length of the anterior aspect of the articular surface, the maximum mediolateral length of the posterior aspect of the articular surface, the maximum mediolateral length at the midpoint of the articular surface, the maximum anteroposterior width of the most medial aspect of the articular surface, the maximum anterioposterior width of the most lateral aspect of the articular surface, and the maximum anteroposterior width at the midpoint of the articular surface (Figure 3.1). Measurement error, assessed by repeating these measures on forty specimens a month after the original measurements were taken, was within 5%. The geometric mean 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 geometric mean, following the size adjustment protocol established by Darroch and Mosimann (1985). This approach has been used in previous paleoanthropological studies (Richmond and Jungers, 1995; Madar et al., 2002; DeSilva et al., 2006; Richmond and Jungers, 2008) including a study of the primate ankle (Seiffert and Simons, 2001). This approach essentially asks the question: Given an equal amount of bone, *where* in the joint does the primate distribute this limited resource? The following fossils were complete enough for these measures to be taken accurately: NAP I'58, BUMP 764, KNM-MV 2, KNM-RU 1939, KNM-RU 2036, KMM-RU 3589, KNM-MB 11973, and KNM-BG 35250. The KNM-BG 35250 tibiae are severely distorted and results should be interpreted with caution.

TALUS

2.) The talus was measured in a slightly different way. Three measurements were taken on isolated tali: the maximum width of the talar trochlea at its most anterior aspect, the maximum width of the talar trochlea at its most posterior aspect, and the maximum length of the malleolar facet on the medial side of the talar body. Although some have

Figure 3.1. Measurements taken on articular surface of the distal tibia

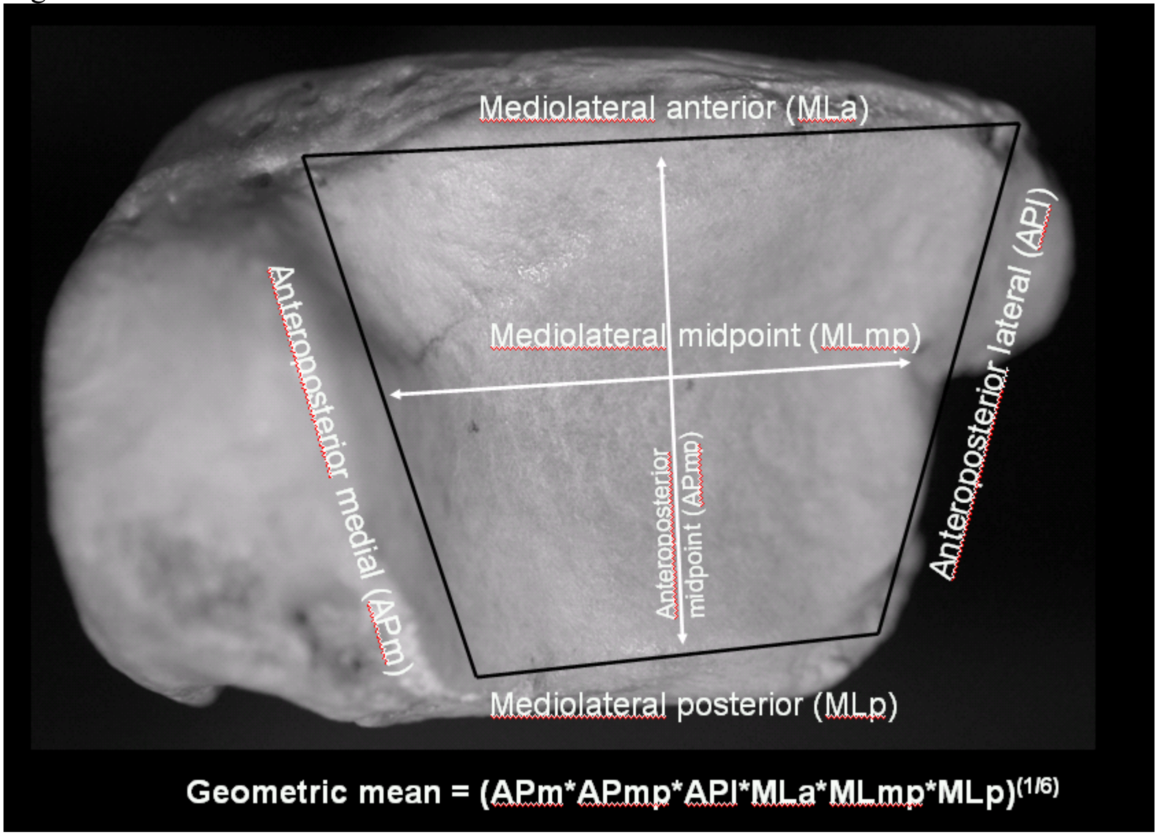


Figure 3.1. Six measurements were taken on the articular surface of the distal tibia and are illustrated here on a left gorilla distal tibia in inferior view. The geometric mean of these six measures was calculated used to size-standardize each of the measurements as explained further in the text.

simply divided the anterior width of the talus by the posterior width to assess the degree of talus wedging (Barnett and Napier, 1952), Brenner et al. (2003) recently suggested that another approach is more appropriate to account for the possible role of body size in talar scaling. The primate talus is modeled as a partial cone with the apex of the cone positioned medially, and both the lateral and medial aspects of that cone sharing a similar radius of curvature (Inman, 1976; Bremer, 1985; Latimer et al., 1987; Donatelli, 1990). The wedging of the talus, or the expansion of the anterior aspect of the bone relative to the posterior articular surface was quantified using the geometry of a trapezoidal shape extracted from the partial cone (Figure 3.2). Talar wedging was calculated as the angle formed between a line drawn along the lateral body of the talus from the posterolateral corner to the most anterolateral extent of the articular surface, and a line drawn from the same posterolateral corner of the talar trochlea perpendicular to the medial aspect of the bone (Figure 3.2). This angle was calculated as the arctangent of the difference between the anterior and posterior widths of the talar trochlea, over the medial length of the talar surface following the protocol of Brenner et al. (2003). This was converted into degrees by multiplying the result by (180/π). This approach treats the anterior and posterior widths of the talar trochlea as parallel measurements. This approach was compared to the simple division of anterior width by posterior width mentioned above and the pattern of the results obtained were the same. The following fossil tali were complete enough for this measure to be taken: CA 1305, LG 621, SO 389, SO 392, SO 478, SO 967, SO 968, SO 1402, RU 1743, RU 1744, RU 1745, RU 1748, RU 1896, RU 2036, RU 5940, RU 5945, BG 35250, MB 9422, and RUD 27. Damage exists on the anterior, posterior or medial aspects of SO 1705, WK 17171, WK 18120, and GSP 10785 was but the wedging angle could still be calculated with confidence. Damage was too severe on the posterior aspect of BMNH M26309, RU 3105, RU 5872, RU 1663 and MY 34 for an accurate wedging angle to be calculated.

TALOCRURAL MOBILITY

3.) The mobility of the talocrural joint was measured as a function of the depth of the distal tibial surface. Photographs were taken of all tibiae in lateral view with a ruler in the same plane as the measurement to be taken, and imported into the program Image J. The line tool was used to measure the distance between the anterior and most posterior

Figure 3.2. Measurements and calculations used in the study of the anthropoid talus

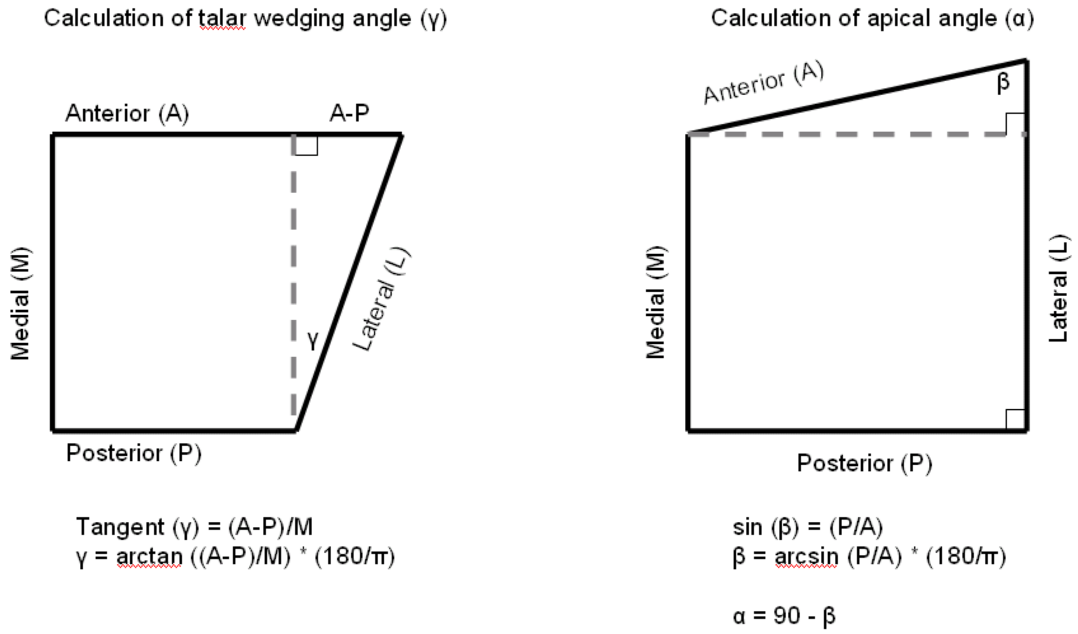


Figure 3.2. Measurements and calculations used to assess the degree of wedging and the apical angle of the anthropoid talus. On the left, the geometry of the talus is roughly trapezoidal in superior view, allowing the angle γ to be calculated as the arctangent of the difference of the anterior and posterior widths of the bone over the length of the medial facet. The talus can be modeled as a cone (right), with the apical angle calculated as described in the figure. These measurements are related to one another with an increased wedging of the talus resulting in, or from, a larger apical angle.

distally extending lips of bone. A perpendicular line was drawn from this line to the point of greatest depth of the tibial articular surface (Figure 3.3). Tibiae that are flatter in the anteroposterior direction are hypothesized to facilitate more dorsiflexion. A tibial surface with a greater depth (i.e. more concave) is hypothesized to result in the most anterior aspect of that surface hitting the talar neck before significant dorsiflexion can be achieved. The depth of the tibial surface was measured on the following fossil tibia: LG 583, BUMP 99, BUMP 764, NAP I’58, RU 1939, RU 2036, RU 3589, BG 35250, MB 11973, and all of the fossil *Theropithecus* tibiae listed in Table 3.3. Damage to the

Figure 3.3. Method for calculated depth of tibial surface and radius of curvature

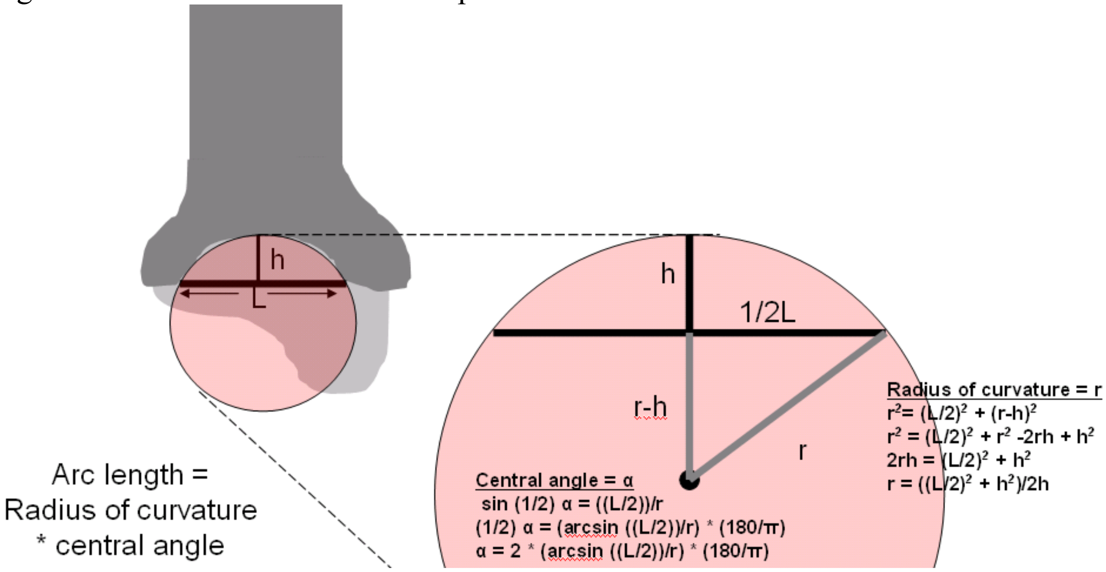


Figure 3.3. Anthropoid distal tibia illustrated in lateral view. The depth of the tibial articular surface was measured as shown in the diagram to the left and calculated as (h/L)*100. In addition, the arc length of the distal tibia was calculated as the radius of curvature of the tibial surface * the central angle. With the tibial facet treated as a circle (shown enlarged to the right), the length of a chord (L) and a perpendicular line between that chord and the rim of the circle (h) can be used to calculate the radius of curvature and the central angle. The same methods were employed on the medial and lateral aspects of the talus to calculate the radii of curvature of that bone.

anterior and/or posterior rims prevented accurate tibial depth measurements in KNM-MV 2.

4.) The mobility of the talocrural joint was also measured as a ratio of the amount of bone in the anteroposterior aspect of the distal tibial metaphysis versus the amount of bone in the mediolateral dimension. It is hypothesized that species with a more rectangularly shaped distal tibia will have a greater range of movement over the talus than those species with a more square shaped distal tibia. 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 width perpendicular to the mediolateral dimension. This measurement was taken in the following Miocene catarrhine tibiae: MV 2, LG 583, BUMP 99, BUMP 764, NAP I'58, RU 1939, RU 2036, RU 3589, BG 35250, MB 11973, and all of the fossil *Theropithecus* tibia listed in Table 3.3. The KNM-BG 35250 *Nacholapithecus* distal tibiae are so severely distorted that it was not possible to measure these elements with any accuracy.

Abduction

With the talus modeled as a partial cone, the apical angle should be proportional to the degree of abduction, with a high apical angle resulting in a greater degree of abduction than a low apical angle (Figure 3.2). This is because the distance traveled by the tibia on the lateral aspect of the talus is greater than the distance traveled on the medial side of the talus. The apical angle can be approximated using the geometry shown in Figure 3.2, following the protocol of Bremer (1985). Using the relationship of a right triangle, the arcsin of the posterior width of the talar trochlea over the anterior width of the talar trochlea gives the approximate angle (in radians) opposite the apical angle. This value is converted to degrees by multiplying the resultant by $(180/\pi)$, and the apical angle is calculated by subtracting this final angular value from 90˚. This approach regards the lateral and medial rims of the talar trochlea as being roughly parallel with one another. Although morphologically this is not the case, it is suggested that this assumption is a reasonable one when estimating the apical angle. The tali complete enough to take this measure of talar abduction were the same as those for which talar wedging could be assessed (listed above).

The measure on the talus described above assumes that the corresponding tibia has equal sides to the lateral and medial aspect. In cases where isolated tali are being studied, this must be assumed; however, the degree of foot abduction possible in the ankle can also be assessed as the ratio of distance traveled by the tibia over the talus on the lateral side of the joint to the distance traveled by the tibia over the talus on the medial side of the joint. The total distance traveled along a curved surface is approximately the radius of curvature * the central angle (Figure 3.3). The radius of curvature was calculated using the following equations relating the radius of curvature (r) to the length of a chord measured as the length of the tibial articular surface (L), the height of the chord measured as the depth of the tibial surface (h):

1.) $r^2 = (L/2)^2 + (r-h)^2$

2.) $r^2 = (L/2)^2 + r^2 -2rh + h^2$

3.) $2rh = (L/2)^2 + h^2$

4.) $r = ((L/2)^2 + h^2)/2h$

The central angle was calculated using the following equations relating the radius of curvature and the length of the chord:

1.) $\sin (1/2)\, \alpha = ((L/2))/R$

2.) $(1/2)\, \alpha = (\arcsin ((L/2))/R) * (180/\pi)$

3.) $\alpha = 2 * (\arcsin ((L/2))/R) * (180/\pi)$

The same equations were used to calculate the total distance traveled along the medial and lateral aspects of the talar surface. Tali were photographed in medial and lateral view with a Nikon D100 digital camera, and the images were imported into the program Image J. All of the photographs had a ruler positioned in the same plane as the malleolar surface of the talus. In Image J, a chord was drawn from the most anterior to the most posterior aspect of the articular surface equal in length to what was measured with digital calipers on the actual bone. A line was drawn perpendicularly from this chord to the most superior point on the talar dome and measured to the nearest tenth of a millimeter. With the chord length and the height, the radius of curvature and the central angle of the medial and lateral aspects of the talar joint surfaces were calculated using the equations above.

Data on the tibia and tali from the same individuals were aligned and the arc length on the lateral aspect of the tibia was subtracted from the arc length on the lateral aspect of the talus to get a raw measurement in mm of the total distance that the tibia could travel along the talus. The same was done for the medial aspect of the talocrural joint. Because this study is interested in abduction during dorsiflexion, only one-half of the total movement of the tibia on the talus was considered. The angle of abduction during dorsiflexion was calculated as the arctangent of the width of the talus at its midpoint divided by the difference between the distance traveled laterally and the distance traveled medially. This angle was then subtracted from 90° to obtain the angle that the foot would take relative to the tibial shank during dorsiflexion.

Applications of this value to the hominin fossil record necessitate the presence of associated tibia and tali, for which only the KNM-RU 2036 ankle is complete enough for this calculation to be made.

Inversion

When the ankle is loaded in inversion, stress shifts to the medial aspect of the joint and is borne in part by the medial malleolus of the distal tibia. 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 medial malleolus was complete enough on all tibiae listed in Table 3.3 for this measurement to be taken.

Additionally, it has been shown that there is a correlation between increasing body mass and decreasing radius of curvature of the talus in primates (Latimer et al., 1987), and thus an adaptation to efficiently distributing the load borne on the talus may include a flattening of the joint. In an isolated talus, the ratio of the radius of curvature on the medial side of the joint to the radius of curvature on the lateral side of the joint may provide evidence for whether the ankle was being loaded on the medial or lateral side. The radius of curvature values for the medial and lateral sides of the talus were calculated using the methods described in the "abduction" section above, and are reported as a ratio of one another. This ratio could be calculated on those same tali listed in the "abduction" section above.

Multivariate analysis on the distal tibia

A non-stepwise discriminant function analysis was performed on the size-adjusted measures of the distal tibia using SPSS 14.0. Included in this analysis were the 6 dimensions of the distal tibia and also three dimensions of the medial malleolus: the maximum anteroposterior length, maximum mediolateral width, and maximum superoinferior height. The geometric mean (GM) of these nine measurements was calculated and each raw value divided by the GM, which were then all entered into the discriminant function. All of the fossils were entered as separate groups. This provided a test of the hypothesis that the measures predicted to be biomechanically relevant were in fact the ones that best discriminate the distal tibiae of vertically climbing apes and atelines, cercopithecoids, and *Cebus*.

Allometry

The influence that an increase in body size may have on some of these parameters was also tested. Rafferty et al. (1995) has found that the mediolateral width of the midpoint of the tibial articular surface correlates strongly with body mass in catarrhine primates ($r = .982$). Therefore, mediolateral width of the trochlear surface of the distal tibia can be used as a proxy for body mass in testing how features scale with increase in size. Before this is done, however, it is important to establish that the mediolateral width of the tibial surface scales geometrically with body mass. Isometric scaling between the mediolateral width of the tibial surface and body mass would necessitate a relationship in which the mediolateral width of the distal tibia scales with $(\text{body mass})^{1/3}$ and thus a predicted isometric scaling equation between body mass and mediolateral width of the tibial surface would be:

$\mathrm{Log}_{10}(\text{mediolaterally width}) = \log_{10}(\text{body mass}) * 0.333 - \text{constant}$

The equation presented in Rafferty et al. (1995) is:

$\mathrm{Log_eBW} = \mathrm{log_eTIBWI} * 2.721 - 4.376$

"BW" is body weight and "TIBWI" is the mediolateral width of the tibial surface. $\mathrm{Log_eBW}$ is converted to $\mathrm{log_{10}BM}$ using the following relationship:

$\mathrm{Log_eBW} = \mathrm{log_{10}BW} * \mathrm{Log_e10}$

$\mathrm{Log_e10} = 2.303$

Therefore, $\mathrm{Log_eBW} = \mathrm{log_eTIBWI} * 2.721 - 4.376$ is the same as:

$\mathrm{Log_{10}BW} *2.303 = \mathrm{log_{10}TIBWI} * 2.303 * 2.721 - 4.376$, which simplifies to:

$\mathrm{log_{10}TIBWI} = \mathrm{Log_{10}BW} * .3675 - .698$

Though slightly larger than the .333 predicted for isometric scaling, the calculated slope of .3675 using Rafferty et al.'s (1995) equation is similar enough to isometry, that it can be reasonably argued that the mediolateral width of the tibial surface scales isometrically with the cube root of body mass. Given that relationship, allometric scaling of skeletal correlates of vertical climbing in the distal tibia was tested. Tests of allometry were limited to the anterior width of the distal tibia, and the mediolateral width of the medial malleolus because *post hoc* these measurements best discriminate vertical climbing primates and the potential effect of size on these results must be considered.

These measurements were $\log_{10}$ transformed for all primate tibia examined. The regression equation between each of these variables and the $\log_{10}$ transformed mediolateral width of the distal tibia at its midpoint was calculated using reduced major axis regression using RMA v.1.17 (Bohonak, 2004) which was chosen over least squares regression because of the error associated in measuring the dependent variable (Sokal and Rohlf, 2001). The 95% confidence interval was calculated for the slope of the regression line for all species and some larger taxonomic categories (i.e. ateline, apes, cercopithecoids) to test whether the thickness of the medial malleolus or width of the anterior aspect of the tibial articular surface exhibits allometric scaling.

The potential role of size in affecting the morphology of the distal tibia in fossil hominoids was assessed by testing the hypothesis that the large *Proconsul major* distal tibia (NAP I'58) is a size-scaled version of the *Proconsul nyanzae* distal tibia (KNM-RU 1939). The eleven measurements taken on the distal tibiae (six measurements on the articular surface, three measurements of the medial malleolus, and two measurements on the metaphysis) were size-standardized by taking the geometric mean (GM) of these measures, and dividing each raw measurement by the value of the GM. Euclidean distances between the fossils were then calculated as the square root of the squared sum of differences between the eleven size standardized values.

This value of morphological distance between the NAP I'58 tibia and the KNM-RU 1939 tibia was then compared to three models models of a size-scaled version of the distal tibia. The first was an intraspecific model in which size scaled versions of a similar morphology were males and females of a sexually dimorphic species. Three species were used in this model: *Nasalis larvatus* (males 20.4 kg; females 9.8 kg); *Pan troglodytes* (males ~50 kg, females ~40 kg); *Gorilla gorilla gorilla* (males ~170 kg; females ~72 kg) (Smith and Jungers, 1997). Euclidean distances between males and females of the same species were determined by an exact resampling method. The Euclidean distance between the size standardized values of the distal tibia for every pairing of male and female within *Nasalis*, *Pan troglodytes*, and *Gorilla gorilla gorilla* was calculated. A histogram showing the distribution of values for all possible pairings within a species was constructed and the morphological distance between NAP I'58 and KNM-RU 1939 within that distribution was determined. The second model calculated a distribution of morphological distances between species of a difference size that engaged in a similar form of locomotion. *Gorilla gorilla gorilla* and *Pan troglodytes* were selected to represent this model and the distribution of morphological variation between the distal tibiae of these species was calculated using an exact resampling approach. Every chimpanzee distal tibia was matched with every gorilla tibia and the Euclidean distance between each pair was calculated. The morphological distance between NAP I'58 and KNM-RU 1939 was assessed within the distribution of morphological variation that exists between chimpanzee and gorilla tibia. Finally, a third model tested the range of morphological variation that exists between taxa of differing body size *and* differing locomotor modes. *Pan troglodytes* and *Papio* spp. were selected and the distribution of morphological variation in the distal tibia was calculated using the exact resampling approach mentioned above.

Results

Dorsiflexion

DISTAL TIBIA

1.) Vertically climbing apes and the ateline primates have a relatively wide anterior aspect of the tibial articular surface, whereas the cercopithecoids and *Cebus* have a narrowed anterior tibial articular surface (Figure 3.4). Terrestrial cercopithecoids and arboreal cercopithecoids have a statistically identical width of the anterior aspect of the distal tibia ($p=0.99$) as do the genera *Hylobates* and *Symphalangus* ($p=0.48$). This measurement is also the same between *Pan* and *Pongo* ($p=0.32$) and each of these apes and the atelines ($p=0.53$ for atelines and *Pongo* and $p=0.99$ for *Pan* and the atelines). The relative size of the anterior aspect of the distal tibia has the following relationship in anthropoids: *Gorilla* > (*Pan* = *Pongo* = atelines) > *Hylobates* > cercopithecoids > *Cebus*. This measure distinguishes apes and the atelines from the cercopithecoids and *Cebus* and is thus a potentially very useful indicator of frequent vertical climbing involving extreme dorsiflexion (Figure 3.5). In addition, body size does not appear to be impacting this measure as the anterior width of the tibial surface scales isometrically within all species studied. There is a slight allometric effect within the great apes ($m= 1.112$; 95% C.I.: 1.044-1.181), though the hominoid clade displayed isometric scaling ($m=1.024$; 95% C.I. 0.999-1.049). The role of body size in vertical climbing adaptations is addressed more in the discussion.

Figure 3.4. Size-standardized shape of articular surface of the anthropoid distal tibia.

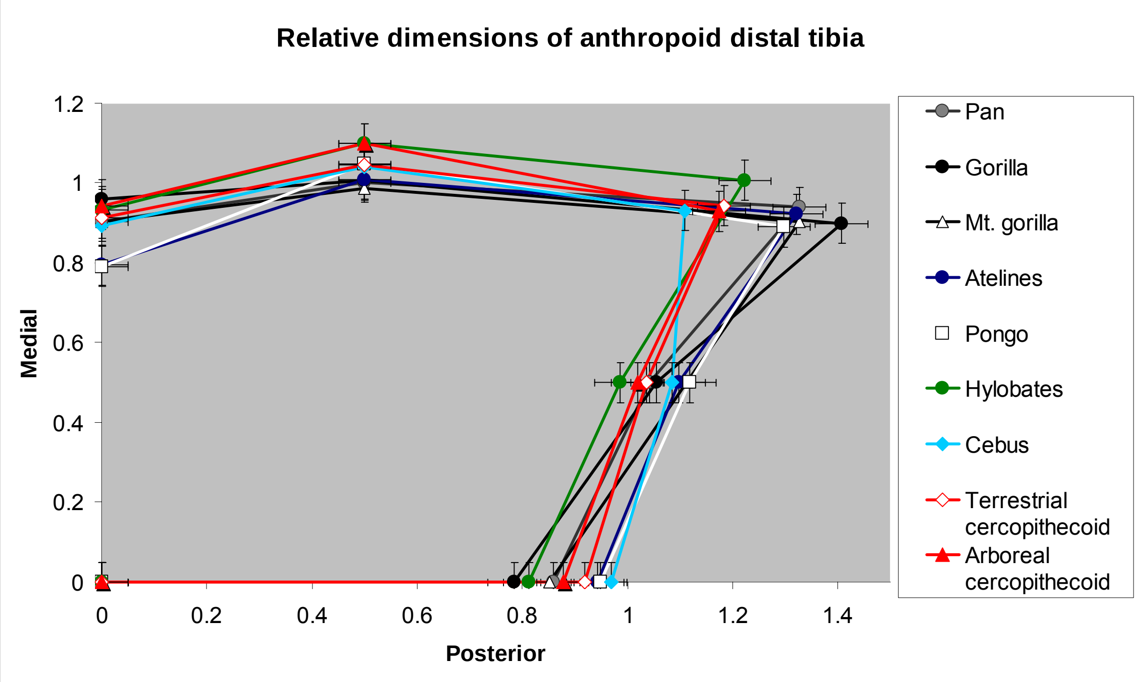


Figure 3.4. Size standardized representation of the shape of the distal tibia in the catarrhine primates: chimpanzees (dark gray circle), lowland gorillas (black circle), mountain gorillas (white triangle), orangutans (white square), hylobatids (green circle), arboreal cercopithecoids (red triangle), terrestrial cercopithecoids (white diamond with red edge), atelines (blue circle), *Cebus* (light blue diamond). Plotted are the mean values and the bars represent one standard deviation. Anterior is towards the top, posterior the bottom, lateral towards the right, medial the left. Apes and atelines differ from the cercopithecoids and *Cebus* primarily in having a wider anterior surface to the distal tibia.

All of the Miocene tibiae fall within or below the range of values known for modern cercopithecoids and *Cebus*. However, the NAP I'58 distal tibia from *P. major* has the widest anterior aspect to the tibial surface of any Miocene specimen, most similar in morphology to modern hylobatids.

Figure 3.5. Size-standardized anterior width of tibial articular surface.

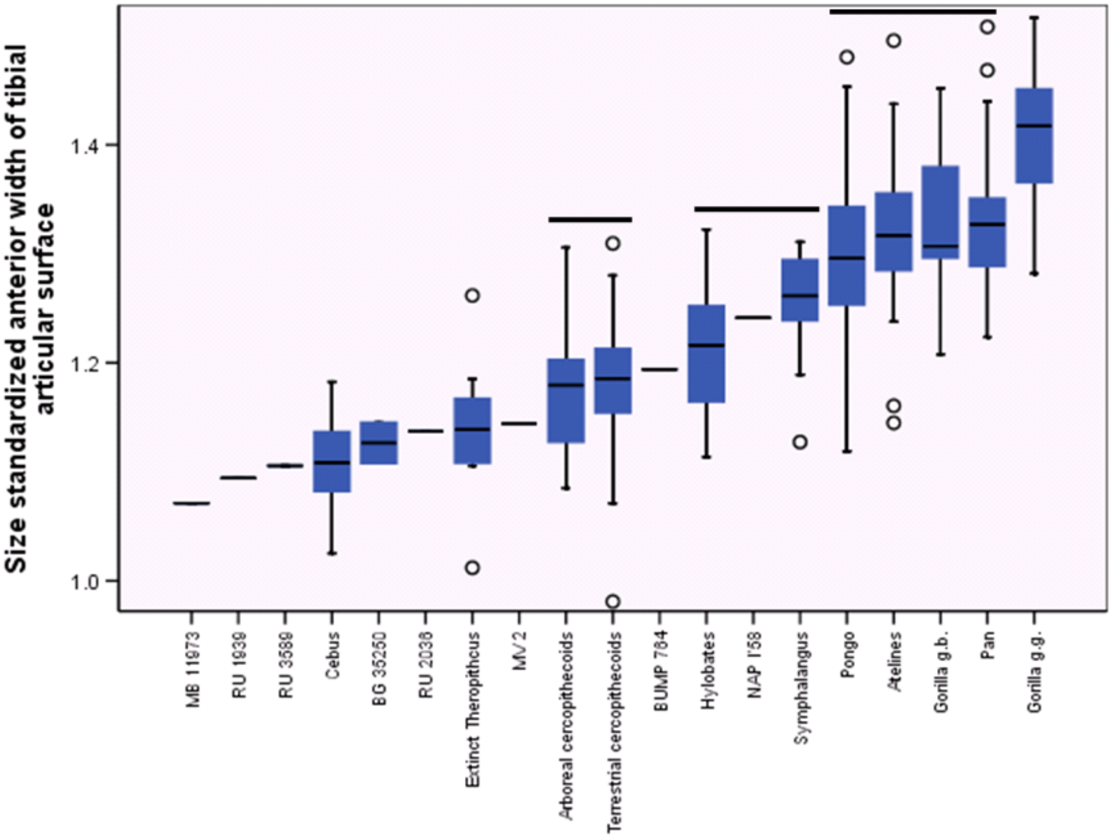


Figure 3.5. Boxplots of the size-standardized anterior width of the articular surface of the distal tibia show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Vertically climbing apes and ateline primates cluster to the right of the graph and are statistically distinct from cercopithecoids and *Cebus*. The *P. major* NAP I'58 distal tibia has an elongated anterior aspect, much like modern hylobatids.

TALUS

2.) The wedged morphology of the talus was hypothesized to be a skeletal indicator of vertical climbing with a more wedged talus adaptive for the loads incurred during extreme dorsiflexion. Although *Gorilla*, *Pan*, and the atelines had the most wedged tali, this measure did not discriminate climbing *Pongo* and *Hylobates* from terrestrial cercopithecoids (Figure 3.6). *Gorilla* has equal talar wedging as atelines (p= 0.08) and the atelines are statistically equivalent to *Pan* (p= 0.81). *Hylobates* and

Symphalangus are statistically identical to one another (p= 0.84) and to *Pongo* (p= 0.99), and terrestrial cercopithecoids (p = 1.0). The arboreal cercopithecoids and *Cebus* have the least wedged tali and are statistically equivalent (p = 0.99). The known fossil tali for which this measure was possible span the range of talar wedging measured in extant primates. All of the tali fall within the range of terrestrial and arboreal cercopithecoids.

Figure 3.6. Degree of wedging in the anthropoid talus.

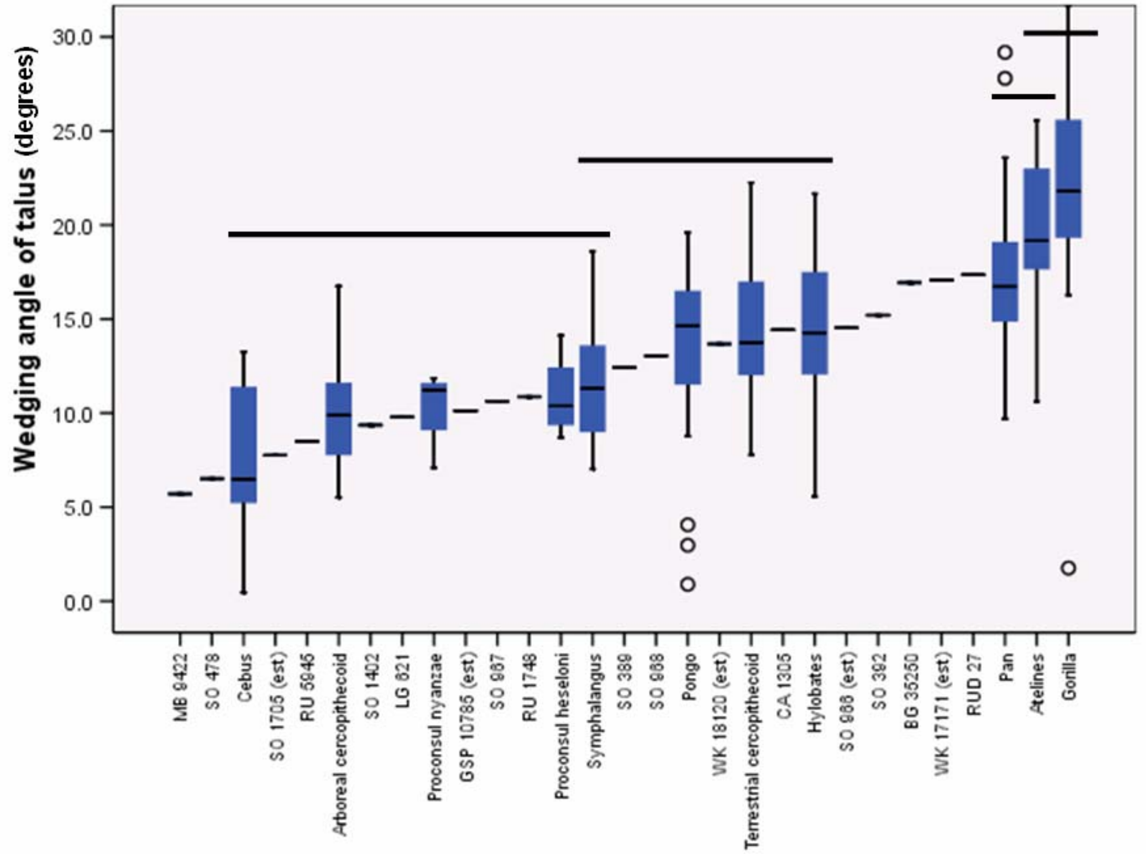


Figure 3.6. Boxplots of the wedging angle on the superior surface of the talus in primates show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Because of the number of tali, well represented Miocene taxa were grouped together: *P. nyanzae* (RU 1743, RU 1896, RU 5940) and *P. heseloni* (RU 2036 left and right, RU 1744, RU 1745). *Pongo*, hylobatids and terrestrial cercopithecoids have statistically equivalent wedging angles, limiting the utility of this measure as a vertical climbing correlate. *Nacholapithecus* (KNM-BG 35250), *Simiolus* (KNM-WK 17171), and *Anapithecus* (RUD 27) have the most wedged tali, like modern African apes and atelines.

The most wedged tali closer to the *Pan* range and just outside the interquartile range of the terrestrial cercopithecoids are the *Anapithecus* talus RUD 27, the *Simiolus* talus KNM-WK 17171, and the *Nacholapithecus* talus KNM-BG 35250.

TALOCRURAL MOBILITY

3.) The depth of the tibial articular surface was not a good skeletal correlate of vertical climbing in primates. *Pongo* and the atelines had the most shallow tibial surface and were statistically identical to one another (p= 1.0). However, the depth of the tibial surface was not distinguishable between the African apes and terrestrial cercopithecoids (p=0.99), or between *Hylobates* and the arboreal cercopithecoids (p=0.4). The relationship between living taxa is thus: (*Pongo* = atelines) < (*Symphalangus* = *Pan* = *Gorilla* = terrestrial cercopithecoid = *Hylobates* = *Cebus*) < arboreal cercopithecoids, with the latter group also statistically identical to *Hylobates* and *Cebus*. Interestingly, many *Proconsul* specimens, KNM-RU 3589, NAP I'58 and KNM-RU 2036 and the *Nacholapithecus* tibiae have relatively shallow, *Pongo* and ateline-like tibial surfaces (Figure 3.7). Caution should be used in interpreting the KNM-BG 35250 *Nacholapithecus* tibiae as both the left and right were distorted in the fossilization process. The small ape tibia BUMP 764 and KNM-LG 586, potentially from a *Limnopithecus* or *Micropithecus* also have a shallow tibial depth. The *P. nyanzae* tibia KNM-RU 1939, *Victoriapithecus* KNM-MB 11973, and unassigned small tibia from Napak BUMP 99 have deeper tibial facets, more like modern cercopithecoids, *Hylobates*, and African apes.

Figure 3.7. Depth of inferior surface of anthropoid distal tibiae.

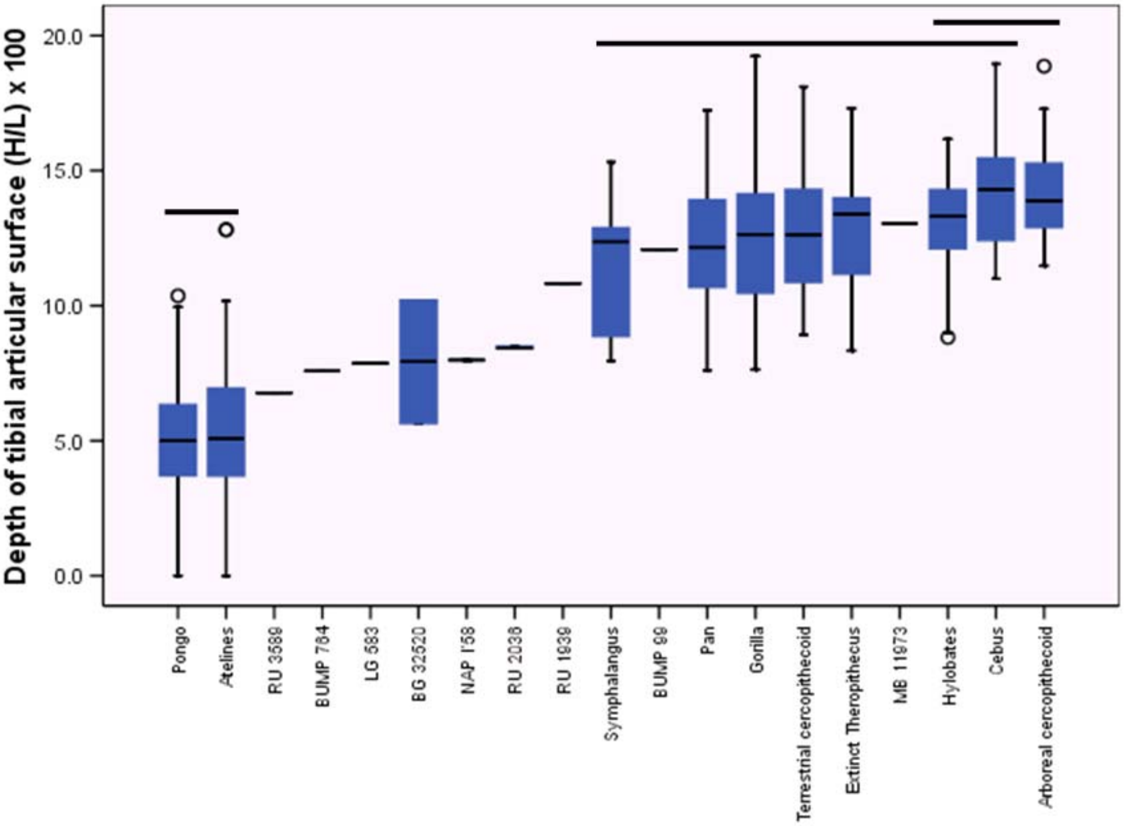


Figure 3.7. Boxplots of the depth of the articular surface of the distal tibia show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. This measurement is calculated as a ratio of the depth of the inferior surface (H) and the anteroposterior length of the distal tibial surface (L). This measurement does not distinguish vertically climbing apes and atelines from more generalized quadrupedal primates. Interestingly though, many Miocene tibiae have relatively shallow tibial depths away from the cercopithecoid and African ape morphology, and more similar to that found in modern atelines and *Pongo*.

4.) The shape of the metaphysis of the distal tibia tends to be mediolaterally wider in vertically climbing primates (Figure 3.8). Arboreal cercopithecoids and terrestrial cercopithecoids have a statistically similar shape to the distal tibia (p=0.84). Mountain gorillas have a slightly more square-shaped distal tibia than lowland gorillas. The shape of the tibia is most rectangular in the genus *Pongo* and most square shaped in terrestrial

Figure 3.8. Shape of metaphysis in anthropoid distal tibia.

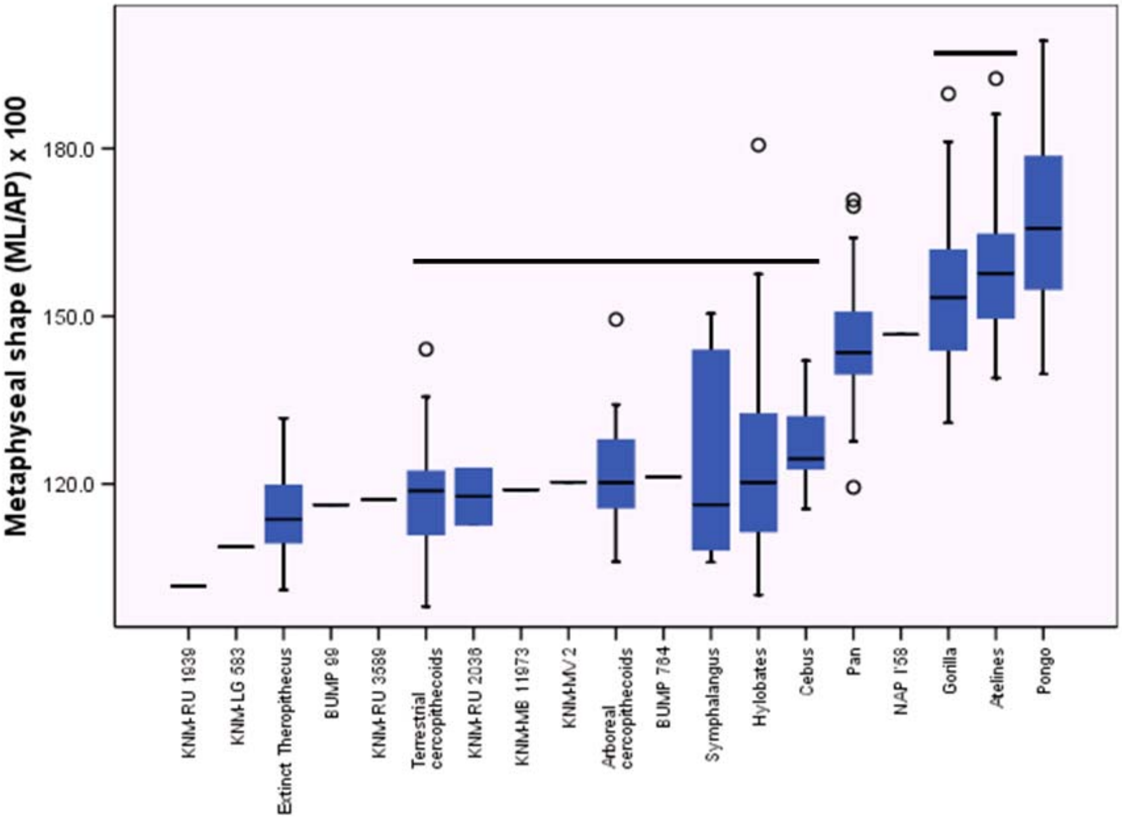


Figure 3.8. Boxplots of the shape of the metaphysis of the primate distal tibia show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Cercopithecoids, *Cebus* and the hylobatids have a statistically identical morphology of the metaphysis of the distal tibia (indicated by black bar). All of the Miocene tibiae have a similar morphology except for the *P. major* NAP I'58 specimen which falls between *Pan* and *Gorilla* for this measure.

cercopithecoids with the following relationship: *Pongo* > (ateline = *Gorilla gorilla gorilla*) > (*Pan* = *Gorilla gorilla beringei*) > (*Hylobates* = *Cebus* = arboreal cercopithecoids = terrestrial cercopithecoids). Because *Hylobates* cannot be distinguished from cercopithecoids, the utility of this measure as a skeletal correlate of vertical climbing is uncertain. However, the clear separation of the great apes and atelines from the cercopithecoids does suggest that a mediolaterally wide metaphysis helps promote dorsiflexion. All of the Miocene tibiae have a cercopithecoid and hylobatid-like morphology except for the *P. major* tibia NAP I'58, which has a metaphyseal geometry most like modern African apes *Pan* and *Gorilla*.

Abduction

Skeletal correlates of foot abduction at the ankle did not distinguish vertical climbing apes and atelines from cercopithecoids and *Cebus* in this study. Although *Gorilla* has the greatest capacity for abduction at the talocrural joint, this measure in isolated tali is statistically equivalent between *Pan*, *Hylobates*, atelines, *Gorilla gorilla beringei*, and terrestrial cercopithecoids (Figure 3.9). *Pongo* and the terrestrial cercopithecoids have indistinguishable values (p = 0.98) as do *Pongo* and arboreal cercopithecoids (p = 0.46). Fossil tali span the range of possible primate values with KNM-SO 478 and KNM-MB 9422 having values only in the range of modern *Cebus* to RUD 27 and KNM-WK 17171 having values within the range of modern apes and atelines, outside of the interquartile ranges of the cercopithecoids.

Measuring the tibia and tali together demonstrates that the angle of abduction at the talocrural joint may not be strictly a vertical climbing adaptation. *Pongo* and *Cebus* have similar measures of foot abduction at the ankle (p= 0.99). The atelines, hylobatids, *Pan* and arboreal cercopithecoids have indistinguishable average values for abduction at the ankle (Figure 3.10). Terrestrial cercopithecoids are statistically identical to *Pan* (p = 0.07), arboreal cercopithecoids (p = 0.14), and *Gorilla* (p = 0.88). The only associated ankle in the Miocene complete enough for this measure to be taken is from the *Proconsul heseloni* KNM-RU 2036 skeleton. The range of abduction measured at the ankle falls directly between the range occupied by *Pan* and arboreal cercopithecoids on one side,

Figure 3.9. Apical angle of the anthropoid talus.

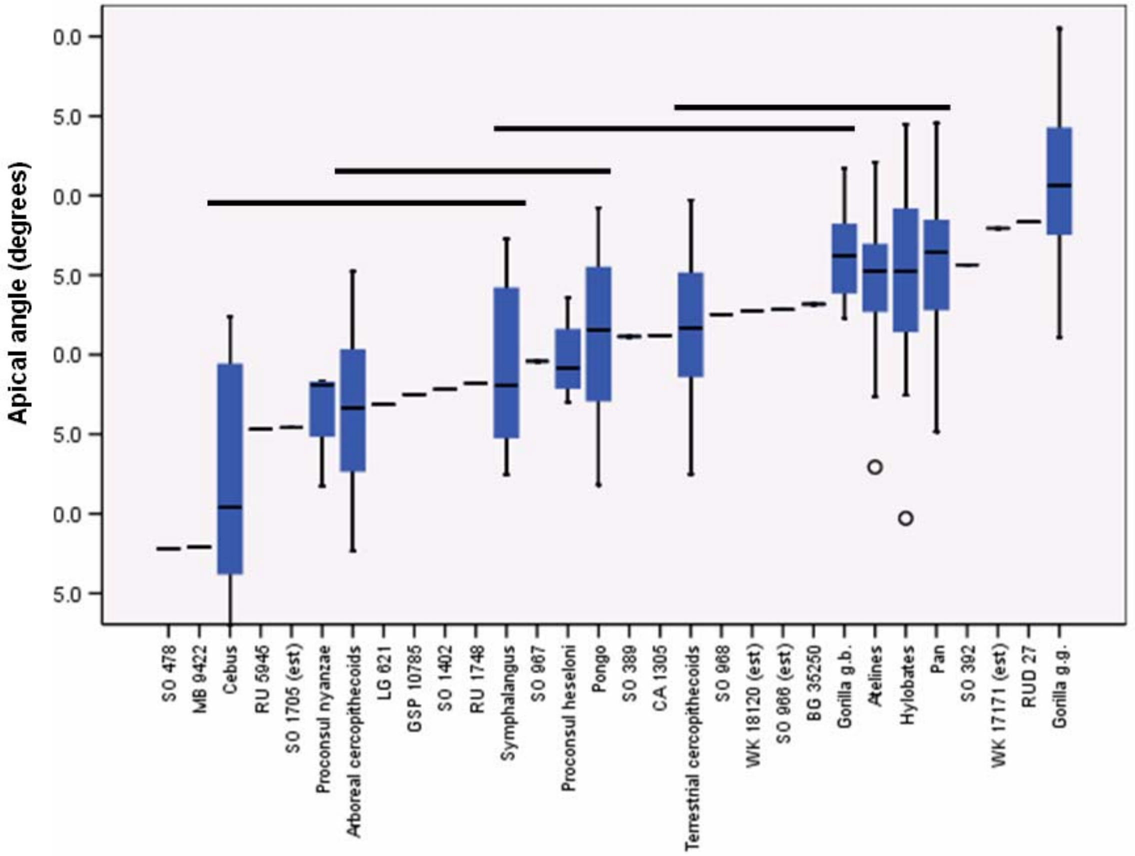


Figure 3.9. Boxplots of the apical angle of isolated tali show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. This measure did not clearly discriminate locomotor modes, suggesting that foot abduction is an important motion regardless of climbing frequency or abilities among primates. All of the apes were statistically equivalent to terrestrial cercopithecoids for this measure except for *Gorilla*. Because of the number of tali, well represented Miocene taxa were grouped together: *P. nyanzae* (RU 1743, RU 1896, RU 5940) and *P. heseloni* (RU 2036 left and right, RU 1744, RU 1745).

and terrestrial cercopithecoids and *Gorilla* on the other. Little can be said about locomotion using this measure.

Figure 3.10. Angle of abduction in anthropoid ankle.

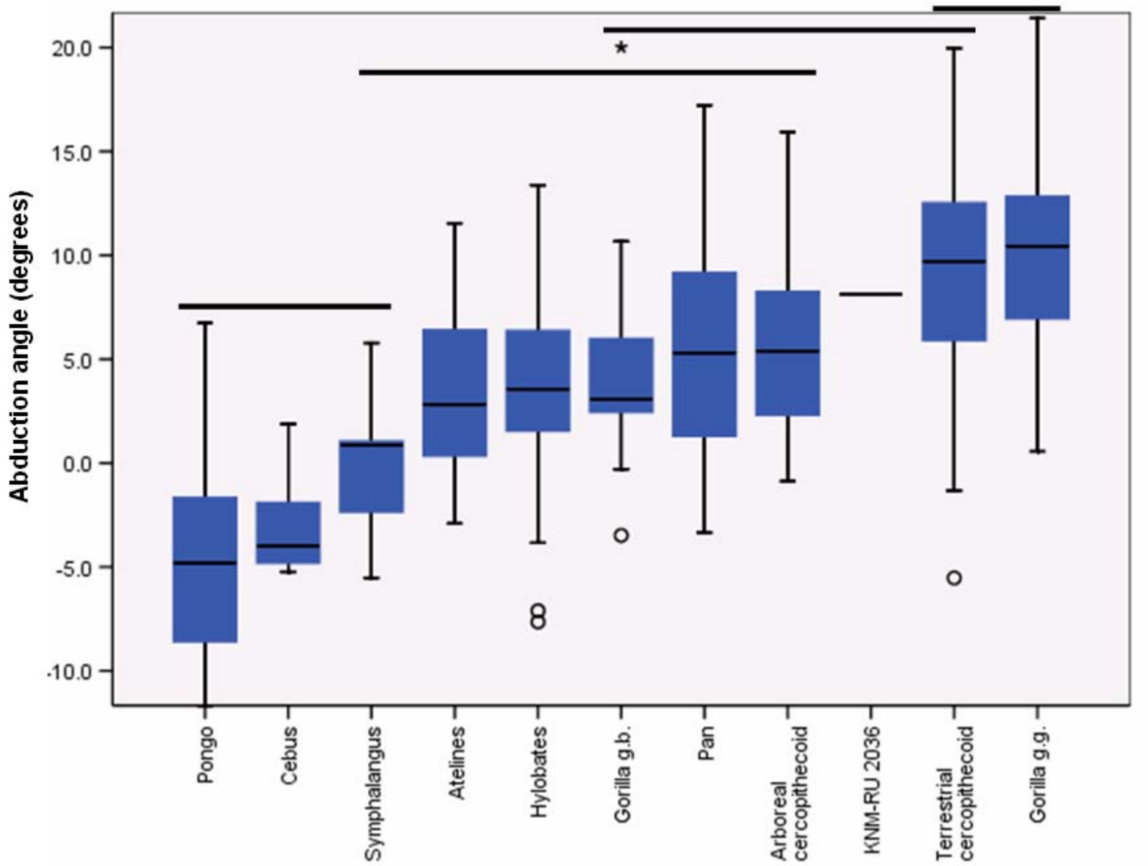


Figure 3.10. Like the apical angle on isolated tali, the total abduction angle calculated from associated tibiae and tali, also did not identify different locomotor modes among the primate ankles studied. Boxplots of the abduction angle of isolated tali show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Note that the African apes were statistically equivalent to the terrestrial cercopithecoids for this measure. The only associated Miocene ankle measured was the *P. heseloni* KNM-RU 2036 tibia and talus, which fell within the range occupied by the arboreal cercopithecoids and *Pan* on one side and the terrestrial cercopithecoids and *Gorilla* on the other.

Inversion

The medial malleolus is significantly thicker in apes and atelines than in cercopithecoids or the platyrrhine genus *Cebus*. The ateline genera *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix* were similar in this measure and collectively atelines had an equivalent thickness to the medial malleolus as the genus *Pongo* (p=0.99) and *Symphalangus* (p=0.82). Despite the different locomotor modes practiced by extant cercopithecoids, the more terrestrial genera (*Papio, Mandrillus*, *Theropithecus*, *Macaca nemestrina*) were equivalent to the more arboreal (*Nasalis*, *Macaca fascicularis*) in having a relatively thin medial malleolus (p=0.99). The relative thickness of the medial malleolus across anthropoids is thus: (ateline = *Pongo*) > *Pan* > *Gorilla* > *Hylobates* > (*Cebus* = cercopithecoid) (Figure 3.11).

The thickness of the medial malleolus scales isometrically within most genera, though there is positive allometry within the hylobatids (m=1.404; 95% C.I. 1.051-1.758). There is also positive allometry for the thickness of the medial malleolus within ceropithecoids (m=1.164; 95% C.I. 1.077-1.251), and weak positive allometry for the thickness of the medial malleolus within hominoids (m=1.104; 95% C.I. 1.006-1.203).

Fossil tibiae from the Miocene tended to have thicker medial malleoli than modern cercopithecoids or *Cebus*, but were generally closer to the cercopithecoid range than the ape and ateline range. Two tibiae from Napak, NAP I'58 and BUMP 764, had medial malleoli that were within the interquartile range of *Hylobates* and outside of this same range in cercopithecoids. Likewise, the *Nacholapithecus* tibiae from the KNM-BG 35250 skeleton had thick medial malleoli, though distortion to this specimen limits the confidence of this measure.

Medial flattening of the talar body is suggestive of an increase load on the talocrural joint during positions of foot inversion. The difference between the radius of curvature on the lateral aspect of the talus and the medial side of the talus distinguished the African apes from the other apes, cercopithecoids, atelines, and *Cebus*. This measure is statistically indistinguishable for all of the extant taxa, except for *Pan* and *Gorilla*

Figure 3.11. Thickness of the anthropoid medial malleolus.

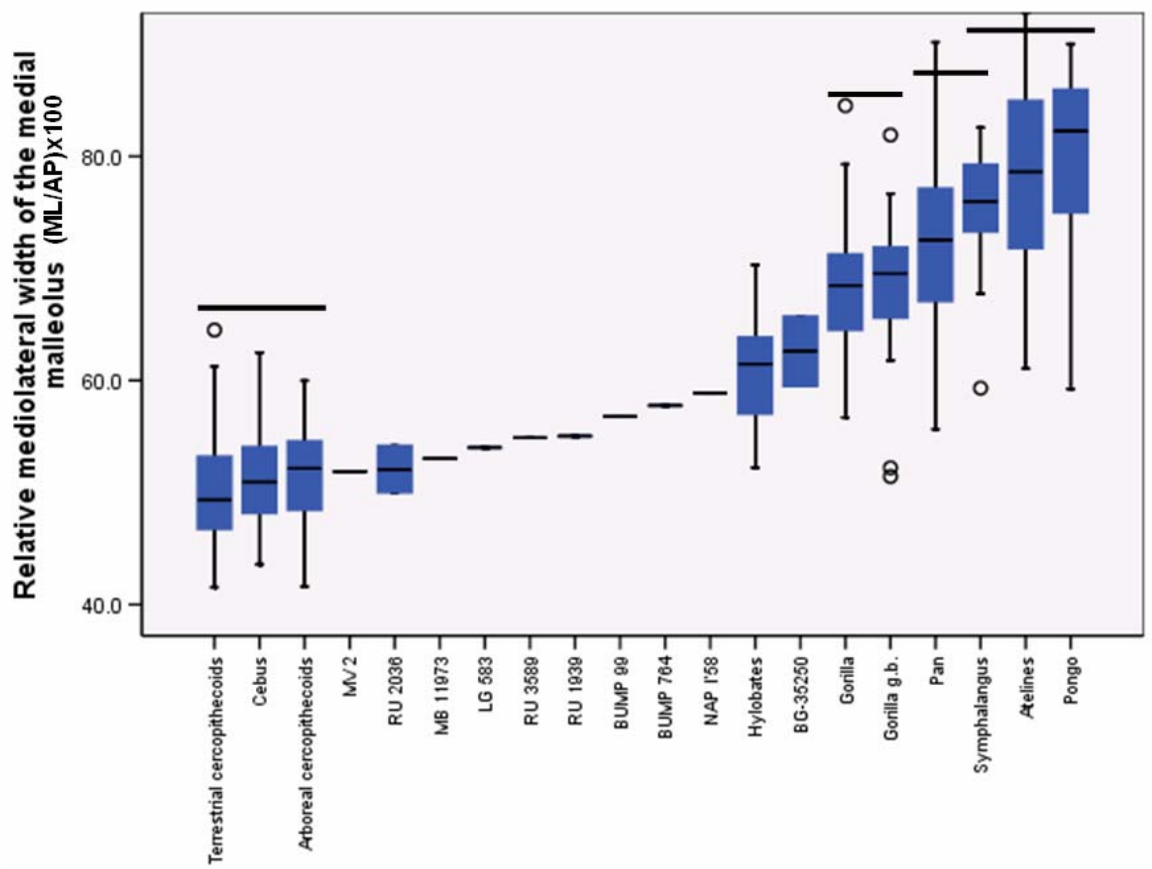


Figure 3.11. Boxplots of the relative width of the medial malleolus show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Vertically climbing hylobatids, African apes, *Pongo*, and the atelines have a significantly thicker medial malleolus than the cercopithecoids or *Cebus*. The Miocene tibiae studied almost all fall directly between the ape/ateline morphology and the cercopithecoid morphology. The large hominoids *P. major* NAP I'58, and *Nacholapithecus* KNM-BG 35250 have the thickest medial malleoli.

(Figure 3.12). Most of the Miocene tali share a similar morphology; however, five tali have medially flattened trochlear surfaces and are thus more African ape like. These are three fossils often assigned to *Rangwapithecus*: KNM-SO 1402, KNM-SO 968, and BMNH M26309. In addition, the *Simiolus* tali KNM-WK 17171, and unassigned talus KNM-RU 5945 have a medially flat surface.

Figure 3.12. Radius of curvature of the anthropoid talus.

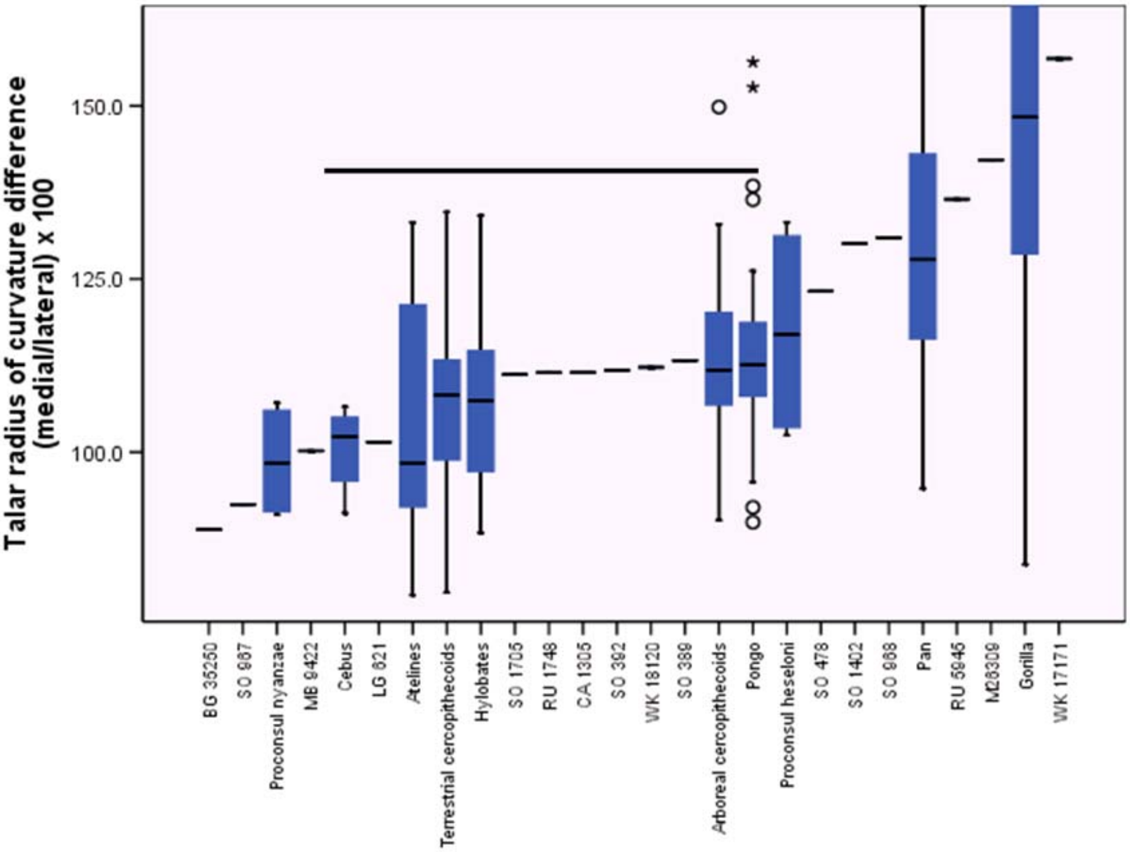


Figure 3.12. The African apes have a medially flattened talus relative to other apes and anthropoids. Boxplots of the radius of curvature on the medial side of the talus relative to the lateral side show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Miocene tali with a flattened medial side include the *Rangwapithecus* specimens SO 1402, SO 968, and M26309, and the *Simiolus* talus WK 17171. Because of the number of tali, well represented Miocene taxa were grouped together: *P. nyanzae* (RU 1743, RU 1896, RU 3105, RU 5940) and *P. heseloni* (RU 2036 left and right, RU 1744, RU 1745).

Multivariate analysis of distal tibiae

The distal tibiae of vertically climbing great apes and atelines can be separated from the cercopithecoids and *Cebus* primarily along Function 1 of the discriminant function analysis. Along this axis, the hylobatids fall in the morphospace between the apes and atelines and the cercopithecoids. The first function is being driven primarily by the mediolateral width of the anterior surface of the distal tibia (+0.637), and the mediolateral width of the medial malleolus (+0.601). Terrestrial and arboreal cercopithecoids cannot be easily distinguished in this discriminant function analysis. Miocene tibiae generally fall within the distribution of the cercopithecoids and hylobatids, though the *P. major* tibia NAP I'58 has a morphology between the hylobatids and the genus *Pan*.

Figure 3.13. Discriminant function analysis of anthropoid distal tibia.

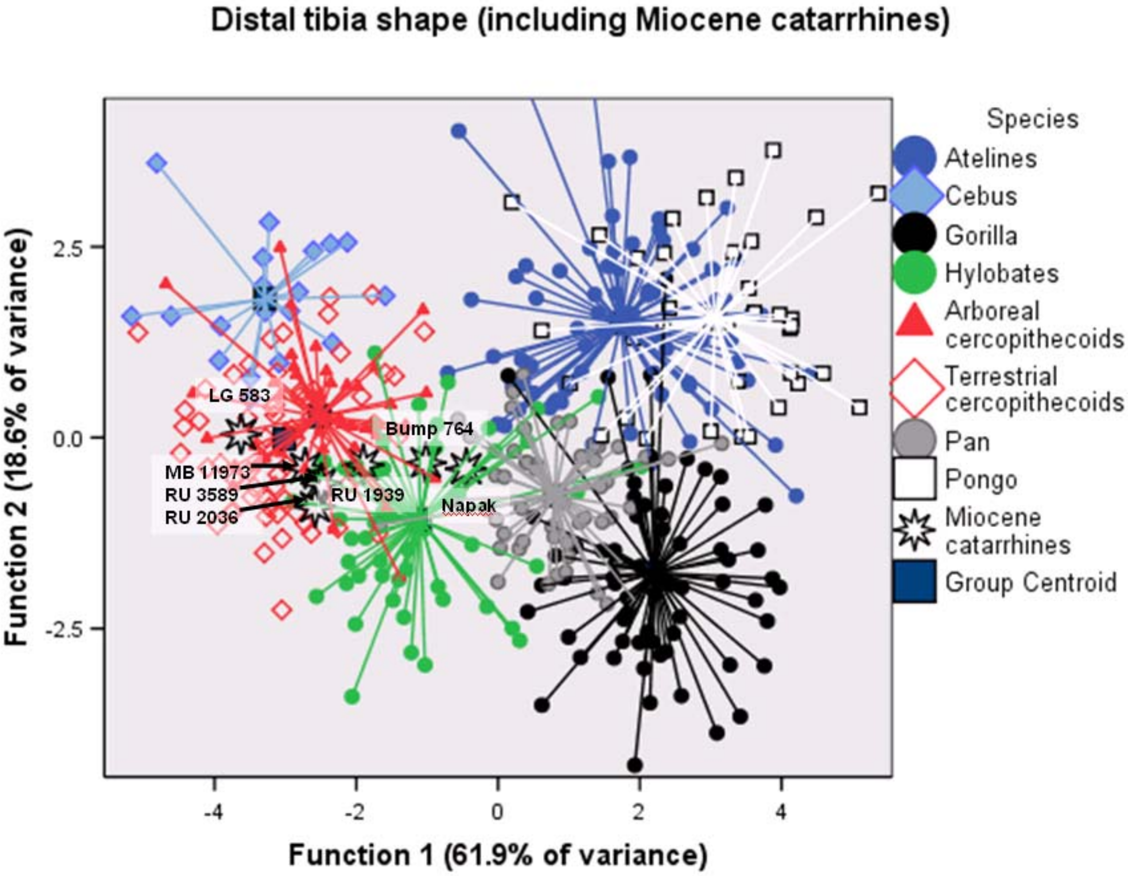


Figure 3.13. Discriminant function analysis on size-standardized measures of the articular surface of the distal tibia. Vertical climbers (atelines, hylobatids, African apes and *Pongo*) are distinguished from the cercopithecoids and *Cebus* along Function 1, which explains 61.9% of the variance. This function is driven primarily by the mediolateral length of the anterior aspect of the tibial surface (+.637) and the thickness of the medial malleolus (+.601). The *Proconsul major* tibia NAP I'58 falls between *Pan* and the hylobatids, whereas the other *Proconsul* tibia fall near the cercopithecoid mean.

Allometry

The hypothesis that the *Proconsul major* distal tibia (NAP I'58) is a size-scaled version of the *Proconsul nyanzae* distal tibia (KNM-RU 1939) was also tested. The Euclidean distance between the morphology of KNM-RU 1939 and NAP I'58 is 0.464. The 95% confidence interval of the mean for the Euclidean distance between male and female pairs of the same species is: *Nasalis* (0.277-0.294), *Gorilla* (0.304-0.322), *Pan* (0.310-0.329). The 95% CI for the mean Euclidean distance between *Gorilla* and *Pan* is 0.372-0.378, whereas the 95% CI for the mean difference between *Pan* and *Papio* is 0.442-0.450.

In 342 possible combinations resampled from *Nasalis* males and females, 7 pairs (2.1%) had a morphology more distinct than NAP I'58 and KNM-RU 1939 (Figure 3.14). In 342 possible combinations resampled from *Pan troglodytes* males and females, 29 (8.5%) had a morphology more distinct than NAP I'58 and KNM-RU 1939. In 418 possible combinations resampled from *Gorilla gorilla gorilla* males and females, 33 (7.9%) had a morphology more distinct from NAP I'58 and KNM-RU 1939. Therefore, although it is statistically possible to sample from a sexually dimorphic species (*Nasalis*, *Gorilla*, *Pan*) a large distal tibia and a small distal tibia that are morphologically as distinct from one another as NAP I'58 is from KNM-RU 1939, it is unlikely. It is noteworthy that the tails of these distributions all skew to the right, suggesting that the pairs that exhibit the greatest differences are being caused by a few morphologically unusual tibiae. The hypothesis that NAP I'58 is a scaled up version of KNM-RU 1939 in the same way that *Gorilla* is a scaled up version of *Pan*, was better supported. In 2,107 possible combinations resampled from *Gorilla gorilla gorilla* and *Pan troglodytes*, 360

Figure 3.14. Shape differences of the distal tibia within and between sexually dimorphic anthropoids.

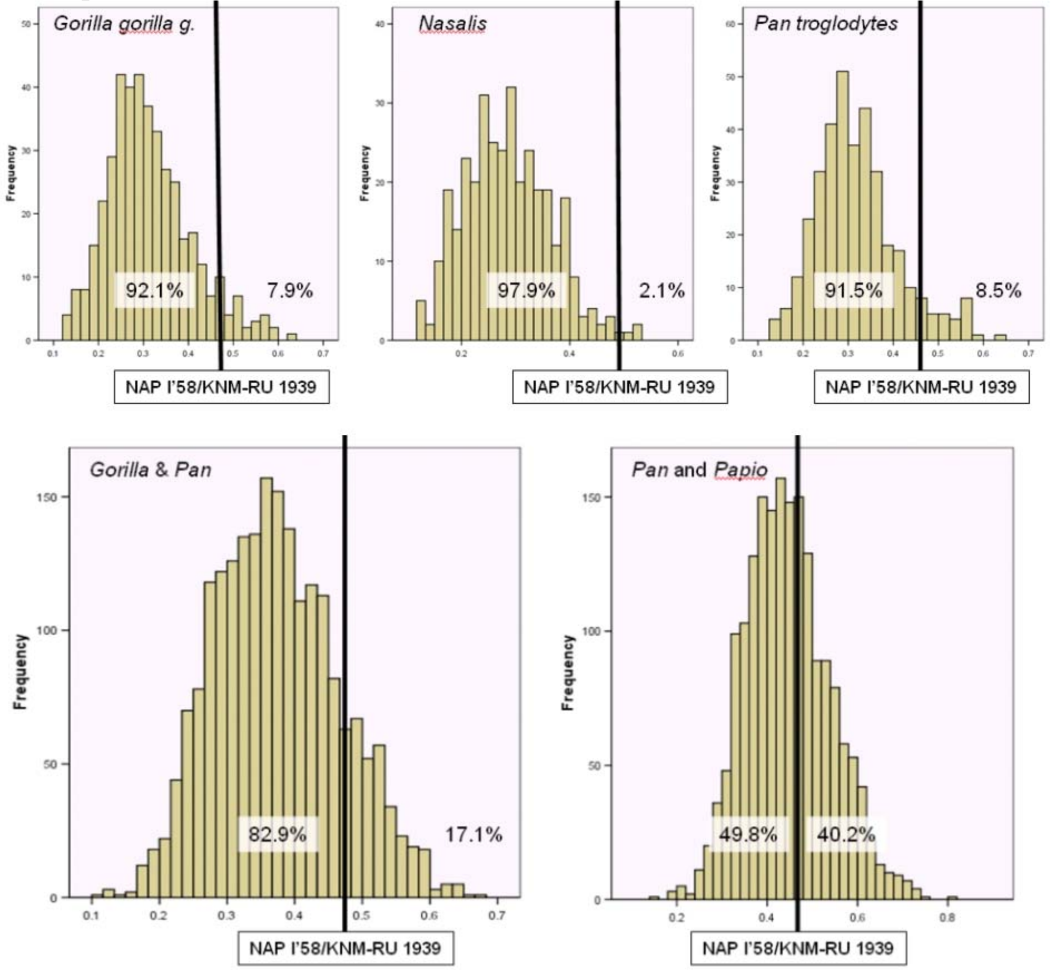


Figure 3.14. Histograms showing the distribution of Euclidean distances calculated through exact resampling of all possible pairs of distal tibial morphologies drawn from five different populations. The top three histograms show the distribution of expected differences between males and females drawn from the sexually dimorphic primates *Gorilla gorilla gorilla*, *Nasalis larvatus*, and *Pan troglodytes*. In each, the Euclidean distance between NAP I'58 and KNM-RU 1939 is represented as a vertical black line and the percentage of pairs more similar to one another than the fossil pair to the left of the line and the percentage of pairs more different to one another than the fossil pair to the right. The two graphs on the bottom show the frequency of Euclidean distances calculated through exact resampling of two different species (*Gorilla gorilla gorilla* and *Pan troglodytes* on left; *Pan troglodytes* and *Papio* spp. on right). Again, the Euclidean distance between NAP I'58 and KNM-RU 1939 is represented as a vertical black line and the percentage of pairs more similar to one another than the fossil pair to the left of the line and the percentage of pairs more different to one another than the fossil pair to the right. The difference between NAP I'58 and KNM-RU 1939 is best modeled by the difference between *Pan* and *Papio*, though distal tibia with these morphological distinctions could conceivable by drawn from any of the five modeled populations.

(17.1%) had a morphology more distinct than NAP I'58 and KNM-RU 1939. The pattern of difference observed between NAP I'58 and KNM-RU 1939 is best accommodated by the differences calculated from resampling from *Pan* and the smaller *Papio*. In 1,813 possible resampled pairs, 728 (40.2%) had a morphological difference greater than that calculated for NAP I'58 and KNM-RU 1939; and 1,085 pairs (49.8%) had a difference less than what is calculated between the two *Proconsul* tibiae. The morphological distance between NAP I'58 and KNM-RU 1939 is thus best modeled with species whose size and locomotor patterns differ.

The question of *where* there are morphological differences in the distal tibia of sexually dimorphic taxa, differently sized species of similar locomotor mode, and differently sized species of different locomotor modes, can be used to better interpret the observed differences between the NAP I'58 and KNM-RU 1939 tibiae. The coefficient of variation in the distal tibia of *Pan*, *Gorilla* and *Pongo* is relatively invariant in the anterior width of the tibial articular surface (Table 3.5). Both *Pan* and *Gorilla* exhibit the greatest variance in the SI height of the medial malleolus, the posterior width of the articular surface and the lateral length of the articular surface. The SI height of the medial malleolus and the posterior width vary considerably in *Pongo* and in *Nasalis* as well, with the third most variant feature being the medial length of the tibial articular surface and the width of the medial malleolus for *Pongo* and *Nasalis* respectively. Like *Nasalis*, *Papio* has a variant width to the medial malleolus, like *Pongo*, a variant medial trochlear length, and like *Pan* and *Gorilla*, a variant lateral trochlear length. If NAP I'58 and KNM-RU 1939 differed in only these regions that are variant in extant catarrhines, then the differences between them may be regarded as functionally insignificant. For the four most distinct features separating NAP I'58 and KNM-RU 1939, only one, the medial width of the tibial articular surface is often a variant feature in *Papio* and *Pongo* (though quite invariant in *Nasalis*). The width of the anterior aspect of the tibial surface is quite invariant in the African apes and is hypothesized to be related to vertical climbing, and the overall shape of the tibial metaphysis may reflect a distinct loading regime on the distal tibia. Interestingly, functionally significant features are relatively invariant in modern taxa and differ considerably between NAP I'58 and KNM-RU 1939.

Table 3.5. Coefficient of variation for size-standardized measures of the distal tibia.

	ML epiph	AP epiph	AP L. troch	AP mid	AP M. troch	ML A. troch	ML mid	ML P. troch	SI height	AP length	ML width
Pan	6.91	🟨 5.77	🟥 7.90	7.08	6.76	🟨 4.09	🟨 4.78	🟥 7.78	🟥 9.39	6.16	7.57
Gorilla	7.00	6.93	🟥 7.53	🟨 6.09	6.89	🟨 3.86	6.24	🟥 7.05	🟥 7.97	🟨 4.63	6.43
Pongo	7.20	6.27	8.15	🟨 5.14	🟥 10.39	6.09	🟨 5.76	🟥 8.73	🟥 13.99	🟨 5.38	8.22
Papio	5.48	5.43	🟥 7.16	🟨 4.84	🟥 10.46	5.37	🟨 4.43	5.71	6.15	🟨 4.39	🟥 6.26
Nasalis	6.93	5.73	6.79	🟨 3.91	🟨 4.25	4.81	🟨 4.60	🟥 7.34	🟥 8.09	5.79	🟥 7.00
NAP I'58 RU 1939	🟥 14.03	🟥 11.78	5.66	4.44	🟥 11.42	🟥 8.31	5.83	🟨 3.79	🟨 1.42	🟨 1.02	🟨 3.79

Yellow = Relatively low variation
Red = Relatively high variation

Discussion

Apes and atelines possess a talocrural joint adapted for frequent bouts of vertical climbing. Relative to cercopithecoids, apes and atelines have a relatively broader anterior aspect to the distal tibia (Figures 3.4, 3.5, and 3.13), which may allow more efficient distribution of forces through the joint while it is loaded in extreme dorsiflexion. Additionally, the medial malleolus is relatively mediolaterally thicker in the apes and atelines than in cercopithecoids (Figures 3.11 and 3.13). This morphology may adapt the ankle to withstand the increased medial loads incurred by the joint while loading the foot in inversion, as is known from kinetic studies on vertically climbing chimpanzees (Wunderlich, 1999).

In addition, the distal tibia is mediolaterally wide, or rectangular, at the metaphysis in apes and atelines that vertically climb. This morphology was hypothesized to be related to joint mobility, with an anteroposteriorly reduced tibial length permitting an increased range of dorsiflexion. However, this measure does not distinguish the vertically climbing hylobatids from cercopithecoids. Isler (2003) has noted that hylobatids do not pull themselves as close to the vertical substrate as the larger apes because the cost of climbing may be less due to their smaller body mass. Hylobatids may therefore not possess all of the vertical climbing adaptations found in the ankle of great apes, though it is important to note that although hylobatids do not have a mediolaterally wide tibial metaphysis, the similarly sized atelines primates do. The significance of this difference is unclear, though more detailed comparative kinematic analysis of atelines and hylobatids may reveal important differences at the ankle.

Similarly, the African apes and ateline primates have a more strongly wedged talus than cercopithecoid monkeys (Figure 3.6). This morphology was thought to represent the reciprocal of the mediolaterally wide anterior aspect of the distal tibia. However, unlike the distal tibia, the talus is morphologically similar in *Pongo*, the hylobatids, and the terrestrial cercopithecoids for degree of talar wedging. This may reflect loading of the talocrural joint in positions of both dorsiflexion and plantarflexion and in *Pongo* may be a result of occasional hindlimb suspension and grasping. In addition, the radii of curvature on the medial and lateral aspects of the talus distinguish African apes from the other anthropoids, but this measure is no different in Asian apes or atelines from the cercopithecoids (Figure 3.12). Interestingly, African apes have relatively thinner medial malleoli than *Pongo* or the atelines. It is possible that African apes do not load their talocrural joints in as extreme a position of inversion as *Pongo* and atelines and thus the medial aspect of the tibia and talus bear the brunt of the load in *Gorilla* and *Pan* whereas the medial malleolus and cotylar fossa of the talus absorbs the majority of the force during climbing in *Pongo* and the atelines. These variations in morphology of the talocrural joint may reflect subtle differences in locomotion and vertical climbing kinematics among the apes and ateline primates. Additional kinematic data during vertical climbing bouts in all apes and ateline primates will be necessary to test the hypothesis presented here that these shared morphological features are functionally related to vertical climbing and not some other form of locomotion in which the ankle is loaded in dorsiflexion and inversion.

Though the tibia and talus of vertical climbing primates differ from cercopithecoids and *Cebus* in some respect related to dorsiflexion and inversion, there appear to be no locomotor related differences among the primates for measures of abduction (Figures 3.9 and 3.10). There were also few differences in overall morphology of the talocrural joint between terrestrial cercopithecoids and more arboreal cercopithecoids.

Explaining Gorillas

Although the mediolaterally wide anterior aspect of the distal tibia is consistent with predictions from the biomechanical model of vertical climbing (Chapter 2), and the vertically climbing atelines and apes can be distinguished from cercopithecoids and

Cebus for this measure, it is unclear why the greatest average value is found in lowland gorillas (*Gorilla gorilla gorilla*). The anterior width of the tibial facet scales isometrically within gorillas, within the African apes, and within the non-human hominoids so there is little evidence that this morphology can be explain simply as an effect of body size. Lowland gorillas are quite arboreal (Remis, 1995; Kuroda et al., 1996; Tutin, 1996), and thus it should not be surprising that they are adapted for vertical climbing. Remis (1995) has even suggested that female gorillas are as suspensory and arboreal as chimpanzees. However, lowland gorillas may vertically climb in a slightly different way than the other apes. A study of vertical climbing kinematics found that, in general, apes vertically climb in a kinematically similar way, with the knees, elbows, and hips quite flexed. However, this study also found that *Pan* climbs with a more flexed knee than *Gorilla* (Isler, 2003). Isler (2003) noted that both *Pan* and *Gorilla* kept their bodies closer to the vertical substrate than what is observed in cercopithecoids and thus *Gorilla* may achieve functional equivalence with *Pan* and compensate for a less flexed knee than *Pan* with even greater flexion at the ankle. Although not enough climbing bouts were observed for statistical tests to be applied, it is intriguing that *Gorilla* appeared to have a slightly greater degree of dorsiflexion than *Pan* in the data presented in Chapter 2. Further controlled analyses should be done on the kinematics of climbing to test whether there are differences in dorsiflexion at the ankle among the great apes.

In addition, the role of juvenile positional and locomotor behaviors must be considered. Bone is most sensitive and most likely to adapt to frequent loads of great magnitude in the juvenile skeleton (reviewed in Pearson and Lieberman, 2004). In humans, the number of osteoblasts is significantly less in adults than in children and thus the ability of the skeleton to remodel itself becomes less efficient with age (Nishida, 1999). Although the idea that the adult skeleton is a reflection of juvenile loadings has been disputed (Ruff et al., 2006), many have argued that pattern formation during embryological development (Type I and II traits in Lovejoy et al., 1999) and/or chondral modeling during adolescence (Type IV traits in Lovejoy et al., 1999) are important factors for interpreting adult skeletal morphology (Hamrick, 1999; Lovejoy et al., 1999; Lovejoy et al., 2002). Although lowland gorillas may be as arboreal as chimpanzees (Remis, 1995), mountain gorillas are not (Tuttle and Watts, 1985). However, Doran (1997) has found that mountain gorillas climb quite frequently right up to the age of five years old and during childhood, mountain gorillas climb as frequently as chimpanzees. This activity early in life may shape the morphology of the ankle in mountain gorillas and may explain why the shape of the talocrural joint in these largely terrestrial apes is so similar to the morphology of the chimpanzee ankle.

Vertical climbing in *Proconsul major*

All of the *Proconsul* fossils studied had, in general, a cercopithecoid-like morphology, consistent with other claims that this Miocene catarrhine was a pronograde, above branch arboreal quadruped (Walker and Pickford, 1983; Rose, 1993; Rose, 1994; Walker, 1997). Le Gros Clark (1952) noted that the tali of *P. nyanzae* are “strikingly” cercopithecoid-like and this author concurs.

Data from the Napak distal NAP I’58, however, tentatively suggests that *Proconsul major* may have been capable of some degree of modern ape-like vertical climbing. The anterior aspect of the bone is enlarged, a feature found only in the distal tibia of apes and atelines. This distribution of bone gives the articular surface a trapezoid-like appearance in contrast to the more rectangular shape of the distal tibia in cercopithecoids and in other proconsulid distal tibiae (Figure 3.15). In addition, like the morphology found in apes and atelines, the *P. major* medial malleolus is mediolaterally wide relative to the anteroposterior length of the malleolus. The increased width of the medial malleolus and the increased width of the anterior aspect of the articular surface may be adaptations for distributing forces through a bone loaded in inversion and dorsiflexion, positions critical for efficient vertical climbing. Furthermore, like the condition of modern great apes and atelines, the Napak tibia is mediolaterally wide, relative to its anterioposterior length. This morphology would allow increase range of motion at the ankle, and permit greater dorsiflexion. These data are in contrast to suggestions that the *P. major* tibia is morphologically similar to the smaller *Proconsul* tibiae (Rafferty et al., 1995). Instead, it is suggested here that *P. major* may have be capable of more modern ape-like positional behaviors than other members of its genus. These data support other suggestions for a more modern ape-like morphology of the ulna of *P. major* (Nengo and Rae, 1992), the calcaneocuboid joint (Gebo, 1989), and are consistent with evidence for an enhanced range of pronation and supination at the elbow present in a recently discovered distal humerus and proximal radius of *P. major* from Napak (MacLatchy et al., 2007; pers. obs.). Others have also suggested that *Proconsul major* (= "*Ugandapithecus*" *major*) engaged in tree climbing activities and was well adapted to arboreality based primarily on the morphology of the femur (Gommery et al., 1988; Gommery et al., 2002).

Figure 3.15. Shape of distal tibiae in *Proconsul*.

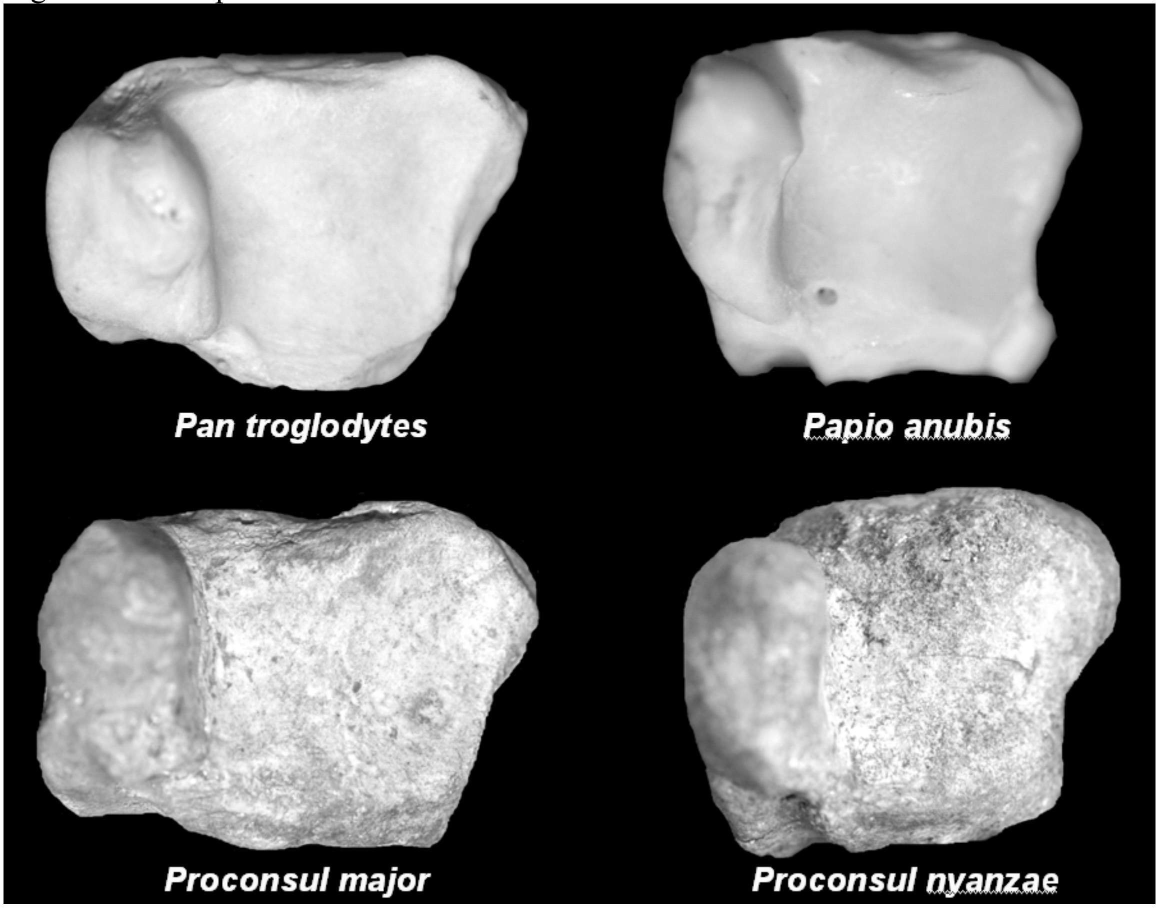


Figure 3.15. Left tibiae of (top) *Pan troglodytes* and *Papio anubis*; and (bottom) NAP I'58 and KNM-RU 1939. The specimens have been scaled to approximately the same size. Notice the square-shape to the articular facet on the *Papio anubis* and *Proconsul nyanzae* tibiae, and the more rectangular shaped facet on *Pan troglodytes* and *Proconsul major*.

The KNM-SO 389 talus is very similar to tali from *P. nyanzae* and thus the tarsal side of the ankle in *P. major* may not be as adapted for vertical climbing as the tibia (Figure 3.16). It is unclear how to interpret this apparent discrepancy, though it may be important to note though that the distal tibia is from an ape that would have been approximately 77 kg, whereas the talus was from a smaller individual of 50 kg. The role of body mass in vertical climbing adaptations is discussed more below. Despite many similarities to *P. nyanzae* tali, the SO 389 talus differs from other tali of *Proconsul* in two important qualitative ways. The distolateral aspect of the trochlear surface is robust and projecting in known tali from *P. nyanzae* and *P. heseloni*, and the articular surface on the anterior aspect of the talus is U-shaped, suggesting limited loading in dorsiflexion. This morphology is found in modern cercopithecoid tali and in the genus *Cebus*. KNM-SO 389, though still more like *Proconsul* than modern apes or atelines for this feature, has a weaker distolateral aspect to the talus, and an articular surface that extends to a more distal location than in any of the five *P. nyanzae* tali known. This morphology is consistent with increased loading in a position of dorsiflexion in *P. major*. In addition, the KNM-SO 389 talus has a robust lateral tubercle. The posterior talofibular ligament, an important ankle stabilizer during dorsiflexion (Leardini et al., 2000), inserts on the lateral tubercle and a strongly developed tubercle in the *P. major* talus may suggest frequent dorsiflexion in this species. A large lateral tubercle can be found in modern gorillas, chimpanzees, and is particularly large in the genus *Pongo*. A tubercle is often absent in cercopithecoids and is variably present in hylobatids. This morphology is also absent from the other *Proconsul* tali except for KNM-SO 1705, which may be from *P. africanus*, and KNM-RU 5940 (*P. nyanzae*), which has a weakly developd lateral tubercle. In sum, these data from the ankle suggest that the postcranial anatomy of *Proconsul major* may not have simply been scaled-up version of the smaller *Proconsul* species and may have been adapted to more frequent bouts of vertical climbing. The overall functional morphology of this large ape should be revisited.

These data are important in addressing the hypothesis that increased body size may have resulted in evolutionary changes related to forelimb suspension, orthogrady, vertical climbing and quadrumanous climbing. The possibility that an increase in body size may

Figure 3.16. *Proconsul* tali.

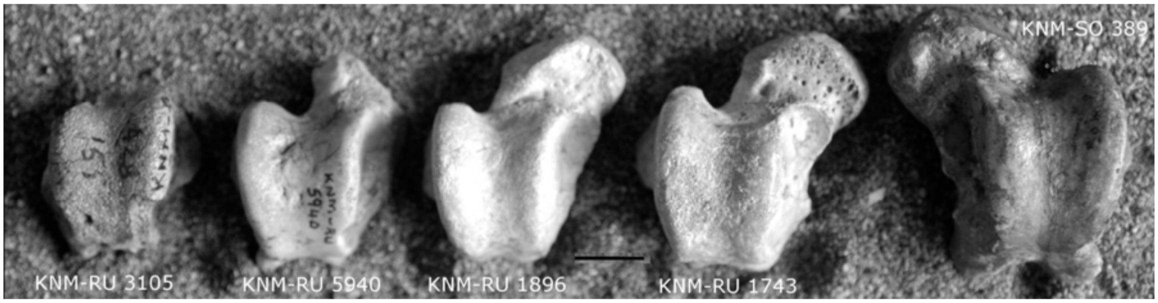


Figure 3.16. Fossil tali of *Proconsul nyanzae* from Rusinga Island (left to right): KNM-RU 3105, KNM-RU 5940, KNM-RU 1896, KNM-RU 1743, and *Proconsul major* from Songhor, KNM-SO 389 in superior view. Note the similar morphology among the tali, though also note the robust lateral tubercle and the weakly extended anterolateral articular surface on the *P. major* talus.

have provided the selection pressures for the evolution of the postcranial adaptations found in modern apes has been suggested elsewhere (Cartmill and Milton, 1977; Wheatley, 1987; MacLatchy, 2004 Model I). *Proconsul major* is reconstructed as a 50-80 kg ape (Rafferty et al., 1995). An animal of that size would not be able to remain an above-branch arboreal quadruped without restricting its movement to large branches that could sustain the force of a very large ape. At a certain body mass, catarrhines must either become terrestrial or evolve adaptations to better distribute the increased weight to many different supports. The latter scenario may necessitate the evolution of increased forelimb suspension capacity and increased orthogrady. The morphology of the *P. major* distal tibia and the unpublished elbow do not possess adaptations that would stabilize either joint in a strictly terrestrial environment. For instance, the tibia lacks a strong medial keel, present in cercopithecoid tibiae and argued to stabilize the ankle joint (Chapter 6). Thus, *P. major* was probably at least partially arboreal, and because of its large body size, may have evolved modern ape-like adaptations to navigate in this environment safely and efficiently. This interpretation of *Proconsul major* will have important implications for reconstructing the behavior and locomotion of this large Miocene ape.

Other vertical climbers in the Miocene?

The tali from Songhor hypothesized to belong to *Rangwapithecus* (KNM-SO 966, KNM-SO 968, KNM-SO 1402, BMNH M26903) have a distinct morphology suggestive of loading during extreme dorsiflexion of the ankle, and perhaps vertical climbing. The anterior aspect of the talus is expanded and the articular surface for the tibia encroaches onto the talar neck and almost to the talar head. The distolateral extension of the articular surface, and sulcus between this projection and the talar neck present in cercopithecoid and *Proconsul* tali is conspicuously absent from these four tali assigned to *Rangwapithecus*. Because the distolateral projection of bone is not present in any infant primate tali (Figure 3.17), it may be reflective of talar use, and perhaps of increase lateral loading of the talocrural joint in cercopithecoids and in the platyrrhine genus *Cebus*. This morphology is therefore evidence of a specific foot functional morphology that results in loading of the lateral aspect of the ankle joint. The similarity between these four tali and tali from atelines, *Hylobates*, *Pongo*, and the African apes in shifting the articular surface to a more medial and distal position may be evidence for vertical climbing in *Rangwapithecus*. It is possible that this morphology is related to leaping abilities in *Rangwapithecus*. However, unlike the tali of leaping primates (Gebo and Simons, 1987), the four tali described here have a relatively shallow talar groove and therefore reflect a joint adapted for mobility rather than stability. Medial cuneiforms perhaps assignable to *Rangwapithecus* are also suggestive of increase hallucial abduction and arboreal climbing

Figure 3.17. Development of talar morphology in anthropoids.

Figure 3.17. Ontogeny of the anterolateral lip in the primate talus. On the top row are three tali of *Pongo* and across the bottom are three tali of *Nasalis* all scaled to roughly the same size. The talus on the far left is from a juvenile, the middle an adolescent, and the right an adult. Notice that the anterolateral lip present in the *Nasalis* adult was absent in the juvenile and adolescent, suggestive that it is a bony adaptation perhaps to loading of the lateral talus. This morphology is present in the KNM-SO 1705 talus (circle), but absent in KNM-SO 1402. KNM-SO 1402 has, like *Pongo*, an anteriorly expanded articular surface of the tibia which extends onto the neck of the bone (arrows).

(Nengo and Rae, 1992). The femoral neck of the KNM-SO 399 femur assigned to *Rangwipithecus* has a neck shaft angle in the range of modern atelines and *Pongo* and may indicate the capacity for increased abduction of the hip (Harrison, 1982).

Others have recognized the similarities between KNM-SO 966, KNM-SO 968, and BMNH M26903 and suggested that they belong to *Rangwapithecus* (Langdon, 1986). However, Langdon (1986) regarded KNM-SO 1402 and KNM-SO 1705 as both belonging to *Proconsul africanus*. Although it is agreed here that KNM-SO 1705 has a talar morphology almost identical to the other *Proconsul* tali from Rusinga Island and is most probably from *P. africanus*, KNM-SO 1402 shares with SO 966, SO 968 and M26903 the distinct extension of the articular surface onto the talar neck and absence of the distolateral sulcus and is suggested to be from a large male *Rangwapithecus*. There is the possibility that KNM-SO 1705 belongs to *Rangwapithecus* and the four anatomically similar tali KNM-SO 966, KNM-SO 968, BMNH M26903, and KNM-SO 1402 belong to *P. africanus*. However, I find this unlikely because *Rangwapithecus* craniodental remains are twice as common as *P. africanus* fossils at Songhor (Cote, in preparation). A more detailed analysis of the postcranial remains from Songhor should be undertaken to test the hypothesis proposed here that *Rangwapithecus* may have been adapted for vertical climbing. There are currently no distal tibia known from *Rangwapithecus*, though a distal tibia from this primate, when located, is hypothesized to have a mediolaterally wide medial malleolus, an expanded anterior aspect to the talar facet, and a mediolaterally wide metaphysis. In addition, the intercollicular groove on the medial malleolus should be weakly developed (Chapter 54).

The extension of the tibial articular facet onto the talar neck described above for the four purported *Rangwapithecus* tali can also be found in the small fragmentary talus from Kalodiir KNM-WK 17171 assigned to *Simiolus*. Importantly, there are many limb bones assigned to *Simiolus* and these reflect some adaptations for forelimb suspension (Rose et al., 1992). Evidence from the talus suggests that extreme dorsiflexion during vertical climbing may have been a part of the locomotion of *Simiolus* as well.

Conclusion

The talocrural joint of vertical climbing primates has an expanded anterior aspect of the distal tibia, a mediolaterally wide medial malleolus, and a mediolaterally wide metaphysis. Aspects of the talus and distal tibia are suggestive of a different loading regime on the ankle in African apes than in the Asian apes which may be reflective of a different overall locomotor pattern, or subtle differences in climbing kinematics at the foot. The Miocene catarrhine fossil record is comprised primarily of primates adapted to an above branch, pronograde lifestyle. However, the distal tibia from *Proconsul major* is distinct from other *Proconsul* tibiae and possessed morphologies functionally correlated with vertical climbing. In addition, tali from the 10-20 kg catarrhine *Rangwapithecus* provide evidence that this primate loaded its talocrural joint in extremes of dorsiflexion. These data suggest that there may have been more locomotor diversity in the Miocene than previously suggested, including catarrhines adapted for bouts of modern ape and ateline-like vertical climbing.

CHAPTER 4
Vertical climbing adaptations in the ape ankle and the likelihood of arboreality in early hominins.

Abstract

The climbing ability of Plio-Pleistocene hominins has been an ongoing point of contention in the paleoanthropological literature. Despite its role in positioning the foot properly against the substrate and in distributing forces from the lower limb through the foot, the ankle joint has played only a minor role in this debate. Data from wild chimpanzees (*Pan troglodytes*) suggest that during vertical climbing, apes position their foot in abduction, inversion, and extremes of dorsiflexion. Based on this kinematic work, it was hypothesized that skeletal morphology of the distal tibia correlated with inversion and abduction, and extremes of dorsiflexion will distinguish vertical climbing primates from those that do not include vertical climbing in their locomotor repertoire. Linear and angular measurements were taken on the distal tibia and tali of modern humans, and wild-shot chimpanzees and gorillas. This study finds that African apes have a distinct ankle morphology adapted for extremes of dorsiflexion, inversion, and abduction typical of vertical climbing, including a broad anterior aspect of the distal tibia and talus, an obliquely oriented tibia over the talar surface, and a thick medial malleolus.

Using the modern chimpanzee as a kinematic model, morphological correlates of vertical climbing in the distal tibia and talus were used to interpret fossil ankles of Plio-Pleistocene hominins. Fourteen hominin distal tibia and 15 tali were studied from

Members 4 and 5 from Sterkfontein, South Africa, the Hadar formation in Ethiopia, the Lake Turkana region of Northern Kenya, and Olduvai Gorge. These fossils span a timescale of human evolution from 4.2 to 1.5 million years ago. In general, the hominin tibia and tali show an overall human-like morphology, one poorly adapted for vertical climbing. These data from the talocrural joint suggest that if hominins were vertically climbing, they were doing so in a manner kinematically different than that practiced by modern apes.

Introduction

The locomotion of early hominins remains a contentious topic in paleoanthropology. Although it is almost universally agreed that the australopiths and other early hominins engaged in terrestrial bipedality, the extent to which hominins also utilized arboreal resources remains unclear. Some have argued that adaptations for bipedality have sacrificed just about any arboreal behavior in our ancestors (Latimer and Lovejoy, 1987; Latimer and Lovejoy, 1990; Latimer, 1991; Lovejoy, 2005), while others examining the same fossilized remains have regarded australopiths as “gifted climbers” (Preuschoft and Witte, 1991), or at least adept in an arboreal setting (Stern and Susman, 1983; Susman et al., 1984). A study of climbing in our ancestors should start with what is known kinematically about climbing in modern primates, and then proceed to identify skeletal correlates of climbing in hominins using these extant models. Without testing an extant model, it is possible that individual aspects of hominin anatomy that may appear more ape-like than human-like will, by default, be regarded as evidence for ape-like behavior in our ancestors, including frequent and skilled vertical climbing. In this study, kinematic data on climbing in wild chimpanzees is used to identify skeletal correlates of vertical climbing in the ankle joint of African apes. These data are used to interpret the functional morphology of 29 fossil tibia and tali from Plio-Pleistocene hominins to test the hypothesis that any known hominin species possessed an ankle adapted for vertical climbing bouts.

Evidence for climbing in hominins

Vertical climbing has served an important role in studies of the origin of bipedalism. Based on EMG and kinematic studies, many have argued that morphological adaptations for vertical climbing preadapt a primate for bipedalism and may have served as an important biomechanical link between arboreality and terrestrial bipedality in our ancestors (Stern, 1971; Tuttle and Basmajian, 1974; Vangor, 1977; Fleagle et al., 1981; Stern and Susman, 1981; Vangor and Wells, 1983; Yamazaki and Ishida, 1984; Senut, 1988; Hirasaki et al., 1993; Hirasaki et al., 2000).

If vertical climbing preadapted hominins for bipedality, then some of the earliest hominins may still have retained the ability to climb, or at the very least, retained morphological features of their climbing ancestry. It is difficult to know whether the plesiomorphic features that some early hominins share with vertically climbing apes were being maintained by natural selection and therefore still of adaptive value, or were simply not being selected against and were morphological remnants from an arboreal past (Ward, 2002). It is notable in this context that most of the arboreal characters found in the postcrania of early hominins can be found in the upper limb. The earliest purported hominin postcranial remains belong to the species *Orrorin tugenensis*. The humeral shaft fragment BAR 1004'00 from this 5.8 mya species has a strong attachment for the brachioradialis muscle, an important flexor and supinator of the forearm, the manual phalanx BAR 349'00 is curved, and a distal thumb phalanx BAR 1901'00 has adaptations for climbing (Senut et al., 2001; Gommery and Senut, 2006). These features of the forearm are suggestive of arboreal behavior in *Orrorin*. However, the three *Orrorin* femora have been interpreted as the earliest evidence of bipedalism in the hominin fossil record (Senut et al., 2001; Pickford et al., 2002; Richmond and Jungers, 2008).

Postcranial fossils of the 4.4-5.8 mya genus *Ardipithecus* are scant. What has been revealed about this genus suggests that it was bipedal based on the dorsally oriented facet on the proximal end of pedal phalanges (Haile-Selassie, 2001; Semaw et al., 2004). However, like *Orrorin* and later australopiths, *Ardipithecus* also possessed a long, robust upper limb (White et al., 1994) and long manual phalanges (Semaw et al., 2004).

The KNM-KP 29285 tibia of the 4.2 mya *Australopithecus anamensis* is well-adapted for terrestrial bipedalism with anteroposteriorly flattened condyles and a perpendicularly oriented distal articular surface relative to the shaft of the bone (Leakey et al., 1995; Ward et al., 2001). The femoral shaft is similar to the *A. afarensis* A.L. 288-1 femur from Hadar (White et al., 2006). However, Heinrich et al. (1993) identified features of the *A. anamensis* radius from Sibilot Hill KNM-ER 20419 consistent with the hypothesis that vertical climbing was still an important component of the locomotion of this hominin. The *A. anamensis* radius has a well developed brachioradialis crest, and the orientation of the articular surface of the radial head suggests that this bone was loaded in a pronated position, which would increase the mechanical advantage for the brachioradialis. Furthermore, the long radial neck would increase the mechanical advantage for the biceps brachii. This is a very long bone likely to have belonged to an individual with long, ape-like forearms (Ward et al., 2001). As in *Ardipithecus*, *A. anamensis* appears to have possessed relatively long manual phalanges as well (White et al., 2006). Although it is clear from the morphology of the tibia that bipedality was selectively advantageous for *A. anamensis*, the available evidence from the forelimb suggests that *A. anamensis* was partially arboreal or retained these morphologies from an arboreally adapted ancestor (Heinrich et al., 1993; Ward et al., 2001).

The debate regarding arboreality in our ancestors has focused primarily on the ~3.0-3.5 mya species *Australopithecus afarensis* and emphasized the partial skeleton A.L. 288-1. The history of the debate has been detailed in Stern (2000) and Ward (2002). Fortunately, *A. afarensis* is one of the best known hominin taxa with many skeletal elements represented by multiple fossils, so that individual variation and sexual dimorphism can be considered in studies of functional morphology. As with *Orrorin* and *A. anamensis*, the long, robust, powerfully muscular arms and forearms of *A. afarensis* are often cited as evidence for arboreality (Stern and Susman, 1983; Susman et al., 1984; Senut, 1988; Preuschoft and Witte, 1991; Hunt, 1994; Hunt, 1998). The intermembral index of the A.L. 288-1 skeleton falls roughly between that of modern humans and the value in African apes (Jungers, 1982; Stern and Susman, 1983; Susman et al., 1984). Recently, the gorilla-like shape of the scapula and curved manual phalanges of the juvenile *A. afarensis* from Dikika, Ethiopia was presented as evidence for arboreality in at least the young of this species (Alemseged et al., 2006). These data on a young hominin are important because bone may be more responsive to loads in juveniles than in adults (Pearson and Lieberman, 2004).

Preuschoft and Witte (1991) suggested that australopiths were “gifted climbers” and “well adapted vertical climbers” based on their short hindlimbs, and powerful forelimbs. Many have argued that australopiths were adapted for both bipedality and arboreality (Prost, 1980; Stern and Susman, 1983; Susman, 1983; Susman et al., 1984; Senut, 1988; Rose, 1991). In addition to the powerful forearms, it has been suggested that a robust fibula and curved pedal phalanges are evidence for climbing in the lower limb (Stern and Susman, 1983; Susman et al., 1984; Susman et al., 1985). A posterior tilt to the distal tibia in A.L. 288-1 also puts the ankle in a plantarflexed set and may be an adaptation for reaching in branches and/or hindlimb grasping and suspension (Stern and Susman, 1983; Susman et al., 1984). This plantarflexed set is not found on the other two, larger, distal tibia from Hadar, A.L. 333-6 and A.L. 333-7 and have led some to suggest that there may be sex-related differences in locomotion in the australopiths (Stern and Susman, 1983; Susman et al., 1984, but see Drapeau et al., 2005). Susman et al., 1984 (pp. 137) put forth the most detailed hypothesis of climbing kinematics in australopiths:

> We suggest that these early hominins climbed vertical trunks with their forefoot (and at times midfoot also) applied to the surface, and that on smaller supports, while they grasped with their toes they emphasized use of their powerful hands. The sort of foot postures we envision for *afarensis* during vertical climbing are those common to all primates when they are on large trunks, viz. the foot is applied to the surface and the hallux is not necessarily opposed to the lateral toes.

Stern and Susman (1991) further argued that the lack of an abducted hallux would not preclude arboreal climbing in *A. afarensis*, and cited the absence of a large divergent hallux in the capable climber *Pongo* as an example. The lack of a large divergent toe in orangutans has been noted by others as well (Straus, 1926; Keith, 1928; Schultz, 1963; Tuttle and Rogers, 1966; Gomberg, 1981). However, Latimer and Lovejoy (1990) convincingly countered that the absence of a large grasping hallux in *Pongo* is compensated for with even more extreme adaptations for climbing including long curved digits. Orangutans also have the largest intermembral and brachial indices of any of the great apes (Aiello and Dean, 2002). The idea that a climbing australopithecine would require even more exaggerated climbing features in regions not related to bipedality (i.e. upper limb) to compensate for the loss of lower limb morphology suitable for climbing has been suggested by others as well (Wolpoff, 1996; Coffing, 1998; Ward, 2002). Besides the arguments over whether the absence of a divergent toe precludes climbing, some have proposed that *A. afarensis* actually *did* have a grasping hallux based on the convex shape of the medial cuneiform (Hunt, 1994, Hunt, 1998; Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004). This hypothesis would necessitate the presence of another species of hominin at this time period, such as *Kenyanthropus* (Leakey et al., 2001 but see White, 2003), or increased variability in morphology because the near-contemporary footprints from the site of Laetoli are definitively absent of a divergent great toe (White, 1980; White and Suwa, 1987).

The arboreal nature of australopiths has been considered for *A. africanus* as well. The "Little Foot" fossil (StW 573) from Member 2 deposits in the Sterkfontein Cave, South Africa was originally described as having a divergent toe (Clarke and Tobias, 1995), though more recent studies of the medial cuneiform suggest that the toe was in-line with the rest of the pedal digits as in modern humans (Harcourt-Smith, 2002; McHenry and Jones, 2006). Nevertheless, the limb proportions of *A. africanus* have been reconstructed to be even more ape-like than those of *A. afarensis* (Green et al., 2007), suggesting that this species had relatively longer arms and therefore may have been even more arboreal than *A. afarensis*. A study of the pedal bones of the Sterkfontein collection regarded many elements as deriving from an arboreal hominin and others from a primitive biped that would have incorporated an arboreal component into its locomotor repertoire (Deloison, 2003). Furthermore, the convexity of the lateral condyle of the *A. africanus* StW 514 proximal tibia would encourage greater mobility at the knee, and is possibly indicative of arboreality in this species (Berger and Tobias, 1995).

Arguments for arboreality in the hominin lineage extend into the early Pleistocene as well. The OH 7 hand is robust and may be evidence for strong arboreal grasping in *Homo habilis* (Stern and Susman, 1982). In addition to powerful hands, some have suggested that the *H. habilis* foot, based on the assumption that the OH 8 specimen belongs to this species, was equipped with a divergent great toe and other features related to arboreality (Oxnard and Lisowski, 1980; Kidd et al., 1996). The presence of a divergent toe in OH 8 has been refuted by more detailed studies (Harcourt-Smith, 2002; McHenry and Jones, 2006). In addition, Gebo and Schwartz (2006) regard the OH 8 specimen as belonging not to *H. habilis*, but to *Paranthropus boisei*, and suggest that features of the OH 8 talus and the TM 1517 *P. robustus* talus may better adapt these animals for an arboreal environment. The limb proportions of two early *Homo habilis* skeletons (OH 62, KNM-ER 3735) have been reconstructed as possibly possessing relatively longer arms than earlier hominins (Leakey et al., 1989; Hartwig-Scherer and Martin, 1991; Haeusler and McHenry, 2007), though there is considerable error in reconstructing these limb lengths and the evidence for such an evolutionary reversal is not currently convincing (Reno et al., 2005). There is even the suggestion that some of these later *Homo habilis* postcranial remains, specifically KNM-ER 3735, may be better adapted for an arboreal environment than the Hadar *A. afarensis* fossils (Haeusler and McHenry, 2007). Finally, Erik Trinkaus remarking on the 1.77 million year old postcranial fossils of *Homo* from Dmanisi noted that "If you're a primate and you sleep on the ground at night, you do not wake up in the morning" (Owen, 2007).

Others have found the postcranial anatomy poorly adapted for modern ape-like climbing and have suggested the possibility that hominins may have climbed in a kinematically unique manner (Jungers, 1982; McHenry, 1991; MacLatchy, 1996; Sanders, 1998). Still others have dismissed the arguments for arboreality in early hominins, particularly *A. afarensis,* outright (Lovejoy, 1978; Latimer et al., 1987; Latimer and Lovejoy, 1989; Latimer and Lovejoy, 1990a; Latimer and Lovejoy, 1990b; Latimer, 1991; Lovejoy, 2005a; Lovejoy, 2005b; Lovejoy, 2007; Sayers and Lovejoy, 2008). By evolving adaptations for bipedality, these studies argue, hominins sacrificed their ability to climb almost entirely. In this view, if hominins did climb, they performed as poorly as modern humans do today (Latimer et al., 1987). Latimer (1991) argued that modern chimpanzees occasionally die when they fall from trees, and thus if early hominins were climbing, natural selection would maintain adaptations for moving in an arboreal environment. Instead, Latimer (1991) argued that the morphology of the post-cranial skeleton of early hominins was evolving in a direction *away* from the ape condition, and towards the human one. These evolutionary changes would have compromised their ability to safely operate in an arboreal environment, or at least changed the type of arboreal conditions in which hominins could navigate. Sayers and Lovejoy (2008) present a list of morphological traits found in the *A. afarensis* skeleton that would prevent much arboreal activity in early hominins. These include an elongated lumbar region of the vertebral column, which Lovejoy (2005) regards as “antithetical” to ape-like arboreality because a critical adaptation for vertical climbing or bridging in apes is a short, stiff lumbar region (Keith, 1923; Cartmill and Milton, 1977; Jungers, 1984). In the lower limb, the metatarsophalangeal joints are decidedly human-like in their orientation, and though the phalanges are more curved than modern humans, they are short and straight compared to modern chimpanzee phalanges (Latimer and Lovejoy, 1990). The talocrural joint (discussed more below) and the calcaneus have evolved morphologies related to obligate bipedality at the expense of adaptations for climbing (Latimer et al., 1987; Latimer and Lovejoy, 1990). Latimer and Lovejoy (1990) also provided a convincing morphological argument that *A. afarensis* had an adducted hallux (contra Hunt, 1994, Hunt, 1998; Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004). In fact, Lovejoy (1978, 2005) has suggested that australopiths may have been more adept bipeds than modern humans, with a more efficient abductor mechanism at the hip joint. The differences found between the australopithecine postcranial anatomy and the modern human skeleton is hypothesized to be related to differences in neonatal brain size and thus obstetric constraints (Lovejoy, 1978; Lovejoy, 2005).

This study adds to the current debate about vertical climbing in our hominin ancestors by augmenting the talocrural joint study by Latimer et al. (1987) to include all hominin distal tibia and tali and to test adaptations for climbing in the non-human hominoid and hominin talocrural joint using new kinematic data of vertical climbing in wild chimpanzees (Chapter 2). Functional predictions of skeletal differences in African apes and in humans are based on kinematic data of climbing in wild chimpanzees, cadaver studies, and kinetic work.

Vertically climbing apes and some atelines place their foot in positions of abduction, extreme dorsiflexion (Lewis, 1980; Chapter 2), and load the medial side of their foot (Wood-Jones, 1916; Morton, 1922; Vançata, 1985; Langdon, 1986; Wunderlich, 1999) as a result of foot inversion. The ability to achieve these joint positions in addition to loading of the joint surface at these times yields specific predictions regarding the morphology of the talocrural joint in primates that vertically climb. It is therefore predicted that vertically climbing apes possess skeletal correlates of foot mobility, and particularly the capacity to achieve extreme dorsiflexion, abduction, and inversion at the ankle. These are discussed in more detail in the material and methods sections.

Studies on human cadavers have found that during dorsiflexion, the contact point between the tibia and the talus shifts anteriorly (Driscoll et al., 1994; Corazza et al., 2005). Vertically climbing primates utilize positions of extreme foot dorsiflexion during climbing bouts, and therefore it is hypothesized that vertically climbing primates will produce a loading environment at the talocrural joint with high anterior forces. Because stress is equal to force divided by a given surface area, increased bone in the anterior aspect of the talocrural joint would help reduce the pressure in this region despite the high forces being incurred. Thus, it is predicted that vertically climbing primates will have broad anterior aspects of the talocrural joint.

Inversion at the talocrural joint in the human ankle shifts the contact point medially on the articular surface and onto the medial malleolus (Calhoun et al., 1994; Kura et al., 1998). Detailed kinetic work on the primate foot demonstrated that the force on the foot shifts medially in vertically climbing chimpanzees whereas it remains in a lateral position in cercopithecoids (Wunderlich, 1999). It is therefore hypothesized that vertically climbing apes will produce a loading environment at the talocrural joint with high medial forces. Again, because pressure is equal to force divided by a given surface area, increased bone in the medial aspect of the talocrural joint would help reduce the pressure in this region despite the high forces being incurred. Thus, it is predicted that vertically climbing primates will have more robust medial malleoli.

Given these data from the orthopaedic and primate literature, it is possible to address two questions about the ankle anatomy of extinct hominins: 1) Based on the morphology of the distal tibia and talus, did fossil hominins have the range of motion necessary to achieve the joint positions observed in vertically climbing wild chimpanzees? If so, 2) based on the distribution of bone in the distal tibia and talus, did fossil hominins load their talocrural joint in a position of dorsiflexion, inversion, and abduction?

Materials and Methods

The right distal tibia and talus of adult wild-shot African apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla gorilla*, *Gorilla gorilla beringei*) were studied at the Cleveland Museum of Natural History, Harvard Museum of Comparative Zoology, American Museum of Natural History (New York), National Museum of Natural History (Washington D.C.), Peabody Museum (Yale), and Field Museum (Chicago). The numbers of tibia and tali, and the sexes of the specimens are listed in Tables 4.1 and 4.2. The human tali were from the 9th-12th century PaleoIndian Libben population housed at Kent State University (Lovejoy et al., 1977) and the Hamann-Todd collection at the

Table 4.1. Extant tibiae measured in this study.

Species	Male	Female	Sex unknown	Total
Homo sapiens	25	34	77	136
Pan troglodytes	18	20	10	48
Pan paniscus	2	1	1	4
Gorilla gorilla gorilla	23	19	2	44
Gorilla gorilla beringei	15	6	1	22

Table 4.2. Extant tali measured in this study.

Species	Male	Female	Sex unknown	Total
Homo sapiens	13	21	11	45
Pan troglodytes	17	20	9	46
Pan paniscus	2	1	1	4
Gorilla gorilla gorilla	23	19	3	45
Gorilla gorilla beringei	10	3	0	13

Cleveland Museum of Natural History. The human tibia were from the 9th-12th century PaleoIndian Libben population housed at Kent State University (Lovejoy et al., 1977), the Hamann-Todd collection at the Cleveland Museum of Natural History, and an unprovenienced sample of human tibia from the University of Michigan Department of Anthropology. For all measures, the three populations were first treated as separate groups and only when they did not statistically differ for any measure were the results combined.

Fossil hominin tibia and tali (Table 4.3) were studied at the Transvaal Museum in Pretoria, South Africa, the Department of Anatomy at the University of Witwatersrand in Johannesburg, South Africa, the Kenya National Museum in Nairobi, and the Tanzania

Table 4.3. Fossil hominin tali and tibiae measured in this study.

Accession number	Element	Geological age	Taxon	Talocrural angle (˚)
KNM-KP 29285	Tibia	4.12[0]	*Australopithecus anamensis*	93.1
A.L. 333-6	Tibia	3.2[1]	*A. afarensis*	91.2
A.L. 333-7	Tibia	3.2[1]	*A. afarensis*	90.0
A.L. 288-1	Talus	3.18[1]	*A. afarensis*	90.3
A.L. 288-1	Tibia	3.18[1]	*A. afarensis*	91.2
StW 181	Tibia	2.6-2.8[2]	*A. africanus?*	93.7 (est.)
StW 347	Talus	2.6-2.8[2]	*A. africanus?*[8]	Damaged
StW 358	Tibia	2.6-2.8[2]	*A. africanus?*[8, 20]	94.7
StW 363	Talus	2.6-2.8[2]	*A. africanus?*[23]	91.6
StW 389	Tibia	2.6-2.8[2]	*A. africanus?*[8, 20]	94.3
StW 88	Talus	2.6-2.8[2]	*Homo habilis?*[6,7, 20] *A. africanus?*	90.4
StW 514b	Tibia	2.6-2.8[2]	*A. africanus?*[8, 18]	90.8
StW 486	Talus	2.6-2.8[2]	*A. africanus?*[8]	93.7
StW 102	Talus	2.4-2.8[2]	*H. habilis?*[7, 20] *A. africanus?*[8]	91.9
Omo 323-76-898	Talus	2.2[3]	*Homo?*[9,10]	94.5
TM 1517	Talus	1.9-2.0[4]	*Paranthropus robustus?*[20]	91.1
SKX 42695	Talus	1.5-2.0[5]	*P. robustus?*[5] *Homo?*[5]	Damaged
KNM-ER 1481	Tibia	1.9[3]	*H. habilis?*[20, 21] *H. erectus*[22]	90.5
KNM-ER 1500	Tibia	1.9[3]	*P. boisei?*[15, 20]	87.4
KNM-ER 2596	Tibia	1.9[3]	Hominin[25] Cercopithecoid?	107.0
KNM-ER 1476	Talus	1.88[3]	*P. boisei?*[10, 11]	93.7
OH 8	Talus	1.85	*H. habilis?*[12, 13, 20] *P. boisei?*[10, 14, 15]	92.0
OH 35	Tibia	1.85	*H. habilis?*[13, 20] *P. boisei?*	89.0
KNM-ER 813	Talus	1.85[3]	*Homo*[10, 14]	93.2
KNM-ER 1464	Talus	1.7[3]	*P. boisei?*[15, 20] *Homo?*	93.5
StW 567	Tibia	1.4-1.7[2]	*Homo*[2, 24]	91.2
KNM-ER 5428	Talus	1.6[3]	*H. erectus*[19, 26]	92.6
KNM-ER 803	Talus	1.53[3]	*H. erectus*[16, 19, 20, 26]	Damaged
KNM-WT 15000	Tibia	1.5[17]	*H. erectus*[17]	86.7

[*] Based on human-regression equations from McHenry (1992).

[0]Leakey et al., 1998; [1]Walter et al., 1994; [2]Kuman and Clarke, 2000; Deloison, 2003; Pickering et al., 2004; [3]Feibel et al., 1989; [4]McKee, 1995; [5]Susman et al., 2001; [6]Clarke, 1985; [7]Christie, 1990; [8]McHenry and Berger, 1998; [9]Deloison, 1997; [10]Gebo and Schwartz, 2006; [11]Leakey, 1973; [12]Leakey et al., 1964; [13]Susman and Stern, 1982; [14]Wood, 1974; [15]Grausz et al., 1988; [16]Day and Leakey, 1974; [17]Walker and Leakey, 1993; [18]Berger and Tobias, 1996; [19]Antón, 2003; [20]McHenry, 1994; [21]Trinkaus, 1984; [22]Kennedy, 1983; [23]Fisk and Macho, 1992; [24]Curnoe and Tobias, 2006; [25]Leakey and Walker, 1985; [26]Walker, 1994.

National Museum and House of Culture in Dar es Salaam. High quality research casts of the Hadar *A. afarensis* tibiae and tali were measured at the Cleveland Museum of Natural History and the University of Michigan Department of Anthropology. All linear measurements on fossil and extant tibiae and tali were taken with digital calipers.

The ankle morphology of African apes and humans was quantified to assess features related to the three types of movement that typified vertically climbing wild chimpanzees (Chapter 2): dorsiflexion, abduction, and inversion.

I. Dorsiflexion

Four separate analyses were undertaken on the tibia and talus to assess both the capacity for extreme dorsiflexion, and to test whether loading occurred in the joint during periods of extreme dorsiflexion. These are described in detail in Chapter 3 and will not be repeated here, except to note on which fossils these measures could be accurately taken.

DISTAL TIBIA

1.) The Mosimann size-standardized shape analysis of the distal tibia allows the following question to be addressed: given an equal amount of bone, *where* in the joint does the primate distribute this limited resource? The following fossils were complete enough for measures to be taken accurately: KNM-KP 29285, A.L. 333-6, A.L. 288-1, StW 358, StW 389, KNM-ER 1481, KNM-ER 1500, KNM-ER 2596, OH 35, StW 567, and KNM-WT 15000. The anterolateral corner of A.L. 333-7 was damaged and thus the mediolateral length of the anterior surface and the anteroposterior width of the lateral aspect of the bone were estimated. The anterior aspect of StW 181 and the posterior region of StW 514 were both sheared away and thus the dimensions of these tibiae could not be assessed with any accuracy.

In addition, a non-stepwise discriminant function analysis was performed on the six size-adjusted measures using SPSS 14.0. All of the fossils were entered as separate groups. This provided a test of the hypothesis that the measures predicted to be biomechanically relevant were in fact the ones that best discriminate the distal tibia of humans and African apes.

TALUS

2.) Wedging of the talus was assessed as described in Chapter 3. The following fossil tali were complete enough for this measure to be taken: A.L. 288-1, StW 88, StW 363, Omo 323-76-898, KNM-ER 1476, KNM-ER 813, KNM-ER 1464, and KNM-ER 5428. There is damage to the posterolateral corner of the talar trochlea in OH 8, though this width could be reasonably estimated. Likewise, the posterior edge is not preserved on TM 1517 and thus these values should be considered minimums. The damage is too severe on StW 102, StW 347, StW 486, and SKX 42695 for an accurate measure of this angle to be calculated.

TALOCRURAL MOBILITY

3.) The mobility of the talocrural joint was measured as a function of the depth of the distal tibial surface following the protocol described in Chapter 3. In addition to the depth measurement, with the images in lateral view, the posterior or anterior “tilt” of the distal tibia relative to the long axis of the shaft was also measured on all tibiae. This angle was taken by drawing a straight line through the most inferior aspects of the distal tibial (as described above) and measuring the angle that this line forms with the long axis of the tibia, following the protocol of Stern and Susman (1983). This measure has been previously used to argue that A.L. 288-1 had an ape-like plantarflexed set to its talocrural joint (Susman and Stern, 1983; Susman et al., 1984) though others have argued instead that this measure is quite variable and holds little functional significance (Latimer et al., 1987). The depth of the tibial surface and the tilt of the tibial axis in the sagittal plane were measured on the following fossil tibia: KNM-KP 29285, A.L 288-1, A.L. 333-6, A.L. 333-7, StW 358, StW 389, KNM-ER 1500, KNM-ER 1481, KNM-ER 2596, StW 567, and KNM-WT 15000. The anterior and/or posterior rims were too badly damaged on StW 181, StW 514 to accurately assess the depth of the tibial articular surface and the tilt of the joint surface in the sagittal plane. Also, damage inflicted perhaps by a crocodilian (Njau and Blumenschine, 2007) to the anterior rim of the OH 35 tibia makes it difficult to get a precise measurement of the tibial depth, though a minimum value could be estimated.

4.) The mobility of the talocrural joint was also measured as a ratio of the amount of bone in the anteroposterior aspect of the distal tibial metaphysis versus the amount of bone in the mediolateral dimension following the protocol described in Chapter 3. The metaphyseal region was preserved well enough for this measurement to be taken with accuracy on the following hominin distal tibia: KNM-KP 29285, A.L. 288-1, A.L. 333-6, A.L.333-7, StW 358, StW 389, KNM-ER 1500, KNM-ER 1481, KNM-ER 2596, OH 35,

Figure 4.1. Models illustrating the effect of tibial depth on dorsiflexion.

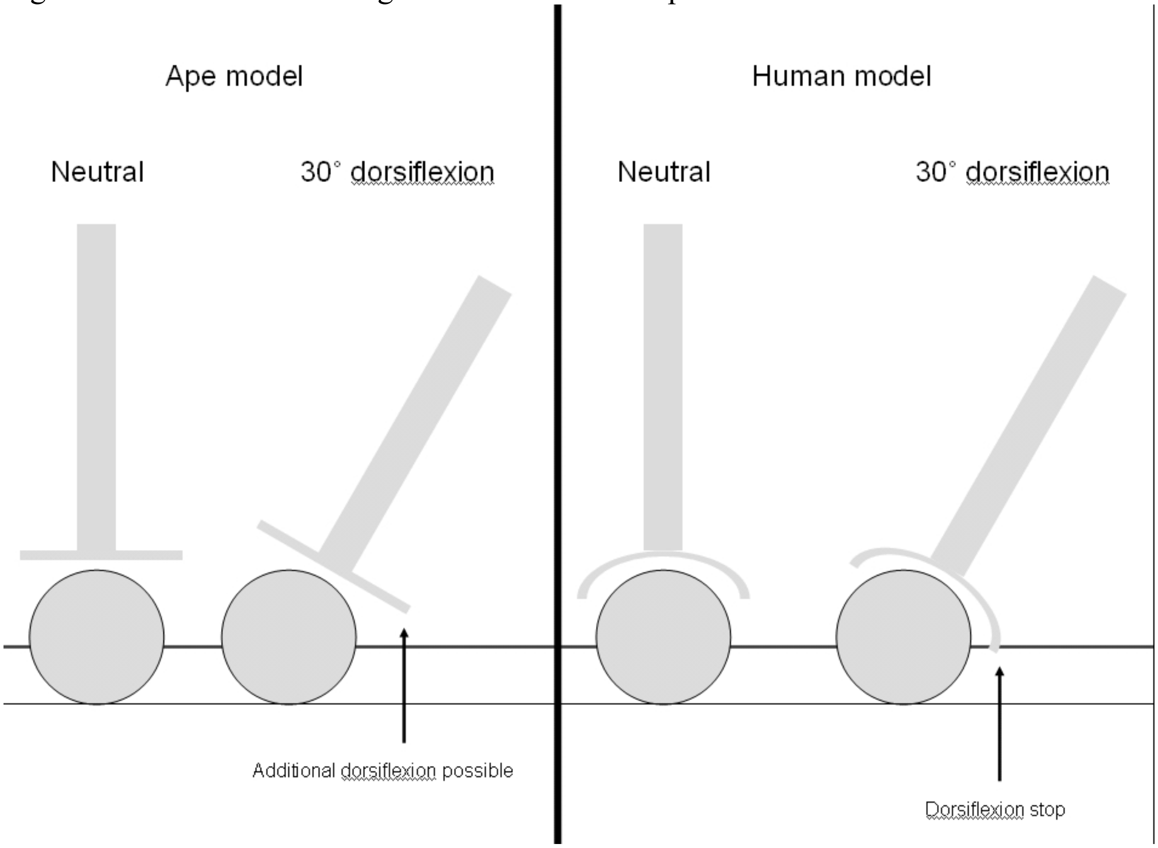


Figure 4.1. Models illustrating how the depth of the tibial surface can limit dorsiflexion in the ankle. The circles represent the talus, vertical rectangles represent the long axis of the tibia and gray horizontal lines the distal tibia. The ape model on the left shows a flat tibial surface dorsiflexing 30˚ over a curved talar surface. The rim of the distal tibia does not reach the black line drawn through the talus representing the talar neck. However, a curved surface, the same exact length as the flat one, reaches the black line upon 30˚ of dorsiflexion. These models illustrate how the flatness of the tibial articular surface may be correlated with an increased range of dorsiflexion.

and KNM-WT 15000.

II. Abduction

The apical angle of the talus is hypothesized to be proportional to the degree of foot abduction, with a high apical angle resulting in a greater degree of abduction than a low apical angle. The methods employed to calculate the apical angle are described in detail in Chapter 3. As with the measure of talar wedging, the tali complete enough to take this measure of talar abduction were: A.L. 288-1, StW 88, StW 363, Omo 323-76-898, KNM-ER 1476, KNM-ER 813, KNM-ER 1464, and KNM-ER 5428. TM 1517 should be considered a minimum as there is damage to the posterior aspect of the bone.

The degree of foot abduction possible in the ankle can also be assessed as the ratio of distance traveled by the tibia over the talus on the lateral side of the joint to the distance traveled by the tibia over the talus on the medial side of the joint. The methods employed to calculate the degree of abduction on an associated tibia and talus is described in Chapter 3.

Applications of this approach to the hominin fossil record necessitate the presence of associated tibia and tali. These data are available for the *A. afarensis* skeleton A.L. 288-1 (Johanson et al., 1982), and potentially for the OH 8/OH 35 talocrural joint (Stern and Susman, 1982 though see Aiello et al., 1998; Wood et al., 1998). Additionally, the *A. africanus* tibia StW 358 has been hypothesized to articulate with the StW 363 talus (Fisk and Macho, 1992) or the StW 347 talus (Deloison, 2003). Although the StW 358 tibia morphologically fits well with either of the two tali and all share the same patina, it is argued here to belong with StW 363 (Figure 4.2). The two were found in adjacent grids (R/43 and Q/43 respectively) and at the same depth of 13’6”-14’6”. Although the StW 347 talus was also found in an adjacent grid (P/43), it was at a shallower depth of 11’2”-12’3”. Furthermore, there is damage to the inferolateral aspect of the anterior aspect of the StW 358 tibia and what appears to be corresponding damage to the inferior aspect of the lateral talar body and malleolar facet on the StW 363 talus.

Figure 4.2. Ankle of *Australopithecus africanus*.

Figure 4.2. Potentially associated tibia (StW 358) and talus (StW 363) of *Australopithecus africanus* from 2.6-2.8 mya Member 4 deposits in the Sterkfontein cave, South Africa, in anterior view (left) and medial view (right).

III. Inversion

An inverted set to the talocrural joint is a function of the angle that the long axis of the tibia forms with the articular surface of the ankle (Latimer et al., 1987). This was assessed in two different ways. The angle that the long axis of the tibia forms with the distal articular surface of the tibia was measured using a carpenter's contour guide on wild-shot chimpanzees (n=31), lowland gorillas (n=29), and on modern human tibia (n=28) from the Hamman-Todd Collection at the Cleveland Museum of Natural History. The tibia were pressed into the carpenter's contour guide with care taken to be sure that the contour pins were parallel to the long axis of the tibial shaft. The impression of the articular surface made on the contour guide was then laid flat, and photographed with a Nikon D100 digital camera. The images were imported into the program Image J and the angle formed between the plane formed by the contour pins and the long axis of the tibia as inferred by the unmoved straight contour pins was measured.

This angle formed between the long axis of the tibia and the ankle joint surface was measured in this same manner on casts of the following hominin tibia: KNM-KP 29285, A.L. 288-1, A.L. 333-6, A.L. 333-7, KNM-ER 1481, KNM-ER 1500, KNM-ER 2596, and OH 35. Two other methods were employed to measure this angle on the tibia as well. Plaster casts of the above hominin tibia were produced and sectioned in the coronal plane with a handsaw. The angle formed between the tibial axis and the articular surface was then measured directly with a protractor. This approach allowed the results of this study to be compared directly to the results of Latimer et al. (1987) who employed a similar cast sectioning method to measure the angle that the long axis of the tibia forms with the ankle. The results from the carpenter's contour guide method were within 1˚ of the angles measured on sectioned casts. In addition, the following original fossil tibia were studied: StW 181, StW 358, StW 389, StW 514, StW 567, KNM-KP 29285, KNM-ER 1481, KNM-ER 1500, KNM-ER 2596, OH 35, and KNM-WT 15000 (Table 4.3). These fossils were scanned with a Next Engine portable 3-D desktop laser scanner. The specimens were scanned at the maximum resolution possible of 0.1 mm. The 3-D models were imported into the program ScanStudio and using the crop tool, the bones were digitally sectioned in the coronal plane. Images of the digitally sectioned fossils were captured with the program Jing, and imported into Image J, where the angle formed between the long axis of the tibia and the articular joint surface was measured with the angle tool as described above. Measured angles were within 1˚ of one another for specimens in which all three methods were employed (KNM-KP 29285, KNM-ER 1481, KNM-ER 1500, and KNM-ER 2596) allowing results from the three methods to be used interchangeably.

The set of the tibia on the talus was estimated using isolated tali as well (Figure 4.3). This was possible because the angle formed between the long axis of the tibia and the axis of rotation of the talocrural joint is conserved in humans and African apes, approximately 80˚ (Latimer et al., 1987). Because the angles of a triangle sum to 180˚, if 80˚ is conserved between humans and African apes, then there remains 100˚ between the remaining two joint angles to differentiate the two primate groups. Because humans have a perpendicularly aligned tibia relative to the ankle (an angle of ~90˚), the angle formed between the articular surface of the ankle and the axis of rotation of the joint is roughly 10˚; whereas a more obliquely angled tibia over the talus (~75˚), would necessarily mean a higher joint angle (~25˚) between the axis of rotation and the ankle joint surface in the African apes. Because the axis of rotation of the talocrural joint runs through the tips of the malleoli (Inman, 1976; Latimer et al., 1987), this axis can be estimated on isolated tali as the line that runs between the most inferior aspect of the articular surfaces for the medial and lateral malleoli. The angle that the axis of rotation forms with the articular surface of the talocrural joint can then be determined by measuring the angle between this line connecting the inferior malleolar facets and the superior surface of the talus. This angle was measured on isolated tali from *Homo sapiens* (n=45), *Pan troglodytes* (n=51), *Gorilla gorilla gorilla* (n=45), and *Gorilla gorilla beringei* (n=13). The tali were positioned in distal view and photographed with a Nikon D100 digital camera. The images were imported into the program Image J, and the angle between the most inferior extent of the facets for the medial and lateral malleoli and the superior surface of the talus

Figure 4.3. Geometry of the hominoid ankle.

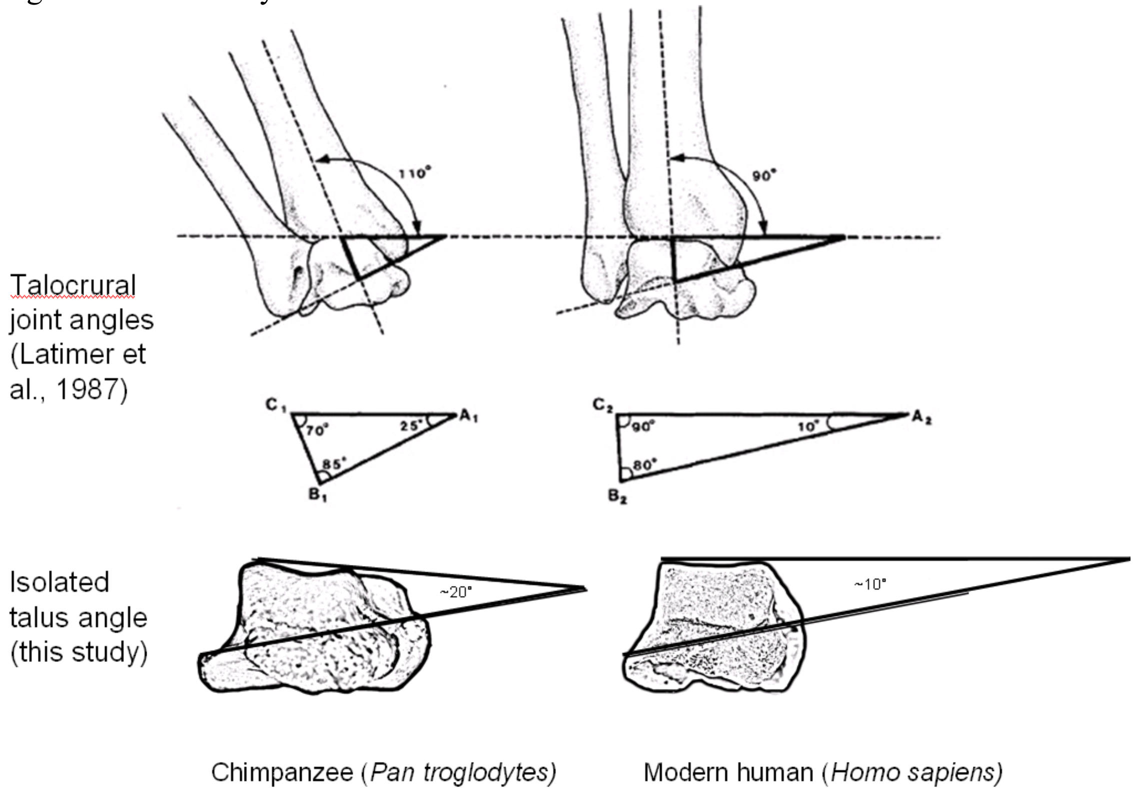


Figure 4.3. Lines drawn through the long axis of the tibia, the talocrural axis, and the plane of the talocrural joint form a triangle. The angle formed between the long axis of the tibia and the axis of rotation of the ankle joint is conserved between humans and African apes (Latimer et al., 1987). Thus a measure of either of the other angles can be used to calculate the third angle. The angle formed between the axis of rotation of the ankle and the plane of the talocrural joint, even if taken on isolated tali, can be used to calculate the angle that the long axis of the tibia formed with the articular surface of the tibia. Reproduced with permission from Latimer et al. (1987) and reprinted with permission from Wiley-Liss, Inc.Wiley Publishing Inc., a subsidiary of John Wiley & Sons, Inc.

was measured with the angle tool. Twenty randomly selected specimens were measured a second time a month after the original measurement to assess repeatability. The average difference between the two measures was 1° ± 0.5° with a maximum difference between two measures of 1.93°.

This angle was also measured on the following original fossil tali: StW 88, StW 102, StW 363, StW 486, OH 8, TM 1517, KNM-ER 1476, KNM-ER 1464, KNM-ER

813, and KNM-ER 5428. This angle was taken on high quality research casts of A.L. 288-1 and Omo 323-76-898. The original fossil hominin tali StW 347, SKX 42695, and KNM-ER 803 were too badly damaged along the medial or lateral aspect of the talar body to accurately take this angle.

A measure of the relative thickness of the medial malleolus and the ratio of the medial and lateral radii of curvature on the primate talus follows the protocol described in detail in Chapter 3. The medial malleolus was complete enough for the thickness ratio to be calculated on the following hominin fossils: KNM-KP 29285, A.L. 333-6, A.L. 333-7, A.L. 288-1, StW 358, StW 515, KNM-ER 1500, KNM-ER 1481, KNM-ER 2596, StW 567, and KNM-WT 15000. Although the malleolus is broken in OH 35, enough of the malleolar junction with the tibial articular surface is present that mediolateral thickness and anteroposterior width can be estimated. The relative radii of curvature on the hominin talus could be assessed with accuracy on those tali with relatively complete medial and lateral trochlear rims: A.L. 288-1, StW 88, StW 363, StW 486, Omo 323-76-898, TM 1517, KNM-ER 1476, OH 8, KNM-ER 813, KNM-ER 1464. and KNM-ER 5428.

Significance was assessed for all measures in this study using Fisher's least squares difference (LSD) test for planned comparisons, after first performing a one-way analysis of variance (ANOVA) test. When *Gorilla* and *Pan* were treated collectively, significant differences between humans and the African apes were assessed using a t-test.

Results

Dorsiflexion

1.) The size standardized shape of the distal tibia is clearly different between humans and African apes (Table 4.4; Figure 4.4). Humans have a statistically equivalent anteroposterior length at the midpoint of the distal tibia to all of the African apes (*Gorilla* p=0.30, *Pan* p=0.14), and a statistically similar mediolateral width at the midpoint of the tibial articular facet (*Gorilla* p=0.043; *Pan* p=0.74). These results imply that anteroposterior and mediolateral measurements taken at the midpoint of the tibial articular surface do not distinguish African apes and humans and differences instead exist at the edges of the talocrural joint. The anteroposterior length on the medial side is significantly longer in African apes than in humans (t=7.97, p<0.0001). The mediolateral width of the anterior aspect of the distal tibia is dramatically longer in African apes than in humans (t=26.8, p<0.0001). In contrast, humans have an anteroposteriorly longer lateral aspect of the distal tibia than African apes (t=16.97, p<0.0001), and have a broader mediolateral width of the posterior aspect of the bone as well (t=15.03, p<0.0001). The two features that differentiate ape and human distal tibia most clearly are the broader mediolateral width of the anterior aspect of the distal tibia in the apes, and an elongated anteroposterior width of the lateral aspect of the distal tibia in humans (top right corner of Figure 4.4). When the 12 complete fossil hominin distal tibia are graphed with humans and African apes, it is clear that they are morphologically similar to modern humans, and conspicuously lack the broad anterior aspect of the distal tibia that is characteristic of vertically climbing primates (Chapter 3). The earliest hominin tibia from *A. anamensis*

Table 4.4. Size-standardized dimensions of distal tibia in humans, African apes, and fossil hominins.

Species/specimen	AP lateral	AP midpoint	AP medial	ML anterior	ML midpoint	ML posterior
African ape	0.92 ± 0.06	1.00 ± 0.06	0.92 ± 0.07	1.36 ± 0.07	1.06 ± 0.06	0.83 ± 0.07
Human	1.04 ± 0.05	0.99 ± 0.05	0.87 ± 0.05	1.17 ± 0.05	1.04 ± 0.04	0.94 ± 0.05
KNM-KP 29285	1.04	0.97	0.82	1.16	1.09	0.96
A.L. 333-6	1.00	1.00	0.88	1.12	1.04	0.97
A.L. 333-7	1.01	0.99	0.84	1.17	1.05	0.96
A.L. 288-1	1.10	0.97	0.82	1.17	0.97	1.01
StW 358	1.07	1.02	0.90	1.10	1.01	0.92
StW 389	1.03	0.98	0.89	1.11	1.03	0.97
KNM-ER 1481	0.97	1.01	0.89	1.15	1.08	0.93
KNM-ER 1500	1.17	1.05	0.83	1.20	0.97	0.85
KNM-ER 2596	1.04	1.06	0.92	1.21	1.01	0.81
OH 35	1.10	0.89	0.90	1.18	1.08	0.90
StW 567	1.04	0.98	0.89	1.11	1.03	0.97
KNM-WT 15000	1.12	1.03	0.90	1.09	0.97	0.92

(KNM-KP 29285), *A. afarensis* (A.L. 288-1, A.L. 333-6, and A.L. 333-7), and *A. africanus* (StW 358, StW 389) have a shape of the distal tibia distinct from the African ape shape, and similar to that found in modern humans (Figure 4.5). All six of the tibiae were within two standard deviations of the modern human mean for all six measures. They were unlike African apes in having an elongated lateral side to the distal tibia, and in having a shortened anterior aspect to the articular surface. Similarly, the six Plio-Pleistocene tibia, KNM-ER 1481, KNM-ER 1500, KNM-ER 2596, OH 35, StW 567, and KNM-WT 15000 were all unlike the African ape distal tibia in lacking the broad anterior aspect to the joint surface (Figure 4.6). KNM-WT 15000, KNM-ER 1481, StW 567, and OH 35 were within two standard deviations of the human mean for all measures. However, there was more variation in these later tibiae, with KNM-ER 1500, and KNM-ER 2596 being the most distinct from the modern human form. Both of these specimens

Figure 4.4. Size-standardized dimensions of African ape and human distal tibia.

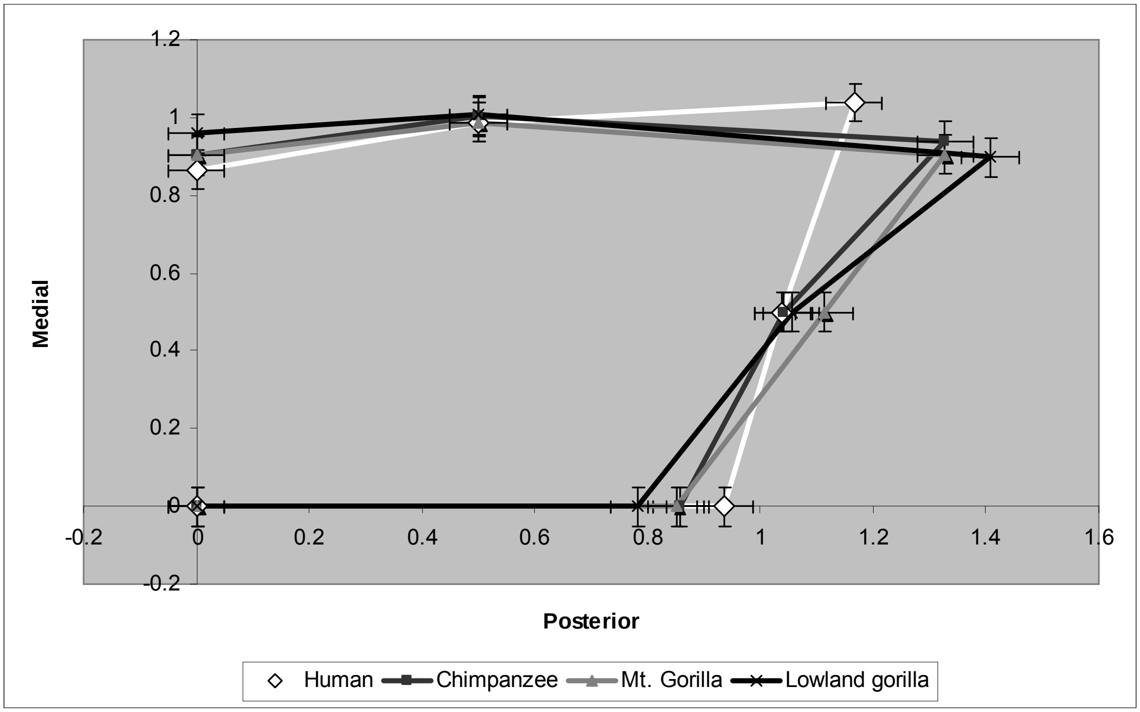


Figure 4.4. Size standardized representation of the shape of the distal tibia in humans (white diamond), chimpanzees (grey square), lowland gorillas (black x) and mountain gorillas (gray triangle). Plotted are the mean values and the bars represent one standard deviation. Anterior is towards the top, lateral towards the right. Humans differ from the African apes in having broader posterior and longer lateral aspects to the distal tibia while African apes have broader anterior and longer medial sides. Note that measures taken at the midpoints of the bone would not discriminate humans from African apes.

have relatively shortened posterior aspects to the distal tibia and KNM-ER 1500 in particular has a lengthened lateral aspect relative to what is found in modern humans. None of the tibiae differ from humans in having African ape-like broader anterior or medial aspects of the joint surface though.

Figure 4.5. Size-standardized shape of articular surface of fossil hominin distal tibia (4.2-2.6 mya).

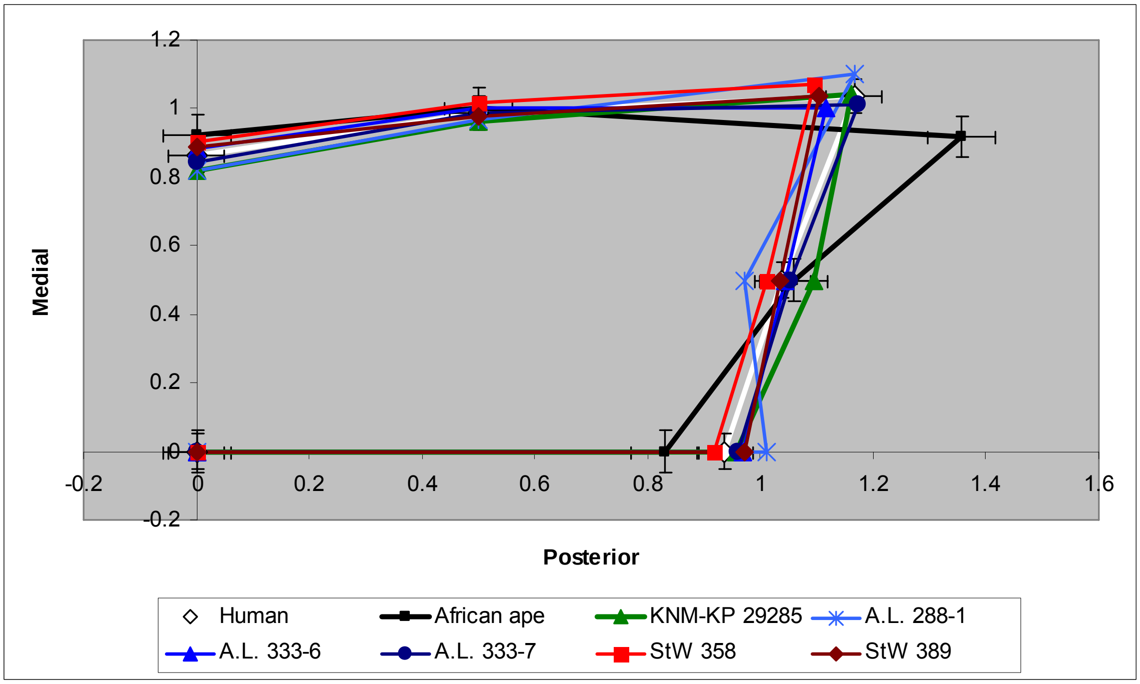


Figure 4.5. Size standardized representation of the shape of the distal tibia in humans (white diamond), African apes (black square), and Pliocene hominins (colors). Plotted are the mean values and the bars represent one standard deviation. Anterior is towards the top, posterior on the bottom, lateral towards the right, and medial to the left. The hominins all lack the relatively broad anterior aspect of the distal tibia typical of African apes and are all human-like in the geometry of the articular surface of the ankle.

Figure 4.6. Size-standardized shape of articular surface of fossil hominin distal tibia (2.0-1.5 mya).

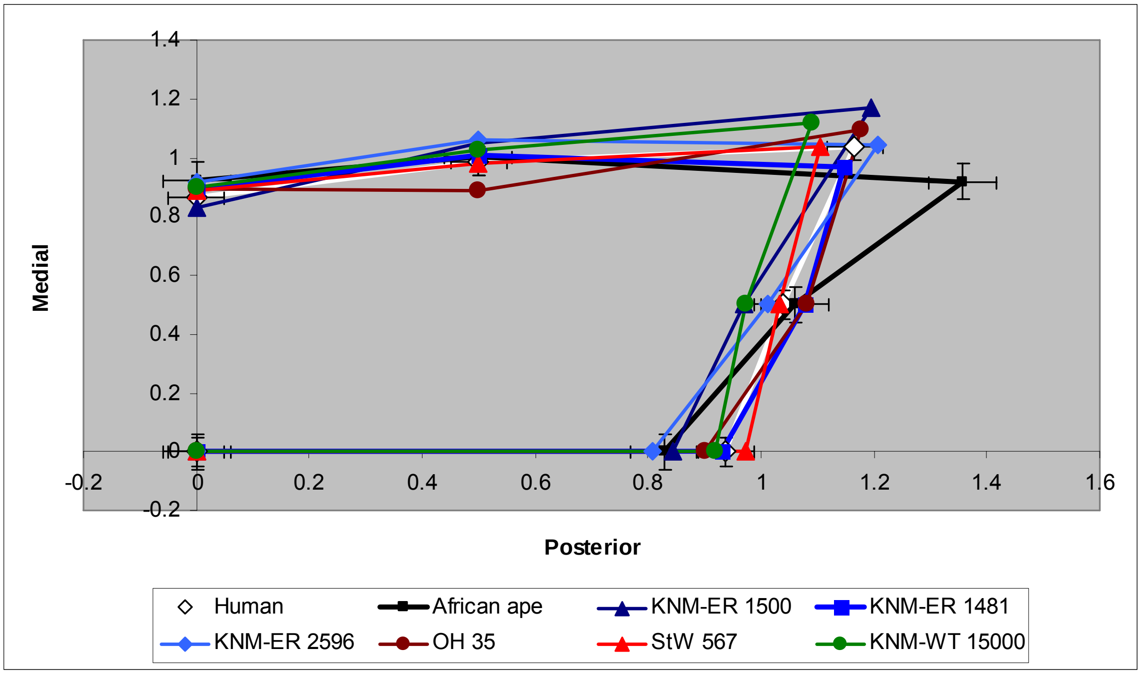


Figure 4.6. Size standardized representation of the shape of the distal tibia in humans (white diamond), African apes (black square), and Pleistocene hominins (colors). Plotted are the mean values and the bars represent one standard deviation. Anterior is towards the top, posterior on the bottom, lateral towards the right, and medial to the left. The hominins all lack the relatively broad anterior aspect of the distal tibia typical of African apes.

When these variables are entered into a discriminant function analysis, humans and African apes can be clearly differentiated, especially along the first function which accounts for 94.8% of the variation (Figure 4.7). Separation on this axis is being driven primarily by the mediolateral width of the anterior aspect of the distal tibia (-0.855), the anteroposterior length of the lateral side of the bone (+0.531), and the mediolateral width of the posterior aspect of the bone (+0.492). All of the fossil hominins entered into the discriminant function analysis clustered with modern humans, with the possible exception of KNM-ER 2596, which was predicted by the discriminant function to group with modern humans, but the hypothesis that it belonged with the chimpanzee group

Figure 4.7. Disciminant function analysis of distal tibial shape in fossil hominins.

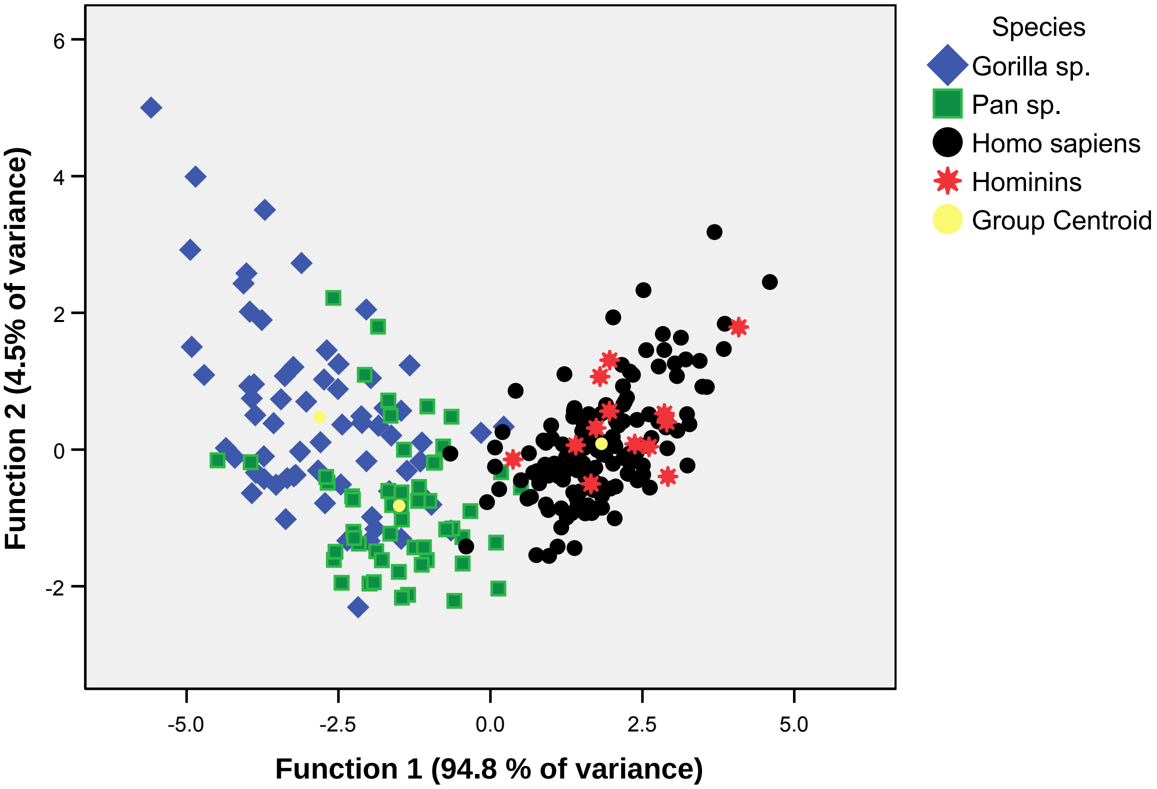


Figure 4.7. Discriminant function analysis on the size-standardized measures of the articular surface of the distal tibia separate the African apes (blue and green) from modern humans (black). Hominins (red stars) fall within the human distribution, though KNM-ER 2596 is the specimen nearest to the ape distribution. Function 1, which explains most of the variance is driven primarily by the anterior mediolateral width of the tibial articular surface (-0.855) and the lateral anteroposterior length of the tibial articular surface (+0.531).

could not be refuted (p=0.286). KNM-ER 2596 differs mostly from modern humans in having a shortened posterior width of the tibial surface.

The results both from the univariate analysis and the discriminant function analysis make it clear that two features best differentiate African ape and human tibia: African apes have broad anterior aspects of the distal tibia, while modern humans have long lateral widths to the bone. When just these two size-standardized dimensions are plotted, all twelve hominin tibiae for which these measures are known cluster tightly

Figure 4.8. Shape of the articular surface of the distal tibia in fossil hominins

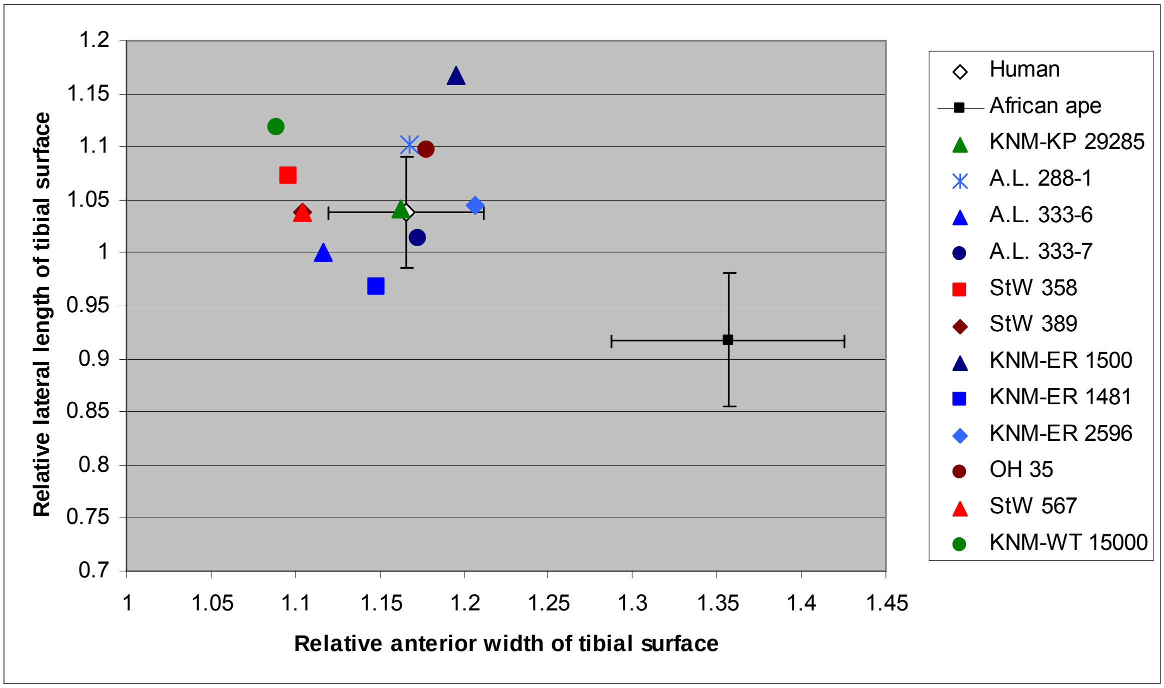


Figure 4.8. Ape distal tibiae have relatively broad anterior surfaces while human distal tibiae have relatively long lateral aspects. When just these two size-standardized measures are plotted, they clearly separate human tibiae (white diamond) from ape tibiae (black square). Plotted are mean values and the bars represent one standard deviation. All of the fossil hominins cluster with modern humans.

around the human distribution (Figure 4.8). Importantly, for those specimens that deviate from the human range (i.e. KNM-ER 1500), they do so in the direction *away* from the morphospace occupied by the African apes, and KNM-ER 2596 is within a standard deviation of the human mean for both of these critical measures.

2.) The wedged shape of the superior surface of the talus was measured by modeling the superior surface of the talus as a cone and taking the angle formed between lateral edge of the talus and a line starting at the most posterolateral corner of the talus and drawn parallel to the medial edge of the talus. This angle is significantly different between humans and the African apes (Figure 4.9), although care should be taken in interpreting this result because this feature did not identify vertical climbing per se in a broader comparative study (Chapter 3). Humans have a weakly wedged talus with an

Figure 4.9. Degree of wedging in the hominin talus.

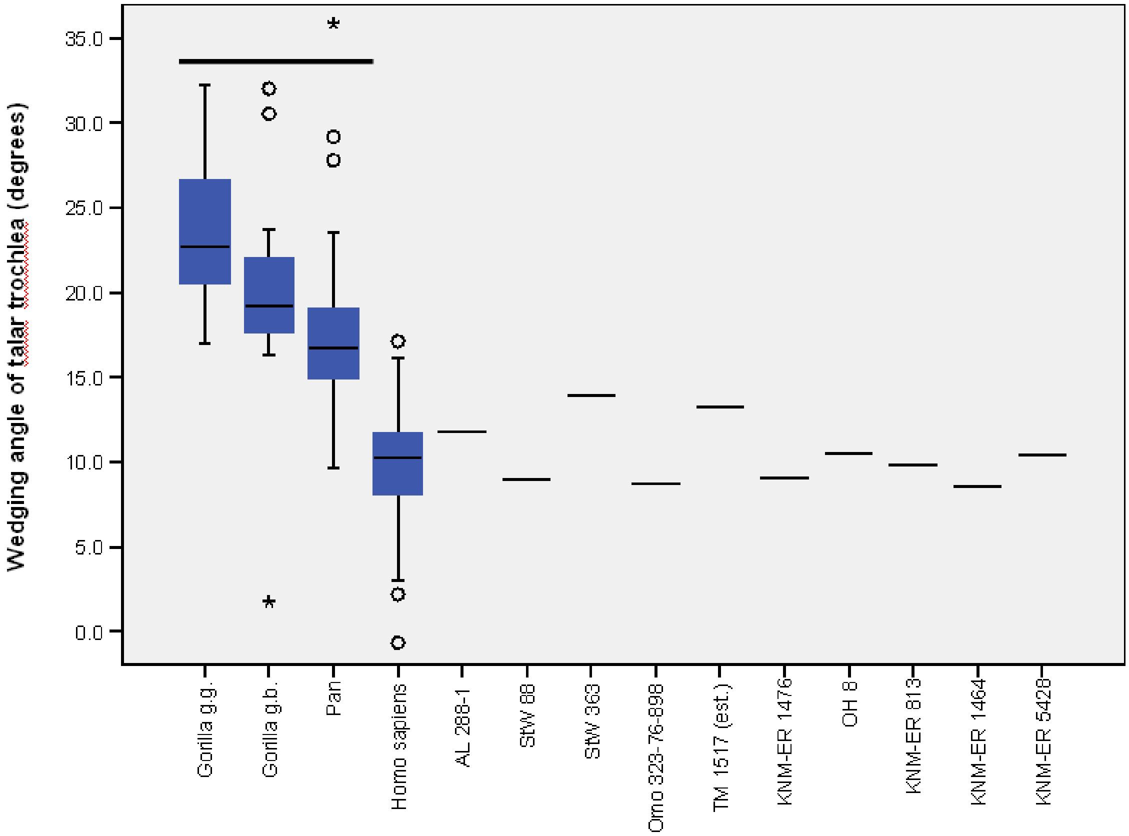


Figure 4.9. Boxplots of the talar wedging angle show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Ape tali have a higher wedging angle, reflecting a broad anterior aspect of the bone. Humans have more even sided lateral and medial talar rims and thus have a more square-shaped talar surface and a lower angle. All of the hominins studied fall within the range of modern humans for this measure.

angle of 10.0˚ ± 3.0˚. This angle is a significantly larger in chimpanzees ($p<0.001$), and in gorillas ($p<0.001$), which have statistically similar angles ($p=0.13$). All of the hominin tali complete enough for this measurement to be made are within one standard deviation of the human mean except TM 1517 and StW 363. These two tali are within two standard deviations of the human mean and within the modern human range, though they have a value closer to the chimpanzee mean for this measure.

3.) Humans have a significantly deeper articular surface of the distal tibia than what is found in the ankle of African apes (Figure 4.10). Again though, this feature did not discriminate vertical climbing primates from other locomotor modes in a wider comparative study (Chapter 3). The human tibial surface has a depth that is 16.1% ± 1.7% of the anteroposterior width of the articular surface. African apes have a flatter tibial surface, only 12.3% ± 2.5% of the tibial width. African apes are statistically equivalent to one another for this measure (*Gorilla gorilla beringei* and *Gorilla gorilla gorilla* (p=0.12); *Gorilla gorilla beringei* and *Pan* (p=0.24); *Gorilla gorilla gorilla* and *Pan* (p=0.58). These difference between the means of each of the African apes and modern humans are statistically significant (p<0.001). The anteroposteriorly flatter tibia of African apes is hypothesized to permit additional range of motion of the tibia over the talus, allowing for the increased dorsiflexion required during vertical climbing. All of the fossil hominin tibia are human-like in having a deeply concave tibial surface, except for OH 35 and KNM-ER 2596. The anterior surface of OH 35 is damaged and thus the inferior extend of the anterior aspect of this tibia could only be estimated. What is presented is a minimum value that would probably have been in the human range in the intact specimen. However, the KNM-ER 2596 distal tibia is striking in its anteroposteriorly flat tibial surface, outside of the range in modern humans.

4.) The dimensions of the tibial metaphysis differed significantly between modern humans and African apes (Figure 4.11). African apes have a more rectangular shape to the distal tibial metaphysis with the anterolateral length representing only 67.2% ± 5.6% the value of the mediolateral width of tibial metaphysis. In contrast, humans have a more

Figure 4.10. Depth of tibial articular surface in fossil hominins.

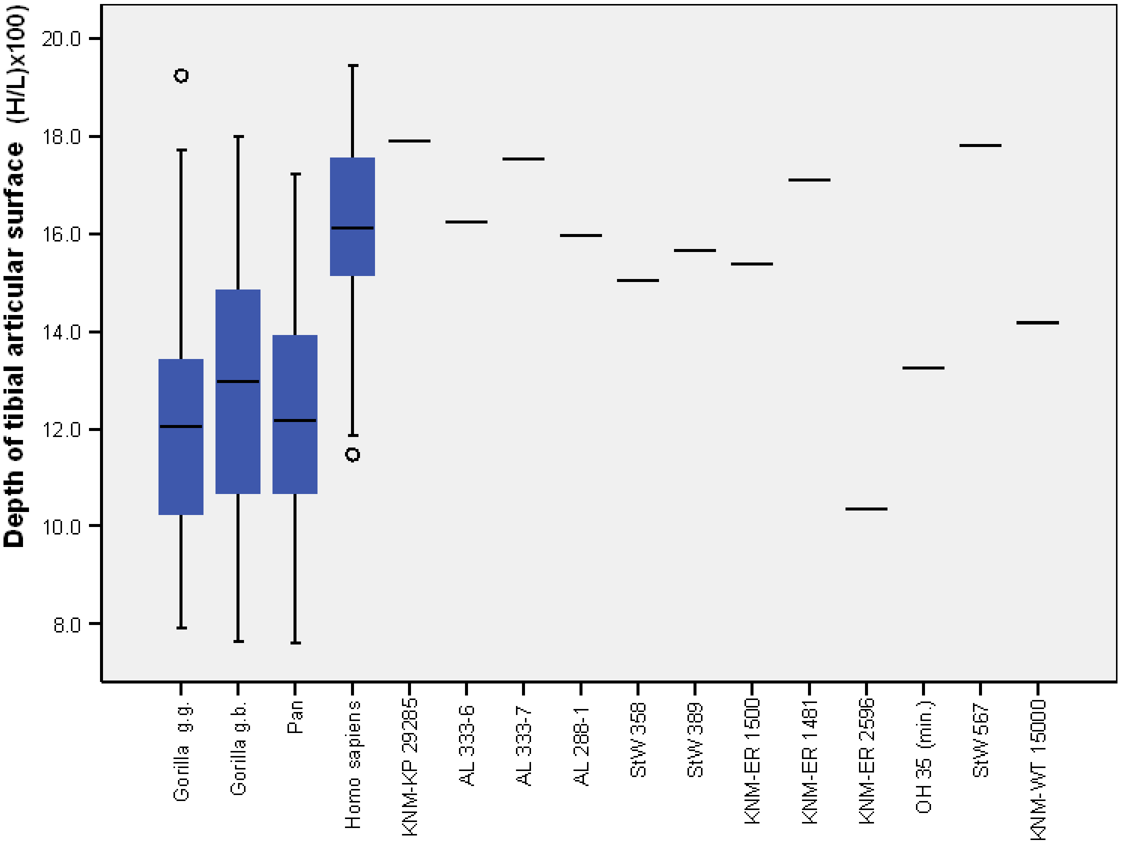


Figure 4.10. The depth of the tibial surface (H) relative to the anteroposterior width of the articular facet (L) distinguishes the flat tibia of African apes from the concave tibia of modern humans. Boxplots of the relative depth of the tibial surface show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Most of the hominin tibiae fall within the range of modern humans except OH 35, which has damage to the anterior aspect of the bone and thus would have had a more concave surface than what is presented here, and KNM-ER 2596, which is quite flat.

square-shaped bone with the anteroposterior length composing 82.2% ± 4.8% of the mediolateral width. *Gorilla gorilla beringei* and *Pan* are statistically equivalent (p=0.43), though *Gorilla gorilla gorilla* has a significantly wider metaphysis (p<0.001) that the other Africa apes. The difference between all of the African apes and humans for this measure is statistically significant (p<0.001). All of the hominin tibiae were distinctly

Figure 4.11. Shape of the metaphysis in the hominin distal tibia.

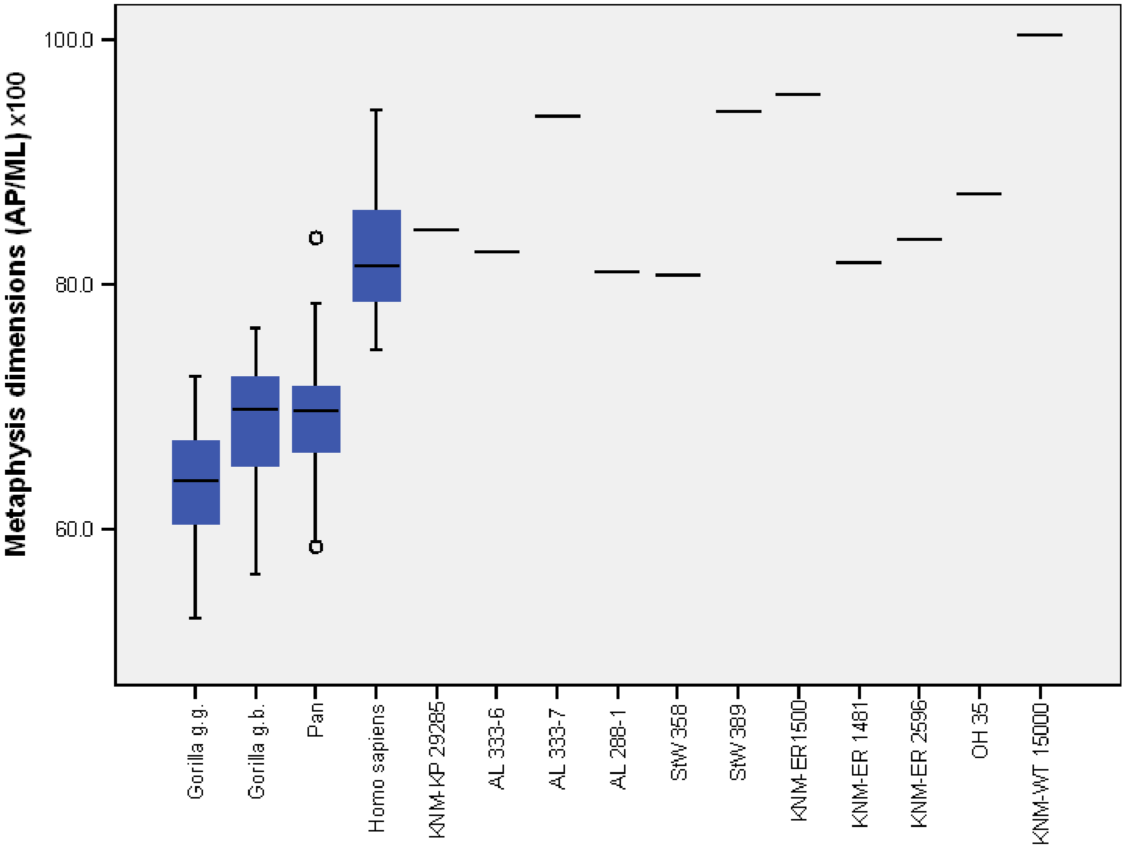


Figure 4.11. The dimensions of the metaphysis of the distal tibia [(ML/AP) *100] differ between the square-shaped human tibiae and the rectangular-shaped African ape tibiae. Boxplots of the shape of the distal tibial metaphysis show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. All of the hominin tibiae are human-like for this measure.

human-like for this measure and did not possess the mediolaterally wide distal tibia typical of African apes.

Abduction

With the talus modeled as a cone, the degree of abduction can be estimated from isolated tali as the apical angle of the cone. The resultant measure is the amount of rotation that occurs when the tibia travels a farther distance over the lateral aspect of the

Figure 4.12. Apical angle of the hominin talus.

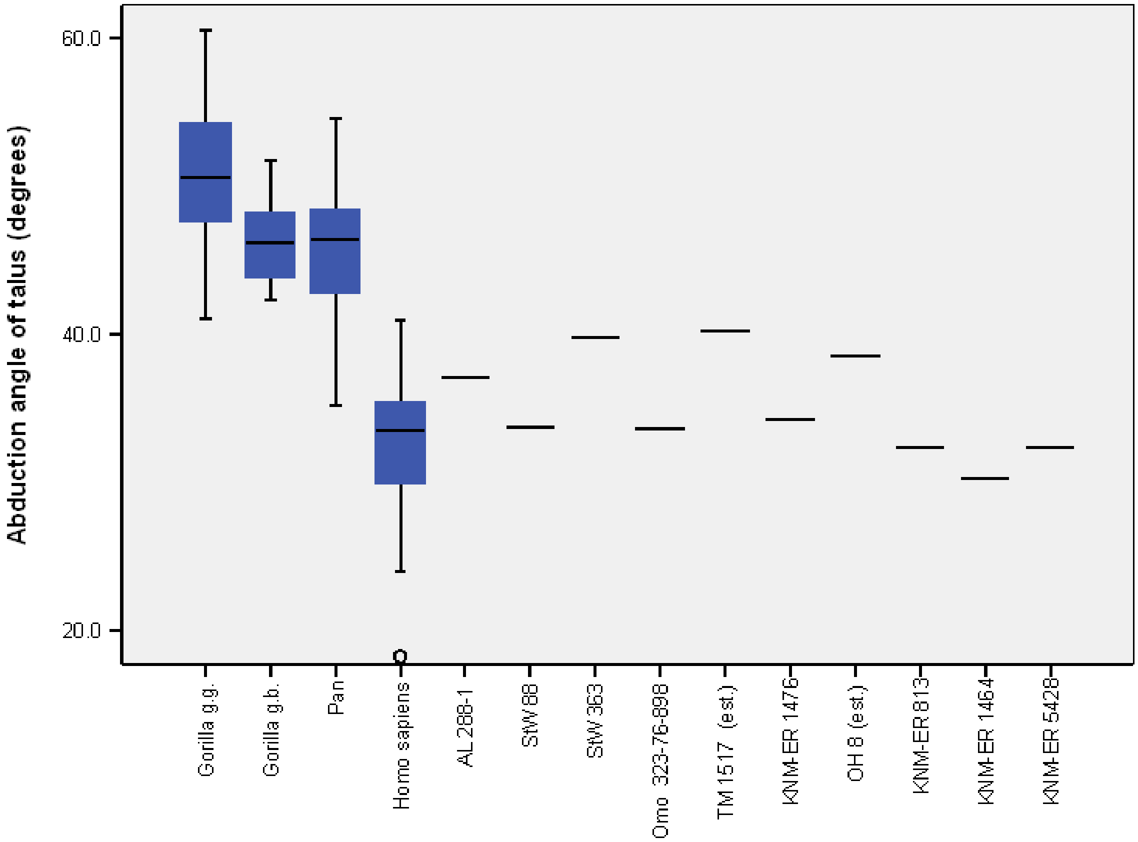


Figure 4.12. With the talus modeled as a cone, the degree of tibial rotation and thus foot abduction can be estimated from isolated tali. Ape tali have much broader anterior and lateral sides which would encourage foot abduction; whereas the human foot experiences less abduction during dorsiflexion. Boxplots of the talar abduction angle (also referred to as the apical angle in the text) show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. All of the hominin tali studied fall within the range of modern humans.

cone than the medial. However, this measure did not discriminate vertically climbing primates from others in a wider comparative study (Chapter 3). Nevertheless, the apical angle of 47.8° ± 6.2° in African apes is significantly greater than the 32.7° ± 4.5° found in modern human tali (t=18.46, $p<0.0001$), and humans have a more acute angle when compared to each of the African ape species individually ($p<0.001$). *Gorilla gorilla beringei* and *Pan* have statistically equivalent apical angles (p=0.40). All of the fossil hominin tali strongly resemble modern humans in the geometry of the talar surface except TM 1517 and StW 363, which both fall between the human and African ape mean (Figure 4.12), within two standard deviations of both.

Adding the tibial dimensions to the talus gives a more accurate representation of the amount of rotation that occurs during dorsiflexion of the tibia over the talus. There was considerable variation within both the African apes and humans for this measure, though *Gorilla gorilla beringei* and *Pan* had statistically equivalent abduction angles ($p=0.67$). African apes collectively have a greater degree of lateral talar rotation under the tibia during dorsiflexion (7.5˚ ± 5.7˚) than do modern humans (-0.08˚ ± 3.4˚) ($t=10.1$, $p<0.0001$), and each African ape species is statistically distinct from modern humans ($p<0.001$). These data suggest that the human talocrural joint is primarily a hinge joint, with very little abduction or adduction occurring during dorsiflexion and plantarflexion. The impact of this morphology on vertical climbing per se is not clear as *Pongo* also possesses a hinge-like morphology. The tibia and talus of A.L. 288-1 falls near the human mean, as does the potentially associated tibia and talus from South African StW 358 and StW 363 (Figure 4.13). The OH 8 and OH 35 bones have a geometry that would force the foot into a<u>d</u>duction during dorsiflexion, opposite of what occurs in the African apes and outside of the modern human distribution. These data suggest that OH 8/OH 35 was moving in a *Pongo*-like manner (Chapter 3) or more likely that these two bones are not from the same individual.

Figure 4.13. Maximum abduction possible in hominin ankle.

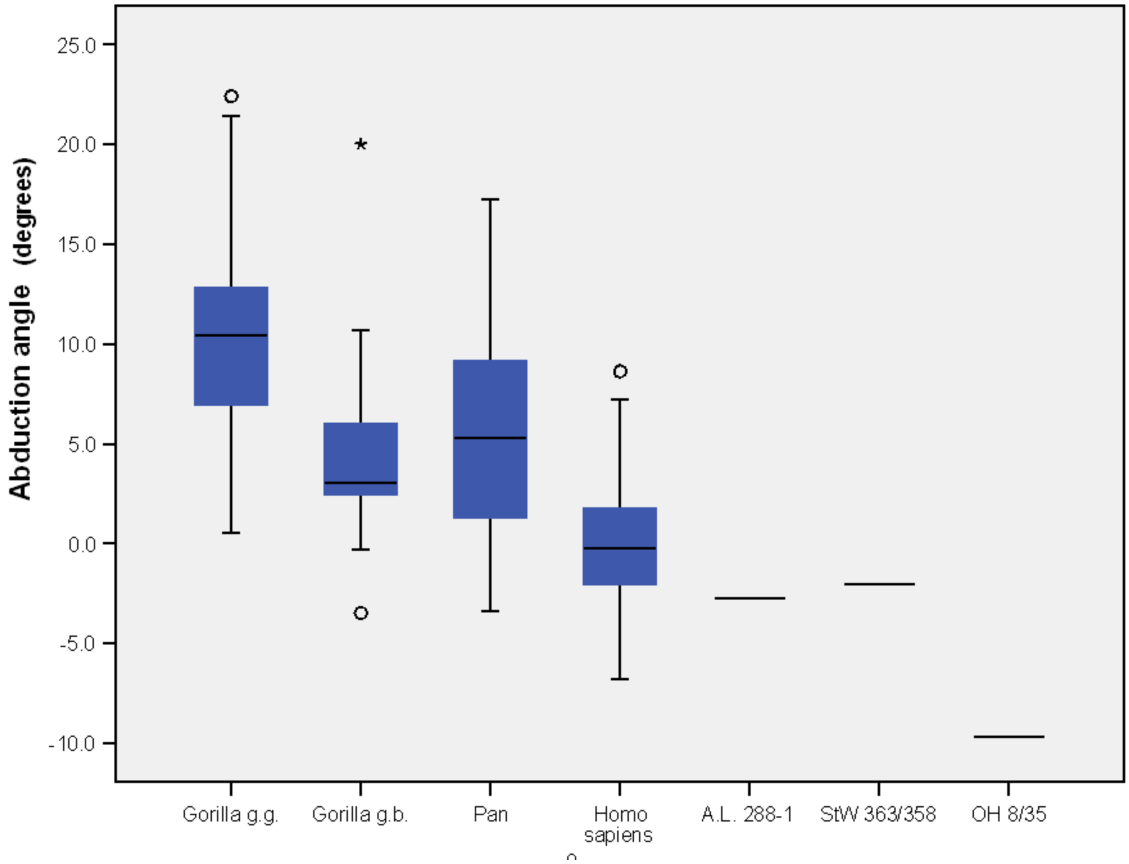


Figure 4.13. By combining the lateral and medial arc lengths of both the tibia and the talus, it can be calculated that African apes have an ankle that permits more internal rotation of the tibia and thus more foot abduction during dorsiflexion than what usually occurs in the human ankle. Boxplots of the total angular abduction at the ankle show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. The fossil tibia and tali from A.L. 288-1 and StW 358/StW 363 are human like in limited abduction. The fossil pair OH 8/OH 35 likely does not derive from the same individual hominin.

<u>Inversion</u>

The angle formed between the long axis of the tibia and the articular surface at the distal end of the bone is 91.1˚ ± 2.4˚ in humans, 102.6˚ ± 4.4˚ in chimpanzees, and 105.7˚ ± 2.5˚ in gorillas (Figure 4.14). The difference between the angle in humans and the African apes is statistically significant ($p<0.001$). KNM-ER 2596 was the only purported hominin specimen to have an ape-like tibia oriented obliquely over the foot at 107.0˚

Figure 4.14. Angle formed between plane of ankle joint and long axis of tibia in hominins.

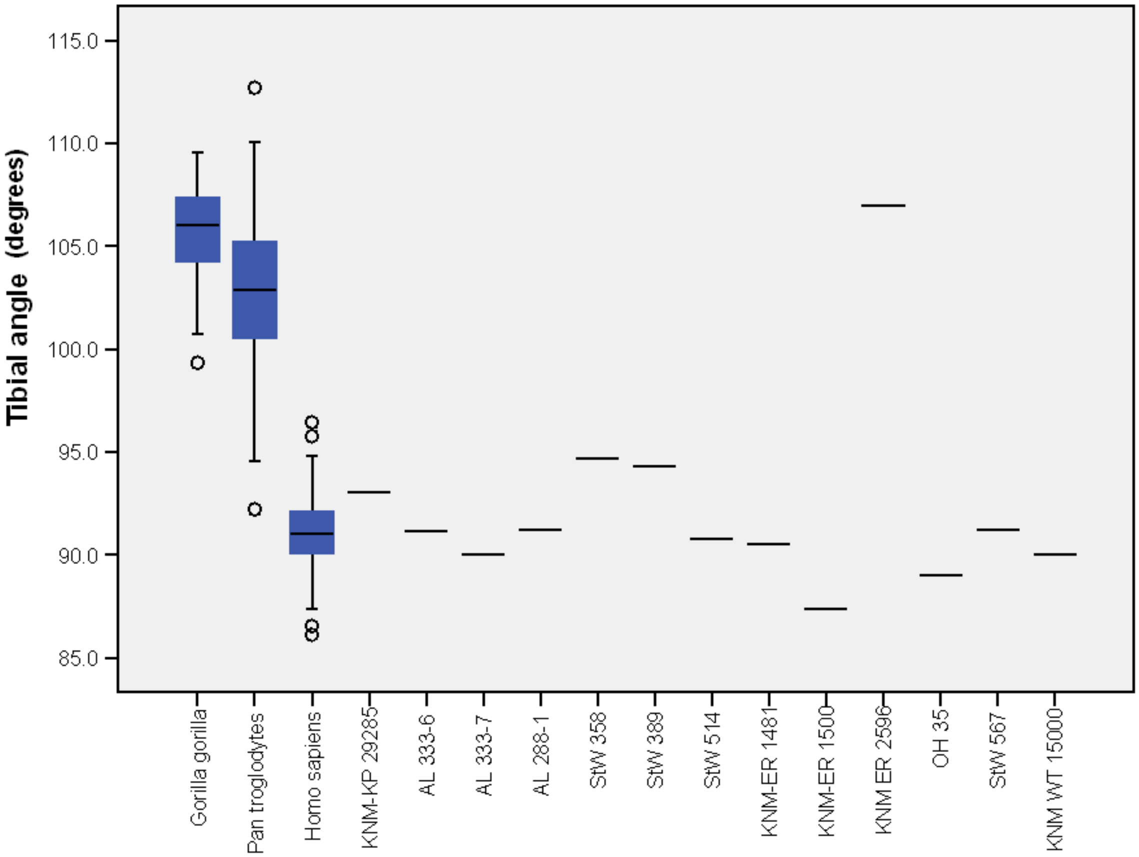
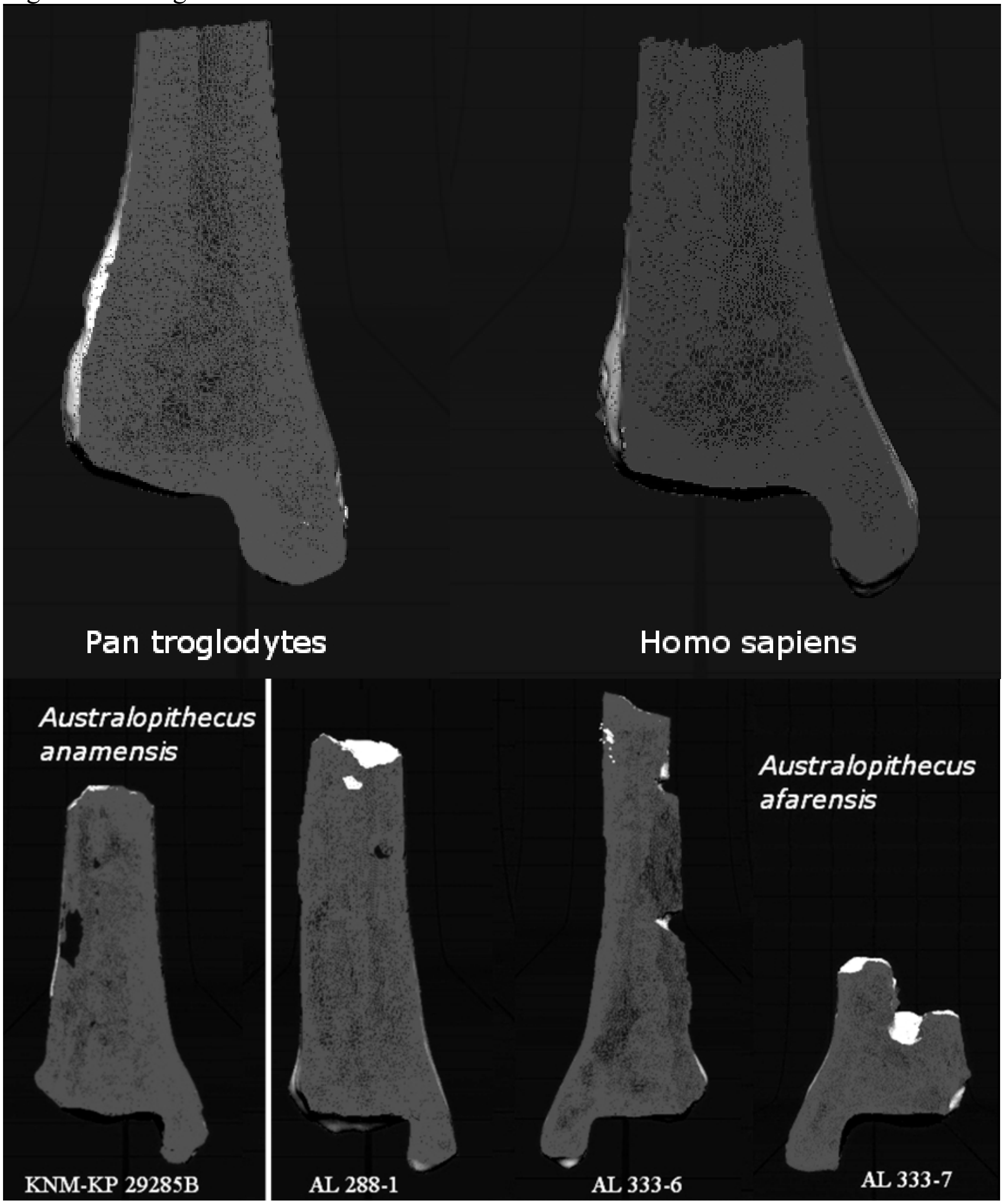


Figure 4.14. Boxplots of the angle formed between the long axis of the tibia and the tibial plafond show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. The long axis of the tibia is perpendicular relative to the talar articular surface in humans and in all hominins except KNM-ER 2596, which shares with the African apes, and other non-human primates, an obliquely oriented joint surface. Interpretations of the KNM-ER 2596 tibia are discussed further in the text.

(Figure 4.15). The *A. anamensis* tibia had a slight tilt to its articular surface of 93.1˚, and two *A. africanus* tibia also had a slight tilt of 94.7˚ and 94.3˚ for StW 358 and StW 389 respectively, though these values are well within the modern range of variation. The *A. africanus* tibia StW 181 was too badly damaged to precisely measure the angle between the articular surface and the long axis of the tibial shaft, though it can be estimated to approximately 93.7˚ by assuming that the distolateral aspect of the tibia shares a conserved angle with chimpanzees and humans. All of the other hominin tibiae were

Figure 4.15. Digital cross-sections of fossil hominin distal tibiae.



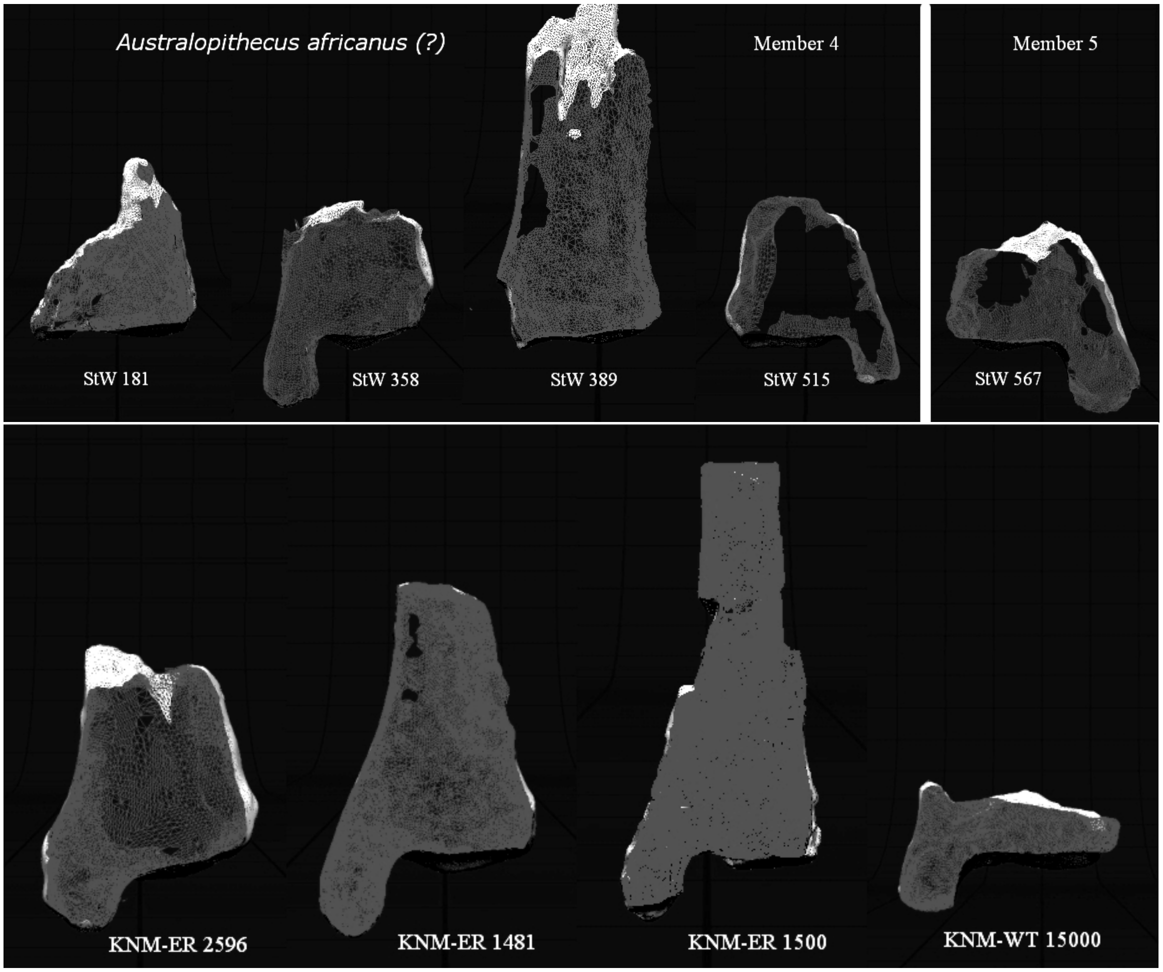


Figure 4.15. Digital cross-sections of the tibiae of a chimpanzee (top left), human (top right), Pliocene East African australopiths (2nd row), South African australopiths and *Homo* (3rd row), and Kenyan Pleistocene hominins (4th row). 3D scans of original fossils and fossil casts (Hadar *A. afarensis*) were acquired with a NextEngine desktop scanner and digital cross-sectioned along the coronal plane using the trim tool in the software ScanStudio. All of the fossils have a human-like horizontal articular surface relative to the long axis of the tibia except KNM-ER 2596 which possesses a valgus ankle. See text for details.

within one standard deviation of the modern human mean, except for KNM-ER 1500 which had a lower angle of 87.4˚, though this too is within the modern human range (Figure 4.14).

The angle formed between the long axis of the ankle and the articular surface of the talocrural using isolated tali discriminated African apes from humans (Figure 4.16).

The angle in chimpanzees is 15.5˚ ± 2.9˚, in lowland gorillas 18.8˚ ± 2.5˚, and 14.2˚ ± 2.8˚ in mountain gorillas. The angle in the human talus is 10.2˚ ± 2.3˚, significantly distinct from the average value measured in the talus of the African apes (t=12.1, p<0.001). Among the African apes, *Gorilla gorilla beringei* and *Pan* have statistically equivalent angles between the axis of rotation and superior surface of the talus (p=0.11). All twelve hominin fossils measured were within the range of variation found in modern humans, though interestingly all twelve have values *below* the human mean, and thus quite distinct from the African ape condition. StW 486, KNM-ER 1476, KNM-ER 813, KNM-ER 1464, and Omo 323-76-898 are within one standard deviation below the human mean, OH 8, TM 1517, StW 363, and KNM-ER 5428 within two standard deviations below the human mean, and A.L. 288-1 and StW 88 are within three standard deviations below the human mean, though all are within the modern human range. When these values are converted to a measure of the angle that the long axis of the tibia forms with its articular surface, the 12 hominin tali give a range of 90.3˚-94.5˚, well within the range of the modern human ankle.

African apes, especially chimpanzees and lowland gorillas, have thicker medial malleoli relative to the mediolateral width of the tibial articular surface than what is found in modern humans (Figure 4.17). Relative to its anteroposterior length, the width of the medial malleolus in African apes is 70.1% ± 6.4%, whereas in humans the relative width of the medial malleolus is 56.6% ± 5.6%. Mountain and lowland gorillas are statistically identical for this measure (p=0.99), though they together have significantly thinner malleoli than chimpanzees (p=0.01). The African apes collectively have a significantly thicker medial malleolus than modern humans (t=19.7, p<0.0001). All of the

Figure 4.16. Geometry of hominin ankle assessed from isolated tali.

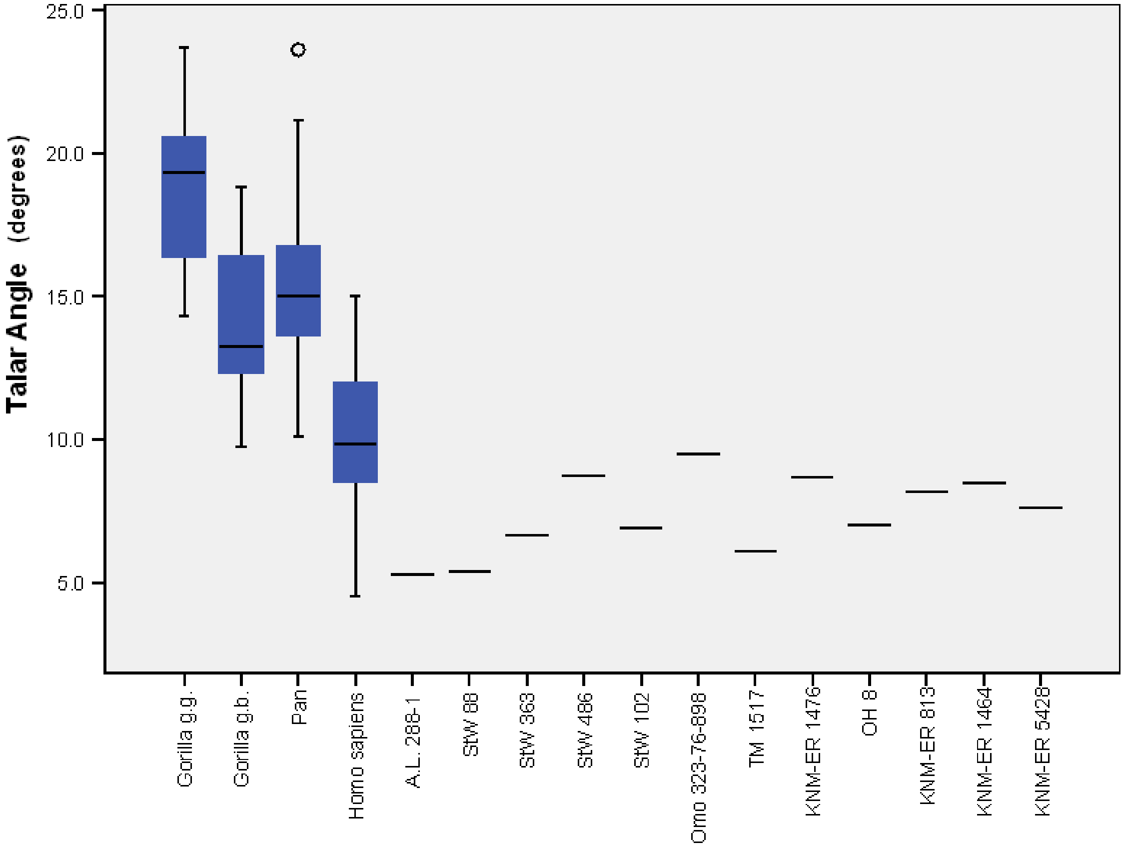


Figure 4.16. Boxplots of the angle formed between the axis of rotation of the talocrural joint and the superior surface of the talus show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. This angle differs between African apes and humans with the low angle in humans directly related to the perpendicular position of the tibia over the talus and consequently a valgus knee. All of the hominins studied had a human-like angle, suggestive of a perpendicular tibia and a valgus knee.

hominin tibiae are human-like, possessing mediolaterally thin medial malleoli, except KNM-ER 1481 and KNM-ER 1500 which both have a relatively thick medial malleolus though still within the range of modern humans. These bones fall between the human and ape condition, within two standard deviations of the mean for both groups.

Human tali have a medial and lateral side with equal radii of curvature (Figure 4.18). However, African ape tali have a flatter medial side of the talus with a larger radius of curvature than the lateral side. The ratio of the medial radius of curvature to the lateral

Figure 4.17. Thickness of the hominin medial malleolus

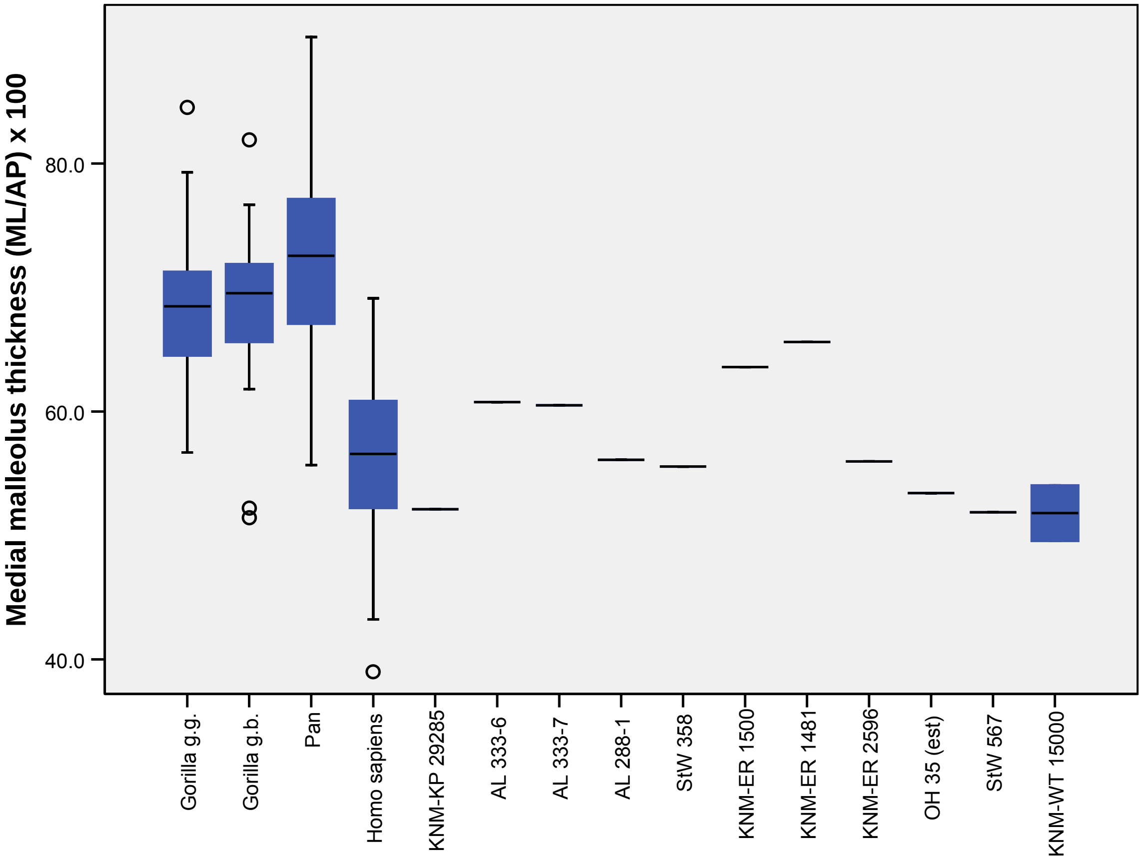


Figure 4.17. Vertically climbing apes have a thicker medial malleolus (ML) relative to the anteroposterior length of the medial malleolus (AP) than modern humans do. Boxplots of the thickness of the medial malleolus show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. KNM-ER 1481 and KNM-ER 1500 have relatively thick medial malleoli, but still fall within the range of modern humans with all of the other fossil hominin tibiae.

radius of curvature is significantly smaller in modern humans than in either *Pan* or *Gorilla* ($p<0.001$). *Gorilla gorilla beringei* and *Pan* have statistically equivalent flattening of the medial side of the talus ($p=0.87$). South African fossil hominin tali StW 486 and TM 1517 have the relatively flattest medial side to the talus and are thus the most African ape-like; however, they, like all other known hominin tali, fall within the modern human range for this feature.

Figure 4.18. Radius of curvature of hominin talus.

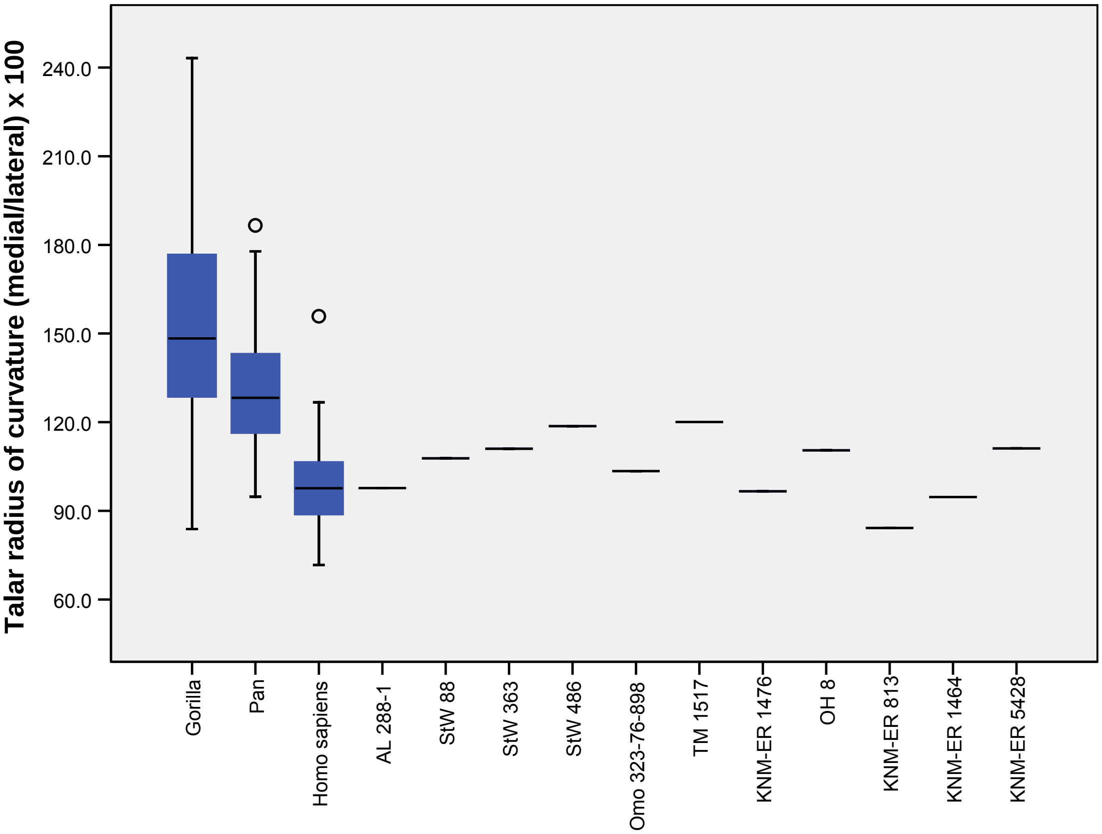


Figure 4.18. Boxplots of the relative radii of curvature in the talus show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. African apes have a lower radius of curvature on the medial side of the talus than modern human tali, which have an equal radius of curvature on the medial and lateral sides. Fossil hominins all fall within the range of modern humans for this value, though StW 486 and TM 1517 have the most medially flattened tali.

Discussion

Early hominins were not chimpanzees, though some have argued that the last common ancestor of humans and chimpanzees was probably quite chimpanzee-like (Wrangham and Pilbeam, 2001), including in its locomotion (Gebo, 1996; Richmond et al., 2001). The use of the chimpanzee as a model for early humans both in terms of behavior and locomotion has been questioned (Sawyer and Lovejoy, 2008). However, when the likelihood of vertical climbing in hominins is discussed in the paleoanthropological literature, the model that is employed is often a chimpanzee one, as exemplified by the biomechanical scenario put forth by Susman et al. (1984) and detailed in the introduction. Sawyer and Lovejoy (2008) have recently argued that the tendency to regard early hominins and australopiths as chimpanzee-like is becoming more and more prevalent. I suggest that climbing adaptations in early hominins have been promoted with the chimpanzee model in mind, but without a rigorous test of the utility of this model. With this study, I attempt to correct that trend by testing whether hominins had adaptations for vertical climbing in an ape-like manner focusing specifically on the morphology of the ankle. It is important to emphasize that this study did not test whether hominins vertically climbed per se, but whether hominins vertically climbed specifically in a manner kinematically similar to that practiced by modern apes, though the results do inform questions of arboreality in general.

During vertical climbing bouts, chimpanzees and gorillas pull their bodies close to the vertical substrate in part via extreme dorsiflexion at the talocrural joint (Chapter 2). In addition, there is inversion and abduction of the foot relative to the long axis of the tibia. Based on data from both orthopaedic and primate studies, it was hypothesized that vertically climbing primates would produce a loading environment at the talocrural joint with high anterior and medial forces and therefore would possess distal tibia with broad anterior and medial aspects and a large medial malleolus. Additionally, the ankle of vertically climbing apes would have a geometry that encourages dorsiflexion, abduction, and inversion. There are some measures used in this study that have been demonstrated to be reliable skeletal indicators of vertical climbing across a wide range of primates (Chapter 3). These include the broad anterior aspect of the tibial articular surface, a mediolaterally wide medial malleolus, and a mediolaterally wide metaphysis. Absence of these morphologies in the hominin talocrural joint provides strong evidence against substantial ape-like vertical climbing in fossil hominins. However, the other morphologies examined in this study, though not particularly effective for identifying vertical climbing per se, are still useful in reconstructing the overall function of the ankle in fossil hominins. These other morphologies, such as the relative tibial depth and the radii of curvature on the talus, may not be adaptations specifically for vertical climbing, but by moving away from this general primate morphology, humans and their fossil predecessors would become even less capable of vertical climbing and more poorly adapted in the ankle for bouts of ape-like arboreal locomotion. These are explained in more detail below.

A size-standardized measure of the distribution of bone on the articular surface of the distal tibia reveals that relative to modern humans, African apes have dramatically broader anterior aspects (Figure 4.4). None of the twelve fossil hominin tibiae ranging in time from 4.12 to 1.5 mya have a broad anterior surface (Figures 4.5 and 4.6), suggesting that no known hominin was adapted to loading its talocrural joint during extremes of dorsiflexion. In contrast, human tibiae are adapted to withstand loads along the posterior and lateral aspects of the ankle. Forces at the ankle are highest during heel strike and push-off, which both occur when the foot is in a position of plantarflexion (Seirig and Arvikar, 1975; Morris, 1977; Stauffer et al., 1977; Burdett, 1982; Czerniecki, 1988; Rodgers, 1978; Nordin and Frankel, 1989), and thus it is suggested here that the broad posterior aspect of the tibial articular surface is an adaptation for reducing these peak forces. This increase in joint force in a position of plantarflexion is also reflected by increased bone strength in the posterior portion of the distal tibia (Hvid, 1985) and an increase in bone volume density and trabecular number, thickness, and orientation in the posterior portion of the distal tibia (Lai et al., 2005). The reasons for the broader lateral aspect of the joint are not as clear, though the rapid pronation of the foot after heel contact (Matsusaka, 1986) may be a factor. Additionally, the increased length of the lateral aspect of the tibia may be a means by which the hominin tibia has minimized the amount of rotation that occurs as the tibia moves over a cone shaped talus. This minimization of tibial rotation over the talus during dorsiflexion, quantified as 0˚ (Figure 4.13 this study); 2.5˚-3˚ (Close, 1956), 2.5˚ (Michelson and Helgemo, 1995), or as great as 6˚ (Leardini et al., 1999) is significantly less than the 8.75˚ estimated for the great apes (Latimer et al., 1987; Figure 4.3 this study). The lower value of rotation of the tibia over the talus estimated in this study is most certainly a result of using only dry bone specimens, and ignoring the role that the deltoid ligament has in limiting movement on the medial aspect of the ankle and encouraging some internal rotation of the tibia during dorsiflexion (Michelson and Helgemo, 1995). However, regardless of approach, by reducing tibial rotation during dorsiflexion, lateral movement is minimized and the human foot remains more or less in the anteroposterior plane of forward movement. In contrast to other studies (Christie, 1977), this study found that the arc lengths of the tibia and corresponding talus of the *A. afarensis* hominin A.L. 288-1 (Lucy) were strikingly human-like and would have resulted in very little foot abduction during dorsiflexion. These data are consistent with results from Latimer et al. (1987). The same results were found on the *A. africanus* StW 358/StW 363 ankle as well (Figure 4.13). This reduction of tibial rotation limits the amount of abduction that occurs at the ankle during dorsiflexion in humans and extinct hominins and is, in part, a function of an elongated lateral aspect of the tibial articular surface. This last statement is particularly the case in interpreting the *A. africanus* fossils given that the StW 363 talus by itself may have suggested more foot abduction (Figure 4.12) than the entire ankle would allow (Figure 4.13). The incongruence between OH 8 and OH 35 (Figure 4.13) lends support to the hypothesis that these two bones do not belong to the same individual (Aiello et al., 1998; Wood et al., 2001; contra Stern and Susman, 1982).

By having more bone devoted to the lateral and posterior portions of the distal tibia, humans necessarily reduce the relative amount of bone that is along the anterior and medial portion of the joint surface. There appears to be a trade off in the distal tibia in which adaptations for efficient force distribution through the talocrural joint surface during bipedalism renders the bone maladapted for joint movements and force distribution incurred during bouts of ape-like vertical climbing. An idealized distal tibia of a hominin well adapted to withstanding the loads incurred on the joint during bipedality and during ape-like vertical climbing may require joint surfaces that are anteriorly and medially large for climbing, and posteriorly and laterally wide for bipedality. It is possible that the size-standardized method employed in this study would not recognize such a bone as both a climber and a biped. However, this hypothetical bone would increase the mass of the distal portion of the tibia and increase the energetic costs of lifting that bone during terrestrial locomotion (Hildebrand, 1985; Steudel, 1990; Minetti et al., 1994). For tibia in which the proximal and distal portions of the tibia are both present (KNM-KP 29285, A.L. 288-1, KNM-ER 1481), the proximal end predicts a hominin of larger mass than the distal end (McHenry, 1992; Leakey et al., 1995). These data suggest that in accordance with the energetic constraints of walking bipedally, hominins by 4.12 mya already had reduced the amount of bone in the distal end of the tibia, slightly reducing the costs of lifting that bone during walking. With the amount of bone at a minimum, the question of where in the joint the hominin distributes that bone becomes even more important in addressing the question of locomotion. The morphology of the known hominin tibiae with long lateral and posterior aspects of the bone, but shortened anterior widths (Figure 4.8), suggest strongly that the evolution of bipedalism rendered their ankles maladapted for ape-like vertical climbing.

Adaptations for distributing force through a dorsiflexed ankle can also be observed in the African ape talus, which has a broad anterior aspect and is thus considered more ‘wedged’ than human tali (Sewall, 1904; Lewis, 1980; Gomberg, 1981; Langdon, 1986; Gebo, 1992; this study Figure 4.9). Because the talus can be modeled as a cone (Inman, 1976; Bremer, 1985; Latimer et al., 1987), a more wedged talus also has a longer lateral than medial side in comparison with a talus that is only weakly wedged. Therefore, the angular measure for talar wedging (Figure 4.9) mirrors the results for the measure of talar abduction (Figure 4.12). The relationship between dorsiflexion and abduction in the ankle is a well established one in humans (Close, 1956; Lewis, 1980; Bremer, 1985; Sigeler et al., 1988; Scott and Winter, 1991; Michelson and Helgemo, 1995; Leardini et al., 1999) and has been argued to be a primate synapomorphy (Dagosto, 1985). African ape tali, with longer arc lengths along the lateral aspect of the joint than the medial, provide a geometry over which the tibia will become internally rotated during dorsiflexion and puts the foot in a position of abduction. The longer lateral side also creates a geometry on the superior aspect of the talus in which the anterior aspect of the articular surface is broad and capable of efficiently distributing forces through a joint loaded in extreme dorsiflexion. Thus, adaptations for dorsiflexion in the talus of African apes result in a joint morphology that increases foot abduction as well. All of the hominin tali studied have a human-like architecture to the superior surface of the talus except perhaps StW 363 and TM 1517. Though towards the ape-like morphology, StW 363 and TM 1517 are still within the range of modern human variation. When StW 363 is combined with the associated tibia StW 358, it lacks the foot abduction typical of vertical climbing African apes (Figure 4.13).

Additional differences between human and African ape ankles demonstrate that adaptations for bipedality result in morphologies that would make vertical climbing in a ape-like manner more difficult, if not impossible. These include morphologies related to the valgus knee of bipedal hominins.

The bicondylar angle of the distal femur has long been argued to represent a critical adaptation for bipedality by positioning the knees directly under the center of mass (Walmsley, 1933; LeGros Clark, 1947; Heiple and Lovejoy, 1971). Work on the talocrural joint (Latimer et al., 1987) linked the ankle to the knee by demonstrating that tibia oriented perpendicularly over the foot occurs only in a lower limb that possesses a valgus knee. Therefore, isolated distal tibia can be used to assess whether that individual hominin had a bicondylar angle of the undiscovered distal femur or not (Figure 4.19). Using the angular relationships developed in Latimer et al. (1987), this study extends distally the elements that can be used to determine whether a hominin had a bicondylar angle. Because of the known relationship between the axis of rotation of the ankle and the superior surface of the talus (Latimer et al., 1987), isolated tali can be used to reconstruct

Figure 4.19. General angular geometry of lower limb in apes and humans.

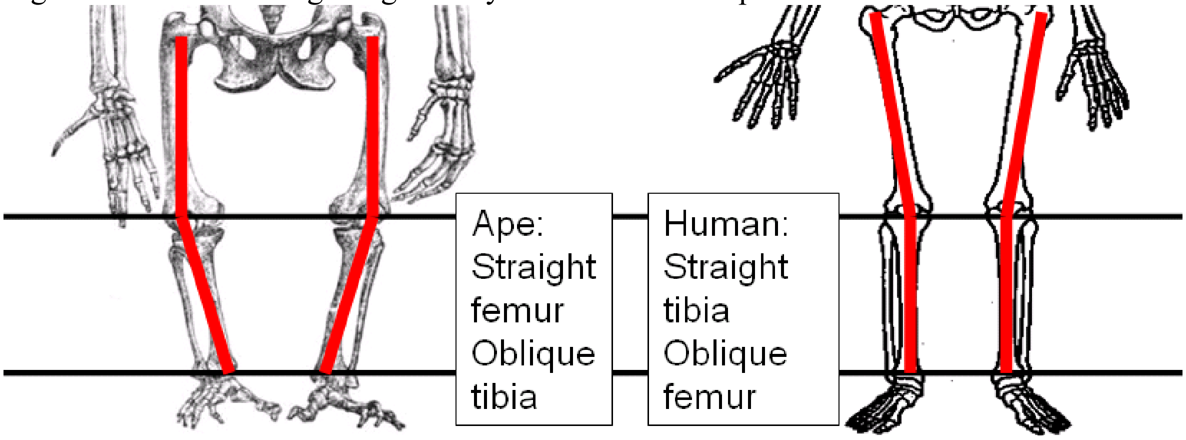


Figure 4.19. Relationship between the bicondylar angle and the angle formed between the long axis of the tibia and the talocrural joint in apes (left) and humans (right). In apes, the femoral shaft is straight or slightly bowed, and the tibia is obliquely oriented over the feet. This orientation positions the feet under the center of gravity, but not the knees, which allows the foot to be easily inverted against a tree during vertical climbing bouts. However, humans (right) have both the knees and the ankles under the center of gravity. This is obtained by obliquely orienting the femur, while evolving a straight tibia relative to the plane of the talocrural joint. This morphology is adaptive for bipedalism, and maladaptive for climbing.

the orientation of the long axis of the tibia over the foot (Figure 4.3), and therefore determine whether the knee was in a varus or valgus position. These data imply that an isolated talus may be used to reconstruct the general geometry of the entire lower limb, from the orientation of the tibia over the foot, to the position of the knee. The angle of the tibia in 12 hominin tibia and 12 hominin tali are in the modern human range and either directly or indirectly demonstrate that these 24 hominins had a perpendicularly oriented tibia over the foot, and therefore all 24 hominins would also possess a valgus knee and bicondylar angle. Specimens for which a distal femur is also present (A.L. 288-1, KNM-ER 1481, KNM-ER 1500, and KNM-WT 15000) corroborate this hypothesis. A single purported hominin distal tibia, KNM-ER 2596, has an obliquely angled tibia over the talus and thus would have had a varus knee position. The implications of this are discussed below.

The presence of a perpendicularly oriented tibia over the talus and a valgus knee in all but one of the hominin fossils studied, suggests these individuals were adapted for bipedality by positioning both the knee and ankle directly under the center of gravity. However, this adaptation for upright walking maladapts the lower limb for vertical climbing in an ape-like manner. An obliquely oriented tibia over the talus naturally puts the foot in an inverted position. Chimpanzees place the sole of their foot against the side of the vertical substrate during vertical climbing bouts. Having an obliquely oriented tibia relative to the talus allows the ape to keep its leg close to the tree and close to the center of gravity while still maintaining an inverted position of the foot against the side of the tree (Preuschoft, 1970; Chapter 2). However, having a perpendicularly oriented tibia over the talus, as is the case in modern humans and in fossils hominins (except KNM-ER 2596), precludes climbing in this ape-like manner. Instead, this morphology forces a climbing hominin to adopt one of two other climbing strategies. 1.) The sole of the foot is placed along the side of the tree as in modern chimpanzees and the knees are splayed outwards. 2.) The sole of the foot is positioned on the anterior portion of the tree and extreme dorsiflexion at the talocrural joint brings the climbing hominin close to the vertical substrate. Given that data from the tibial articular surface already suggest that hominins were not loading their joint in positions of extreme dorsiflexion (Figures 4.5, 4.6 and 4.9) and given that they may not have been capable of positions of extreme dorsiflexion at all (Chapter 5; Figure 4.10), the more likely climbing strategy is one in which that knees splay laterally and the hominin ascends vertically in a pulse like manner. This is occasionally practiced in modern human populations (Devine, 1985) and has been observed as a climbing strategy in modern baboons (Hunt, 1991; Chapter 2) and orangutans (MacKinnon, 1974). This approach would increase the shear forces on both the ankle and the knee during climbing (Latimer et al., 1987). Thus, the orientation of the tibia over the talus in all but one fossil hominin demonstrates that if these early bipeds were climbing, they were probably not climbing in a manner similar to that practiced by modern apes.

The adoption of bipedality by early hominins increased the load being absorbed by the distal tibia. Adaptations to this increased load include both an increase in the anteroposterior dimensions of the bone (Figure 4.11), and the depth of the articular surface of the distal tibia (Figure 4.10). However, both of these adaptations hinder the ability of the hominin to dorsiflex to the extremes at the ankle necessary to vertically climb like a chimpanzee or a gorilla. Having anteroposteriorly short and mediolaterally wide distal tibia with relatively flattened articular surfaces, Africa apes are able to both increase their range of flexion, and efficiently distribute mediolateral forces through the ankle joint. An expansion of the anteroposterior dimensions of the distal tibia in hominins allow them to more efficiently distribute axial forces that occur during bipedal walking, however, this also implies that during dorsiflexion, the anterior edge of the bone will meet the talar neck sooner than in bones with shortened anteroposterior dimensions. In addition, the deeply concave articular surface of the distal tibia may serve two roles. First, a curved surface increases the area of the bone, without increasing any of its linear dimensions. Treated as a flat surface, an average human distal tibia has a surface area of about 7.7 cm^2, but when the average curvature of 16.1% the length of the tibial surface

(Figure 4.10) is considered as well, the area increases to 8.3 cm^2, an addition of roughly 8%. The pressure on the distal tibia is reduced by having a curved surface. In addition, and perhaps more importantly, forces are best distributed through a joint if they remain perpendicular to the articular surface maximizing the compressive component of the force (where bone is strongest), and minimizing shear forces (Latimer et al., 1987; Hamrick, 1999). During walking, humans range from 20 degrees of dorsiflexion to 50 degrees of plantarflexion (Donatelli, 1990) and only a curved surface permits forces to remain perpendicular through the entire range of motion. The curved arch of the distal tibia has been hypothesized to be critical for maintaining joint strength (Lauge-Pedersen et al., 2002).

All of the fossil hominin tibiae studied possessed anteroposterior dimensions within the human range, and distinct from the mediolaterally expanded tibia found in the African apes. The depth of the articular surface was human-like and reflective of committed bipedality in all hominin tibia except OH 35 and KNM-ER 2596. As explained in the results section, the OH 35 tibia is damaged anteriorly and a minimum depth of the articular surface could only be estimated. These data imply that the adoption of bipedality resulted in adaptations related to the efficient distribution of forces through the joint surface that are in direct conflict with the motions necessary to climb in a ape-like manner. An anteroposteriorly wide distal tibia with a deeply concave articular surface would not be able to achieve the ranges of dorsiflexion that permit apes to pull their bodies close to the vertical substrate thus reducing their climbing costs. However, the KNM-ER 2596 tibia is decidedly flat in the anteroposterior direction, and thus unlike that found in modern humans or the other extinct hominins. The implications of this morphology are discussed below.

Posterior tilt

Much has been made of the posterior tilt of the tibial articular surface in the sagittal plane. It has been suggested to reflect a “plantarflexed set” to the talocrural joint, which would aid in arboreality and perhaps even in hindlimb hanging positions (Stern and Susman, 1983; Susman et al., 1984; Hunt, 1994). The posterior tilt to the joint axis occurs in A.L. 288-1 (Stern and Susman, 1983) and though suggested for the *A. africanus* tibia StW 514b (Berger and Tobias, 1996), it is not complete enough to make this determination (pers. obs.). There is also great variation in this feature and its functional significance is unclear (Latimer et al., 1987).

If this feature was related to hindlimb grasping, the species that engages in hindlimb grasping the most of the apes (*Pongo*) should have the most plantarflexed set to the joint. This is clearly not the case (Figure 4.20). Instead, all of the apes have roughly the same angle, considerably less than what is found in modern humans and in most hominins. Only A.L. 288-1, and the presumably *Homo* distal tibia StW 567 have anteriorly prolonged articular surfaces outside of the range of modern humans, and thus a plantarflexed set to the joint. It is not entirely clear what this morphology would have meant for these individuals though it is suggested here that this morphology is neither functionally ambiguous (contra Latimer et al., 1987) nor does it aid in arboreality (contra Stern and Susman, 1983; Susman et al., 1984; Hunt, 1994).

Figure 4.20. Dorsiflexed “set” to the hominin ankle in the sagittal plane.

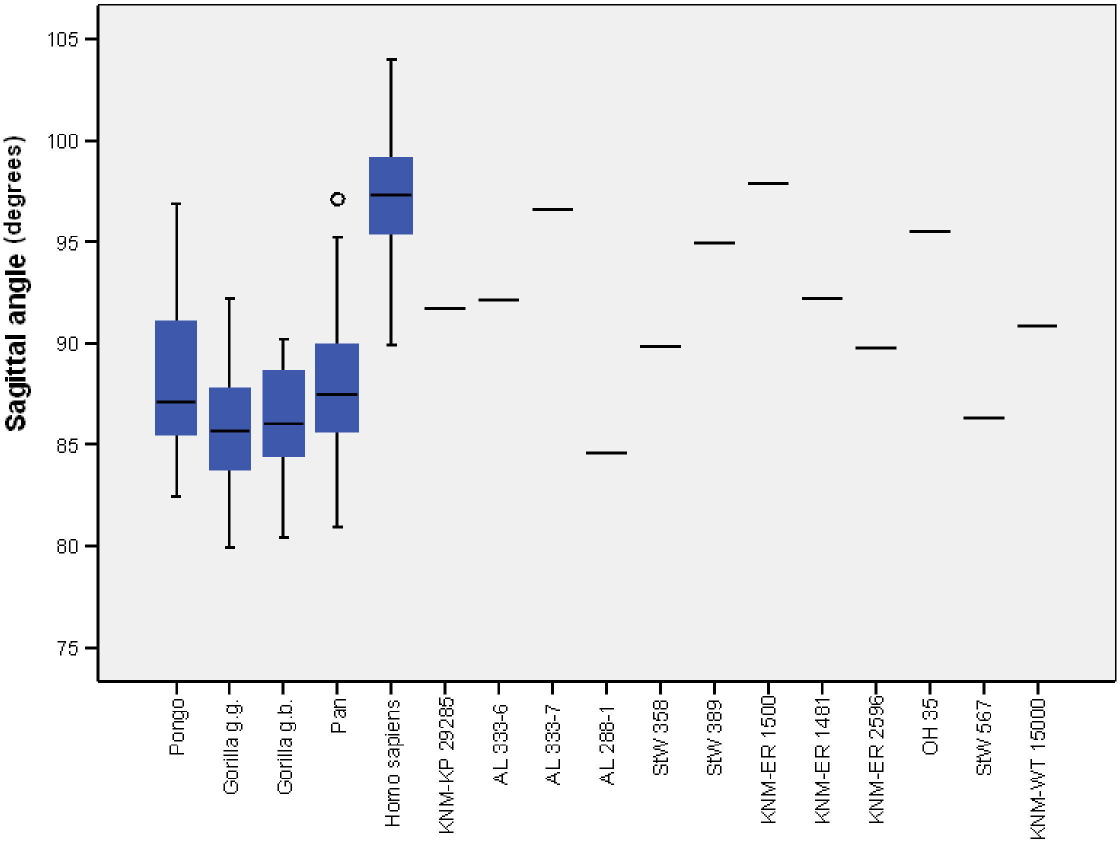


Figure 4.20. The angle formed between the articular surface of the distal tibia and the long axis of the tibia in the sagittal plane in humans, apes and hominins. Boxplots of this angle show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Humans have a posteriorly tilted joint surface, whereas the apes have a perpendicular or anteriorly tilted joint surface. There is no difference between the African apes and orangutans for this measure. The hominins fall within the human distribution except for A.L. 288-1 and StW 567 (explained in text).

If the articular surface is to remain perpendicular to the talar trochlea throughout the range of motion, the sagittal plane of the distal tibia should tilt posteriorly in individuals with a longitudinal arch (Figure 4.21). This morphology can be found in most modern humans. One ramification of this morphology has to do with the range of dorsiflexion and plantarflexion, and loading of the joint in these directions. As is apparent from the model in Figure 4.21, those with a longitudinal arch would have a limited capacity for dorsiflexion because anterior aspect of the distal tibia would impinge on the dorsally tilted talar neck after only slight dorsiflexion; whereas a flat-footed individual would have the opportunity for more substantial dorsiflexion. If this were the case, then within the human population there should be a relationship between the tilt of the tibial surface in the sagittal plane and the morphology of the anterior aspect of the distal tibia. Specifically, modern humans with a greater posterior tilt to the distal tibia should have a greater potential for dorsiflexion and therefore an expanded anterior aspect of the talar facet. The posterior tilt to the distal tibia and the size-standardized with of the anterior aspect of the tibia are indeed correlated (Figure 4.21) (r=0.279, df=67, t=2.38, p=0.01). Importantly, though the sagittal angle of A.L. 288-1 and StW 567 suggest that these two individuals may have had lower arches or even flat feet, neither hominin loaded the anterior aspects of their distal tibia more than the average modern human with or without flat feet (Figure 4.22). Even though these two hominins may have been capable of more dorsiflexion given the geometry of their tibia, they did not load their tibia in positions of extreme dorsiflexion, and thus probably did not engage in much, if any, ape-like vertical climbing. Therefore, it is argued here that the posterior tilt to the distal tibia is not, by itself, evidence for arboreal activities in early hominins (contra Stern and Susman, 1983; Susman et al., 1984; Hunt, 1994). Instead, this morphology in A.L. 288-1 and StW 567 would have enabled these hominins to have a greater range of dorsiflexion, although the distribution of bone on the articular surface suggests that they did not regularly load their talocrural joint in this manner.

Figure 4.21. Models of flatfootedness in early hominins.

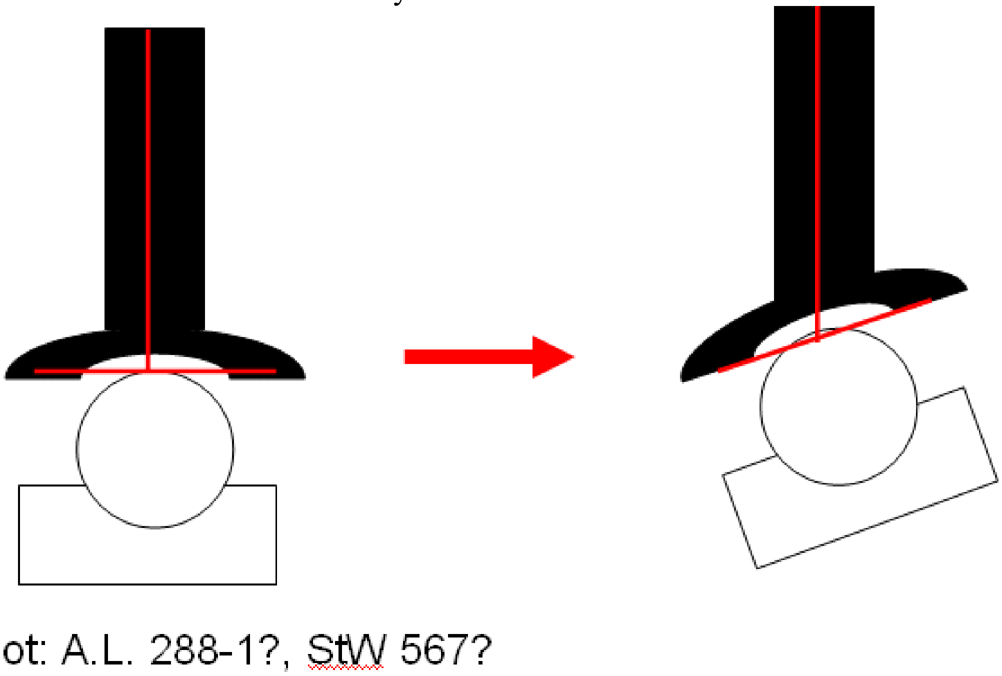


Figure 4.21. Model of the relationship between the plantarflexed tilt of the distal tibia in sagittal view and the presence of a longitudinal arch. In order to maintain a tibia perpendicular to the ground, the articular surface of the distal tibia must be posteriorly tilted in feet with a high longitudinal arch (figure on right), whereas a flatter foot (left) can be tilted anteriorly or be perpendicular to the long axis of the bone. A low medial arch in the foot of AL 288-1 and StW 567 may explain the relatively low sagittal angle found in these tibiae (Figure 4.23).

The unusual morphology of A.L. 288-1 and StW 567 reveals information about these two as individuals, rather than saying anything about general species level morphology or behavior. A.L. 333-6, and A.L. 333-7, other members of *A. afarensis*, have a modern human-like sagittal tilt to the articular surface of the distal tibia. Although A.L. 288-1 may have had relatively flat feet, her species may have had individuals with well developed longitudinal arches as demonstrated by other tibia, foot bones (see Chapter 7), and the Laetoli footprints (White, 1980; White and Suwa, 1987). Additionally, StW 567, most likely a distal tibia of *Homo erectus* (Kuman and Clark,

Figure 4.22. Relationship between plantarflexed set to human ankle and shape of articular surface.

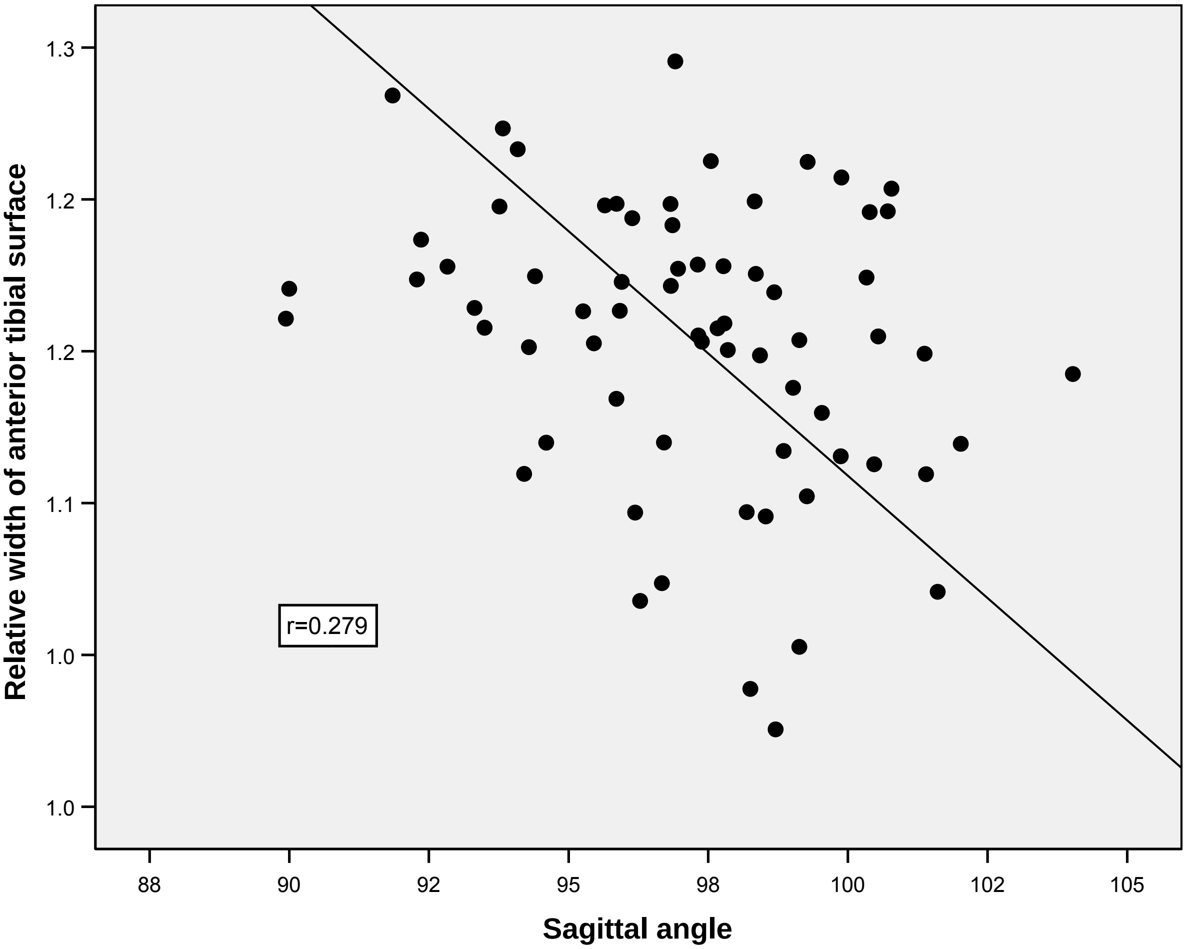


Figure 4.22. The relative width of the anterior surface of the talar facet on the distal tibia of modern humans (n=69) is expanded in tibia with a “plantarflexed set”, measured by the low angle between the long axis of the tibia and the articular surface in the sagittal plane. The line drawn is the RMA regression line (m=-0.016, b=2.72). The broad anterior surface on plantarflexed tibia may be evidence that this angle is related to the height of the medial arch as modeled in Figure 4.24.

2000; Curnoe and Tobias, 2006) is one member of a species that almost certainly had a high proportion of individuals with a well developed longitudinal arch (Bramble and Lieberman, 2004; Lordkipanidze et al., 2007; Chapter 7) including KNM-WT 15000 and perhaps KNM-ER 1481 (Figure 4.21). Thus, just as in the modern human population today, flat-footedness may have been variably present.

The issue of KNM-ER 2596

KNM-ER 2596 has not been described in detail but was identified by Walker and Leakey (1985) as a hominin, though notes at the National Museum of Kenya suggest it may be from a *Theropithecus*. This is the first thorough treatment of this fossil.

The results from this study demonstrate that many of the adaptations for bipedality in the ankle joint of early hominins would have maladapted them for the positions and loading environments encountered in the ankle joint of vertically climbing African apes. These include a perpendicularly oriented tibia over the foot, and a deeply concave articular surface of the distal tibia which would limit inversion and dorsiflexion respectively. However, for both of these measures, the distal tibia KNM-ER 2596 is unlike modern humans (Figures 4.10, 4.14, 4.15). This tibia has an oblique orientation of the long axis over the articular surface, implying that this individual did not possess a valgus knee and therefore may have walked with a bent hip-bent knee (Lovejoy, 2005), whether bipedally or quadrupedally. In addition, the shallow depth of the articular surface would have allowed an increased range of dorsiflexion at the ankle. However, even though this individual would have been able to achieve positions of inversion and dorsiflexion at the ankle, there is little evidence that the ankle was frequently loaded in these joint positions. The medial malleolus, though short and stout, does not have the relative thickness found in modern ape medial malleoli (Figure 4.17), and unlike African apes, this tibia does not possess the broad anterior surface adaptive for bouts of vertical climbing (Figure 4.6). There is also the complete absence of a distal fibular facet, which

Figure 4.23. Distal tibia KNM-ER 2596.

Figure 4.23. The 1.9 mya distal tibia from Koobi Fora, Kenya KNM-ER 2596 in (from left to right) anterior, lateral, posterior, medial, and inferior views. Notice in anterior and posterior view the valgus tilt to the articular surface (also clear in Figure 4.18). In the lateral view image, note the expanded metaphysis relative to the tibial shaft.

implies that unlike apes, this individual did not have a strong grasping hallux (Figure 4.23).

The obliquely tilted tibia, square shaped articular facet, weakly developed medial malleolus, and absence of a distal fibular facet are all features present to varying degrees in cercopithecoid distal tibia of the same general size. However, this bone is not from the similarly sized and contemporary *Theropithecus oswaldii* (Figure 4.23). The distal tibiae of *Theropithecus* have very strongly keeled anteroposteriorly directed midline to the distal tibia, and the medial malleolus has both a bulbous anteromedial portion and a deep intercollicular groove for the posterior tibiotalar ligament (Chapters 3 and 5). KNM-ER 2596 has a mediolaterally flat tibial surface, and a very weak attachment for the posterior tibiotalar ligament on an anteromedially flat medial malleolus. However, there is another large-bodied primate from the Koobi Fora deposits, *Rhinocolobus* (Leakey, 1982). There are two distal tibia identified as coming from *Rhinocolobus* in the Kenya National Museum: KNM-ER 1542 and KNM-ER 45613, though the second of these two is quite unlike ER 1542 and likely to be from a *Theropithecus oswaldii* instead. KNM-ER 1542, like KNM-ER 2596 has a relatively flat anteromedial portion of the medial malleolus, and a mediolaterally flattened articular surface of the distal tibia when compared to *Theropithecus*. There are adaptations in the upper limb of the KNM-ER 1542 skeleton for arboreality and likewise, the KNM-ER 1542 distal tibia has morphology consistent with an arboreal large-bodied colobine (Chapter 3). KNM-ER 2596, however, possesses a key morphology thought to be related to terrestriality, and in particular bipedality.

The metaphysis of KNM-ER 2596 is expanded to a degree only found in modern humans and hominins (Figure 4.24). This expanded metaphyseal volume has been argued to be an adaptation for absorbing the large forces incurred during bipedalism (Kunos and Latimer, 2000) and has been used as evidence for bipedality in early hominins such as *A. anamensis* (Leakey et al., 1995; Ward et al., 2001). Importantly, *Rhinocolobus* does not have this expanded volume. The more terrestrial *Theropithecus* possesses a larger relative metaphyseal volume than *Rhinocolobus*, though still significantly less than what is present in KNM-ER 2596 (Figure 4.26).

The combination of morphology present in the KNM-ER 2596 tibia is perplexing. The expanded metaphyseal volume suggests strongly that this individual was terrestrial, and perhaps even bipedal. However, the obliquely oriented tibia over the articular surface is evidence that the individual did not possess a valgus knee and may have walked in a bent-hip, bent-knee fashion. The inverted set to the articular surface also adapts KNM-ER 2596 for bouts of climbing. Additionally, this individual would have been capable of extreme dorsiflexion, both because of the shallow depth of the tibial articular surface and the absence of a strong attachment for the deltoid ligament (Chapter 5). However, there is little evidence for frequent loading of the joint in these positions of inversion and dorsiflexion because the medial malleolus is not robust, and the tibial articular surface

Figure 4.24. Expansion of distal tibial metaphysis in hominins.

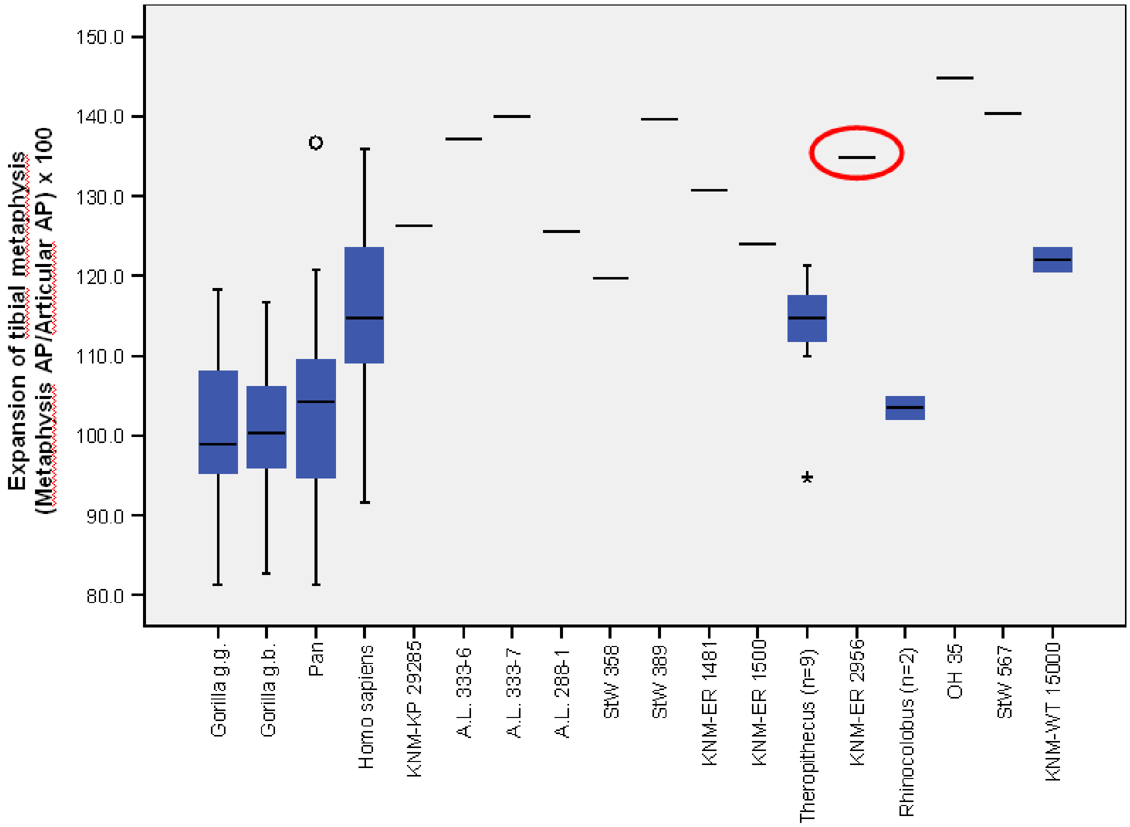


Figure 4.24. The length of the metaphysis of the distal tibia in the anteroposterior direction over the length of the articular surface of the distal tibia in the anteroposterior direction is graphed along the y-axis. Boxplots of this ratio show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Note that humans and fossil hominins all have an expanded metaphysis compared to the African apes. The KNM-ER 2596 distal tibia is circled in red and shares with hominins an expanded metaphysis. It is thus quite unlike the Pleistocene cercopithecoid *Rhinocolobus* in this morphology.

lacks the anterior expansion of the joint typical of a vertical climber.

A conservative explanation is that KNM-ER 2596 was misidentified as a hominin and instead is a distal tibia from the large-bodied cercopithecoid *Rhinocolobus*. This would dramatically increase the variation known for this taxa, and would suggest a significant degree of terrestriality in this colobine. This hypothesis would also suggest that an expanded metaphyseal volume is not solely a bipedal adaptation and thus its utility in identifying hominins in the fossil record would be limited.

An alternative hypothesis is that KNM-ER 2596 possesses a combination of features consistent with an occasional biped that has the capacity to climb. Some have argued that *H. habilis* may have undergone an evolutionary reversal to possess even stronger adaptations for climbing that its Pliocene ancestors (Haeusler and McHenry, 2007). Could KNM-ER 2596 be evidence for such a reversal? A potential problem with such an interpretation is that by having a varus knee this would not be a particularly efficient biped, and by not having a thick medial malleolus or wide anterior aspect of the articular surface of the tibia this would not be a particularly well adapted climber either. There are three other distal tibiae from this time period: KNM-ER 1481, KNM-ER 1500, and OH 35. All three have a perpendicularly aligned tibia relative to the articular surface. Furthermore, for all relative and absolute measures done in this and other studies (Chapter 6), KNM-ER 1500 and OH 35 are nearly identical to one another and it is suggested here that they are from the same sex of the same species (Figure 4.25). A fragmentary mandible of KNM-ER 1500 has features that may link it to *P. boisei* (Grausz et al., 1988, but see Wood, 1992; Wood and Constantino, 2007). If KNM-ER 1500 is *P. boisei*, then some of the original suggestions that the OH 35 tibia and fibula were associated with the OH 5 Zinj skull, found between 11-20 feet away (from Figure 4.21 in Leakey, 1971), may have been correct. The contemporary KNM-ER 1481 has been regarded by many to be from the genus *Homo* (Kennedy, 1983; Antón, 2003), and results of this study are consistent with this assessment. Thus, if OH 35 and KNM-ER 1500 are

Figure 4.25. Cross-section of hominin distal tibiae OH 35 and KNM-ER 1500.

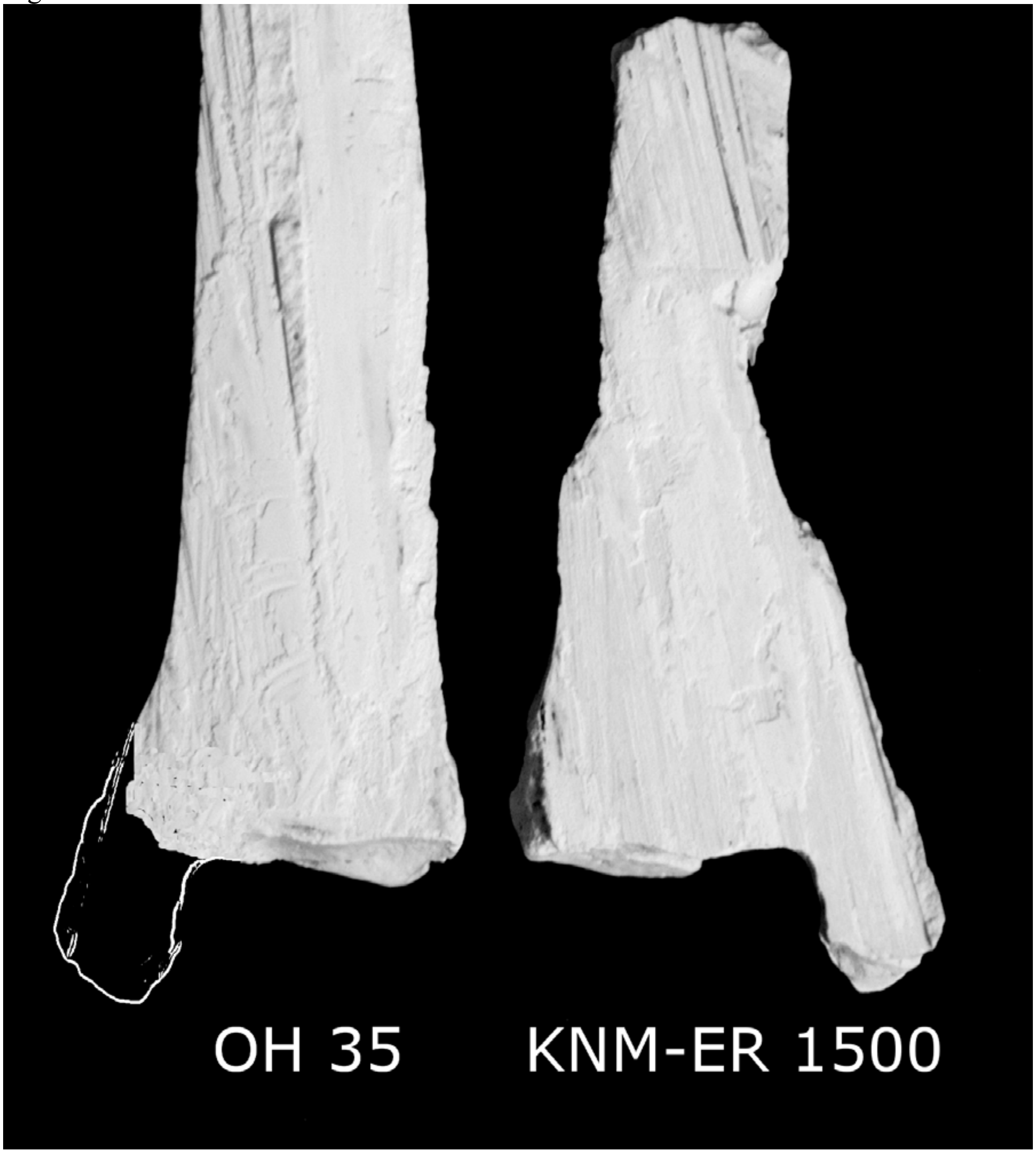


Figure 4.25. Cross section of plaster casts of OH 35 (left) and KNM-ER 1500 (right). The images have not been size adjusted and instead show how similar in size and shape these two fossils are to one another. The medial malleolus of the KNM-ER 1500 specimen has been copied and mirrored onto OH 35, which is missing its medial malleolus. The absolute size and morphology of these two specimens is so similar that they are suggested here to represent the same sex of the same species (see text for details). If, as has been argued (Grausz et al., 1988), KNM-ER 1500 belongs to *P. boisei*, the OH 35 may also be a *P. boisei* tibia, and not a tibia from *H. habilis* as has been hypothesized by others (Susman and Stern, 1982).

P. boisei, and KNM-ER 1481 is from *Homo*, it is difficult to find a taxonomic home for the morphologically distinct KNM-ER 2596.

A final hypothesis is that KNM-ER 2596 is a hominin with valgus deformity of the ankle. This can occur in humans today as a result of many different causes including injury to deltoid ligament, muscular imbalance due to damage to the tendon of the posterior tibialis muscle, or malunion of a fractured tibia or fibula (Gibson and Prieskorn, 2007). Wiltse (1972) noted that a malunion of a fractured proximal fibula in children less than 12 years old will quite often result in a valgus ankle. It is not clear at this time which of these three hypotheses is best supported by the evidence though this author finds the pathological argument the most compelling.

How will we know if early hominins were climbing?

Findings from this study suggest that the evolution of bipedalism resulted in changes to the hominin ankle that rendered them poorly adapted for vertical climbing in a manner like modern chimpanzees. Kinematic data obtained from vertically climbing apes in this study (Chapter 2) and others (i.e. Isler, 2003) should be used to continue to test the chimpanzee model of vertical climbing on other joints of the postcranial skeleton. However, given the results obtained here, it is likely that the same conclusion will be reached: if currently known hominins were vertically climbing it was performed in a manner unlike that practiced by modern chimpanzees. Therefore, it is suggested that other models of climbing, including a cercopithecoid model (see Chapter 7) and a modern human-like model of climbing should be tested as well. It will also be important to test these models using skeletal elements or morphologies that are more likely to be sensitive to the loading environment and thus epigenetically informative about the actual behavior of the animal (Ward, 2002). Other, indirect, methods discussed below may also be used to test for the likelihood for vertical climbing in our hominin ancestors.

The consequences of being a poorly adapted climber, and still attempting to climb, is an important issue and is precisely the kind of approach needed to assess how natural selection shapes postcranial anatomy in apes and hominins. Pontzer and Wrangham (2004) argued that chimpanzees move less often in the trees than on the ground, yet they are postcranially better adapted for an arboreal environment. They suggested that although this anatomy comes at the expense of energetically efficient terrestrial travel (i.e. short hindlimbs), it is maintained by natural selection because of the severe consequences for being an occasionally arboreal animal, poorly adapted for traveling arboreally (Pontzer and Wrangham, 2004).

The suggestion that falls from the canopy have helped shape chimpanzee and ape anatomy in general is supported by behavioral data on wild apes and by study of their skeletal remains. In two years of data collection at Gombe, Goodall (1986) observed 51 chimpanzee falls from trees, including 13 from heights of over 10 meters. Of the 51 individuals who fell from these heights, two died. Assuming the Goodall team observed all of the falls from the canopy over that two year period (which most likely they did not), the danger from falling and the selection pressures for retaining features that may prevent falling from a high canopy may both be quite high.

Fractures have been found in gibbon (Schultz, 1956) and orangutan (Lovell, 1990) skeletons consistent with falls from a great height. In a comprehensive study of African great ape skeletal remains, Jurmain (1997) found that postcranial trauma is found in 21.7% of chimpanzees (n=92), 17.7% of lowland gorilla skeletons (n=62), and 13.3% of bonobo postcranial remains (n=15). Of the 13 postcranial skeletons available from studied chimpanzees at Gombe, 30.8% of them had suffered fractures of the postcranial skeleton (Jurmain, 1997). Much of the craniodental trauma was related to inter and intragroup aggression and fractures of the ulna are consistent with the chimpanzee warding off blows from an attacker; however, much of the remaining trauma of the postcranial skeleton was consistent with falls from an arboreal environment (Jurmain, 1997). Recently, Carter et al. (2008) studied the postcranial remains of 12 chimpanzees from study sites in the Kibale National Park, Uganda, and found some degree of postcranial trauma in 11 of them (91.7%). This includes a fractured pelvis and radius of an individual (KFB 107) who most likely died from a tree fall.

What is striking about these data is not only the frequency of tree falls from apes so well adapted for life in an arboreal setting, but also how often the skeletal record preserves evidence that severely damaged bones had healed. Recovery from severe falls has been noted by Goodall (1986), and does not require care by conspecifics.

Therefore, if early hominins still included climbing as part of their locomotor repertoire, and if, as has been demonstrated here and elsewhere, hominins were not as adept in an arboreal environment as modern chimpanzees, then one may expect a higher likelihood of hominins falling to the ground and suffering trauma, if not death. Given that scenario, it may be more likely that if hominins utilized an arboreal resource, they did so in a manner quite unlike chimpanzees. They presumably were unable to move quickly through the canopy to avoid predation, navigate aggressive intergroup encounters, or to hunt monkeys. However, even if they moved cautiously and only built night nests for example, hominins still would have to get into the tree, and get out of the tree, thus increasing the risk of a fall. Furthermore, females with young either climbed with one arm, or the young still retained the ability to grasp onto the still retained body hair of the mother. Nevertheless, if hominins included climbing as part of their daily repertoire, *even if they were as adapted for this environment as chimpanzees*, they would, like every other ape species known, occasionally fall. A prediction from a hypothesis of frequent and adept climbing in the hominin fossil record may therefore include a high frequency of healed fractures in the hominin fossil record.

A preliminary survey of the literature on hominin paleopathology and a study of femora, tibia, and foot bones of australopiths in the Kenya National Museum, and Department of Anatomy at the University of Witwatersrand by this author reveals a striking absence of healed fractures in the postcranial anatomy of early hominins. A healed compression fracture of the calcaneus is present in an *A. africanus* specimen from Sterkfontein (Fisk and Macho, 1992). The OH 8 foot preserves osteoarthritis or healed trauma on the anterolateral aspect of the metatarsals (Day and Napier, 1964; Stern and Susman, 1982; pers. obs.). The australopithecine femur KNM-ER 738 preserves evidence for a healed fracture on the femoral shaft (Leakey et al., 1972; pers. obs.). There may not be enough postcranial fossils yet to test this hypothesis of healed fractures as evidence for climbing and there may be taphonomic or collection bias that would reduce the apparent numbers of healed fractures in the hominin fossil record. However, this hypothesis should be tested with a more rigorous study of hominin postcrania and be reassessed as the hominin fossil record grows.

In addition, as proposed by Pontzer and Wrangham (2004), biomechanical models need to be developed and tested that address how a hominin may be adapted in an arboreal environment to specifically avoid falling. Instead of focusing on getting into the tree, perhaps we should be testing whether an early hominin could keep itself in that tree without losing its balance and falling. Along those same lines, we should begin to ask questions about compensatory anatomies that may permit arboreal activities despite all of the lower limb adaptations that maladapt the hominin for a life in the trees. For example, without a grasping hallux, the arboreal orangutan has evolved even longer pedal digits and even longer arms than its African ape cousins. In the context of hominins, we need to begin to ask whether a robustly built arm is enough to pull an animal with an adducted hallux, valgus knee (this Chapter), longitudinal arch (Chapter 7), and long lumbar region up into a tree, and to keep it there safely. This approach becomes even more critical when supposed climbing adaptations begin to be explained in non-arboreal ways. For example, the arboreally adapted convex lateral condyle (Hunt, 1994; Berger and Tobias, 1995) does not discriminate modern humans and apes (Organ and Ward, 2006) and is absent in most australopithecine tibia anyway (Lovejoy, 2005). Additionally, strong peroneal musculature (Stern and Susman, 1983; Susman et al., 1984; Hunt, 1994) may be an adaptation for preventing ankle dislocation suffered from rapid inversion during terrestrial bipedalism (Chapter 6). Therefore, *if* hominins were climbing, they would need even more exaggerated adaptations in the parts of their bodies not effected by the adoption of bipedalism (i.e. upper limb) to compensate for the loses of so many other arboreal adaptations (Wolpoff, 1996; Coffing, 1998; Ward, 2001). A biomechanical study of the upper limb in this context should be undertaken.

Modern chimpanzees primarily climb trees to obtain food (Hunt, 1998) and to avoid predation (Preutz et al., 2007). In recent work at the chimpanzee sites of Fongoli and Assirik, Pruetz et al. (2007) found a relationship between the height of the nest that chimpanzees built and the risk of predation by lions, leopards, spotted hyenas, or wild dogs. Without predators, chimpanzees at Fongoli often make ground nests (Preutz et al., 2007). Our Pliocene ancestors may have been able to acquire terrestrial food resources; however, it is not likely that they were able to entirely avoid predation. In fact, evidence for predation is present in the hominin fossil record, SK 54 the victim of a leopard (Brain, 1969), the Taung child possibly an eagle (Berger and Clarke, 1995; Sanders et al., 2003; Berger, 2006), and Olduvai hominins taken by crocodiles (Njau and Blumenschine, 2007). It is difficult to understand how a 30 kg bipedal primate, poorly adapted to an arboreal environment, could survive by building night nests and thus risking falls from the canopy or by remaining terrestrial at night and risking predation from felines. Yet, that is precisely the paleobiological scenario presented by the remains left by early hominins. Given these data, the hypothesis that australopiths were aggressive appears quite reasonable (Carrier, 2007). Certainly a more detailed reconstruction of the paleoenvironment of early hominins and continued biomechanical studies of the postcranial bones are needed to help better reconstruct the behavior and locomotion of the early bipeds.

Conclusion

Many have used the postcranial remains of early hominins to reconstruct an animal adept at both terrestrial bipedalism and ape-like vertical climbing. However, these reconstructions have not fully considered the kinematics of climbing in modern apes. Based solely on the morphology of the ankle, I suggest that early hominins did not, and could not, vertically climb like a modern African ape. In fact, many of the adaptations for terrestrial bipedalism found in the ankle of early hominins produce a joint geometry that would limit the ability to climb and is potentially maladaptive, given the danger associated with falling from the forest canopy. Based on the morphology of the hominin ankle, *if* hominins were climbing at all, they were doing so in a manner kinematically distinct from modern African apes.

CHAPTER 5

Dorsiflexion, vertical climbing, and the evolution of the deltoid ligament.

Abstract

During vertical climbing bouts, non-human hominoids reduce their energy costs by pulling themselves close to the vertical substrate in part via extreme dorsiflexion at the ankle. This is in contrast to climbing cercopithecoids, which flex primarily at the midfoot. Modern humans are capable of only limited dorsiflexion without severe injury. Dissections of gorilla, chimpanzee, macaque, baboon, and human ankles reveal that the posterior tibiotalar portion of the deltoid ligament, known to inhibit dorsiflexion, is well developed in terrestrial monkeys and humans. This ligament, however, is relatively small in apes. Furthermore, in apes and atelines, the posterior tibiotalar ligament attaches close to the axis of rotation of the ankle, limiting its role to a joint stabilizer. This morphology helps facilitate the extreme dorsiflexion characteristic of vertically climbing primates. In contrast, the posterior tibiotalar ligament attaches more distantly from the axis of rotation in humans and cercopithecoid monkeys and thus serves the role as a motion inhibitor in the ankle of these primates. Though there is considerable variation, osteological correlates of a strong, dorsiflexion-restricting posterior tibiotalar ligament can be found in the distal portion of the medial malleolus and may provide another tool for interpreting the locomotion of extinct primates, including hominins.

Introduction

The presence and attachment point of ligaments have played an important role in interpreting the functional morphology of fossil hominoids and hominins. For example, a strong iliofemoral ligament which helps balance the human body in an upright position, often produces a roughened surface called the intertrochanteric line (Lovejoy and Heiple, 1972). This feature of the proximal femur has been used to infer the bipedal nature of fossil hominins (Aiello and Dean, 2002). Additionally, attachments for a strong nuchal ligament on the occipital region of the skull may be evidence for head stabilization during long distance running in early *Homo* (Bramble and Lieberman, 2004). Soft tissue and ligamentous characters of the knee have also been used to interpret how stable the knee of early hominins was during extended leg upright walking (Tardieu, 1999; Lovejoy, 2007).

Because the ligaments of the ankle both guide and restrict motion (Leardini et al., 1999; Stagni et al., 2004; Wolf, 2006), kinematics of the ankle in both human and non-human primates may be partially explained by ligamentous strength and orientation within the joint. Correlation between joint mobility, ligament function, and skeletal indicators of ligament strength and function can be used to interpret the fossil record and infer locomotion of extinct primates.

The ankle contains a structurally complex array of ligaments that function primarily to stabilize the bony connections between the talus and the long bones of the lower leg. The distal tibia and fibula are attached to one another via the anterior and posterior tibiofibular ligaments. Three distinct ligaments, the anterior talofibular, calcaneofibular, and posterior talofibular ligaments, support the lateral side of the ankle joint, whereas the medial side of the joint is anchored by the thick and strong deltoid ligament.

The deltoid ligament, or the medial collateral ligament, of the ankle connects the medial malleolus of the tibia to the talus, navicular, and calcaneus (Figure 5.1). Many anatomical variants of its form have been suggested (Pankovich and Shivaram, 1979; Sarrafian, 1993; Milner and Soames, 1998; Boss and Hintermann, 2002), and the terminology and anatomical descriptions vary. The deltoid ligament is composed of two layers: a superficial and a deep deltoid. The superficial deltoid layer consists of three, and sometimes four, bands that all originate on the anterior and medial aspect of the medial malleolus of the tibia. These are the tibionavicular ligament, tibiospring, tibiocalcaneal, and superficial posterior tibiotalar. The tibionavicular and tibiospring ligaments are always present in the human ankle, whereas the tibiocalcaneal and superficial posterior tibiotalar are variably present (Milner and Soames, 1998). There are some who use the terms tibiospring and tibiocalcaneal interchangeably (Leardini et al., 2000) and some who do not (Boss and Hintermann, 2002). It is important to note in this context that assigning individual fibers to any of the three or four superficial deltoid ligaments is a somewhat arbitrary exercise as these fibers are usually continuous with one another (Sarrafian, 1993). The deep deltoid layer originates from the most medial aspect of the medial malleolus and consists of a deep anterior tibiotalar ligament, and a deep posterior tibiotalar ligament. Although the anterior tibiotalar ligament is variably present in the human ankle, the posterior tibiotalar ligament of the deep deltoid can always be found (Milner and Soames, 1998).

Figure 5.1. Anatomy of the deltoid ligament.

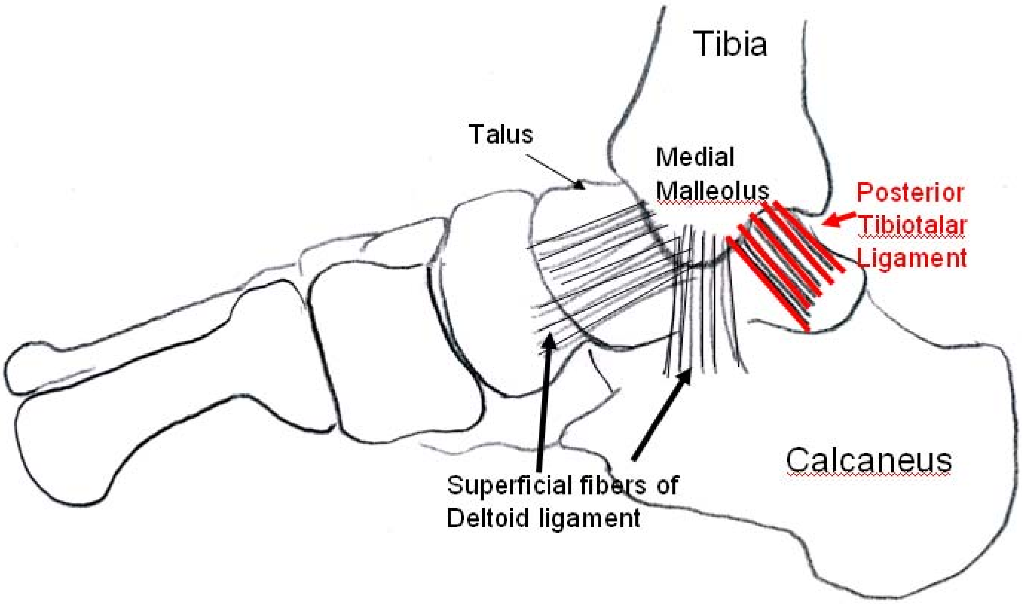


Figure 5.1. The medial side of the primate ankle is supported by deltoid ligament which anchors the medial malleolus of the tibia to the talus, navicular, and calcaneus. This study focuses on the largest of the deltoid fibers, the posterior tibiotalar ligament.

In identifying the different layers, fibers, origins and insertions of the ligaments of the deltoid ligament, Pankovich and Shivaram (1979) also coined terms for bony landmarks on the medial malleolus that serve as attachment points for the posterior tibiotalar ligament. The medial malleolus is shaped like the letter “U”, but with a triangular notch excavated from the inferoposterior aspect of the malleolus. Bordering this notch are two bony projections: the anterior and posterior colliculi (Figure 5.2). The notch between these bony landmarks is known as the intercollicular groove. It is in this groove that the robust posterior tibiotalar ligament anchors.

The relative size and strength of these ligaments have been described using human cadavers. The posterior tibiotalar portion of the deltoid ligament is the thickest (Close, 1956; Klein, 1994; Milner and Soames, 1998) and the strongest (Attarian et al.,

Figure 5.2. Anatomy of the posterior tibiotalar ligament.

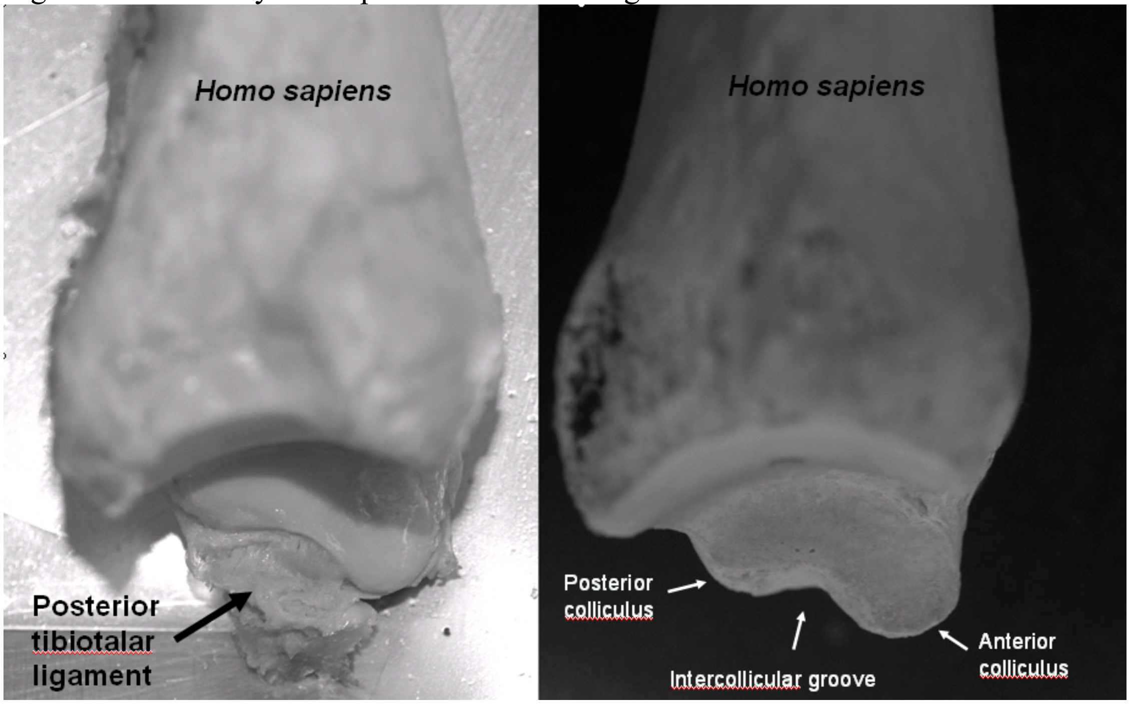


Figure 5.2. Distal tibia of a human cadaver (left) in lateral view showing the posterior tibiotalar portion of the deltoid ligament originating from the medial malleolus. On the right, a prepared osteological human distal tibia shows that the posterior tibiotalar ligament originates in the intercollicular groove, formed between the anterior and posterior colliculi.

1985; Siegler et al., 1988; Sarrafian, 1993; Beumer et al., 2003) ligament in the human ankle. It also occupies the largest insertion area of any ankle ligament (Boss and Hintermann, 2002). The function of the deltoid ligament complex has also been determined primarily in studies using human cadavers, and a recent MR study of the ligament *in vivo* (Wolf, 2006). The posterior tibiotalar ligament primarily inhibits dorsiflexion (Rasmussen, 1985; Siegler et al., 1988; Leardini et al., 2000; Stagni et al., 2004; Wolf, 2006; Figure 5.3) and can rupture when the ankle is forced into extreme dorsiflexion (Rasmussen et al., 1983). In his seminal work on ligament development, Beau (1939) even regarded the posterior tibiotalar ligament to be part of the posterior ligaments of the ankle, despite its position on the medial side of the tibia, further

Figure 5.3. Tightening of the posterior tibiotalar bands during dorsiflexion.

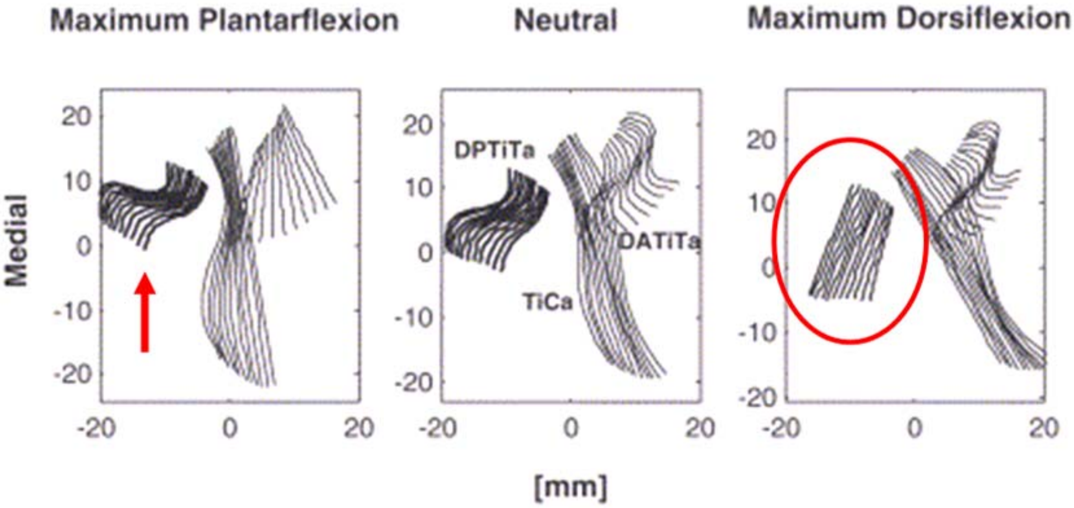


Figure 5.3. Ligaments of the ankle that attach close to the axis of rotation do not change length (remain isometric) through the range of motion. Those attaching distant from the axis of rotation can resist joint motion. In human cadavers, the posterior tibiotalar ligament (DPTiTa) is slack in plantarflexion (arrow), and becomes taut in dorsiflexion (circled). Reproduced with permission from Stagni et al. (2004).

emphasizing this ligament's importance in restricting dorsiflexion. In addition to its primarily role as a dorsiflexion inhibitor, Harper (1987) used 24 cadavers to suggest that the deltoid ligament is a restraint against valgus tilting of the talus relative to the tibia, which would put the foot in a position of dorsiflexion, abduction, and eversion. Stormont et al. (1985) also found that the deltoid ligament resists eversion of the foot. The deltoid ligament is also integral in limiting medial movement of the tibia over the talus, and therefore allowing for some internal rotation of the tibia during dorsiflexion (Michelson and Helgemo, 1995). Finally, cadaver studies have found that sectioning of the posterior tibiotalar portion of the deltoid results in a separation of the tibia and fibula, and thus an increase in the intermalleolar distance (Barnett and Napier, 1953; Close, 1956; Skie et al., 1989).

Thus, the posterior tibiotalar ligament is the largest and strongest ligament in the human ankle and serves primarily to resist dorsiflexion. In Chapter 2, it was shown that vertical climbing great apes have significantly greater dorsiflexion capacity than bipedal humans or terrestrial monkeys. A comparison of these results with the available data from the literature demonstrates that apes (*Pan troglodytes*, *Gorilla gorilla gorilla*, *Pongo pygmaeus*, *Hylobates lar*) can achieve approximately 45˚ of dorsiflexion at the ankle during vertical climbing bouts whereas cercopithecoid monkeys dorsiflex to approximately 15˚-20˚ during their climbing bouts (Yamazaki and Ishida, 1984; Hirasaki et al., 1993; Chapter 2). Reports of dorsiflexion during walking in modern human ankles range from only 8.3˚ to 25.7˚ (Rome, 1996). Additional studies have found that the human ankle can be severely injured when forced beyond 45˚ of dorsiflexion with injuries ranging from avulsions of the deltoid ligament itself to fractures of the medial and lateral malleoli and tears of the flexor hallucis longus, flexor digitorum longus, and tibialis posterior muscles (Begeman and Prasad, 1990; Parenteau et al., 1998).

Based on the preceding considerations, it is hypothesized that the posterior tibiotalar ligament is less developed in the vertically climbing apes, allowing a greater range of dorsiflexion; whereas terrestrial monkeys and bipedal humans have a strongly developed posterior tibiotalar ligament that inhibits dorsiflexion. Ligament strength is a function of its cross-sectional area, and therefore, the area of the ligament relative to the body size of the primate is a proxy for strength (Currey, 2002). Because this ligament attaches to the medial malleolus, differences in the morphology of the medial malleolus may provide skeletal correlates to posterior tibiotalar ligament size and strength.

The use of skeletal correlates to infer the relative size and strength of the posterior tibiotalar ligament assumes that the posterior tibiotalar ligament has the same biomechanical properties in humans and in non-human primates. This study tests that assumption by assessing the strength, toughness, and stiffness of the posterior tibiotalar ligament in baboons (*Papio anubis*). If the biomechanical properties of the ligament are conserved across primates, then skeletal correlates of ligament strength can be applied to questions of locomotion with more confidence.

In addition to cross-sectional area and biomechanical properties of the ligament, the area of attachment of the ligament relative to the axis of rotation of the joint is critical to the ligament's function (Alexander and Bennett, 1987). Ligaments that attach on or close to the center of rotation remain isometric throughout the range of movement of the joint (Alexander and Bennett, 1987). This has been found to be the case for the human calcaneofibular and the tibiocalcaneal ligaments (Leardini et al., 1999; Stagni et al., 2004). The axis of rotation of the ankle runs approximately through the tips of the medial and lateral malleoli (Inman, 1976; Latimer et al., 1987; Lundberg et al., 1989). The calcaneofibular ligament attaches close to the tip of the lateral malleolus (Burks and Morgan, 1994; Hintermann, 2002; Taser et al., 2006), and the tibiocalcaneal ligament attaches close to the tip of the medial malleolus (Pankovich and Shivaram, 1979; Sarrafian, 1993; Leardini et al., 2000). The origin of these ligaments is consistent with observations that their length does not change during a full range of motion of the ankle (Leardini et al., 1999; Stagni et al., 2004) supporting the hypothesis that ligaments originating near the axis of rotation stabilize a joint, but cannot resist motion (Alexander and Bennett, 1987).

Figure 5.4. Model of ligament theory.

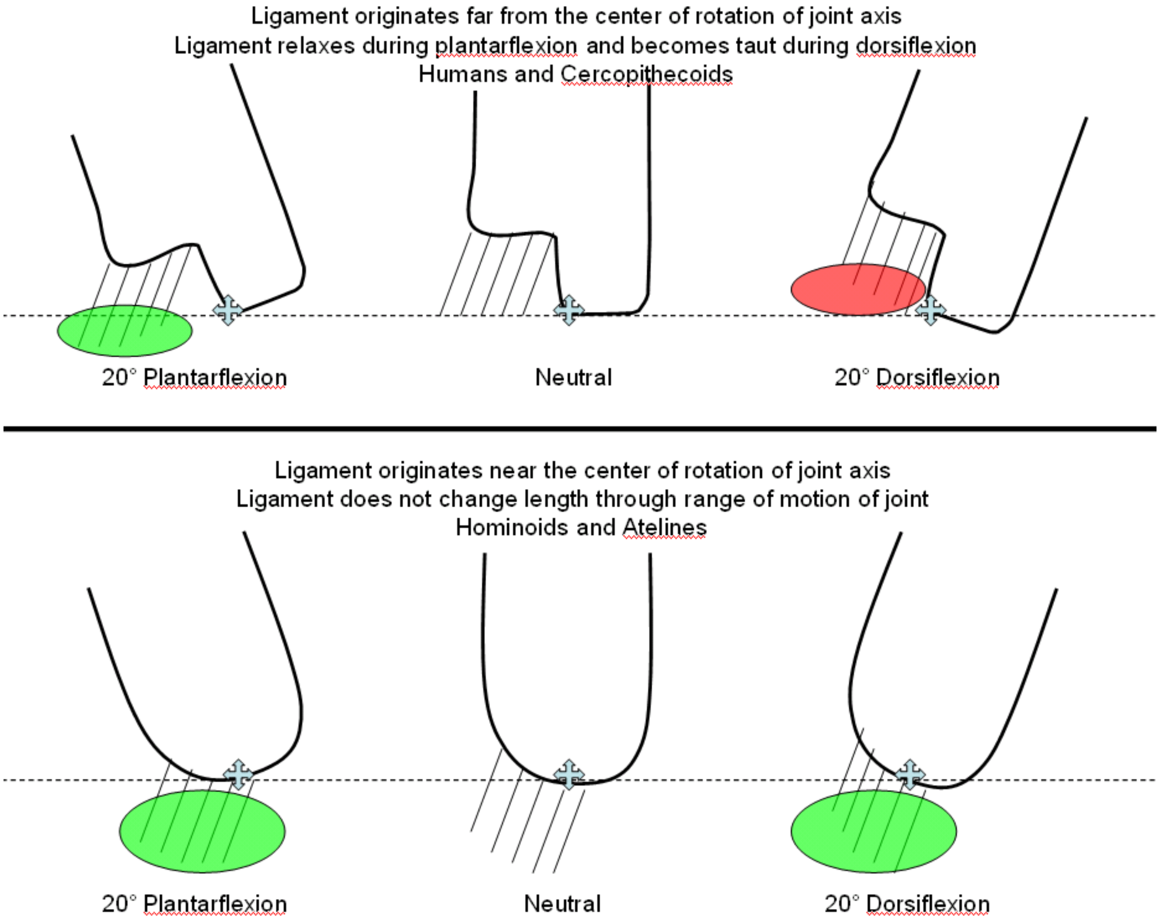


Figure 5.4. Model of the ligament theory proposed by Alexander and Bennett (1987) as applied to the posterior tibiotalar ligament. In all drawings the axis of rotation of the ankle runs through the tip of the medial malleolus of the distal tibia and is marked with a cross. In the model across the top, the ligament originates far from the axis of rotation, becomes slack in plantarflexion (green), but becomes taut in dorsiflexion (red). In the model across the bottom, the ligament originates close to the axis of rotation and thus its length does not change much at all in plantarflexion or in dorsiflexion.

In regards to the posterior tibiotalar ligament, it is hypothesized that a more developed intercollicular groove shifts the origin of the ligament to a more posterior and superior position relative to the tip of the medial malleolus (Figure 5.4). By originating far from the axis of rotation of the ankle, the posterior tibiotalar ligament increases its ability to restrict dorsiflexion and eversion. A weakly formed, or even absent, intercollicular groove positions the origin of the posterior tibiotalar ligament to an area close to the tip of the medial malleolus, and therefore, close to the axis of rotation. This latter scenario would result in a posterior tibiotalar ligament that could guide movement in the sagittal plane, but not restrict it because the ligament would not become taut at any point during the range of motion of the joint.

Only Gomberg (1981) has provided a brief description of the comparative anatomy of the deltoid ligament in different hominoid species. He observed that humans have a strong deltoid whereas chimpanzees and gorillas have a long deltoid ligament (Gomberg, 1981). However, no quantitative description or analysis was done. Additionally, no quantitative description of the differences in medial malleolar shape among the different extant and extinct catarrhine species has yet been attempted.

With this in mind, the following hypotheses will be tested in this chapter:

<u>Ligament size</u>

<u>Ho:</u> There are no differences in the relative size of the posterior tibiotalar ligament (PTTL) in humans, cercopithecoid monkeys, and apes.

<u>H1</u>: Relative to body mass, the PTTL has a significantly larger cross-sectional area in species with limited dorsiflexion (humans and cercopithecoids)

<u>Biomechanical properties of ligament</u>

<u>Ho</u>: There are no differences in material properties of the posterior tibiotalar ligament between humans and a non-human primate.

H1: The material properties of the posterior tibiotalar ligament differ between primate species.

Skeletal anatomy

Ho: There are no differences between the attachment points for the deltoid ligament on the medial malleolus among hominins, apes, cercopithecoids, and atelines.

H1: There are statistically significant differences in the morphology of the medial malleolus between among hominins, apes, cercopithecoids, and atelines and these differences are related to the attachment area and function of the posterior tibiotalar ligament of the deep deltoid.

Materials and Methods

Dissections and ligament testing were performed on four macaques (*Macaca mulatta*) and ten baboons (*Papio anubis*) that had completed research protocols approved by the University of Michigan Institutional Animal Care and Use Committee. Additional dissections were made of five human cadavers at Wayne State University Medical School, and on an adult male chimpanzee of unknown provenience at the Museum of Comparative Zoology (Harvard University) and adult male gorilla from the Cincinnati Zoo at the University of Michigan Museum of Zoology.

The tibia of adult wild-shot primates museum specimens were studied of the following species: *Pan troglodytes* (n=52), *Pan paniscus* (n=4), *Gorilla gorilla gorilla* (n=44), *Gorilla gorilla beringei* (n=22); *Pongo pygmaeus* (n=36), *Hylobates lar* (n=40), *Symphalangus syndactylus* (n=8); *Papio* spp. (n=35); *Mandrillus sphinx* (n=10); *Theropithecus gelada* (n=5); *Macaca fascicularis* (n=5); *Macaca nemestrina* (n=6); *Nasalis larvatus* (n=37); *Alouatta palliata* (n=20); *Ateles* spp. (n=23); *Brachyteles arachnoides* (n=1); *Lagothrix lagotricha* (n=16); *Cebus capucinus* (n=19). The relative numbers of males and females are listed in Table 5.1. The human tibiae were from the 9th-12th century PaleoIndian Libben population housed at Kent State University (Lovejoy et al., 1977), and the Hamann-Todd collection at the Cleveland Museum of Natural History. The non-human primates were studied at the Cleveland Museum of Natural History, Field Museum, American Museum of Natural History, National Museum of Natural History, Museum of Comparative Zoology (Harvard), and Peabody Museum (Yale).

Twenty-nine fossil tibiae were studied (Table 5.2). Original fossils were examined at the Uganda National Museum, Kenya National Museum, and the Department of Anatomy at the University of Witwatersrand in South Africa. High-quality research casts of tibiae from the Ethiopian hominin *A. afarensis* were studied courtesy of the Cleveland Museum of Natural History and the University of Michigan Department of Anthropology.

Comparative morphology of PTTL

The area of the posterior tibiotalar ligament was measured on four macaques (*Macaca mulatta*) and 10 baboons (*Papio anubis*). The baboons were between two-three years old, and thus still had unfused epiphyses on the distal fibula and tibia. They weighed between 6.0-8.4 kg with an average of 7.2 kg. The macaques were adults, approximately 10 kg in mass. Additionally, the cross-sectional area of the posterior tibiotalar ligament was measured on an adult male chimpanzee and an adult male lowland gorilla that weighed approximately 225 kg. The length, width, height, and anatomical origin and insertion of the PTTL was measured using digital calipers at the midpoint of the ligament's length. Mkandawire et al. (2005) have found that the caliper technique can underestimate the ligament cross-sectional area. The data presented in Mkandawire et al. (2005) suggest that the actual cross-sectional area of the PTTL can be estimated using the equation for the area of an ellipse. Dissection of five human cadavers confirmed that the shape of human ankle ligaments is roughly the same as the shape of non-human primate ligaments and this method was therefore used to calculate the cross-sectional area of ligaments in this study. The cross-sectional area of the posterior tibiotalar ligament in humans was taken from Sigeler et. al. (1988), and from the five dissected human cadavers mentioned above.

Because this study samples a range of body masses, the relative strength of the posterior tibiotalar ligament was assessed by dividing the square root of the cross-sectional area of the ligament by the cube root of the mass of the animal.

In addition to measuring the cross-sectional area, the maximum range of dorsiflexion between the foot and the tibial shaft was measured before and after severing the posterior tibiotalar ligament in human cadavers (n=5) and the gorilla (n=1).

Ligament biomechanics

Figure 5.5. Anatomy of baboon (*Papio anubis*) ankle.

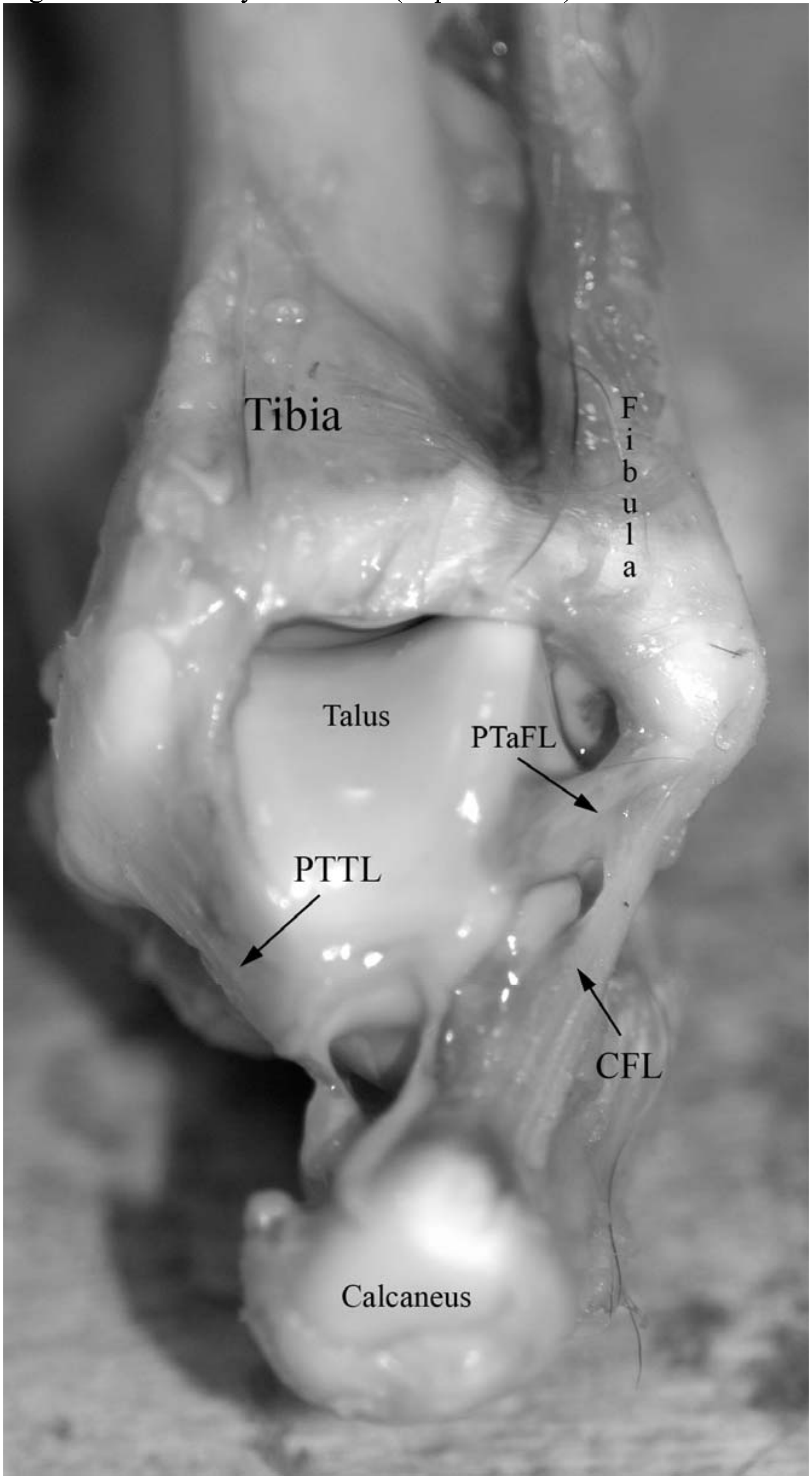


Figure 5.5. Dissected baboon ankle in posterior view. Labeled are the tibia, fibula, talus, and calcaneus, and the three ligaments examined in this study: PTTL (posterior tibiotalar ligament), PTaFL (posterior talofibular ligament), and CFL (calcaneofibular ligament).

When the ligaments were ready for testing, the limbs were thawed for 24 hours at room temperature (~21˚C). Dissections were performed on the right limbs unless the ligaments were damaged during the dissection or tensile mounting, in which case the left limb was used. The calcaneofibular ligament (CFL), posterior talofibular ligament (PTaFL), and posterior tibiotalar ligament (PTTL) were carefully isolated and all surrounding tissue removed (Figure 5.5). Attempts were made to locate the ATaFL. The length, width, height, and anatomical origin and insertion of the three ligaments were measured using digital calipers. As mentioned above, Mkandawire et al (2005) have found that the caliper technique can underestimate the ligament cross-sectional area and that the actual cross-sectional area of the CFL can be approximated using the equation for the area of a rectangle; the PTTL by using the equation for the area of an ellipse; and the PTaFL by averaging the area of a rectangle with the average of an ellipse.

Mounting ligaments and testing the strength and stiffness can be difficult to achieve without slippage. Tests were first performed on pig ankle ligaments to obtain the best mounting protocol. Bone-ligament-bone complexes were prepared by dissecting the calcaneus and talus from the rest of the hindfoot and by separating the tibia and fibula from one another by cutting the anterior and posterior tibiofibular ligaments, the interosseous tissue, and the ligaments anchoring the proximal tibiofibular joint capsule. The shafts of the fibula and tibia were cut with a power rotary tool to properly mount the bone-ligament-bone specimens in the tensiometer. The bones were not potted, but instead were cut along the cortical portion of the shafts to form T-shaped regions of bone that were subsequently mounted proximally in the Instron clamps while the talus or calcaneus

Figure 5.6. Testing biomechanical properties of baboon posterior tibiotalar ligament.

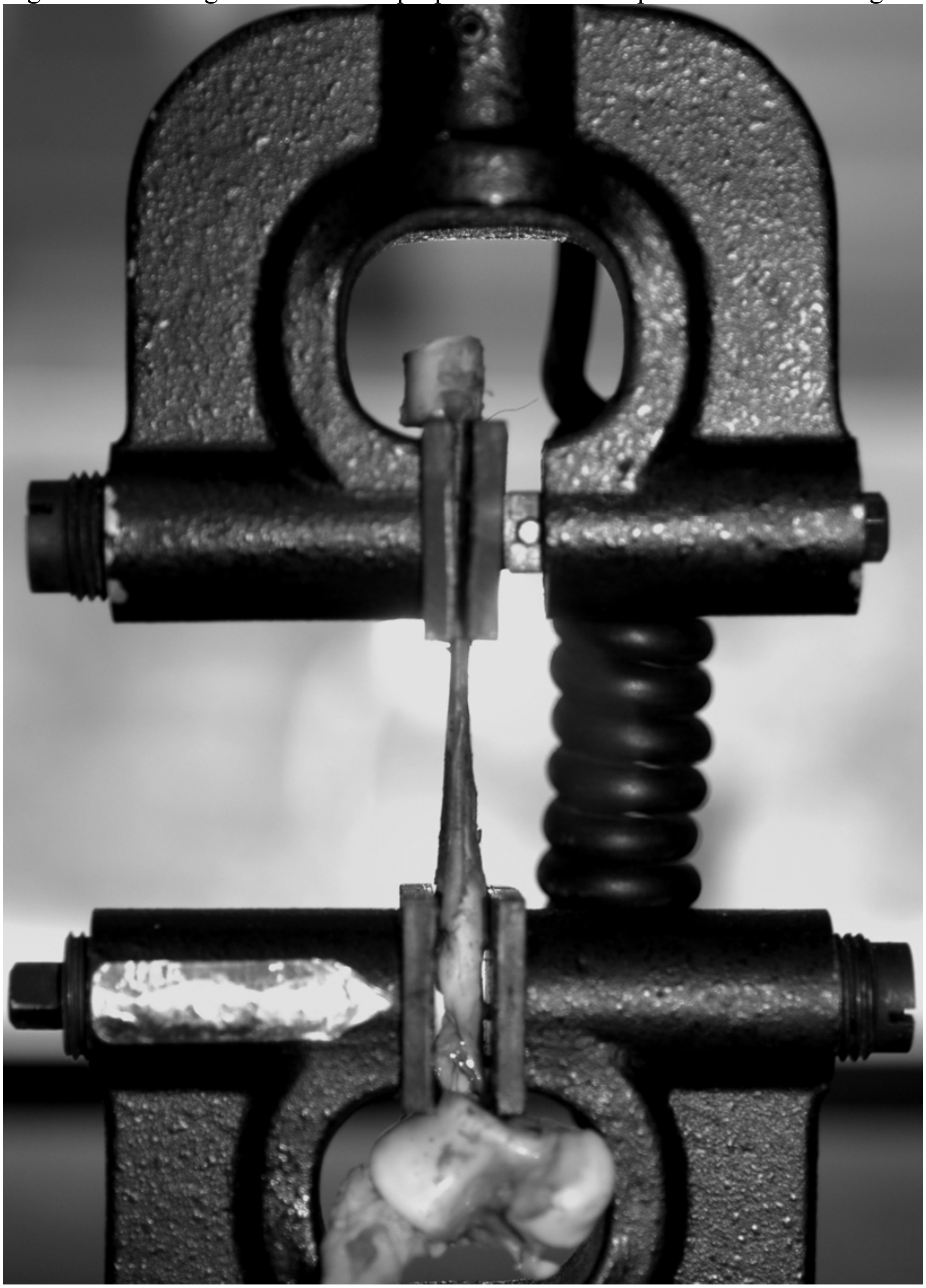


Figure 5.6. Mounting protocol to test the material properties of the posterior tibiotalar ligament (PTTL). Proximally, the bone-ligament-bone complex is clamped into the Instron apparatus and resists slipping downward by the T-shaped cortical bone. Distally, the tibia is cut along the medial malleolus such that it and the posterior tibiotalar ligament can fit between the Instron clamps without interference. The bone-ligament-bone complex is held in place distally by the superior and medial sides of the talus itself.

was mounted distally to the Instron clamps (Figure 5.6). Slippage was minimal as the force-displacement graphs for each ligament were consistent both within a test and between tests. When not being dissected, cut, mounted, or tested, the ligaments were wrapped in a moist paper towel.

Care was taken to cut and mount the bone-ligament-bone complex along the long axis of the ligament. The strength and stiffness of the ligaments were tested in an Instron 4301 tensile test machine using a load cell of 10 kN. Force was applied to the ligament at a low rate of 2.54 mm/min until failure. This rate corresponds to between 15% (CFL) and 40% (PTTL) of the total length of the ligament per minute which is similar to the 12% (CFL) to 27% (PTTL) of total length of the ligament per minute used to test humans (Siegler et al., 1988). Output of force and displacement throughout the test was recorded 1 data point per second in addition to the maximum load and displacement at failure (Figure 5.7). The stress (force/cross-sectional area) and strain (displacement/ligament length) were calculated from the data in the output graphs as was the Young's elastic modulus (stress/strain) and the energy to yield (Nmm). The mode of failure (bony avulsion or ligament tear) and the site of failure were recorded for each ligament.

Because there were a limited number of baboons available, the ligaments were not tested as isolated structures. This did not affect the PTTL ligament as it was the only structure tested on the medial side of the ankle. However, the CFL and PTaFL have a common origin on the distal fibula, though when one ligament was mounted, the other was placed in a position perpendicular to the tensiometer grips and thus was not under a tensile force. For half of the bone-ligament-bone complexes, the CFL was tested first; for the other half, the PTaFL was tested first. The difference in strength or stiffness was not

Figure 5.7. Force-elongation graph of baboon posterior tibiotalar ligament.

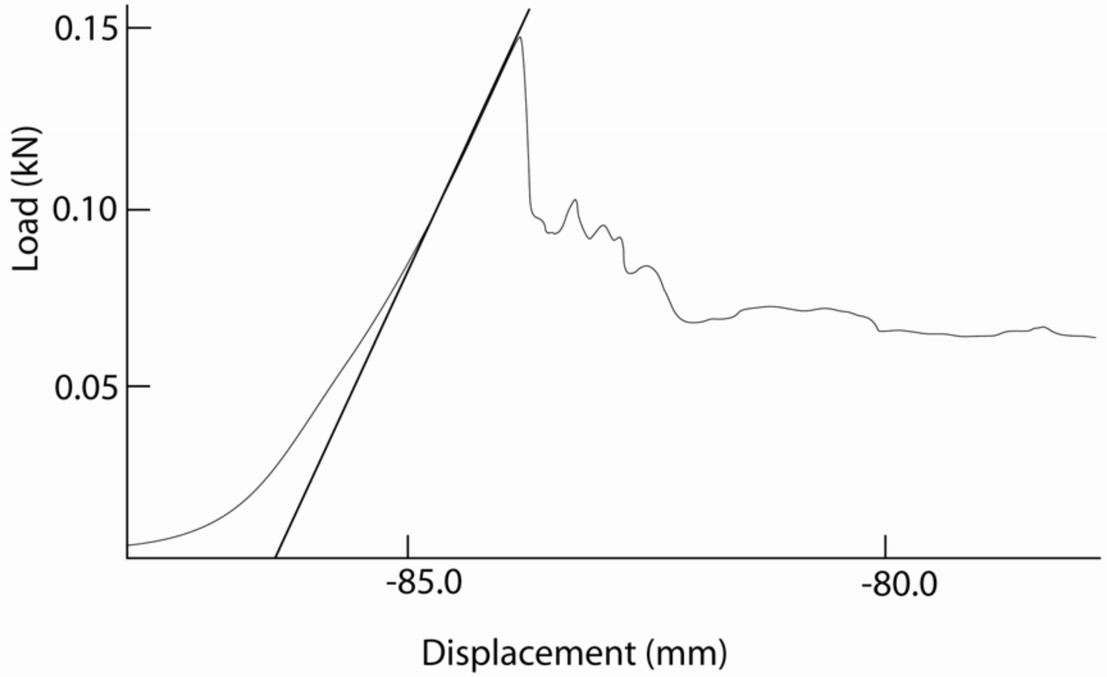


Figure 5.7. An example of the force-elongation graph produced during the testing of a posterior tibiotalar ligament (PTTL). The x-axis is the change of original length of the ligament and the y-axis is the total load. In this example, after about 2.5 mm of elongation, the ligament abruptly failed at a load of approximately 145 N.

different whether the ligament was tested first or second. However, if the ligament failed by pulling the distal fibular epiphysis from the diaphysis, it was not possible to test the second ligament. This occurred three times. Ligament failure or failure of the bone along the epiphyseal plate prior to a 10N load occurred for five CFLs and two PTaFL. It is assumed that in cases of failure at such a low load, the bone was cut too thin during mounting preparation. Data are thus reported for the remaining 10 PTTLs, eight PTaFLs, and six CFLs.

Skeletal morphology

The attachment for the posterior tibiotalar ligament was measured on 379 tibia from wild-shot adult non-human primate specimens (Table 5.1), and 69 human adult human tibia representing two different populations. All of the hominoid genera (*Homo*, *Pan*, *Gorilla*, *Pongo*, *Hylobates*, *Symphalangus*) are represented, as are primarily terrestrial (*Papio, Mandrillus, Theropithecus, Macaca nemestrina*), and more arboreal (*Nasalis, Macaca fascicularis*) cercopithecines. Platyrrhines are represented by the ateline genera (*Ateles*, *Alouatta*, *Brachyteles*, *Lagothrix*) and the arboreal quadruped *Cebus*. Specimens were measured at the Cleveland Museum of Natural History, Field Museum (Chicago), American Museum of Natural History (New York), National Museum of Natural History (Washington D.C.), Museum of Comparative Zoology (Harvard), and Peabody Museum (Yale). The two human populations are the 9th-12th century PaleoIndian Libben population (Lovejoy et al., 1977) housed at Kent State University (n=45), and the Hamann-Todd collection at Cleveland Museum of Natural History (n=24).

Photographs of the tibia were taken in lateral view with a Nikon D100 digital camera. The bone was positioned flat on its medial side such that the anterior or posterior edges of the medial malleolus were not visible (Figure 5.8). Images were imported into Image J and two measures were taken. First, the shape of the intercollicular groove was assessed by measuring the angle that the posterior edge of the intercollicular groove forms with the long axis of the tibia using the angle tool in Image J. This was measured by drawing a line from the posterior colliculus to the deepest point of the intercollicular groove and measuring the angle that this line makes with long axis of the tibia. A second measure was taken to quantify the size of the intercollicular groove. Using Adobe

Table 5.1. Extant tibiae measured in this study.

Family	Species	Male	Female	Sex unknown	Total
Hominoid	*Homo sapiens*	25	34	10	69
	Pan troglodytes	20	21	11	52
	Pan paniscus	2	1	1	4
	Gorilla gorilla gorilla	23	19	2	44
	Gorilla gorilla beringei	15	6	1	22
	Pongo pygmaeus	12	19	5	36
	Hylobates lar	19	20	1	40
	Symphalangus syndactylus	2	5	1	8
Cercopithecoid	*Papio* spp.	18	5	12	35
	Mandrillus sphinx	3	4	3	10
	Theropithecus gelada	3	2	0	5
	Macaca fascicularis	3	2	0	5
	Macaca nemestrina	4	2	0	6
	Nasalis larvatus	18	19	0	37
Platyrrhine	*Alouatta palliata*	11	7	2	20
	Ateles spp.	12	8	3	23
	Brachyteles arachnoides	0	0	1	1
	Lagothrix lagotricha	8	5	3	16
	Cebus capucinus	10	9	0	19

Photoshop, the medial malleolus was cropped from the rest of the tibia, and imported into Image J. Using the line tool, a curve was traced along the anterior edge of the medial malleolus, following the shape of the bone. This line was then inverted, and placed along the posterior edge of the malleolus to represent what a "complete" medial malleolus

Figure 5.8. Comparative morphology of anthropoid medial malleoli.

Figure 5.8. Distal tibia in lateral view of (from left to right) *Papio anubis*, *Pongo pygmaeus*, *Gorilla gorilla gorilla*, *Pan troglodytes*, and *Homo sapiens*. All are from adult right tibia. Notice the large intercollicular groove on the baboon and the human and more rounded medial malleoli on the great ape tibia.

without an intercollicular groove would look like. A threshold tool was then used to convert all of the bone to white pixels, and the background to black pixels. A line was drawn from the posterior colliculus across the medial malleolus, parallel to most superior junction of the medial malleolus with the distal tibia. The region inferior to this line, including the portion representing the intercollicular groove was outlined and the percentage of the area of interest filled with bone was calculated and subtracted from 100%. This value represents the area of the intercollicular groove. The size of the intercollicular groove was not measured relative to the size of the entire medial malleolus because the relative height of the medial malleolus varies between primate taxa (Chapter 3). Significant differences among primate species for this measure were assessed using a one-way ANOVA and the post hoc Tukey honestly significantly different (HSD) test.

These same measures were taken on nine fossil hominin, eight fossil catarrhine or hominoid, and 13 fossil cercopithecoid distal tibiae listed in Table 5.2. These specimens had a complete enough medial malleolus for the measurements described above to be accurately taken. The medial malleolus is not present or is damaged on the Miocene

Table 5.2. Fossil tibiae measured in this study.

Accession number	Geological age	Family	Taxon	Original or cast
NAP I'58	19.5[1,2]	Hominoid	*Proconsul major*[3,5]	Original.
BUMP 764	19.5[1,2]	Catarrhine	?	Original.
KNM-LG 583	19.5[4]	Hominoid? Catarrhine?	*?P. africanus*[5] *?Dendropithecus macinnesi*[3]	Original. National Museums of Kenya (NMK)
KNM-ER 1939	17.8[6]	Hominoid	*P. nyanzae*[3, 7]	Original. NMK
KNM-RU 3589	17.8[6]	Hominoid	*P. heseloni*[3]	Original. NMK
KNM-RU 2036	17.8[6]	Hominoid	*P. heseloni*[3]	Original. NMK
KNM-BG 35250	~15[8]	Hominoid	*Nacholapithecus kerioi*[9]	Original. NMK
KNM-MB 11973	14-15[10]	Cercopithecoid	*Victoriapithecus macinnesi*[11]	Original. NMK
A.L. 333-6	3.2[12]	Hominin	*A. afarensis*	Cast. CMNH
A.L. 333-7	3.2[12]	Hominin	*A. afarensis*	Cast. CMNH
A.L. 288-1	3.18[12]	Hominin	*A. afarensis*	Cast. CMNH
StW 358	2.6-2.8[13]	Hominin	*A. africanus?*[15,18]	Original. Univerisity of Witwatersrand
StW 567	1.4-1.7[13]	Hominin	*Homo erectus*[2,21]	Original. Wits
KNM-ER 1500	1.9[14]	Hominin	*P. boisei*[16, 18]	Original. NMK
KNM-ER 2596	1.9[14]	Hominin? Cercopithecoid?	Hominin [22] Cercopithecoid?	Original. NMK
KNM-ER 1481	1.9[14]	Hominin	*Homo habilis* [18,19] *Homo erectus*[20]	Original. NMK
KNM-WT 15000	1.6[14, 17]	Hominin	*Homo erectus*[17]	Original. NMK
KNM-ER 1542	1.9-2.1[14, 24]	Cercopithecoid	*Rhinocolobus turkanaensis*[23]	Original.NMK.
KNM-ER 45613	1.9-2.1[14, 24]	Cercopithecoid	*?R. turkanaensis*	Original.NMK.
KNM-ER 40443	1.9-2.1[14, 24]	Cercopithecoid	*Theropithecus oswaldi*	Original.NMK.
KNM-ER 3823	1.9-2.1[14, 24]	Cercopithecoid	*T. oswaldi*	Original.NMK.
KNM-WT 16875	1.4-2.1[24]	Cercopithecoid	*T. oswaldi*	Original.NMK.
KNM-WT 16755	1.4-2.1[24]	Cercopithecoid	*T. oswaldi*	Original.NMK.
KNM-ER 3877	1.6-1.9[14, 24]	Cercopithecoid	*T. oswaldi*	Original.NMK.
KNM-ER 5474	1.6-1.64[14, 24]	Cercopithecoid	*T. oswaldi*	Original.NMK.
KNM-ER 597	1.4-1.6[14, 24]	Cercopithecoid	*T. oswaldi*	Original.NMK.

KNM-ER 866	1.4-1.6[14, 24]	Cercopithecoid	*T. oswaldi*	Original.NMK.
KNM-ER 5491	1.4-1.6[14, 24]	Cercopithecoid	*T. oswaldi*	Original.NMK.
KNM-OG 1109	>0.74[24]	Cercopithecoid	*T. oswaldi*	Original.NMK.

[1]Bishop, 1969; [2]MacLatchy et al., 2006; [3]Rafferty et al., 1995; [4]Pickford and Andrews, 1981; [5]Harrison, 1982; [6]Drake et al., 1988; [7]Le Gros Clark, 1952; [8]Sawada et al., 1998; [9]Ishida et al., 1999; [10]Feibel and Brown, 1991; [11]Harrison, 1989; [12]Walter et al., 1994; [13]Kuman and Clarke, 2000; Deloison, 2003; Pickering et al., 2004; [14]Feibel et al., 1989; [15]McHenry and Berger, 1998; [16]Grausz et al., 1988; [17]Walker and Leakey, 1993; [18]McHenry, 1994; [19]Trinkaus, 1984; [20]Kennedy, 1983; [21]Curnoe and Tobias, 2006; [22]Leakey and Walker, 1985; [23]Leakey, 1982; [24]Krentz, 1993.

tibiae KNM-MV 2 and KNM-RU 5872, and on Plio-Pleistocene hominins StW 181, StW 389, StW 515, and OH 35. There is some damage to the inferior tip of the medial malleolus in the Miocene *Victoriapithecus* fossil tibia KNM-MB 11973 and the unpublished catarrhine distal tibia BUMP 764 from the Napak site of northeastern Uganda. Measurements on these fossils should be treated as estimates. There is sufficient crushing to the inferior end of the hominin tibia from *Australopithecus anamensis* KNM-KP 29285 to preclude reliable estimates of the angle or area of the intercollicular groove. The left tibia of KNM-BG 32520 *Nacholapithecus* is severely distorted; however, the right tibia is not as badly distorted (thought still slightly) and the measurements reported are from this right distal tibia. Measurements were taken on original fossils from the Kenya National Museum in Nairobi, Kenya, the Department of Anatomy at the University of Witwatersrand, and the Uganda National Museum. Measurements of three *Australopithecus afarensis* distal tibia were taken on high quality research casts (A.L. 288-1, A.L. 333-6, A.L. 333-7) at the Cleveland Museum of Natural History and University of Michigan Department of Anthropology.

Results

Comparative morphology of PTTL

The posterior tibiotalar ligament originated in the intercollicular groove between the anterior and posterior colliculi and inserted on the medial aspect of the talus in a wide area inferior to the articular facet for the medial malleolus and anterior to the medial tubercle for all primates dissected. In macaque monkeys (n=4), the ligament was 63.0 mm^2 ± 13.8 mm^2 in cross-sectional area. In baboons (n=10), the posterior tibiotalar ligament had a cross-sectional area of 33.5 mm^2 ± 5.0 mm^2. The gorilla (n=1) had a ligament that was 157.1 mm^2 in cross-sectional area, and the chimpanzee (n=1) ligament was 31.4 mm^2 in cross-sectional area. Siegler et al. (1988) found that the human posterior tibiotalar ligament has a cross-sectional area of 141.9 mm^2 ± 99.2 mm^2, whereas the human cadavers measured (n=5) in this study had a larger average cross-sectional area of 212.6 mm^2 ± 65.0 mm^2, although the ranges from the two studies overlap. Because the Siegler et al. (1988) study measured 20 human cadavers and includes mass estimates of the humans, those results are used for comparative purposes throughout the rest of this chapter.

The cross-sectional area of the posterior tibiotalar ligament is known for each of the individual primates in this study; however, body mass is not. Therefore, a measure of cross-sectional area relative to body mass can only be calculated as an average and cannot be statistically analyzed for significance. However, trends can be observed (Table 5.3). The ratio of the square root of the cross-sectional area of the posterior tibiotalar

Table 5.3. Relative size of the posterior tibiotalar ligament in primates.

Species	n	Area of PTTL (mm^2)	Body mass (kg)	$\frac{(\text{PTTL area})^{(1/2)}}{(\text{Body mass})^{(1/3)}}$	Source
Homo sapiens	20 5	141.9 ± 99.2 212.6 ± 65.0	69.1 kg	~2.9	Siegler et al., 1988 This study
Pan troglodytes	1	31.4	33.7-42.7 kg	1.6-1.7	This study
Gorilla gorilla	1	157.1	~225 kg	2.1	This study
Papio anubis	10	33.5 ± 5.0	6.0-8.4 kg	2.9-3.2	This study
Macaca mulatta	4	63.0 ± 13.8	8.8-11.0	3.6-3.9	This study

ligament to the cube root of the mass of the animal is approximately 3.6-3.9 in macaques, 2.9-3.2 in baboons, 2.9 in humans, 2.1 in the gorilla, and 1.6-1.7 in the chimpanzee.

Ligament biomechanics

The largest ankle ligament in baboons is the posterior tibiotalar ligament (10.67 mm^2) followed by the posterior talofibular ligament (6.14 mm^2), and the calcaneofibular ligament (1.25 mm^2). As in humans, the posterior tibiotalar ligament is also the strongest, failing at a load of 141.8 N ± 41.0 N (range 60 N- 210.7 N) after a displacement of 3.4 mm ± 1.2 mm (range 1.3 mm- 4.5 mm). In comparison, the calcaneofibular ligament failed at a load of 55.8 N ± 43.2 N (range 10 N-120 N) after a displacement of 3.6 mm ± 0.9mm (range 2.2 mm- 4.8 mm) while the posterior talofibular ligament failed at a load of 58.7 N ± 19.1 N (range 30.9 N- 85 N) after a displacement of 3.2 mm ± 1.4 mm (range 1.7 mm- 5.8 mm). Baboons do not have an anterior talofibular ligament.

The maximum stress withstood by the posterior tibiotalar ligament was quite similar in the baboon (11.1 ± 4.1 MPa) and in a human study (16.0 ± 15.1 MPa) (Siegler et al., 1988). The strain calculated in the baboon demonstrated that it could stretch approximately half its original length before failure. This value is slightly higher than that reported in one human study (0.25 in Siegler et al. [1988]) and lower than another human study (2.1 in Attarian et al., [1985]).

The elastic modulus of the posterior tibiotalar ligament in the baboon is 28.3 ± 11.0 MPa. Although lower than the average value in humans, it is still within a single standard deviation of the human mean 99.54 ± 79.32 MPa (Siegler et al., 1988).

Skeletal morphology

The average angle that the posterior colliculus formed with the long axis of the tibia differed significantly between humans and all other primate species ($p<0.01$ for all comparisons) (Figure 5.9). The angle was statistically identical between the following groups: terrestrial cercopithecoids (*Papio, Mandrillus, Theropithecus, Macaca nemestrina*) and cebus ($p=0.43$), *Gorilla* ($p= 0.70$) and hylobatids ($p=0.62$); *Gorilla* and hylobatids ($p=1.0$), *Pan* ($p=0.72$), and arboreal cercopithecoids (*Nasalis* and *Macaca fascicularis*) ($p=0.05$); hylobatids and *Pan* (0.87), and arboreal cercopithecoids ($p=0.13$); arboreal cercopithecoids and *Pan* ($p=0.90$) and *Pongo* ($p=0.16$); *Pongo* and Atelines ($p=0.96$). There were no differences between the Ateline genera (*Ateles, Alouatta, Brachyteles,* and *Lagothrix*). There were no differences between males and females for any of the species examined. Thus, the angle that the posterior colliculus forms with the long axis of the tibia is the most acute in humans, and most obtuse in orangutans and New World Atelines.

Figure 5.9. Angle of intercollicular groove in extant anthropoids

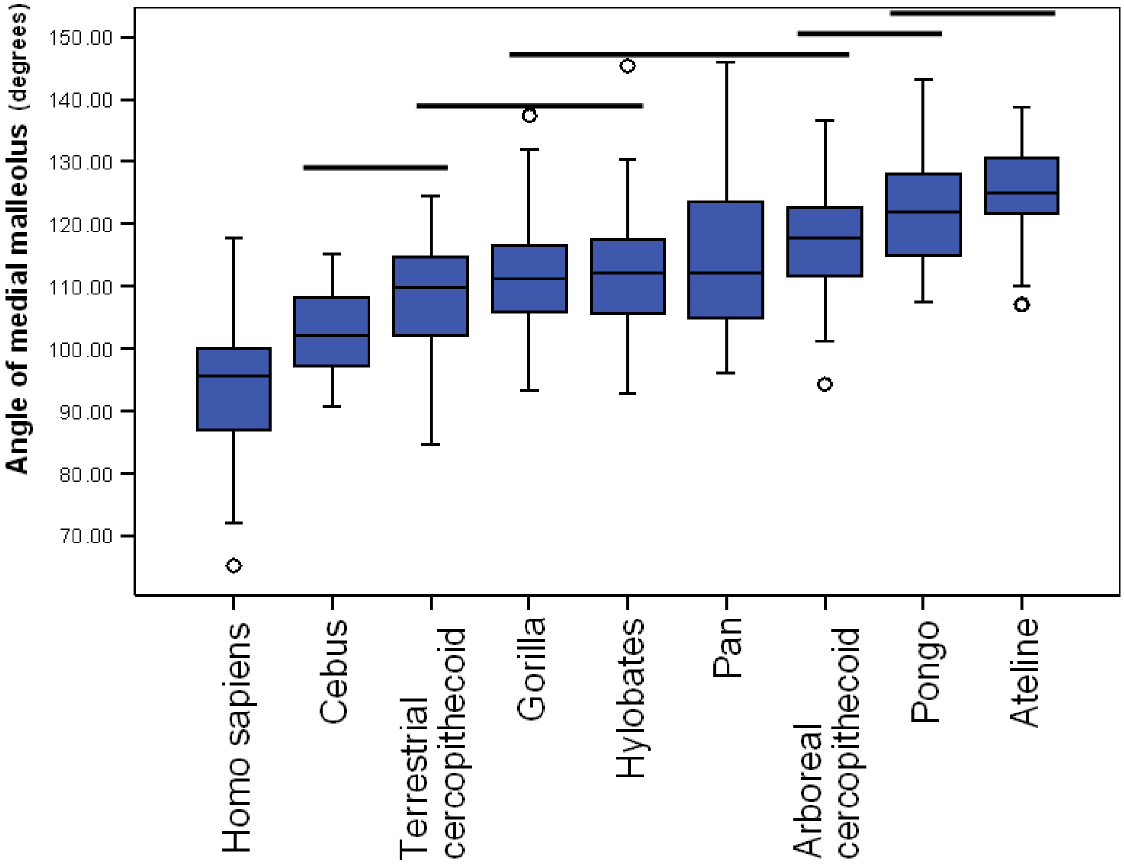


Figure 5.9. The angle that the intercollicular groove forms with the long axis of the tibia is graphed on the y-axis. Box and whisker plots show the median value (black line), interquartile ranges (blue/gray boxes) and full range of values (whiskers). Outliers are represented as circles. This angle is most acute in *Homo sapiens* and the terrestrial cercopithecoids and *Cebus*. The angle gradually becomes more obtuse in species that are more arboreal and more adapted for bouts of vertical climbing (African apes, *Pongo*, and atelines).

The area encompassed by the posterior tibiotalar ligament also differed between the different primate genera studied in a manner quite similar to that observed for the intercollicular angle (Figure 5.10). Statistically identical values were found for the following: *Homo sapiens* and terrestrial cercopithecoids (p=0.33) and *Cebus* (p=0.15); *Cebus* and *Gorilla* (p=0.88) and hylobatids (*Hylobates* and *Symphalangus*) (p=0.61); *Gorilla* and hylobatids (p=0.99) and *Pan* (p=0.07); *Pan* and hylobatids (p=0.49) and

Figure 5.10. Area of intercollicular groove in extant anthropoids.

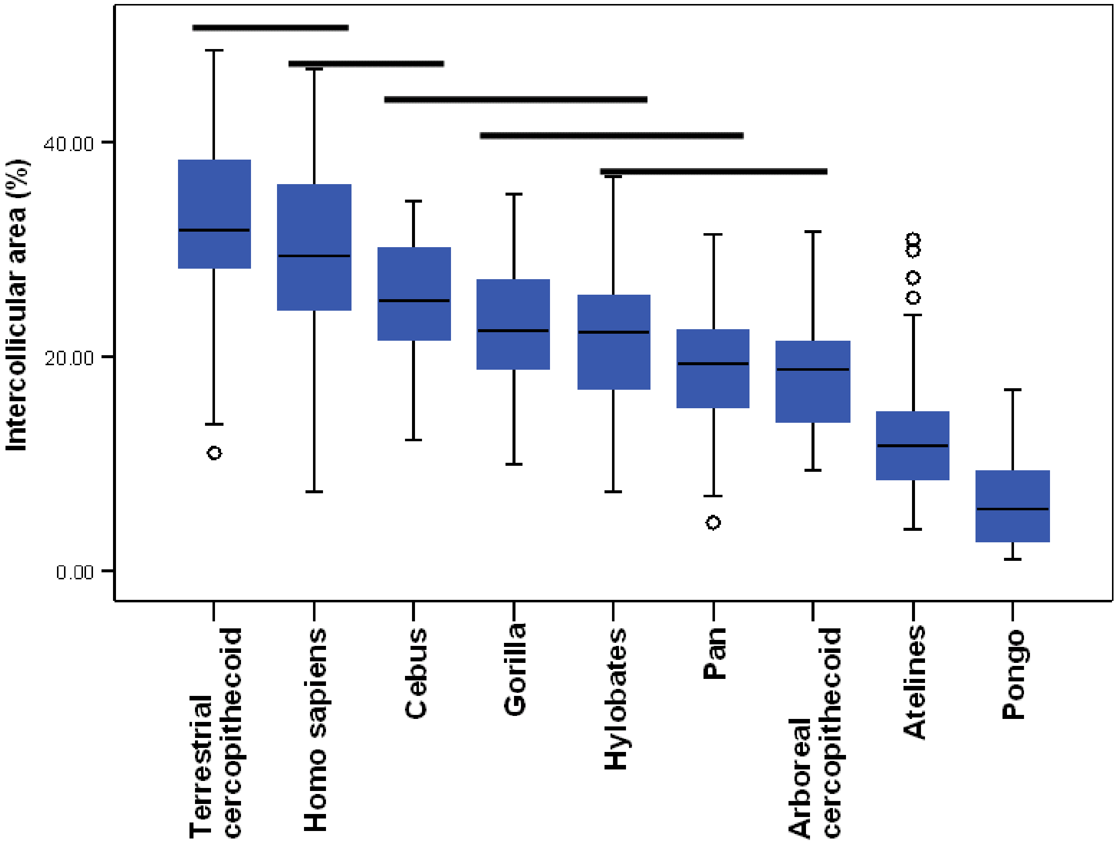


Figure 5.10. The area carved out of the medial malleolus by the intercollicular groove relative to the total area of the medial malleolus is a proxy for the size of the posterior tibiotalar ligament and is graphed on the y-axis. Box and whisker plots show the median value (black line), interquartile ranges (blue/gray boxes) and full range of values (whiskers). Outliers are represented as circles. The area is large in terrestrial monkeys and humans, and becomes gradually less substantial in the more arboreal monkeys, apes, and atelines.

arboreal cercopithecoids (p=1.0); and arboreal cercopithecoids and the hylobatids (p= 0.33). Males and females had statistically identical areas of the posterior tibiotalar ligament in all of the species studied. The area is largest in humans and the terrestrial quadrupeds, and smallest in orangutans and the ateline monkeys.

Morphology of fossil catarrhines from the Miocene

Figure 5.11. Comparative morphology of Miocene catarrhine medial malleoli.

Figure 5.11. Eight relatively complete distal tibia from catarrhines of the early to middle Miocene in lateral view. These are either right tibiae or have been mirrored to represent the right side. The tibiae have been scaled to similar sizes to better compare morphologies. Across the top are four tibiae thought to belong to the genus *Proconsul* (NAP I'58, KNM-RU 1939, KNM-RU 3589, KNM-RU 2036). Note the very similar morphology to the medial malleolus. Across the bottom is an unassigned distal tibia from Napak, Uganda (BUMP 764), a possibly *Dendropithecus* specimen from Legetet, Kenya (KNM-LG 583), *Victoriapithecus* (KNM-MB 11973), and the right tibia from *Nacholapithecus* KNM-BG 35250.

The four purported *Proconsul* distal tibia from the Miocene deposits of Napak (NAP I'58) and Rusinga Island (KNM-RU 1939, KNM-RU 3589, KNM-RU 2036) are strikingly similar in the morphology of the medial malleolus. These fossils share a distinct morphology in which the posterior colliculus bulges posteriorly and slightly inferiorly (Figure 5.11). There are some *Macaca nemestrina* tibiae with a similar morphology. The angle formed between the posterior colliculus and the long axis of the

Figure 5.12. Angle of intercollicular groove in Miocene catarrhines.

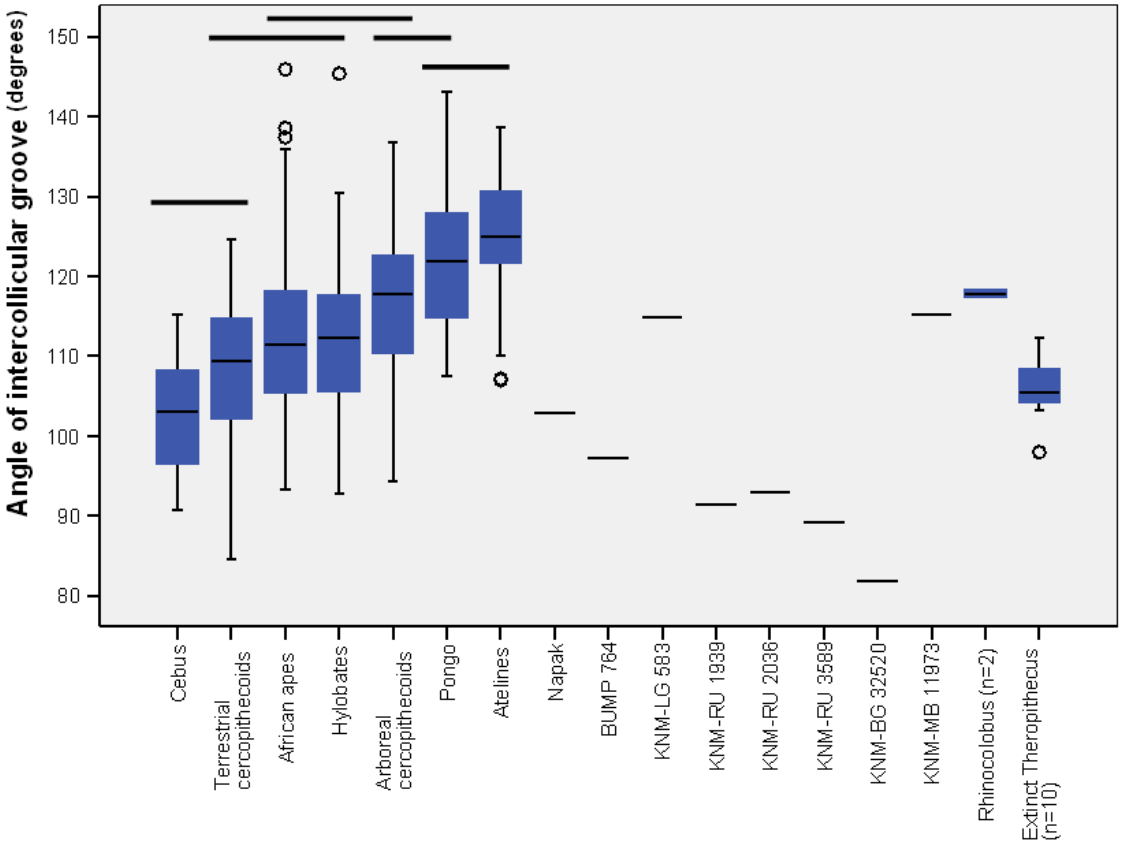


Figure 5.12. Box and whisker plots of the intercolliculr groove angle show the median value (black line), interquartile ranges (blue/gray boxes) and full range of values (whiskers). Outliers are represented as circles. The angle of the intercollicular groove is quite low in specimens assigned to *Proconsul* and *Nacholapithecus* and higher in the *Dendropithecus* and *Victoriapithecus* Miocene tibia, and in the Pleistocene *Rhinocolobus* specimens. The low angle in the Miocene specimens and in the Pleistocene *Theropithecus* fossils may reflect increased terrestriality whereas the higher angle may reflect an increase in arboreal activity.

bone is 102.8˚, 91.4˚, 89.1˚, and 93.0˚ for NAP I'58, RU 1939, RU 3589, and RU 2036 respectively (Figure 5.12). Although an estimate, the smaller Napak fossil BUMP 764 also has a low angle. The low angle formed by the posterior collicular is also present in the later Miocene *Nacholapithecus* tibia KNM-BG 35250, 81.9˚. For this measure, these fossils are most like the genus *Cebus* and the terrestrial cercopithecoids, though there is enough variation in arboreal cercopithecoids, *Hylobates* and the African apes to

Figure 5.13. Area of intercollicular groove in Miocene catarrhines.

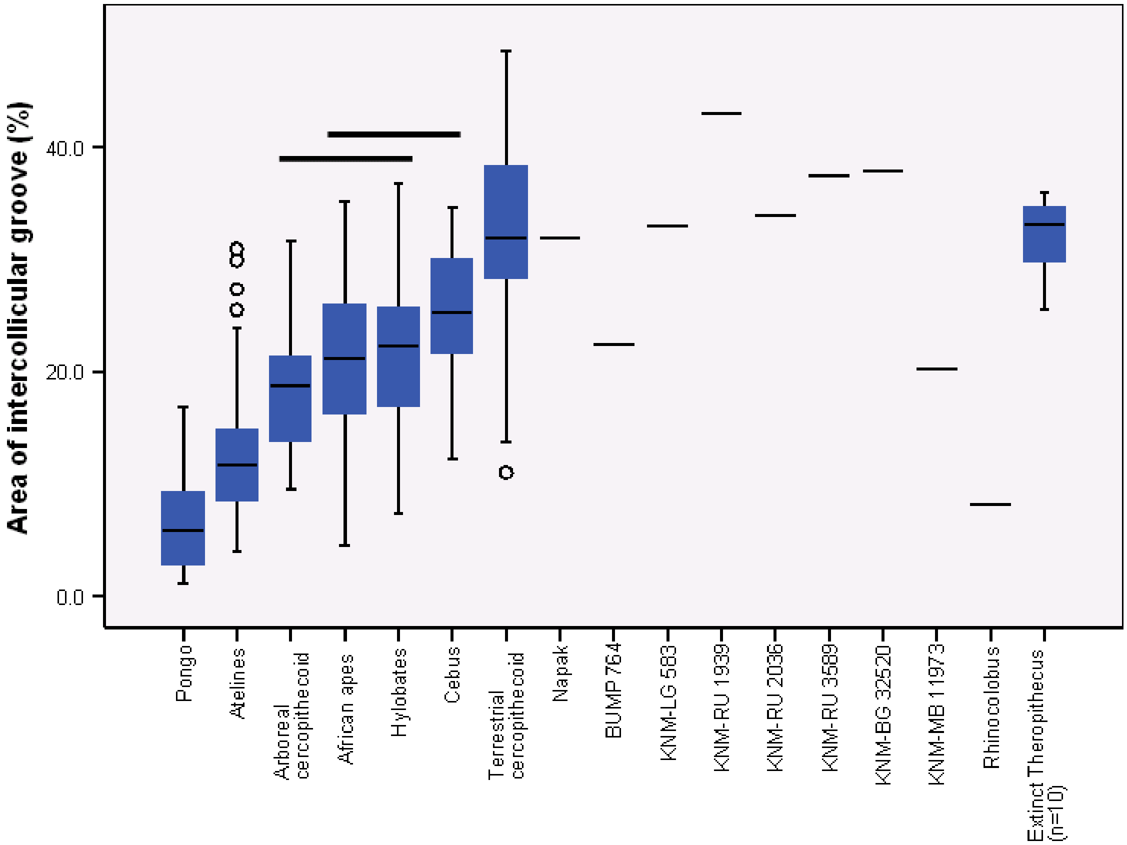


Figure 5.13. Box and whisker plots of the intercollicular area show the median value (black line), interquartile ranges (blue/gray boxes) and full range of values (whiskers). Outliers are represented as circles. Similar to what is illustrated in Figure 5.12, the area formed by the intercollicular groove is relatively high in specimens assigned to *Proconsul* and *Nacholapithecus* and lower in the *Victoriapithecus* tibia, and in the Pleistocene *Rhinocolobus* specimens. The high area in the Miocene specimens and in the Pleistocene *Theropithecus* fossils may reflect increased terrestriality whereas the reduced area for the posterior tibiotalar ligament may reflect a weaker ligament and an increase in arboreal activity.

encompass these values. In contrast, KNM-LG 583 and the later *Victoriapithecus* fossil KNM-MB 11973 have a more obtuse angle of 114.8˚ and 115.3˚ respectively. They are most like the arboreal cercopithecoids for this measure.

The area encompassed by the intercollicular groove is high and terrestrial cercopithecoid-like for all of the Miocene fossils except perhaps for BUMP 764 and the

Victoriapithecus distal tibia KNM-MB 11973 (Figure 5.13). The area measured is 31.9% for NAP I'58; an estimated 22.5% for BUMP 764; 33.0% for KNM-RU 583; 43.1%, 37.6%, and 34.0% for RU 1939, RU 3589, and RU 2036 respectively; 37.9% for KNM-BG 32520; and only 20.3% for KNM-MB 11973.

Morphology of fossil cercopithecoids from the Pleistocene

The two purported *Rhinocolobus* tibia have medial malleoli similar to the arboreal *Nasalis*, though one specimen (KNM-ER 1542) has a more poorly developed intercollicular groove than the other fossil, KNM-ER 45613. The angle formed by the intercollicular groove is 117.4° in ER 1542 and 118.2° in ER 45613, though the area formed by the groove is 8.2% in the former and 25.6% in the latter. In this respect, ER 45613 is more like the large *Theropithecus* fossil tibia and may actually belong to that taxa.

Ten *Theropithecus* tibiae were studied and all of the fossils were quite similar to one another, and all cluster within the distribution occupied by the modern terrestrial quadrupeds *Papio*, *Mandrillus*, *Theropithecus*, and *Macaca nemestrina* (Figure 5.12). The average angle formed by the intercollicular groove is 105.9° ± 4.1° (range 98.0°-112.2°), and the area occupied by the intercollicular groove on the medial malleolus is 33.0% ± 2.5% (range 29.5%-35.9%).

Morphology of fossil hominins (Figure 5.14)

Unfortunately, the oldest hominin tibia KNM-KP 29285 from the 4.12 mya *A. anamensis* has damage to the most inferior aspect of the medial malleolus and the shape

Figure 5.14. Comparative morphology of medial malleolus in fossil hominins.

Figure 5.14. Ten hominin distal tibiae measured in this study shown in lateral view. These are all right tibiae or have been mirrored to represent the right side. The tibiae have been scaled to roughly the same size. Across the top are tibiae from *Australopithecus*, with KNM-KP 29285 from *A. anamensis*, three tibiae from *A. afarensis* (AL 288-1, AL 333-6, AL 333-7), and StW 358 is from *A. africanus*. Across the bottom are latter, Plio-Pleistocene tibiae. KNM-ER 2596, KNM-ER 1500, and KNM-ER 1481 are all 1.9 mya and their taxonomic affinity is unclear though it is thought that ER 1500 may be from *P. boisei* while ER 1481 may be from *Homo*. StW 567 is from later deposits in the Sterkfontein cave and is thought to be from *Homo*. KNM-WT 15000 is from *Homo erectus*. KNM-KP 29285 is the oldest distal tibia, 4.12 mya from *A. anamensis*. The medial malleolus is crushed inferiorly and reliable measurements on the intercollicular groove were not possible.

and size of the intercollicular groove cannot be accurately assessed. However, three complete distal tibiae from *A. afarensis* are preserved. A.L. 288-1 has the most modern human-like medial malleolus of any hominin fossil assessed. The intercollicular groove forms an angle of 95.6˚ with the long axis of the shaft and occupies 27.7% of the medial malleolus. These values are quite similar to the human means of 93.8˚ ± 9.8˚ and 30.7% ±

11.1% respectively. The remaining hominin tibia are between the human range and the African ape range of 112.9° ± 10.1° and 21.0% ± 6.4% for these two measures.

A.L. 333-6 and A.L. 333-7 have similar intercollicular angles of 106.6° and 108.2° and the areas occupied by the intercollicular groove are 28.2% and 23.9% respectively. The *A. africanus* distal tibia StW 358 is quite similar to the Hadar remains. The intercollicular angle is 105.6°, while the groove occupies 24.5% of the area of the collicular region of the medial malleolus. The possibly *P. boisei* (Grausz et al., 1988) distal tibia from the Koobi Fora KNM-ER 1500 has an angle of 91.2° and an area for the posterior tibiotalar ligament occupying 23.8% of the malleolar region. The possibly *Homo* distal tibia from Koobi Fora KNM-ER 1481 has an angle of 110.4° and an area of 23.4%. The KNM-ER 2596 distal tibia from the Koobi Fora deposits has an angle of 104.7° but a strikingly small area for the posterior tibiotalar ligament occupying only 9.4% of the medial malleolus. StW 567, a potentially *Homo* distal tibia from Member 5 deposits in the Sterkfontein cave has a medial malleolus with dimensions very similar to the other Early Pleistocene hominins with an angle of 103.5° and an area of 22.3%. Finally, the KNM-WT 15000 distal tibia forms an angle between the intercollicular groove and the long axis of the tibia of 93.1° and has an intercollicular area of 29.1% of the total collicular region of the medial malleolus.

Discussion

Extreme dorsiflexion is an adaptation for bringing a climbing ape or ateline closer to the substrate during vertical climbing bouts (Chapter 2). Because the posterior tibiotalar ligament is primarily a restrictor of dorsiflexion in humans, it was hypothesized that the size and attachment area for this ligament would be more poorly developed in vertically climbing apes than in the more terrestrial cercopithecoids and humans. Testing this hypothesis required examining whether the ligament had the same biomechanical properties in the human ankle and the ankle of a non-human primate.

The hypothesis that there are no differences in the biomechanical properties of the human posterior tibiotalar ligament and the same ligament from a non-human primate could not be refuted. As in humans (Close, 1956; Attarian et al., 1985; Siegler et al., 1988; Sarrafian, 1993; Klein, 1994; Milner and Soames, 1998; Beumer et al., 2003), the baboon posterior tibiotalar ligament is both the relatively largest and the strongest in the ankle complex. Direct comparisons with the human ligament demonstrate that the maximum stress and strain of the ligament prior to failure is quite similar in the baboon posterior tibiotalar ligament (Table 5.4). Similarly, the Young's modulus calculated for the baboon posterior tibiotalar ligament is within a standard deviation of the human mean for this measure (Table 5.4). Because the biomechanical properties of the ligament are probably conserved between humans and baboons, the size and orientation of the origin and attachment points for this ligament are likely to be functionally informative.

The null hypothesis of no difference in the morphology of the medial malleolus between primates that differ in their locomotion was not supported. Instead, vertically climbing apes and atelines have weakly developed regions of attachment for the PTTL, whereas humans and terrestrial cercopithecoids have much larger areas of attachment for this ligament on the medial malleolus. Furthermore, in the available primate cadavers, the PTTL is larger relative to body mass in baboons, macaques, and humans than what can be found in the chimpanzee or gorilla. Additional data on the size of the PTTL, especially

Table 5.4. Biomechanical properties of posterior tibiotalar ligament in baboon and human ankle.

	Baboons (this study)	Humans
Maximum force (N)	141.8 ± 41.0	[1]713.8 ± 69.3 (n=6) [2]467 ± 289 (n=20) [3]244 ± 71 (n=3) [4]446 ± 51 (n=10)
Stress (Mpa)	11.1 ± 4.1	[2]15.99 ± 15.07
Strain (mm/mm)	0.53 ± .16	[1]2.10 ± .23 [2]0.25 ± .13
E (MPa)	28.3 ± 11.0	[2]99.54 ± 79.32
Energy to yield point (Nmm)	252.8 ± 121.0	[1]747.0 ± 133.0 [2]~508

[1] Attarain et al., 1985; [2] Siegler et al., 1988; [3] Nigg et al., 1990; [4] Beumer et al., 2003

in apes, will be necessary to test this hypothesis with any statistical rigor.

In addition to the area of attachment, the point of attachment of the PTTL in the intercollicular groove of the medial malleolus affects the function of the ligament, from one guiding motion in apes, to one restricting motion in cercopithecoids and humans. In a study of ligament biomechanics, Alexander and Bennett (1987) found that ligaments that attach near to the axis of rotation remain isometric through the entire range of motion of the joint, and thus they serve only to stabilize and guide joint motion rather than restricting it. However, ligaments that insert at a distance from the axis of rotation can become taut at the extremes of joint motion, and thus serve to restrict joint motion (Alexander and Bennett, 1987). Because it is known that the axis of rotation of the ankle runs roughly through the tip of the medial malleolus (Inman, 1976; Latimer et al., 1987; Lundberg et al., 1989), the PTTL attaches near the axis of rotation in species without a developed intercollicular groove, like apes and atelines. The function of the PTTL in these species is thus as an ankle stabilizer on the medial side. However, in humans and terrestrial cercopithecoids, the PTTL anchors in a well developed intercollicular groove, at a distance from the axis of rotation, and thus the posterior fibers of this ligament become taut during extremes of dorsiflexion. The function of this ligament in these species is more of an inhibitor of dorsiflexion.

There are two important caveats to these results. First, these data suggest that a weakly developed posterior tibiotalar ligament is not a vertical climbing adaptation per se. These data are some of the first in the talocrural joint to distinguish arboreal cercopithecoids from terrestrial cercopithecoids (Figures 5.6 and 5.7). In Chapter 3, it was found that the general morphology of the distal tibia and talus of a cercopithecoid, whether more terrestrial like *Papio*, or more arboreal like *Nasalis*, showed only subtle differences. However, the data reported here suggest that the posterior tibiotalar ligament is more strongly developed in terrestrial cercopithecoids, whereas more arboreal cercopithecoids have weakly formed intercollicular grooves and probably do not have a strong dorsiflexion restricting posterior tibiotalar ligament. Pleistocene genera *Theropithecus* and *Rhinocolobus* have distinct medial malleoli, suggestive of a more terrestrial and more arboreal life respectively (Figures 5.12 and 5.13). Fossils from the Miocene genus *Proconsul* are suggestive of a well developed posterior tibiotalar ligament, though these data should be considered in the context of the entire talocrural morphology. For example, while the morphology of the smaller *Proconsul* fossils are quite similar to modern terrestrial cercopithecoids, like *Papio*, the larger tibia from *Proconsul major* has morphologies suggestive of some degree of vertical climbing. It is thus noteworthy that the *P. major* tibia has a less strongly developed intercollicular region than the other *Proconsul* specimens, which have an intercollicular groove that advances to a more anterior region of the medial malleolus. The distal tibia from Legetet, KNM-LG 583 is unlike the other *Proconsul* specimens in having a more obtuse intercollicular angle, and thus may be from another taxon such as *Dendropithecus* as suggested by Rafferty et al. (1995; contra Harrison, 1982). Additionally, the shape of the intercollicular groove in KNM-MB 11973 from *Victoriapithecus* is consistent with others who have suggested agility and at least some arboreality in this Miocene cercopithecoid (Harrison, 1989). These results suggest that a weakly developed posterior tibiotalar ligament is a morphology not only present in the ankle of the vertically climbing atelines and apes, but also in the arboreal cercopithecoids and primitive catarrhines. Dorsiflexion may be important in keeping the center of mass of arboreal cercopithecoids close to the substrate (Meldrum, 1991), though data on the morphology of the ankle is suggestive that arboreal cercopithecoids do not load their ankles in dorsiflexion any more than terrestrial cercopithecoids (Chapter 3), and when climbing, cercopithecoids flex at the midfoot rather than at the ankle (Chapters 2 and 7).

Second, although the mean values of intercollicular area and angle are statistically distinct between vertically climbing apes and atelines and more terrestrial cercopithecoids and humans, tremendous variation can be found within a species or locomotor group. Although there are general trends that find terrestrial primates with a more developed intercollicular area, individuals can be found with poorly developed, ape-like intercollicular regions. Such overlap in morphology and variation within a species makes it difficult to interpret the size and function of the posterior tibiotalar ligament in isolated fossil tibia. However, although individual humans and baboons can be found with more ape-like morphology to the medial malleolus, it was unusual to find climbing apes or atelines with a morphology of the medial malleolus in the far human ranges (Figures 5.9

and 5.10). In other words, humans and baboons display medial malleoli suggestive of a poorly developed posterior tibiotalar ligament, but very few tibiae of apes or atelines have evidence for a strongly developed posterior tibiotalar ligament.

Morphological variation in the talocrural joint is likely due to the fact that the posterior tibiotalar ligament is not the only anatomical element limiting or restricting dorsiflexion in the ankle. As discussed in Chapters 3 and 4, skeletal morphologies related to dorsiflexion restriction may include the depth of the articular surface of the tibia, and the overall geometry of the distal tibia. Shallow, anteroposteriorly shortened tibia have more capacity for dorsiflexion than deeply concave, anteroposteriorly prolonged tibia (Chapters 3 and 4). Therefore, these data on the posterior tibiotalar ligament should be interpreted in a framework that considers the complete morphology of the ankle. The shape of the hominin medial malleolus, falling essentially between the human and African ape distribution (except KNM-ER 2596), may be interpreted in isolation as reflecting an increase in dorsiflexion relative to modern humans (Figures 5.15 and 5.16). However, these tibiae also possessed deeply concave tibial articular surfaces, and demonstratively square-shapes to their distal ends. Both of these morphologies would limit extreme dorsiflexion (Chapter 4). Additionally, and perhaps most importantly to this discussion, the depth of the articular surface and the dimensions of the tibial surface of some hominin tibia are on the high end or even beyond the range of distribution found in modern humans (Chapter 4). Given these osteological elements that would prohibit extreme dorsiflexion in the hominin talocrural joint, the presence of a robust deltoid ligament may be superfluous. However, the morphology of KNM-ER 2596 suggests that this individual had a poorly developed posterior tibiotalar ligament and data from Chapter

Figure 5.15. Angle of intercollicular groove in fossil hominins.

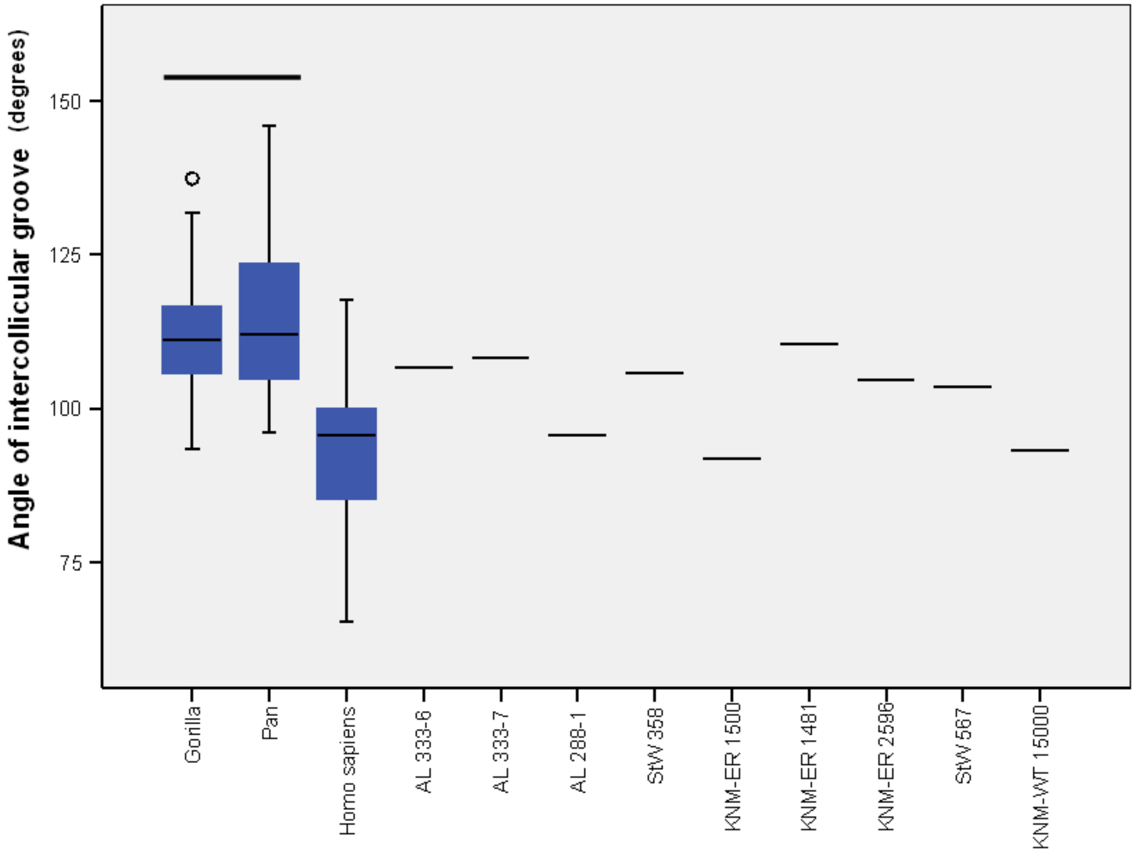


Figure 5.15. Box and whisker plots of the intercollicular groove angle show the median value (black line), interquartile ranges (blue/gray boxes) and full range of values (whiskers). Outliers are represented as circles. The angle formed by the intercollicular groove relative to the long axis of the tibia is higher in African apes than in modern humans. Some fossil tibia fall in the modern human range (AL 288-1, KNM-ER 1500, KNM-WT 15000) while the rest fall between the human and African ape distribution. This is discussed further in the text.

4 suggest that other inhibitors of dorsiflexion are only weakly present in this specimen. Whether KNM-ER 2596 belongs to *Rhinocolobus*, a vertically climbing hominin, or to a pathological hominin is addressed in Chapter 4.

Furthermore, the shape of the intercollicular groove of hominins as existing in the morphospace between the human and African ape distribution needs to be considered in more detail. In Chapter 4, it was found that known hominins have reduced foot abduction relative to African apes and possess a perpendicularly aligned tibia over the foot (except

Figure 5.16. Area of intercollicular groove in fossil hominins.

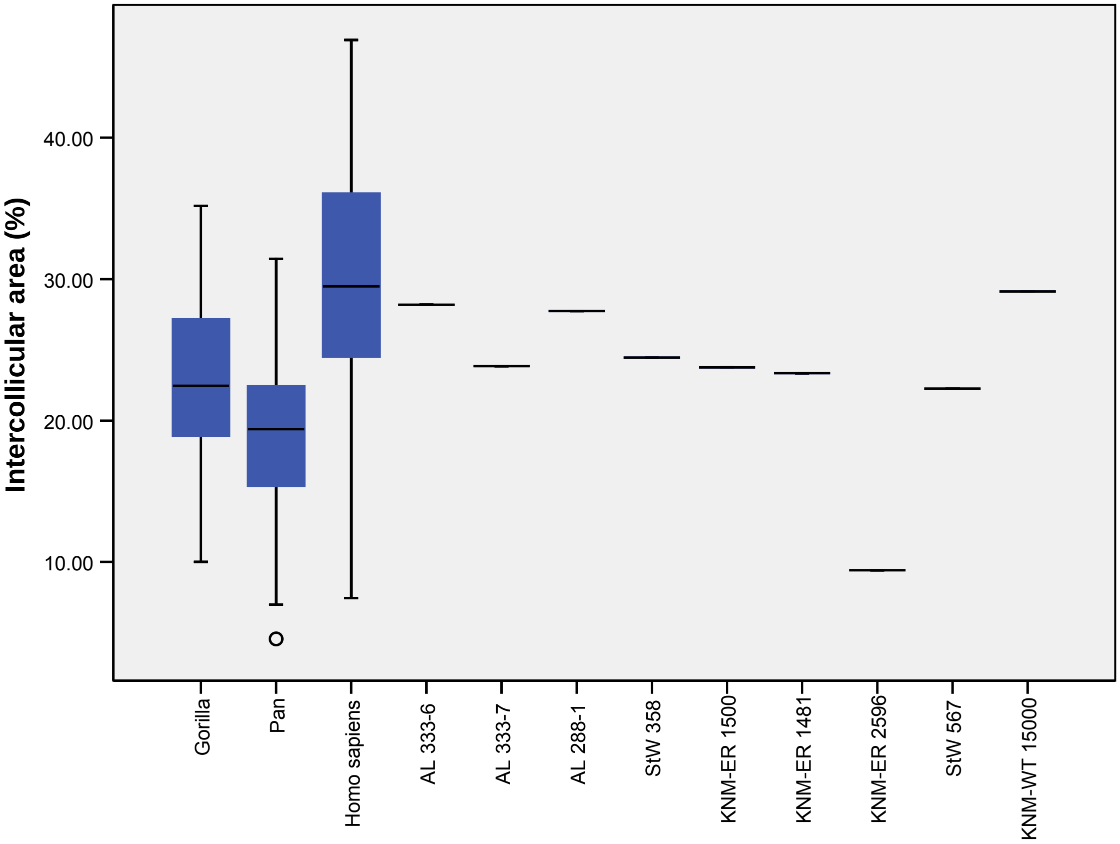


Figure 5.16. Box and whisker plots of the intercollicular area show the median value (black line), interquartile ranges (blue/gray boxes) and full range of values (whiskers). Outliers are represented as circles. The area for the posterior tibiotalar ligament is larger in humans than in the African apes, though there is considerable overlap in this measurement. All of the fossil hominin tibia fall within both the human and African ape range for this measure except for KNM-ER 2596 which is outside the human range for this measure and more closely resembles *Pongo* (see Figure 5.10).

KNM-ER 2596). Both of these morphologies would severely hinder vertical climbing in an ape-like manner. Two potential climbing scenarios were proposed. The first hypothesized that hominins were placing their foot on the anterior aspect of the tree, and because they possessed a perpendicularly aligned tibia, only extreme dorsiflexion even beyond perhaps what African apes are capable of, would pull the hominin closer to the tree, thus reducing its climbing costs. For hominins climbing in this manner, an orangutan-like morphology to the medial malleolus is predicted (Figure 5.8). The second scenario hypothesized that hominins were climbing with their feet against the side of the tree and their knees splayed laterally. A third scenario would posit the absence of climbing altogether in fossil hominins. Therefore, vertical climbing in hominins, with lower limb morphologies that already limit the joint motions adapted for ape-like climbing, would require even more exaggerated features related to climbing in other regions or anatomies. By possessing an “in-between” shape to the medial malleolus, hominins may not have possessed as strong a posterior tibiotalar ligament as possessed by modern humans, but they were moving away from the African ape condition and thus moving away from a morphology that allowed substantial dorsiflexion.

This interpretation of the data is especially relevant for A.L. 288-1, which has been the focus of many of the debates about australopithecine locomotion (Stern and Susman, 1983; Susman et al., 1984; Latimer et al., 1987). The shape of the intercollicular groove on the medial malleolus of A.L. 288-1 is as similar to the modern human morphology as any of the other hominins studied, including the *Homo erectus* tibia KNM-WT 15000. Although there are African apes that have as much area devoted to the posterior tibiotalar ligament attachment on the medial malleolus as A.L. 288-1, few gorillas and no chimpanzees have an intercollicular angle as sharp. By having such an angle, the posterior fibers of the posterior tibiotalar ligament on A.L. 288-1 would have been quite far from the axis of rotation and would have resisted extreme dorsiflexion. These data suggest that this individual *A. afarensis* (Lucy) could not have dorsiflexed her ankle beyond 45° and therefore she could not have vertically climbed like a modern ape. Even if the other hominins studied had an increased capacity for dorsiflexion based on a more weakly developed posterior tibiotalar insertion, there is little evidence that these

Figure 5.17. Distal tibia of "Little Foot" StW 573.

Figure 5.17. The *Australopithecus* sp. fossil StW 573, or "Little Foot", preserves a relatively complete distal tibia. Although this author was not allowed to study this specimen, photographs of the fossil in lateral view suggest a very weakly developed attachment for the posterior tibiotalar ligament. This is discussed further in the text. Image reproduced from Deloison (2003).

individuals actually loaded their ankles in this position of dorsiflexion (Chapter 4). Based on these and other morphologies of the lower limb, continued ape-like vertical climbing in hominins would have required that the morphology of the medial malleolus become even more ape-like, perhaps even orangutan-like, to facilitate the extreme dorsiflexion needed to compensate for all of the other adaptations for bipedalism that maladapted the animal for climbing. Although I was unable to study the StW 573 “Little Foot” distal tibia, the only known published photograph of this specimen in lateral view (Deloison, 2003) shows a strikingly orangutan-like shape to the medial malleolus (Figure 5.17). This weak attachment of the posterior tibiotalar ligament on the medial malleolus of the StW 573 distal tibia is tantalizing and should be studied in more detail on the original specimen.

In addition to skeletal restrictors to dorsiflexion, the Achilles tendon has been suggested as a critical dorsiflexion inhibitor in modern humans (Costa et al., 2006). However, in this study, cutting of the Achilles tendon in both human cadavers and in the gorilla specimen only slightly increased the range of dorsiflexion possible in the ankle. Only after cutting the posterior tibiotalar component of the deltoid ligament was there unrestricted flexion of the tibia over the foot. Furthermore, damage to the human ankle suffered when dorsiflexed beyond 45° included tears of the deltoid ligament, fractures of the medial and lateral malleoli and damage to the posterior tibialis, flexor hallucis, and flexor digitorum longus muscles (Begeman and Pradad, 1990). However, there was no mention of tears of the Achilles tendon. Given the difference between the modern human and hominin posterior tibiotalar ligaments, there is the possibility that a strong dorsiflexion restricting posterior tibiotalar ligament evolved in concert with the strong Achilles tendon.

This study has only considered the effects that the area and angle of attachment of the posterior tibiotalar ligament has on ankle dorsiflexion; however, one also has to consider the possible adaptive functions of the posterior tibiotalar ligament besides dorsiflexion restriction. This ligament serves a critical role in preventing excessive eversion (Stormont et al., 1985; Harper, 1987) and in limiting medial movement of the tibia over the talus (Michelson and Helgemo, 1995). Given that the axis of rotation of the ankle in eversion would be more or less centered on the talar body, the shape of the intercollicular groove would not change the origin of the posterior tibiotalar ligament relative to this axis and thus a deeper intercollicular groove would not increase efficiency of eversion resistance. However, a stronger posterior tibiotalar ligament would hold the medial aspect of the tibia in place as the lateral aspect of the tibia flexes over the talus. This would increase internal rotation of the tibia during dorsiflexion and external rotation during plantarflexion, and may explain why this rotation has been measured as up to 19˚ during walking in living humans (Donnatelli, 1990), but only 0˚ from the skeletal elements alone (Chapter 4). The role that increased tibial rotation would have in the kinematics of normal bipedal walking should be examined more closely in light of these data.

Although the biomechanical properties did not differ between the human and non-human primate posterior tibiotalar ligament, variation observed in the function of this ligament and its ability to restrict dorsiflexion could also include mechanoreceptors in the ligament itself. There are four types of mechanoreceptors in mammalian ligaments, designated Type I-Type IV (Freeman and Wake, 1967). During proprioception, stretching of the ligaments activates these mechanoreceptors, which respond by generating nerve signals to the appropriate compensatory muscles. For example, nerve fibers from the deltoid ligament to the posterior tibialis nerve have been isolated in felines (Solomonow and Lewis, 2002). A histological study of the human ankle found that the anterior talofibular, posterior talofibular, and posterior tibiotalar ligaments had significantly more Type II and Type III mechanoreceptors than what is found in the calcaneofibular and superficial deltoid fibers (Michelson and Hutchins, 1995). These data are consistent with experimental evidence showing that the calcaneofibular and fibers of the superficial deltoid remain isometric through the range of motion in the human ankle (Leardini et al., 1999; Stagni et al., 2004). Type II receptors respond at the beginning of joint motion whereas Type III receptors are activated during the extremes of joint motion (Wyke, 1972; Zimny, 1988). Their presence in high concentrations in the human posterior tibiotalar ligmament is consistent with the hypothesis that this ligament helps restrict dorsiflexion and will recruit muscle action during extremes of dorsiflexion. It is hypothesized that there would be fewer Type II and Type III mechanoreceptors in the ape posterior tibiotalar ligament. However, the possibility exists that variation in the number of mechanoreceptors in the ligament of now extinct catarrhines and hominins may have made the ligament more or less responsive to changes in length. For example, increased Type II receptors in the posterior tibiotalar ligament in the hominin ankle would have triggered a muscular response to an increase in dorsiflexion. This could have compensated for a smaller intercollicular groove than what humans possess today, and would be undetectable in the fossil record. Comparative studies of the frequency and distribution of mechanoreceptors in the primate ankle are needed to begin to address this possibility.

Conclusion

In humans, the posterior tibiotalar portion of the deltoid ligament is a primary restrictor of extreme dorsiflexion in the ankle. The biomechanical properties of the posterior tibiotalar ligament are statistically identical in humans and in *Papio anubis*. Therefore, it is reasonable to assume that differences in cross-sectional area and in the geometry of this ligament relative to the joint axis will reflect differences in its function. Preliminary data on primate cadavers suggest that the ligament has a relatively large cross-sectional area in humans and terrestrial primates, but is relatively smaller in the vertically climbing apes *Pan* and *Gorilla*. In addition, the ligament attaches closer to the axis of rotation of the ankle in vertically climbing apes and atelines, limiting its role to an ankle stabilizer. By shifting this ligament away from the axis of rotation, it changes it role from a stabilizer to a restrictor of extreme dorsiflexion. The early hominoid *Proconsul* had a well developed posterior tibiotalar ligament and probably could not dorsiflex at the ankle like modern apes, limiting their ability to vertically climb. A shift in the function of the posterior tibiotalar ligament towards a dorsiflexion inhibitor is already apparent in early hominin distal tibia as well and provides evidence that ape-like vertical climbing was not a likely locomotion practiced by our hominin ancestors.

CHAPTER 6

Ankle stability and the evolution of the anterior talofibular ligament.

Abstract

Ankle stability is important for terrestrial and arboreal locomotion in primates. Joint stability, however, can be achieved anatomically in three different ways. A joint can be strengthened with muscle, reinforced with strong ligamentous tissue, and via the bony morphology of the joint itself. In humans, ankle stability is maintained in part by the anterior talofibular ligament. However, this ligament, which is one of the most often sprained structures in the human body, is rare or completely absent in non-human primates. Because this ligament attaches to a bony tubercle on the distal-lateral aspect of the talar body, its evolutionary history can be tracked. A comparative analysis of the biomechanical properties of baboon ankle ligaments, the shape of the talar trochlea in Old World primates, and a study of 15 hominin tali from 3.2 million years ago to 1.5 million years ago suggest that all three strategies for stabilizing the ankle joint occurred in early hominin evolution, and that the anterior talofibular ligament may have evolved in the *Homo* lineage. Strong peroneal muscles may have resisted ankle inversion in the earliest bipeds, whereas the keeled bony morphology of the talar trochlea reinforced the ankle in later Plio-Pleistocene hominins. The first evidence of a well-developed anterior talofibular ligament can be found in the four largest tali in the hominin fossil record starting with the 2.2 mya talus from Omo Ethiopia (Omo 323-76-898), and later in

Kenyan specimens KNM-ER 1464, KNM-ER 813, and KNM-ER 5428. These results suggest that the flattening of the talar trochlea, an adaptive response to an increase in body size and perhaps long distance travel in the genus *Homo*, may have selected for the ligamentous, rather than bony means by which hominins stabilized the ankle.

Introduction

The talocrural joint, or the ankle, is formed between the distal tibia, distal fibula and the talus. As obligate bipeds, humans bear all of their weight on the talocrural joint during locomotion and thus have evolved a joint morphology well adapted to absorb and distribute forces through this region (Latimer et al., 1987). Instability of the talocrural joint can result in incongruence of the talus under the tibia (Skie et al., 1989; Harper, 1990; Cass and Settles, 1994; Earll et al., 1996; Sugimoto et al., 1997) which causes an increase in localized stress (Calhoun et al., 1994; Driscoll et al., 1994; Kura et al., 1998; Michelson et al., 2001) and can lead to injury (Harrington, 1979). Stability of the ankle mortise is provided both by bony morphology and by ligamentous support. The distal tibia and fibula are attached to one another via the anterior and posterior tibiofibular ligaments. Three distinct ligaments, anterior talofibular, calcaneofibular, and posterior talofibular, support the lateral side of the upper ankle joint (Figure 6.1), whereas the medial side of the joint is anchored by the thick and strong deltoid ligament.

Cass and Settles (1994) found that during foot inversion, ankle dislocation caused by tilting of the talus plantarly and medially away from the tibia is prevented by the anterior talofibular and calcaneofibular ligaments and that the articular surface of the talocrural joint contributes very little to preventing this motion. However, work by

Figure 6.1. Anatomy of the human ankle (lateral).

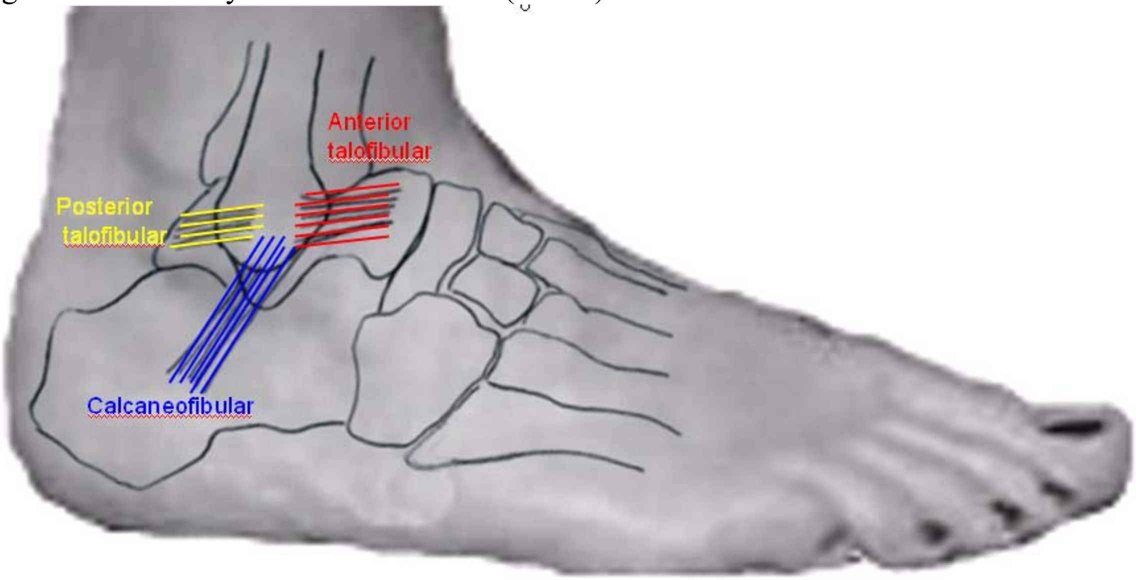


Figure 6.1. Anatomy of the lateral side of the human ankle. The ankle is formed between the tibia, fibula, and talus bones. On the lateral side, the anterior talofibular (red), posterior talofibular (yellow), and calcaneofibular (blue) ligaments provide stability. The anterior talofibular ligament is one of the most often sprained ligaments in the human body.

Tochigi et al. (2005, 2006) suggests that both ligaments and bony articular surfaces help stabilize the ankle. In an unloaded ankle, ligaments helped stabilize the ankle, but only at extremes of motion (Tochigi et al., 2005). When the ankle was loaded in an axial direction, both the articular surface and the ligaments shared the role of limiting inversion and internal and external rotation of the foot (Tochigi et al., 2006). Regardless of the relative contributions of ligaments and the articular surface to joint stability, many studies have concurred that the anterior talofibular ligament (ATaFL) is an important structure limiting inversion at the talocrural joint (Johnson and Markolf, 1983; Rasmussen, 1985; Stormont et al., 1985; Chen et al., 1988; Luo et al., 1997; Hintermann, 2002).

However, during extreme inversion of the foot, it is not uncommon for the talus to tilt away from the talocrural mortise in humans (Cox et al., 1979; Siegler et al., 1988)

Figure 6.2. Talar tilting in human ankle and a sprain of the anterior talofibular ligament.

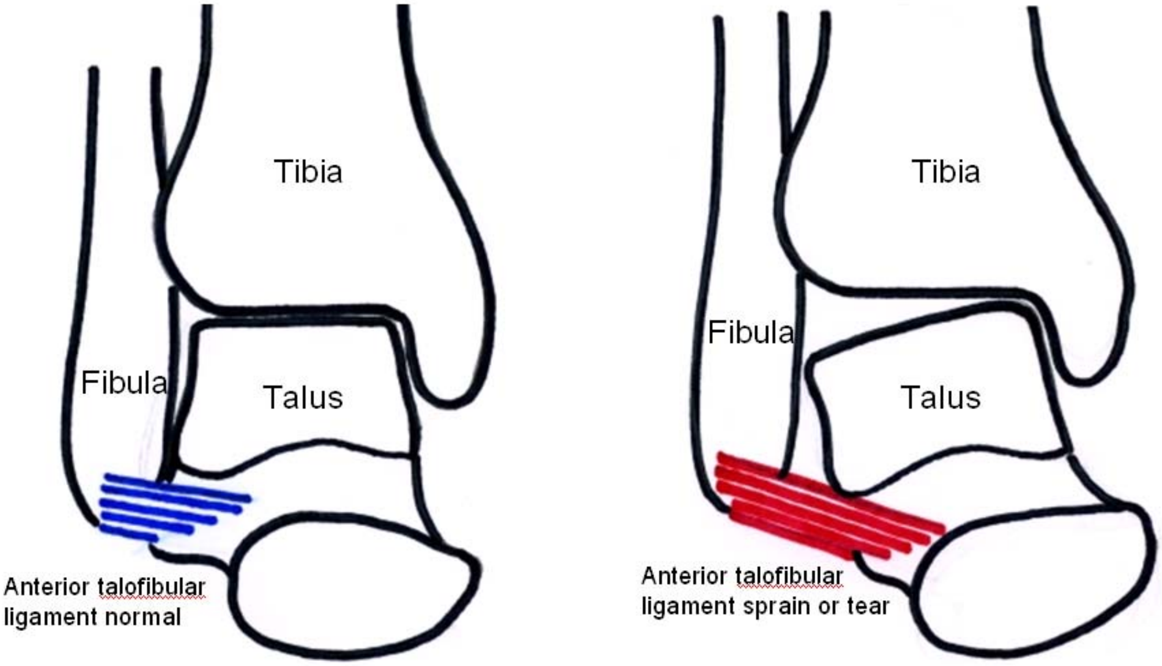


Figure 6.2. Talar tilting. Extreme and sudden foot inversion causes the talus to tilt away from the tibia and fibula. This motion puts strain on the anterior talofibular ligament and can result in a sprain or tear of the ligament.

(Figure 6.2). The degree to which this occurs is directly related to laxity of the anterior talofibular ligament (Inman, 1976; Cass and Settles, 1994; Lentell et al., 1995; Hertel, 2002; Hubbard et al., 2007). Because the anterior talofibular ligament (ATaFL) is the weakest of the ankle complex (Attarain et al., 1985; Siegler et al., 1988), it is also the most often injured ligament in the ankle (Kumai et al., 2002; Taser et al., 2006) and perhaps in the entire body (Butler and Walsh, 2004). The Massachusetts General Hospital Orthopaedic division estimates that one million Americans suffer ankle injuries each year, of which 85% are lateral sprain injuries. Additionally, 38%-45% of all sports related injuries each year occur on the lateral side of the ankle, most of which are inversion sprains to the anterior talofibular ligament (Garrick, 1982; Liu and Jason, 1994). Anyone who has “turned their ankle” and sprained the anterior talofibular ligament knows the pain associated with having their talus tilt away from their tibia.

Interestingly though, this ligament has historically been reported as absent across non-human primates (Keith, 1893-1894; Parsons, 1899; Hill, 1953a; Hill, 1953b). Inman (1976) did not find the ATaFL in dissections of a macaque and chimpanzee, but did observe this ligament in one gibbon. Gomberg (1981) noted the presence of an ATaFL ligament in one captive male lowland gorilla, and one captive female mountain gorilla but not in chimpanzees (n=2) or an orangutan (n=1). Dissections of captive macaques (n=4), and a male captive lowland gorilla and a chimpanzee of unknown provenience by this author showed the ligament to be absent in all. Although there is variation in the number of bands composing it, the anterior talofibular ligament is always present in the human ankle (Milner and Soames, 1997).

Foot inversion is an important motion in the primate lower limb (Conroy and Rose, 1983; Gebo, 1993). During vertical climbing bouts, and arboreal quadrupedalism, primates keep their bodies close to the substrate in part via inversion of the foot (Meldrum, 1991; Chapter 2). Because non-human primates engage in foot inversion and typically do not have an anterior talofibular ligament at all, several questions emerge:

- Without an anterior talofibular ligament, do non-human primates have more talar tilting and is this a strategy by which they achieve additional foot inversion beyond what occurs at the subtalar joint?
- How do non-human primates maintain ankle stability and prevent dislocation of the talus from the ankle mortise?

  - Do non-human primates compensate for the absence of an anterior talofibular ligament with increased strength in the other lateral ankle ligaments?
  - Or have non-human primates instead evolved a talocrural joint shape that provides bony stability?
- Finally, given its absence in most non-human primates, why do humans have an anterior talofibular ligament and under what circumstances did it evolve?

The following hypotheses will be tested in this study:

Talar tilting

The absence of an anterior talofibular ligament permits talar tilting, or inversion at the talocrural joint, in non-human primates.

Ankle ligaments

There are no differences between the geometric and biomechanical properties of the ligaments of human and non-human primate ankles.

Anterior talofibular ligament

There are no differences in talar trochlear shape between species with an anterior talofibular ligament and those without.

Materials and Methods

X-rays of talar tilting in non-human primates

Lower limbs were obtained from ten sub-adult olive baboons (*Papio anubis*) which had completed a research protocol approved by the University of Michigan's Institutional Animal Care and Use Committee. These animals were between two-three years old, and thus still had unfused epiphyses on the distal fibula and tibia. The animals weighed an average of seven kg (range 6.0 - 8.4 kg). Following euthanasia, the legs were amputated at the knee and were frozen for up to one month. A foot from a 500 lb. adult male lowland gorilla (*Gorilla gorilla gorilla*) who died during a veterinary procedure at the Cincinnati Zoo was also x-rayed. After thawing for 24 hours, the baboon feet were positioned in frontal view and xrays were taken using a MinXray HF 100/30 at 50 kVDC for 0.3mAs. The larger gorilla foot was radiographed using a MinXray HF 100/30 at 64 kVDC for 0.8mAs. Radiographs were taken in frontal view with the foot slightly plantarflexed. Radiographs were then taken of the same feet with the midfoot being manually forced into inversion at the talocrural joint to encourage talar tilting.

Biomechanics of ankle ligaments

Materials and methods for testing relative ligament strength, stiffness, and toughness are described in full in Chapter 5.

Skeletal morphology

The shape of the articular surface of the talus was assessed in 219 tali from wild-shot adult primates, and 45 humans listed in Table 6.1. The human tali were from the 9th-

Table 6.1. Extant anthropoid tali measured in this study.

Family	Species	Male	Female	Sex unknown	Total
Hominoid	*Homo sapiens*	13	21	11	45
	Pan troglodytes	19	22	10	51
	Pan paniscus	2	1	1	4
	Gorilla gorilla gorilla	23	19	3	45
	Gorilla gorilla beringei	10	3	0	13
	Pongo pygmaeus	12	18	7	37
	Hylobates lar	17	17	2	36
	Symphalangus syndactylus	4	3	1	8
Cercopithecoid	*Papio* spp.	13	3	8	24
	Mandrillus sphinx	2	2	3	7
	Theropithecus gelada	2	1	0	3

12th century PaleoIndian Libben population housed at Kent State University (Lovejoy et al., 1977). The non-human primates were studied at the Cleveland Museum of Natural History, Field Museum, American Museum of Natural History, National Museum of Natural History, Museum of Comparative Zoology (Harvard), and Peabody Museum (Yale). The tali were photographed in distal view with a Nikon D100 digital camera. Many studies have oriented the talus in standard position with the base of the proximal tubercles on the same plane as the base of the talar head, and with the fibular facet parallel to this basal plane (Lisowski et al., 1974; Kidd and Oxnard, 2005). However, it has long been known that this is not precisely the anatomical orientation of the talus in the live foot (Appleton, 1913; Barnett, 1955). Therefore, the depth of the talar groove was measured without any assumptions regarding the positioning of the talus in the live primate foot. Instead, a line was drawn across the most superior aspect of the talar trochlea and the height of a line drawn perpendicular to this reference line to the depth of the talar groove was measured. This height was standardized by the mediolateral width of the talar trochlea. Significant differences among primate species for this measure were assessed using a one-way ANOVA and the post hoc Tukey honestly significantly different (HSD) test.

The depth of the talar groove was measured as indicated above on 15 fossil hominin tali listed in Table 6.2. Measurements were performed on original fossil specimens at the Kenya National Museum in Nairobi, the Tanzania National Museum and House of Culture in Dar es Salaam, the Transvaal Museum in Pretoria, South Africa, and the Department of Anatomy at Witwatersrand University in Johannesburg, South Africa. High quality casts of the *A. afarensis* talus Lucy (A.L. 288-1) and the Omo talus 323-76-898 from Ethiopia, were measured at the University of Michigan Department of Anthropology.

The tali were also assessed using a known relationship between the axis of rotation of the ankle and the orientation of the tibia relative to the foot in African apes and humans (Latimer et al., 1987). Chimpanzees, gorillas, and humans share a common angle between the axis of rotation of the talocrural joint and the long axis of the tibia (Figure 6.3). Because the axis of rotation of the talocrural joint runs approximately through the tips of the malleoli, this axis can be estimated using the most plantar articular facets of isolated tali. The angle formed between the axis of rotation and a line drawn across the superior surface of the talar trochlea was measured in all of the extant and

Table 6.2. Fossil hominin tali and tibiae measured in this study.

Accession number	Element	Geological age	Taxon	Talocrural axis angle (˚)	Depth of trochlear groove (% of talar width)	*Estimated Body Mass (kg)
KNM-KP 29285	Tibia	4.12[0]	*Australopithecus anamensis*	8.1	7.6	42.9
A.L. 333-6	Tibia	3.2[1]	*A. afarensis*	6.2	2.2	31.1
A.L. 333-7	Tibia	3.2[1]	*A. afarensis*	5.0	2.5	43.3 (est.)
A.L. 288-1	Talus	3.18[1]	*A. afarensis*	5.2	5.1	28.7
A.L. 288-1	Tibia	3.18[1]	*A. afarensis*	6.5	4.4	24.9
StW 181	Tibia	2.6-2.8[2]	*A. africanus?*	Damaged	4.7	32.7 (est.)
StW 347	Talus	2.6-2.8[2]	*A. africanus?* [8]	Damaged	5.3	27.3 (est.)
StW 358	Tibia	2.6-2.8[2]	*A. africanus?* [8, 20]	9.7	6.0	24.4
StW 363	Talus	2.6-2.8[2]	*A. africanus?* [23]	6.6	5.7	31.9
StW 389	Tibia	2.6-2.8[2]	*A. africanus?* [8, 20]	9.3	4.7	34.2
StW 88	Talus	2.6-2.8[2]	*H. habilis?* [6,7, 20] *A. africanus?*	5.4	4.1	32.2
StW 514b	Tibia	2.6-2.8[2]	*A. africanus?* [8, 18]	5.8	6.7	28.5 (est.)
StW 486	Talus	2.6-2.8[2]	*A. africanus?* [8]	8.7	9.1	38.5
StW 102	Talus	2.4-2.8[2]	*H. habilis?* [7, 20] *A. africanus?* [8]	6.9	7.9	33.2
Omo 323-76-898	Talus	2.2[3]	*Homo?* [9,10]	9.5	5.3	46.3
TM 1517	Talus	1.9-2.0[4]	*P. robustus?* [20]	6.1	7.2	31.6
SKX 42695	Talus	1.5-2.0[5]	*P. robustus?* [5] *Homo?* [5]	Damaged	5.9	46.0
KNM-ER 1481	Tibia	1.9[3]	*H. habilis?* [20, 21] *H. erectus* [22]	5.5	5.7	42.9
KNM-ER 1500	Tibia	1.9[3]	*P. boisei?* [15, 20]	2.4	7.5 (est.)	36.7
KNM-ER 2596	Tibia	1.9[3]	Hominin [25] Cercopithecoid?	22.0	5.1	24.9
KNM-ER 1476	Talus	1.88[3]	*P. boisei?* [10, 11]	8.7	7.8	36.4
OH 8	Talus	1.85	*H. habilis?* [12, 13, 20] *P. boisei?* [10, 14, 15]	7.0	10.3	33.5
OH 35	Tibia	1.85	*H. habilis?* [13, 20] *P. boisei?*	4.0	6.8	28.7

KNM-ER 813	Talus	1.85[3]	*Homo* [10, 14]	8.2	9.1	52.2
KNM-ER 1464	Talus	1.7[3]	*P. boisei?* [15, 20] *Homo?*	8.5	9.6	54.6
StW 567	Tibia	1.4-1.7[2]	*Homo* [2, 24]	6.2	5.5	37.6
KNM-ER 5428	Talus	1.6[3]	*H. erectus* [19, 26]	7.6	5.5	94.5
KNM-ER 803	Talus	1.53[3]	*Homo* [16, 19, 20]	Damaged	Damaged	67.4 (based on femur)
KNM-WT 15000	Tibia	1.5[17]	*H. erectus* [17]	5.0	2.8	58.3
Kabwe E691	Tibia	>490k[27] 780k-1.3 mya[28]	*H. erectus*[29] *H. heidelbergensis*[30] *H. rhodesiensis*[28]	7.0	4.1	70.5 (based on proximal tibia)

[*]Based on average of three human-regression equations from McHenry (1992).
[0]Leakey et al., 1998; [1]Walter et al., 1994; [2]Kuman and Clarke, 2000; Deloison, 2003; Pickering et al., 2004; [3]Feibel et al., 1989; [4]McKee, 1995; [5]Susman et al., 2001; [6]Clarke, 1985; [7]Christie, 1990; [8]McHenry and Berger, 1998; [9]Deloison, 1997; [10]Gebo and Schwartz, 2006; [11]Leakey, 1973; [12]Leakey et al., 1964; [13]Susman and Stern, 1982; [14]Wood, 1974; [15]Grausz et al., 1988; [16]Day and Leakey, 1974; [17]Walker and Leakey, 1993; [18]Berger and Tobias, 1996; [19]Antón, 2003; [20]McHenry, 1994; [21]Trinkaus, 1984; [22]Kennedy, 1983; [23]Fisk and Macho, 1992; [24]Curnoe and Tobias, 2006; [25]Leakey and Walker, 1985; [26]Walker, 1994; [27]Millard, 2008; [28]McBrearty and Brooks, 2000; [29]Asfaw et al., 2002; [30]Rightmire, 1998

fossil tali mentioned above. A high angle (~25°) would indicate that the tibia sat obliquely on the talus like in African apes, whereas a lower angle (~10°) would indicate that the long axis of the tibia was perpendicular to the talar trochlea like that found in modern humans (Latimer et al., 1987). A perpendicularly aligned talocrural joint would further indicate that the ankle and knee were both under the center of gravity, and thus the individual would have possessed a valgus knee (Latimer et al., 1987). Significant differences among primate species for this measure were assessed using a one-way ANOVA and the post hoc Tukey honestly significantly different (HSD) test. Twenty randomly selected specimens were measured a second time a month after the original

Figure 6.3. Geometry of the chimpanzee and human talocrural joint.

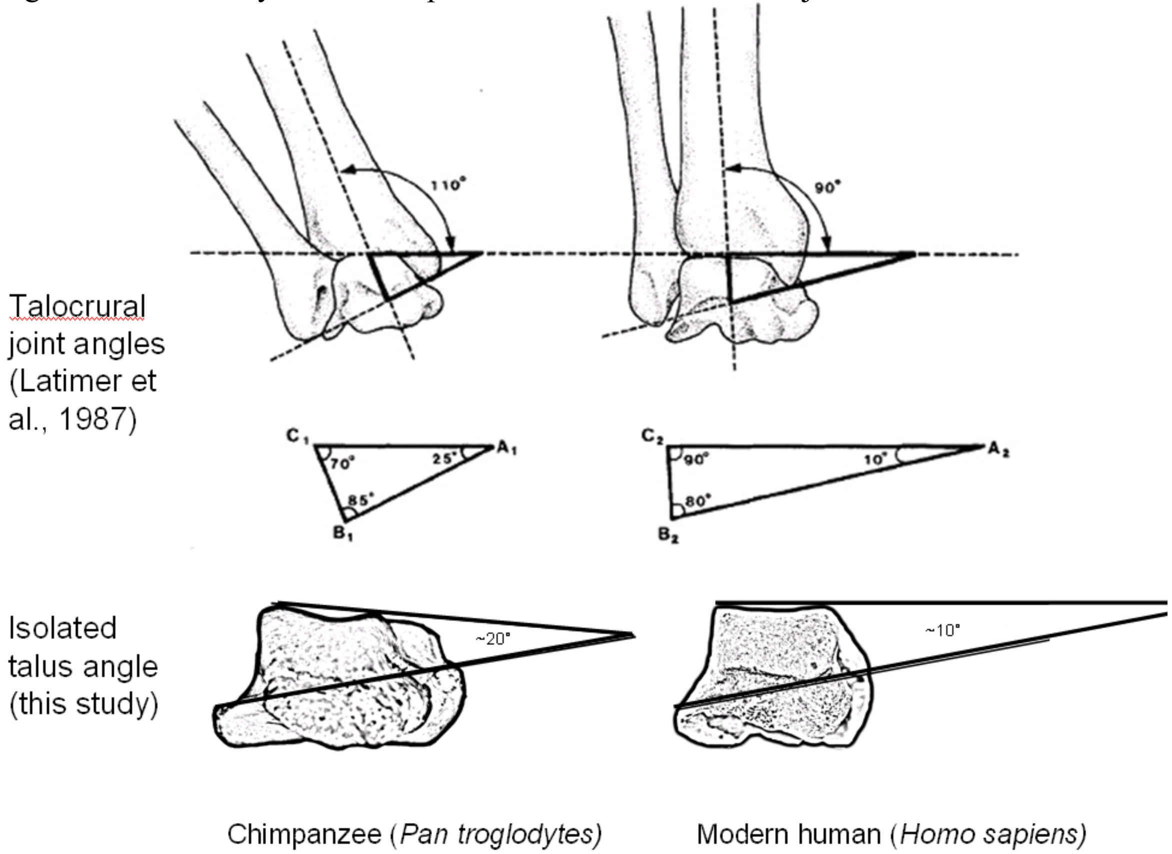


Figure 6.3. The long axis of the tibia is obliquely oriented relative to the plane of the talocrural joint in African apes (left), but perpendicularly oriented in humans (right). Because the angle formed between the long axis of the tibia and the ankle axis of rotation (B) is conserved between African apes (left) and humans (right), the angle formed between the plane of the talocrural joint and the axis of rotation (A) can be taken on isolated tali and can be used to calculate the angle formed between the long axis of the tibia and the talar surface (C). Angle B is greater in African apes than in humans. Reproduced with permission from Latimer et al. (1987).

measurement to assess repeatability. The average difference between the two measures was 1˚ ± 0.5˚ with a maximum difference between two measures of 1.93˚.

It has been found that the shape of the superior surface of the talus and the shape of the articular facet of the distal tibia are near reciprocals of one another (Aiello et al., 1998; Wood et al., 1998) and thus the inverse shape of the distal tibia could be used to estimate the shape of the undiscovered talus from that fossil hominin. To test the congruence of associated tibia and tali using the methods in this study, the shape of these articular facets of these bones were taken with a carpenter's contour guide on chimpanzees (n=31), gorilla (n=28), and modern human (n=29). A photograph was taken of the contour impression of the articular facets, and the depth of the trochlear groove and height of the tibial keel were assessed as function of the length of the articular facet in the program Image J. Although there was more incongruence between associated tibia and tali than expected, the shape of the trochlear groove as determined by the tibia was within 1.5% of the same measure obtained by using only an isolated talus. Interestingly, the curvature of the talar trochlea is overestimated by using the tibia in chimpanzees, but underestimated by using the tibia in gorillas and humans. This implies that the tibia is flatter than the talus in gorillas and humans, whereas the talus is flatter than the tibia in chimpanzees. With those caveats in mind, it is reasonable to use the tibia to estimate the shape of the corresponding talus in an interspecific study such as this one.

Therefore, to increase the sample size of fossil hominins, the depth of the trochlear groove and the axis of the talocrural joint was measured on 13 distal tibia also listed in Table 6.2. These measurements were performed on original fossil tibia at the Kenya National Museum in Nairobi, and the Department of Anatomy at Witwatersrand University in Johannesburg, South Africa. First generation casts of two fossil tibia from Ethiopia (A.L. 333-6, A.L. 333-7) were studied at the Cleveland Museum of Natural History, and high quality research casts of A.L. 288-1, and the tibia from the Broken Hill site of Kabwe, Zambia were also measured at the University of Michigan Department of Anthropology. Distal tibia were scanned with a NextEngine portable 3-D laser scanner. The 3D models were imported into ScanStudio software and cropped such that only an approximately 5 mm (anteroposterior) strip from the midregion of the trochlear surface remained in the coronal plane (Figure 6.4). This was necessary because the anterior and posterior rims of the distal tibia often have slightly different shapes than the actual surface that articulates with the talus. The model was oriented such that the trochlear surface was perpendicular to the long axis of the tibia and this image was captured using the program Jing. The image was then imported into Image J, and the depth of the trochlear groove measured as described for the tali above. The depth of the trochlear groove was also measured using this approach for all 14 of the fossil tali in this study and the results were no different from those obtained using high-resolution photographs (t=1.95, p=0.07; paired two sample for means t-test), and thus results from the two approaches are combined (Table 6.3). To measure the axis of rotation, the 3D scans of the distal tibia were sliced directly in half in the coronal plane and the images captured by the program Jing and imported into Image J. The angle formed between the plane of the talocrural joint and the long axis of the tibia was measured. Because the angle formed between the axis of rotation and the plane of the talocrural joint is conserved in hominoids (Latimer et al., 1987; Figure 6.3), this angle was added to the measured angle and the sum subtracted from 180˚ to approximate the angle formed between the axis of rotation and the superior surface of the talus.

The validity of this method was tested by measuring the angle in question directly on images of 30 human, chimpanzee, and gorilla tali, and then calculating the angle using the above methods on tibia from those same 30 individuals whose tibial axis angle was measured with a carpenter's contour guide. There was a good correlation (r=0.72) between the measured and calculated angle. Differences between the measured and

Table 6.3. Comparison of talar keel depth using different measuring methods.

Fossil hominin talus	Depth using photograph	Depth using 3D scanner
A.L. 288-1	5.1%	6.0%
StW 88	4.1%	4.7%
StW 102	7.9%	8.2%
StW 347	5.3%	4.9%
StW 363	5.7%	6.2%
StW 486	9.8%	9.2%
Omo 323-76-898	5.3%	5.3%
TM 1517	7.2%	7.5%
SKX 42695	5.9%	5.9%
KNM-ER 1476	7.8%	7.8%
OH 8	10.3%	10.5%
KNM-ER 813	9.1%	9.5%
KNM-ER 1464	9.6%	10.1%
KNM-ER 5428	5.6%	5.7%

Figure 6.4. 3-D scan and digital cross-section of fossil *Homo* distal tibia KNM-ER 1481.

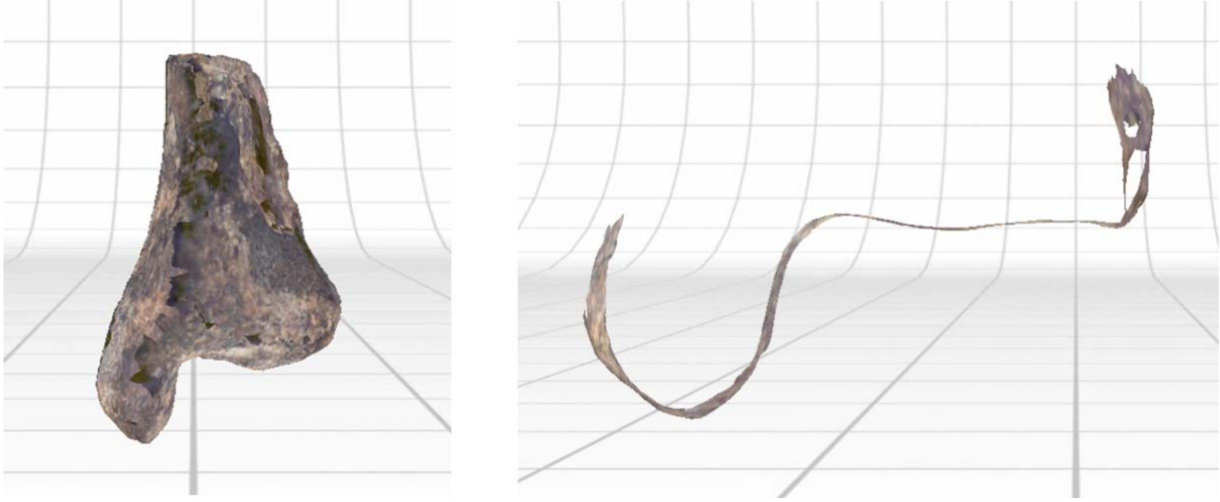


Figure 6.4. 3-D scans of the 1.9 mya hominin distal tibia from Kenya KNM-ER 1481. Scans were obtained using a NextEngine portable 3-D laser scanner on the original fossil at the Kenya National Museum. On the left is the complete fossil specimen in anterior view, and on the right is an enlarged view of the talar articular surface in coronal view. These cropped data were used to measure the depth of the trochlear

calculated angle were typically in the direction of the direct talar measurement being a slight underestimate (~2˚) of the angle as calculated from the angle formed between the long axis of the tibia and its articular surface. Measurements, taken directly from the A.L.

288-1 talus, and calculated indirectly from a measurement of the associated A.L. 288-1 tibia, are only 1.3˚ different, further suggesting the validity of this approach for fossils.

The presence or absence of an anterior talofibular ligament was assessed on all of the tali studied. This was done by visual inspection and palpation for a small tubercle on the distal-lateral body of the talus, midway between the superior and inferior articular surfaces. The presence of this ligament at its point of insertion on the talus was chosen over its origin on the distal fibula for several reasons. This author was unable to detect obvious differences between the anterior distal aspect of the lateral malleolus of the fibula in humans and in chimpanzees related to the presence or absence of the anterior talofibular ligament, and there was considerable variation in the shape of the distal fibula within the a human population despite the fact that all humans have this ligament (Milner and Soames, 1998). Second, the origin of the anterior talofibular ligament overlaps anatomically with the fibers of the calcaneofibular ligament, which also originates on the anterior aspect of the distal fibula, though in a slightly more distal region (Burks and Morgan, 1994; Hintermann, 2002; Taser et al., 2006). These two ligaments may even share fibers at their origin on the distal fibula (Golanó et al., 2006). Therefore, a strong calcaneofibular ligament may result in a broad tubercle on the distal fibula, easily mistaken for the presence of an anterior talofibular ligament. For these reasons, the morphology of the talus, rather than the fibula, was used to assess the presence or absence of this ligament.

Results

X-rays of talar tilting in non-human primates

None of the ten baboon feet forced into inversion displayed any measurable talar tilting (Figure 6.5). The radiographs instead suggested that during forced inversion, tilting of the lateral aspect of the talus is blocked by the lateral malleolus of the fibula, and also hindered by the tibial keel and corresponding groove of the talar trochlea. The role of the fibula in blocking talar tilting, and grooving of the tibiotalar articular surface is also apparent on the gorilla radiograph (Figure 6.5).

Figure 6.5a. Radiograph of talar tilting in baboon ankle.

Figure 6.5a. Radiograph of talar tilting in baboon ankle.

Figure 6.5. Radiographs of a juvenile baboon ankle being inverted (a), and an adult male gorilla ankle being inverted (b). Note that despite exerting a substantial inversion force on the talocrural joint, the lateral corner of the talus does not "tilt" as is possible in human ankles (Figure 6.2), and is instead blocked by the fibula and the tibial keel in both the baboon (a), and the gorilla (b).

Biomechanics of ankle ligaments

None of the ten baboons had an ATaFL. The dimensions and material properties of the major ligaments of the baboon ankle are listed in Table 6.4. In baboons, the largest ankle ligament is the PTTL (10.67 mm^2) followed by the PTaFL (6.14 mm^2), and the CFL (1.25 mm^2). The lateral ligaments were significantly weaker than the PTTL ($t=5.81$, $p<0.001$, $df=22$). The CFL failed at a load of 55.8 N ± 43.2 N (range 10 N-120 N) after a displacement of 3.6 mm ± 0.9mm (range 2.2 mm- 4.8 mm) while the PTaFL failed at a load of 58.7 N ± 19.1 N (range 30.9 N- 85 N) after a displacement of 3.2 mm ± 1.4 mm

Table 6.4. Geometric and material properties of baboon ankle ligaments.

	Calcaneofibular	Posterior talofibular	Posterior tibiotalar
Number of specimens	6	8	10
Length (mm)	17.0 ± 1.2	7.0 ± 1.1	6.4 ± 1.6
Width (mm)	0.5 ± 0.1	1.4 ± 0.4	1.9 ± 0.5
Height (mm)	2.6 ± 0.5	4.8 ± 0.9	7.1 ± 0.9
Area (mm^2)	1.25 ± 0.41	6.14 ± 2.47	10.67 ± 3.6
Maximum force (N)	65.0 ± 41.3	58.7 ± 19.1	141.8 ± 41.0
Maximum elongation (mm)	3.3 ± 0.8	3.2 ± 1.4	3.4 ± 1.2
Maximum stress (MPa)	50.4 ± 22.9	9.8 ± 5.8	11.1 ± 4.1
Maximum strain (mm/mm)	0.20 ± .05	0.45 ± .16	0.53 ± .16
Elastic modulus (MPa)	248.9 ± 86.0	24.8 ± 9.9	28.3 ± 11.0

(range 1.7 mm- 5.8 mm). The PTTL could withstand loads that were almost three times as great. The failure load on this ligament was 141.8 N ± 41.0 N (range 60 N- 210.7 N) while the displacement was 3.4 mm ± 1.2 mm (range 1.3 mm- 4.5 mm) before failure. The ability of this ligament to withstand the largest forces is consistent with this ligament having the largest cross-sectional area of the three ligaments.

Whereas the PTTL was the strongest of the ligaments, it was the CFL that was the stiffest ($t=6.77$, $p<0.001$, $df=22$). This ligament had an elastic modulus of 248.9 MPa ± 86.0 MPa (range 104.3 MPa- 326.6 MPa). The elastic modulus of the PTaFL was 24.8 MPa ± 9.9 MPa (range 11.4 MPa- 40.1 MPa) and the elastic modulus of the PTTL was 28.3 MPa ± 11.0 MPa (range 13.2 MPa- 41.2 MPa). Thus, the CFL was approximately ten times stiffer than the other ligaments. The PTTL and PTaFL have a significantly higher strain value than the CFL ($t=4.00$, $p<0.001$, $df=22$). These ligaments are able to stretch approximately half their original length (PTaFL 0.45 ± 0.16; PTTL 0.53 ± 0.16) before failure.

The toughness as measured by the energy that could be absorbed by the ligament before failure was highest for the PTTL (252.8 ± 121.0 Nmm). The PTTL is significantly tougher ($t=4.06$, $p<0.001$, $df=22$) than the CFL and PTaFL which have statistically equivalent toughness measures of 103.2 ± 85.7 Nmm and 93.7 ± 51.3 Nmm respectively.

Skeletal morphology and fossil hominins

The depth of the groove between the highest points on the medial and lateral aspect of the talar trochlea differentiated the primate groups studied (Figure 6.6). Three apes (chimpanzees, lowland gorillas, and gibbons) were statistically indistinguishable from one another (*Pan* and *Gorilla*: $p=0.42$; *Pan* and *Hylobates*: $p=0.99$; *Gorilla* and *Hylobates*: $p=0.89$). In addition, orangutans and baboons had an identical depth to their talar trochleas ($p=0.83$). Mountain gorillas and modern humans had the flattest articular surfaces and were statistically similar to one another ($p=0.05$) with the following overall relationship: (*Gorilla gorilla beringei* = *Homo sapiens*) < (*Hylobates* = *Pan* = *Gorilla gorilla gorilla)* < (*Papio* = *Pongo*).

The depth of the talar trochlea for fossil hominins is listed in Table 6.2. The flattest talocrural joints most like modern humans and mountain gorillas were the *A. afarensis* Hadar fossils AL 288-1, AL 333-6, AL 333-7, the South African talus StW 88, and the later *H. erectus* tibia from the Nariokotome Boy (KNM-WT 15000). What is preserved of the *H. erectus* talus KNM-ER 803 is also strikingly flat, though not enough of the superior surface of the talus is preserved to take a precise measurement. More keeled specimens though within the range of modern humans include the tali StW 347, Omo 323-76-898, KNM-ER 5428, and the tibia StW 181, StW 389, StW 567, KNM-ER

Figure 6.6. Relative depth of the anthropoid talar trochlea.

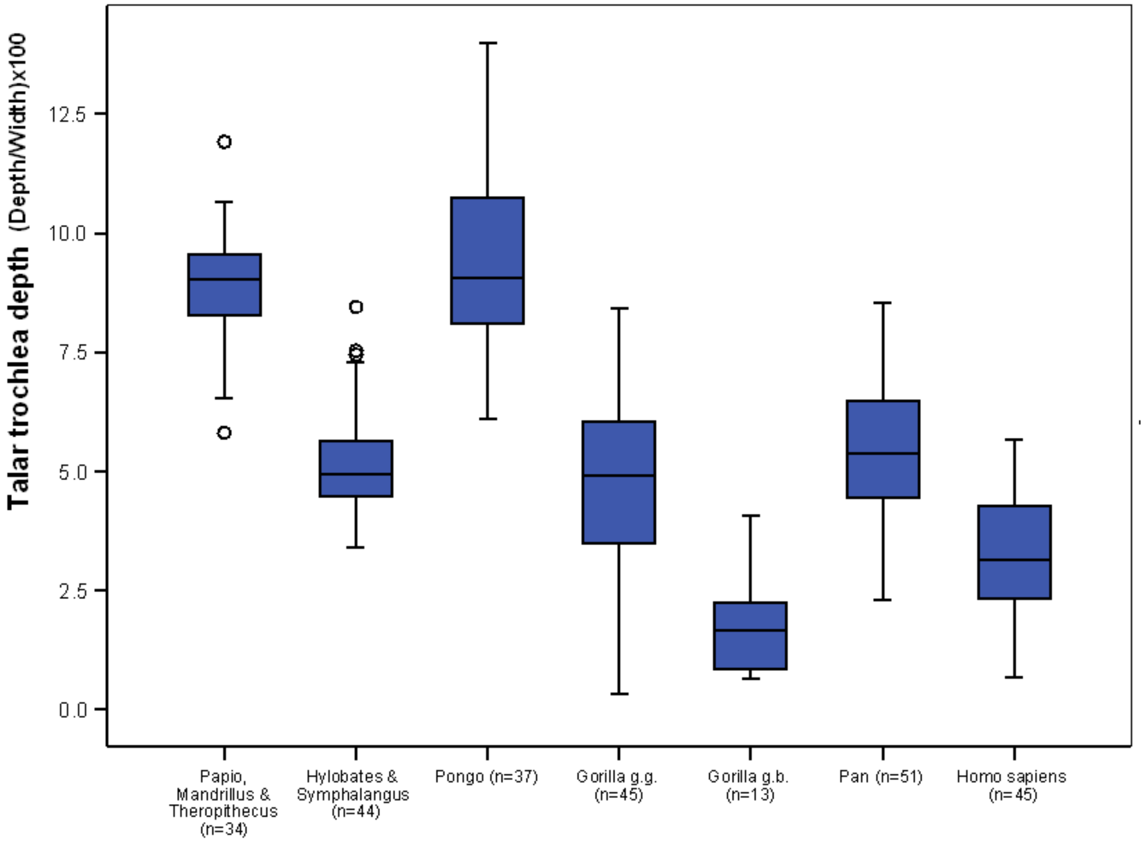


Figure 6.6. Size-standardized depth of the trochlear keel in catarrhine primates. The depth of the trochlear groove was divided by the width of the trochlear surface of the talus and converted to a %. Boxplots show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Humans and mountain gorillas have flat talar surfaces, while baboons and orangutans possess the deepest trochlear groove.

1481, and KNM-ER 2596. A slightly more ape-like grooved talus with a keeled tibial articular surface was present in the tali StW 363, SKX 42695, and the tibiae StW 515, StW 358, OH 35. Baboon and orangutan-like deeply grooved tali and strongly keeled tibiae are present in the StW 102, StW 486, TM 1517, OH 8, KNM-ER 1476, KNM-ER 1464, and KNM-ER 813 tali, and the tibia KNM-KP 29285 and KNM-ER 1500.

As Latimer et al. (1987) found, the angle formed between the axis of rotation of the talocrural joint and the superior surface of the talar body varied between primate groups (Figure 6.7). Humans had a significantly smaller angle of 10.2˚ ± 2.3˚, and thus a talocrural joint more perpendicularly aligned with the long axis of the tibia than the other primate groups studied with the only exception being the hylobatids (p=0.05 using Tukey HSD test; though an insignificant p=0.003 using LSD test for planned comparisons). *Pongo* and *Gorilla gorilla gorilla* were statistically indistinguishable (p=0.99) as was *Gorilla gorilla beringei* and baboons (p=0.23), *Pan* (p=0.12), and hylobatids (p=0.10). Baboons and the hylobatids were also statistically similar (p=0.35). *Pongo* and *Gorilla gorilla gorilla* had the greatest angle between the tibial articular surface and the axis of rotation (~19˚), and *Homo sapiens* and the hylobatids had the most acute angle. With the exception of a single fossil, all hominins measured in this study had human-like angles between the axis of rotation and the superior surface of the talus (Table 6.2), suggesting a perpendicularly oriented tibia and thus a valgus knee. The one fossil with evidence for an obliquely oriented tibial surface is the small distal tibia KNM-ER 2596. Although this fossil shares many features in common with other known hominin specimens, there is a possibility that KNM-ER 2596 is pathological, or from the cercopithecoid *Rhinocolobus*. A more detailed description of this fossil and its possible affinities appears in Chapter 4. The earliest purported hominin talus StW 573 was not studied by this author. However, approximate measurements could be taken from a photo of the specimen in distal view (Deloison, 2003). The fossil lacks the oblique orientation typical of ape-tali and instead has a human-like angle of about 8˚, and is deeply grooved with a depth of about 9% of the talar width, making it quite similar to the earliest hominin tibia KNM-KP 29285 for these measures. It is unclear whether this specimen had an attachment for an ATaFL.

Figure 6.7. Geometry of the anthropoid ankle assessed from isolated tali.

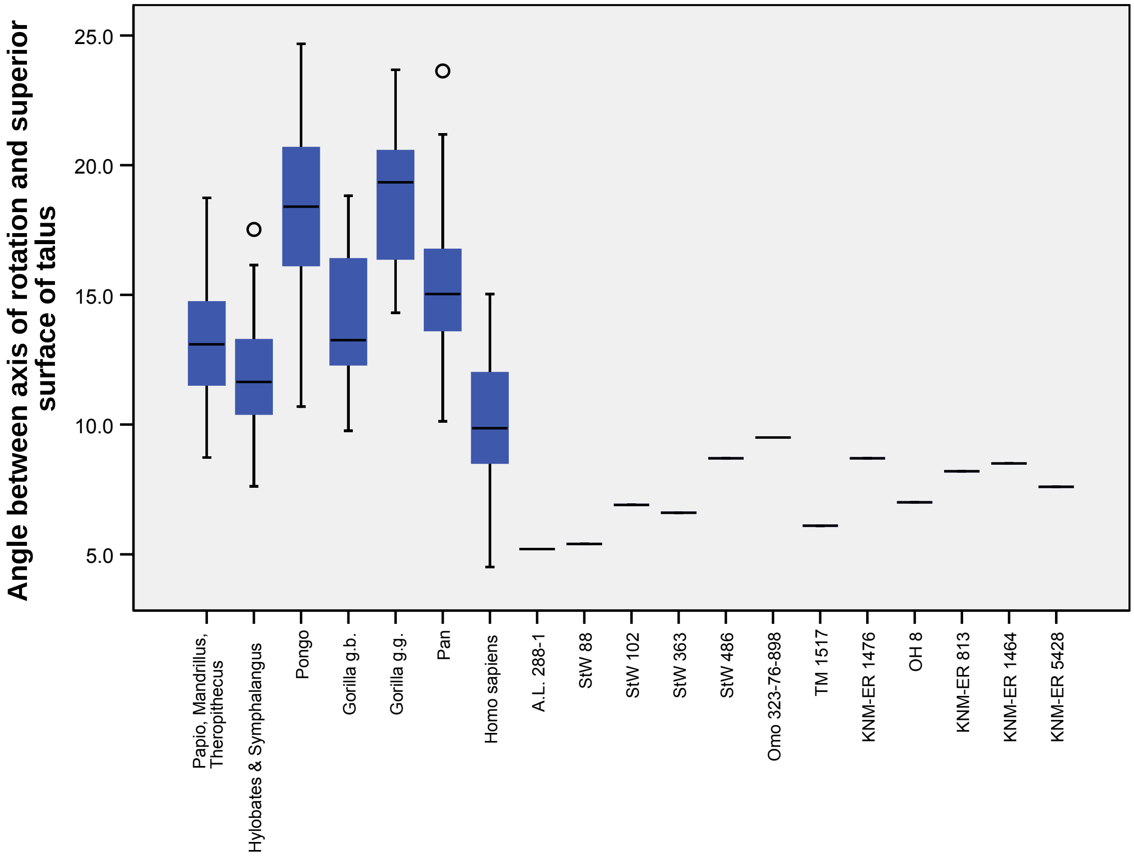


Figure 6.7. The angle formed between the superior surface of the talus and the axis of rotation of the ankle differentiates humans from non-human primates (from Figure 6.3). The black bars represent median values with the blue/gray rectangles representing quartiles in this boxplot; the whiskers show the full range of the data. All twelve of the fossil hominin tali for which this measure was possible fell within the human range implying a perpendicularly oriented tibia, and a valgus knee.

A tubercle for the anterior talofibular ligament was not detected on any tali from *Papio*, *Hylobates*, *Pan*, or *Pongo* (Figure 6.8). However, there were some gorilla specimens that had rugosity in the area most likely to anchor an ATaFL. All gorilla specimens had a buttress running dorsoplantarly along the junction of the talar neck and body. Additionally, many gorilla and chimpanzee specimens had a distally extended articular surface that terminated in a lip of bone anterolaterally. This morphology was not regarded as an indication of the presence of an ATaFL. Only four *Gorilla gorilla gorilla* tali (4/45 = 9%) had a clear tubercle midway between the tibial articular surface and the flaring of the fibular facet on the lateral aspect of the neck-body junction. This tubercle was also present on three *Gorilla gorilla beringei* tali (3/13 = 23.1%). Although all humans have an ATaFL (Milner and Soames, 1997), not all human tali had palpable tubercle for the ATaFL, although this feature was present in nearly all (42/45 = 93.3%). A discernable tubercle for the attachment of the anterior talofibular ligament was present on the hominin tali Omo 323-76-898, KNM-ER 813, KNM-ER 1464, and KNM-ER 5428. On the Omo specimen, there are two weak, but detectable tubercles for the anterior talofibular ligament along the lateral neck-body junction, indicating that this individual had two bands of this ligament, like most humans today (Milner and Soames, 1997). The tubercle on KNM-ER 813 and KNM-ER 5428 is similar in size and location to the Omo specimen, whereas the KNM-ER 1464 tubercle is larger and more projecting. A roughened area on the lateral neck-body junction for ligament attachment was noted in the original description of the KNM-ER 1464 fossil (Day et al., 1976). It is difficult to determine if there was a tubercle for the ATaFL on the KNM-ER 1476 fossil. There appears to perhaps be a small tubercle, but there is also slight damage along the superior aspect of the lateral neck-body junction that may give the illusion of a tubercle. If this is a tubercle for the ATaFL, it is weakly developed. On fossil StW 363, there is a very small tubercle along the lateral edge of the neck-body junction. However, there is glue and matrix in this region, and though it is possible that this is real morphology, this author suggests that this “tubercle” is instead an artifact of preparation. For the fossil talus OH 8, there is some damage to the lateral neck-body junction, though no evidence could be detected for an attachment for the anterior talofibular ligament on the original specimen.

Figure 6.8. Comparative morphology of the anthropoid talus.

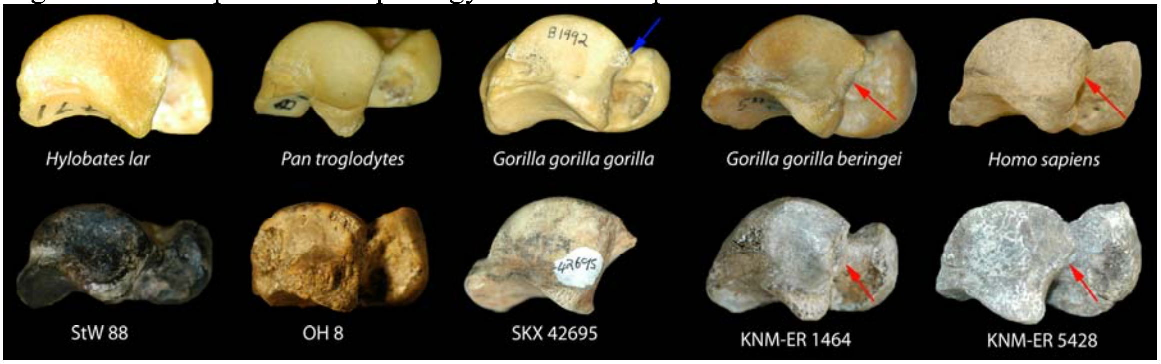


Figure 6.8. Tali from (top: left to right) gibbon, chimpanzee, lowland gorilla, mountain gorilla and human. Across the bottom are fossil tali StW 88, OH 8, SKX 42695, KNM-ER 1464, and KNM-ER 5428. The specimens are in lateral view and have been scaled to approximately the same size. The red arrows indicate the position of the tubercle for the anterior talofibular ligament. Note the absence in the gibbon, chimpanzee, lowland gorilla, StW 88, OH 8, and SKX 42695. The blue arrow on the lowland gorilla calls to attention a lip of bone extending distally not thought to represent an attachment point for the ATaFL.

A study of the Wenner-Gren cast of the OH 8 talus would have led this author to suggest the presence of an ATaFL tubercle, not present on the original fossil. There is no evidence whatsoever for the presence of an ATaFL on the TM 1517, or SKX 42695 South African fossils. On AL 288-1, StW 88, and StW 486, a buttress runs dorsoplantarly along the lateral neck-body junction, and a slight lip is present in the most distal aspect of the lateral trochlear articular surface, like the morphology of some gorilla and chimpanzee tali. However, no evidence for a distinct ATaFL tubercle can be found. Due to damage along the lateral neck-body junction, the presence or absence of an ATaFL tubercle could not be discerned for the StW 102, StW 347, or KNM-ER 803 fossils.

Body mass estimates (Table 6.2) based on the regression equations in McHenry (1992) demonstrate that a definitive tubercle for the anterior talofibular ligament is present on the four tali from the largest hominin individuals (> 46 kg). Only the South African talus SKX 42695 recovered from Swartkrans Cave and belonging to either *Homo* sp. or *Paranthropus robustus* is of that large size and does not have evidence for an ATaFL. Additionally, the three presumably *Homo erectus* ankle fossils younger than 1.6 million years (KNM-ER 5428, KNM-WT 15000, KNM-ER 803) are demonstratively larger than previous specimens, and are more modern human-like in possessing a flat tibiotalar joint surface.

Discussion

In the introduction, several questions were posed related to the absence of the anterior talofibular ligament in most non-human primates. These were:

- Without an anterior talofibular ligament, are non-human primates capable of more talar tilting and is this a strategy by which they achieve additional foot inversion beyond what occurs at the subtalar joint?
- How do non-human primates maintain ankle stability and prevent dislocation of the talus from the ankle mortise?
    - Do non-human primates compensate for the absence of an anterior talofibular ligament with increased strength in the other lateral ankle ligaments?
    - Or have non-human primates instead evolved a talocrural joint shape that provides bony stability?
- Finally, given its absence in most non-human primates, why do humans have an anterior talofibular ligament and under what circumstances did it evolve?

Results from X-rays of non-human primate feet forced into inversion suggest that the answer to the first question is no. Although non-human primates invert their feet during arboreal bouts (Meldrum, 1991; Gebo, 1993; pers. obs.), this movement probably occurs solely at the subtalar joint (Lewis, 1980), and not at the talocrural joint. X-rays of forced inversion on baboon and gorilla ankles suggest that the fibula and the median keel of the distal tibia and the corresponding talar groove both contribute to blocking talar tilting. Thus, the oblique orientation of the tibia on the talus and the keeled shape of the talocrural joint in non-human primates help provide stability to the ankle when the foot is loaded in an inverted position.

The ankle of a non-human primate (baboon) was examined to test whether strong lateral ligaments compensate for the absence of an anterior talofibular ligament. As has been found in studies on humans, the largest and strongest ligament of those tested in the baboon ankle is the posterior tibiotalar portion of the deltoid ligament. This ligament has the largest cross-sectional area and consistently can withstand the greatest load before failure in baboons. In human studies, the PTTL also has the largest cross-sectional area of the ankle ligaments (Siegler et al., 1988; Boss and Hintermann, 2002), and can withstand the greatest loads (Attarian et al., 1985; Siegler et al., 1988). The maximum stress withstood by the PTTL was quite similar in the baboon (11.1 ± 4.1 MPa) and in a human study (16.0 ± 15.1 MPa) (Siegler et al., 1988). The strain calculated in the baboon demonstrated that it could stretch approximately half its original length before failure. This value is slightly higher than that reported in one human study (0.25 in Siegler et al. [1988]) and lower than another human study (2.1 in Attarian et al., [1985]). Given that the PTTL is a dorsiflexion inhibitor, these data are consistent with kinematic studies that demonstrate that ankle flexion is limited in both humans (Begeman and Prasad, 1990; Parenteau et al., 1998) and the cercopithecoid monkeys (Hirasaki et al., 1993; pers. obs).

The lateral ligament complex of the baboon ankle differed strikingly from that of the human ankle. First, the ATaFL, an important stabilizing ligament in the human ankle (Leardini et al., 2000), is completely absent from the baboon ankle. It was hypothesized that in the absence of an ATaFL, the baboon would compensate with a stronger PTaFL and CFL. This was not the case. The PTaFL in baboons is relatively weaker than the same ligament in humans. Siegler et al. (1988) found that the total force that the PTaFL could withstand was roughly the same value as the force at failure in the PTTL (418 ± 191 N for PTaFL; 467 ± 289 N for PTTL). In baboons, however, the PTaFL failed at only one-third the total force that it took to rupture the PTTL. The stress at failure for the human PTaFL is 22.95 ± 24.28 MPa (Siegler et al., 1988) whereas the same value in baboons is only 9.8 ± 5.8 MPa. Baboon ligaments stretched approximately 45% of their total length before failure, between the 17% (Siegler et al., 1988) and 100% (Attarian et al., 1985) found for humans.

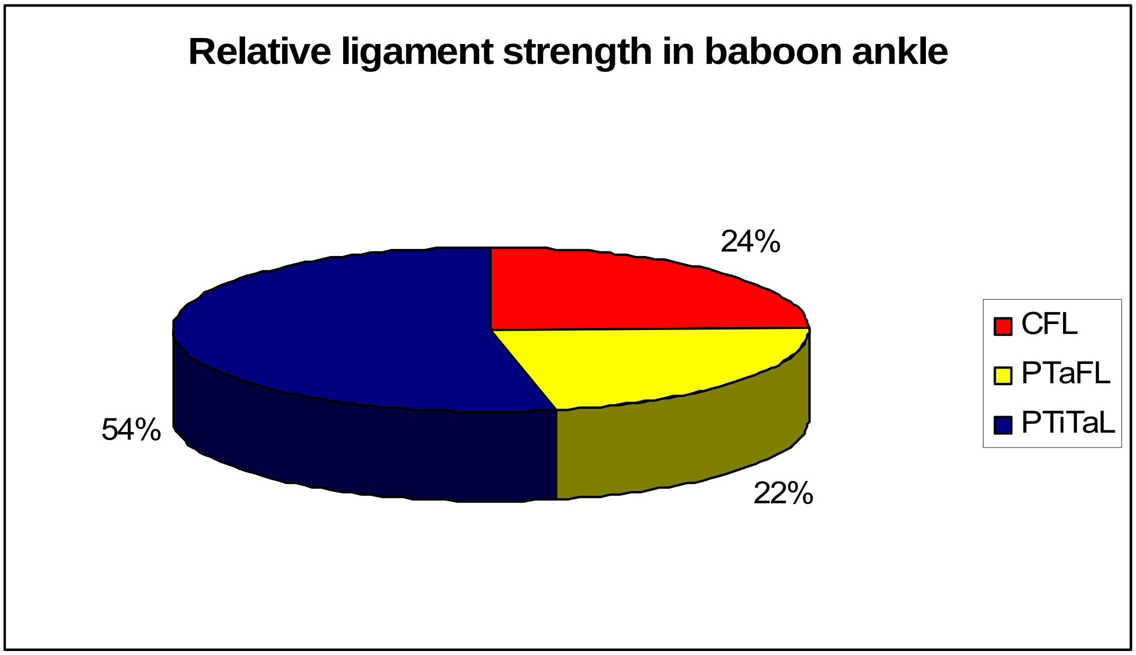
The CFL of the baboon ankle, however, was remarkable similar to the human CFL in almost every respect. The maximum stress that the ligament could withstand before failure was 50.4 ± 22.9 MPa which is comparable to the human value of 46.2 ± 36.6 MPa (Siegler et al., 1988). The ligament stretched 20% before failure in baboons and between 13% (Siegler et al., 1988) and 38% (Attarian et al., 1985) in humans. The elastic modulus of the baboon CFL was the largest of the three ligaments tested indicating that it is the stiffest ligament in the baboon ankle. The CFL has also been found to be the stiffest in the human ankle (Siegler et al., 1988).

It is difficult to determine whether the relative toughness of baboon ligaments is similar or different than values obtained from human studies. In baboons, the PTTL is significantly tougher than the CFL and PTaFL. In humans, Attarain et al. (1985) found the CFL to be twice as tough as the PTTL, followed by the PTaFL, and then the ATaFL. In contrast, Siegler et al. (1988) found the PTaFL to be the toughest followed closely by the CFL and PTTL, with the ATaFL approximately half as tough as the other ligaments. Because the Siegler et al. (1988) study tested more than twice as many ankle ligaments than the Attarain et al. (1985) study (80 versus 38), it may be argued that a more reliable comparison can be made with the Siegler et al. (1988) study. In that case, the baboon ankle differs from the human ankle in having a tougher PTTL and a less tough PTaFL.

These data suggest that the lateral ligaments of the baboon ankle (calcaneofibular and posterior talofibular) are not relatively stronger, stiffer, or tougher than the same ligaments of the human ankle, and thus the baboon does not appear to stabilize its ankle with additional ligamentous reinforcements to compensate for the absence of the anterior talofibular ligament (Figure 6.9).

Instead, these data suggest that bony morphology, in particular a keeled and obliquely oriented talar trochlea, helps stabilize the ankle in species that do not have an anterior talofibular ligament. The congruent keeled shape of the distal tibia and grooved superior surface of the talus limits rotation and translation of the talus under the tibia. Efforts to tilt the talus under the tibia would result in the keeled portion of the tibia blocking the medial aspect of the talar trochlea. Together with the previously mentioned mechanism of the fibula blocking the lateral aspect of the talar trochlea, a keeled and

Figure 6.9. Relative ligament strength on lateral side of baboon and human ankle.



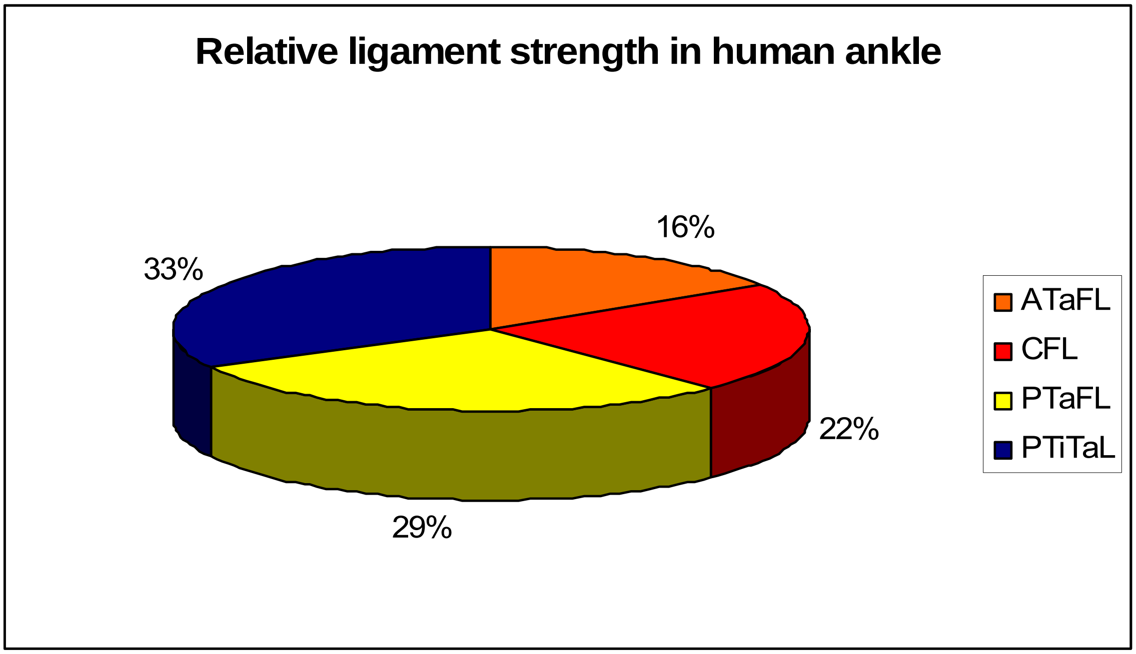


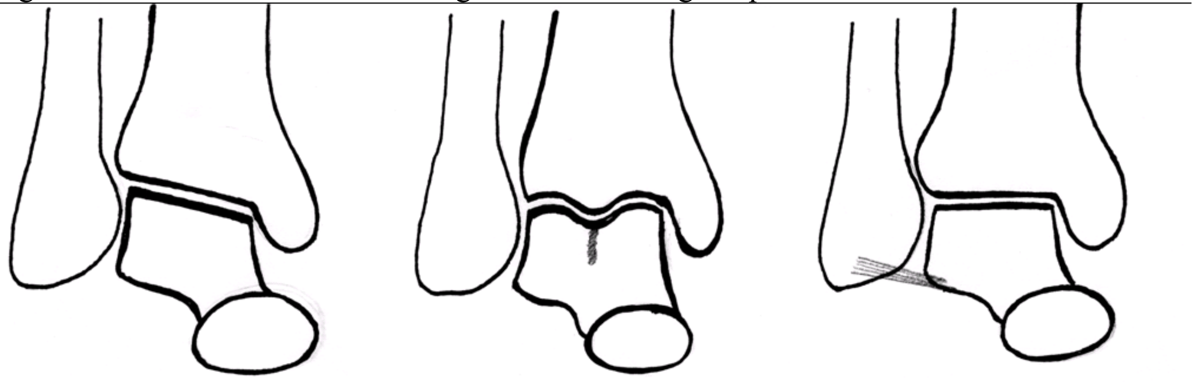
Figure 6.9. Pie graphs representing relative strength of the ankle ligaments in the baboon (n=10) and human (n=20; Siegler et al., 1988) ankles. The absence of the anterior talofibular ligament (orange) in the baboon ankle is not compensated with increased strength in the calcaneofibular or posterior talofibular ligaments (red and yellow respectively). Instead, the posterior tibiotalar ligament appears relatively stronger in the baboon due to the absence of the ATaFL.

obliquely angled talar trochlea is an important morphology in stabilizing the ankle of non-human primates (Figure 6.10).

Both the obliquely oriented talar trochlea and a keeled trochlear surface are absent in the modern human talus (Latimer, et al., 1987; this study). The results of this study are in conflict with Langdon (1986) who found no difference in the depth of the talar trochlea between humans and the African apes. However, the results in this study are compatible with a morphometric study of the talus, which also found that modern humans have a flatter talar trochlea than African apes (Harcourt-Smith, 2002). Because there is limited bony morphology preventing this motion, the talar body can easily tilt away from the tibia during extreme inversion (Cox et al., 1979; Siegler et al., 1988). Humans have evolved an ATaFL, which resists unrestricted tilting of the talus under the tibia during foot inversion. Because the modern human talar trochlea is flat and oriented perpendicular to the long axis of the tibia, there is limited skeletal reinforcement to the lateral side of the ankle and thus the anterior talofibular ligament is particularly vulnerable during foot inversion, and thus is one of the most often injured soft-tissue structures in the human body (Kumai et al., 2002; Butler and Walsh, 2004; Taser et al., 2006). The relationship between the angle of the talocrural joint and talar tilting is further supported by studies that have found that varus tilt of the talocrural joint is a strong predictor of chronic ankle instability (Sugimoto et al., 1997; Beynnon et al., 2001). Non-human primates, in contrast, have a stabilizing valgus tilt to the talocrural joint (Figure 6.10).

The ankles of the gibbon and the mountain gorilla are consistent with the hypothesis that the anterior talofibular ligament evolved as a compensatory stabilizing

Figure 6.10. Three anatomical strategies for stabilizing the primate ankle.



Valgus tilt to tibia
Present in: non-human primates

Inversion blocked by fibula

Grooved talocrural joint
Present in: non-human primates
and early hominins

Inversion prevented by keeled tibia

Anterior talofibular ligament
Present in: modern humans,
some hominins and perhaps
some gibbons and gorillas

Inversion limited by ligament

Figure 6.10. The ankle of can be stabilized in three different, though non-exclusive, ways. The ankle on the left is stabilized via a valgus tilt to the tibia. This morphology which causes the superiolateral edge of the talus to touch the lateral malleolus of the fibula during foot inversion is present in non-human primates and can be seen radiographically in Figure 6.5. The ankle in the middle has a strong trochlear keel, which limits extreme inversion by blocking movement of the superomedial aspect of the talar trochlear with the tibial keel. This morphology is also present in many non-human primates, early hominins and can be seen in Figure 6.5 radiographs as well. In the absence of these two morphologies, humans and some Pleistocene hominins evolved an anterior talofibular ligament (far right). The ligament may also be present in some gibbons and gorillas.

mechanism in the absence of bony stabilization. The gibbon has a more vertically oriented talocrural joint, and the mountain gorilla has a flat tibiotalar joint most similar to the morphology found in modern humans (Figure 6.11). The flat talocrural morphology of the mountain gorilla is likely reflective of a more terrestrial lifestyle than what is found in the other African apes (Tuttle and Watts, 1985; Hunt, 2004). Many skeletal differences related to locomotion and substrate use have been found between mountain and lowland gorillas including a relatively shorter length of the humerus, a lower intermembral index, and a less divergent hallux (Schultz, 1927; Schultz, 1930; Schultz, 1934). More recently and with a larger sample, Taylor (1997) found that the scapula of lowland gorillas is

Figure 6.11. Bivariate plot of depth of talar trochlea and angle of talocrural axis.

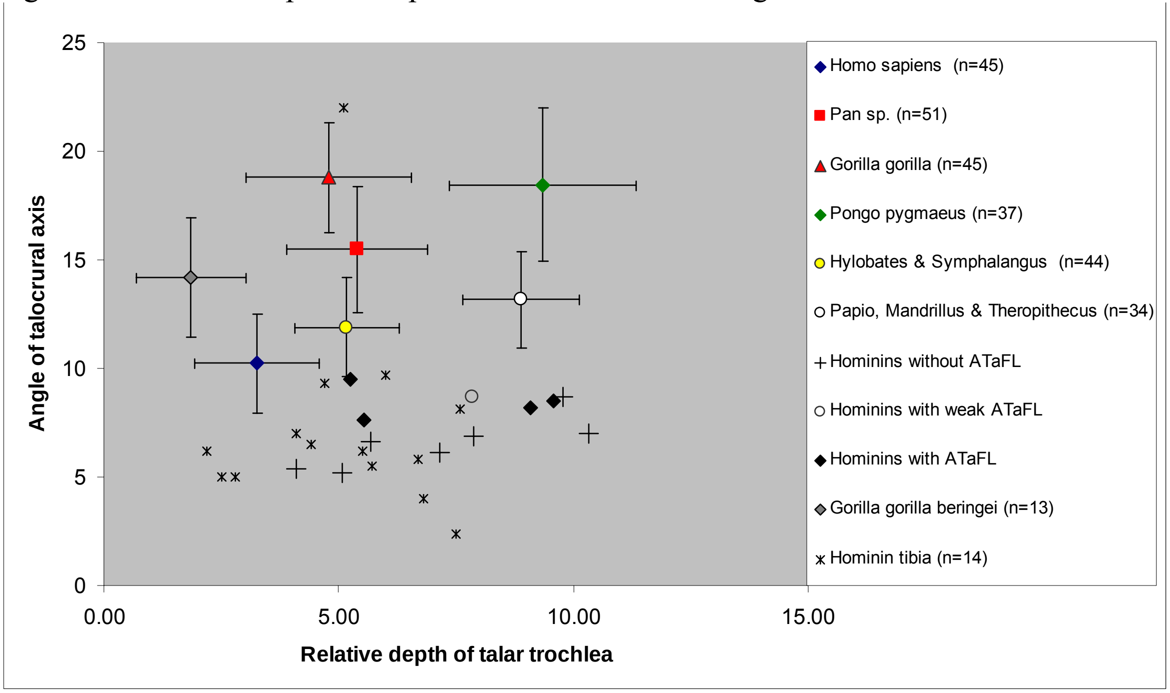


Figure 6.11. Relationship between the keeled topography of the talus (x-axis) and the angle formed between the axis of rotation and the superior surface of the talus (y-axis) in extant anthropoids and extinct hominins. Extant primate data are shown as the mean values and the bars represent one standard deviation from the mean. Note that humans and two other species that may have an anterior talofibular ligament (gibbon and mountain gorilla) have the flattest tali with the most perpendicularly oriented tibia. With the exception of KNM-ER 2596, all of the hominin tibia and tali have a perpendicularly oriented tibia over the talus; however, they vary significantly in the degree of trochlear keeling.

better adapted for loading in an arboreal environment than the scapula of mountain gorillas. This study suggests that in addition to the scapula, the talus may reflect locomotor differences between the different subspecies of *Gorilla*, with a flatter, more perpendicularly oriented tibial shaft over the foot distinguishing the mountain gorilla from the more arboreal lowland gorilla. Although it is unclear why gibbons have evolved a perpendicularly oriented talocrural morphology, the presence of this joint shape may explain why the anterior talofibular ligament has been found in a gibbon (Inman, 1976) and in addition, a flat talar trochlea helps explain why this ligament has been found in a mountain gorilla (Gomberg, 1981). Why the ligament has also been found in a lowland gorilla (Gomberg, 1981) is unclear, though this ligament was not present in a lowland gorilla dissected by this author. More information about the presence or absence of the anterior talofibular ligament from ape dissections is sorely needed.

Because the anterior talofibular ligament anchors on small tubercles on the junction of the neck and body of the lateral side of the talus (Sarrafian, 1993; Golanó et al., 2006), the presence of this ligament can be traced through the hominin fossil record. However, it is emphasized that a bony tubercle for the anterior talofibular ligament is not present in any gibbon talus studied (n=44), though this ligament is known from at least one dissected individual (Inman, 1976). In many mountain and lowland gorilla tali, there is an apparent tubercle on the most superior aspect of the body-neck junction, and often a strong buttress along the body-neck junction running dorsoplantarly. It is suggested here that those morphologies have nothing to do with the presence of an anterior talofibular ligament. However, in a small number of gorilla tali, a diminutive tubercle midway between the superior and inferior aspect of the lateral body-neck junction was detected. Thus, as Gomberg (1981) found, the anterior talofibular ligament may be present in some lowland gorillas, and perhaps a greater percentage of mountain gorillas.

A definitive tubercle for the anterior talofibular ligament is not present in six hominin fossil tali (AL 288-1, StW 88, StW 363, SKX 42695, TM 1517, OH 8), may be weakly present in two specimens (StW 486, KNM-ER 1476), and is present in four tali (Omo 323-76-898, KNM-ER 1464, KNM-ER 813, and KNM-ER 5428). The Omo talus is 2.2 million years old, KNM-ER 1464 and 813 are between 1.85-1.88 mya, and the KNM-ER 5428 talus is 1.6 mya (Feibel et al., 1989). The shape of the talar trochlea fluctuates temporally as well with the earliest published hominin ankle from the keeled 4.1 mya *Australopithecus anamensis* distal tibia, the oldest talus (A.L. 288-1 from *A. afarensis*) and other Hadar tibia having a flat surface, back to many Plio-Pleistocene tali and tibia being quite keeled, and finally to the more recent fossil tali and tibia again having a relatively flat talar surface. Some have suggested that the keeled morphology is ape-like and may reflect more arboreal behaviors in Plio-Pleistocene hominins (Lewis, 1980; Kidd et al., 1996; Hartcourt-Smith, 2002; Deloison, 2003; Kidd and Oxnard, 2005). It is suggested here that this pattern of morphology can also be explained as different strategies for establishing ankle stability in fully bipedal hominins.

Hominin tali can be grouped into those with a flat talar surface with no evidence for an ATaFL; a keeled surface with no evidence for an ATaFL; a keeled surface with an ATaFL; and a flat surface with an ATaFL. Because the angle that the axis of rotation forms with the superior surface of these tali is in the human range for all of these tali, the talocrural joint necessarily was perpendicular to the long axis of the tibia, and thus these species had a valgus knee, and were well adapted for bipedalism (Latimer et al., 1987). Because these hominins were committed bipeds, it was critical for these species to evolve mechanisms of ankle stability.

The earliest hominin tali from the *Australopithecus afarensis* A.L. 288-1 (Lucy) and the three distal tibia from Hadar lack the oblique orientation *and* the keeled shape that stabilizes the ankle in non-human primates. The *A. afarensis* ankle is thus remarkably human-like in its morphology as others have noted (Latimer et al., 1987; Gebo and Schwartz, 2006). Unlike modern humans, however, this talus does not appear to have a detectable tubercle for the anterior talofibular ligament. There is the possibility that the ligament was present, but did not leave a bony tubercle on the talus, as may be the case with gibbons. The possibility exists that a tubercle for the ATaFL might be detectable on the original fossil talus of A.L. 288-1, but not on the cast. Tubercles for the ATaFL were detectable, however, on both the original specimens and casts of KNM-ER 813 and KNM-ER 1464. It is important to note too that in the original description of the Hadar *A. afarensis* distal fibula A.L. 333w-37 and A.L. 333-9b, Lovejoy et al. (1982) describe a tubercle for the anterior talofibular ligament. As mentioned previously, this author is unable to consistently and reliably differentiate a tubercle for the anterior talofibular ligament and one for the calcaneofibular ligament because of anatomical overlap between the fibers of these two ligaments (Burks and Morgan, 1994; Hintermann, 2002; Golanó et al., 2006; Taser et al., 2006). If these distal fibulae are indeed preserving an insertion site for the anterior talofibular ligament, it may have been variably present in *A. afarensis*. The discovery of additional fossil tali and a full description of the A.L. 333-147 talus (Ward et al., 1998) will help assess the nature of this ligament in the ankle of *A. afarensis*. Without the oblique orientation of the tibia, a keeled trochlea, or perhaps even an ATaFL, the question of how *A. afarensis* stabilized its ankle and prevented ankle dislocation during sudden inversion remains unanswered.

One possible explanation is that ankle stability in *A. afarensis* may have been provided by strong peroneal muscles in this species (Figure 6.12). Based on the presence of a wide and deep peroneal groove on all five Hadar distal fibula, A.L. 288-1, A.L. 333-9A, A.L. 333-9B, A.L. 333-85, A.L. 333w-37, and a larger peroneal tubercle on the calcanei A.L. 333-8 and A.L. 333-55, *A. afarensis* was equipped with large peroneal muscles (Johanson et al., 1982; Lovejoy et al., 1982; Latimer et al., 1982; Stern and

Susman, 1983; Latimer and Lovejoy, 1989). Some have suggested that the strong peroneals in *A. afarensis* fossils are evidence for continued arboreality in this species because these muscles are large in apes and active during climbing (Susman, 1983; Susman et al., 1984; Langdon, 1985; Hunt, 1994). Gebo (1992) has supported Stern and Susman's (1983) alternative role of strong peroneals in australopiths as maintaining stability in a biped with more midfoot mobility than modern humans. Latimer and Lovejoy (1989) have added that the peroneals may have served a more dominant role in foot plantarflexion during bipedality prior to the evolution of an enlarged Achilles tendon and a more derived gastrocnemius muscle. It is suggested here that strong peroneals may also have provided a mechanism for stabilizing the ankle joint in the absence of ligamentous or bony reinforcements. The hypothesis posed here and that of Latimer and Lovejoy (1989) and Gebo (1992; citing Stern and Susman [1983]) are not mutually exclusive. In modern humans, weak peroneals (Sugimoto et al., 1997), and a delayed peroneal reaction to foot inversion (Konradsen and Ravn, 1990; Khin-Myo-Hla et al., 1999; Beynnon et al., 2001) are both strong predictors of chronic ankle instability. Studies on modern humans have found that the peroneal muscles react quickly enough to prevent inversion injuries especially if the foot is already inverted during the swing phase of bipedal locomotion (Konradsen and Højsgaard, 1993; Konradsen et al., 1997; Konradsen, 2002). In addition, the peroneal muscles have tendons that wrap around the distal fibula, and thus are close to the center of rotation. This arrangement results in the peroneals having a low mechanical advantage, but in return this muscle group can act quickly (Currey, 2002). In the absence of other means of stabilizing the ankle, *A.*

Figure 6.12. Models of ankle stability in fossil hominins.

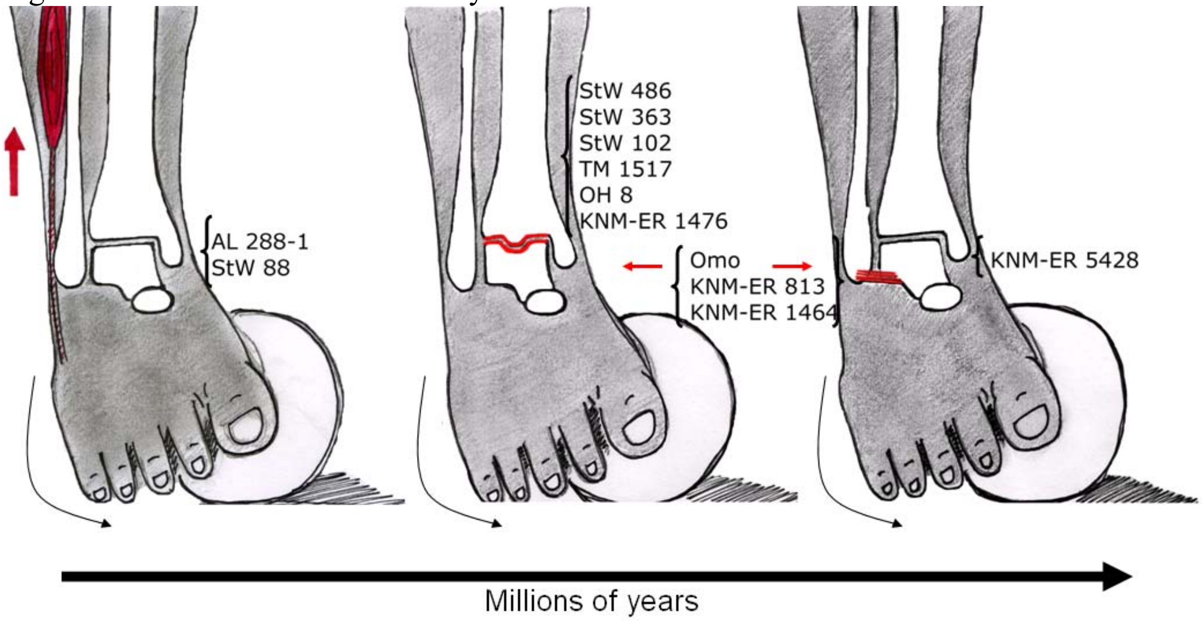


Figure 6.12. Possible mechanisms by which early hominins stabilized their ankles. The hominin on the far left is resisting inversion with strong everting peroneal muscles. This may have been the mechanism of ankle stability used by the A.L. 288-1, and StW 88 individuals. The keeled trochlear surface, a morphology found in many Plio-Pleistocene hominin tali, would have provided ankle stability for the middle hominin. The hominin on the far right resists inversion with ligamentous support on the lateral side of the ankle, a feature found in the talus KNM-ER 5428. Specimens Omo 323-76-898, KNM-ER 813, and KNM-ER 1464 have both a keeled trochlear surface and evidence for an anterior talofibular ligament.

afarensis may have relied on large peroneals to prevent severe ankle injury during sudden foot inversion.

Strong peroneal musculature is evident not only in the *A. afarensis* calcanei A.L. 333-8, A.L. 333-55 from Hadar (Latimer et al., 1982; Latimer and Lovejoy, 1989), but also in the enlarged peroneal process of an *A. africanus* calcaneus StW 352 from the 2.6-2.8 mya Member 4 deposits in the Sterkfontein cave of South Africa (Deloison et al., 2003; pers. obs.). The flattest fossil hominin tali measured in this study also come from the Hadar deposits (A.L. 288-1), and the Member 4 deposits of the Sterkfontein cave in South Africa (StW 88). The 2.36 mya hominin calcaneus from the Shunguru Formation in Ethiopia, Omo 33-74-896 also has a large peroneal tubercle (Deloison, 1986; Gebo and Schwartz, 2006), and although it is damaged on its lateral side, the OH 8 calcaneus is preserved enough to detect the superior aspect of a peroneal tubercle, though it is difficult to tell how large it would have been (pers. obs.). Additional, preferably more recent, fossil calcanei will be needed to test the role of the peroneals in ankle stability by assessing whether the eventual reduction in the peroneal musculature corresponded to the evolution of a stabilizing keeled talar trochlea, or to the evolution of the anterior talofibular ligament. Two more recent distal fibula, KNM-ER 1500 and KNM-ER 1481 from 1.9 mya deposits in the Koobi Fora (Feibel et al., 1989) are notably different from the Hadar fibula in having a much reduced groove for the peroneal tendons (pers. obs.). Day et al. (1975) describe the KNM-ER 1481 fibula as having only a "faint groove" for the peroneal tendons, and Day et al. (1976) remark on the smoothness of the peroneal groove region on the KNM-ER 1500 distal fibula. These two hominins fortunately preserve the distal tibia as well. KNM-ER 1500 has a keeled talocrural joint surface, perhaps as adaptations to stabilize the ankle in the absence of strong peroneals and in the absence of an anterior talofibular ligament (Table 6.2); whereas KNM-ER 1481 has a flatter joint surface and it is predicted that in the absence of strong peroneals, this individual would have had an anterior talofibular ligament like the similarly shaped talus KNM-ER 5428 (Table 6.2). Additional hominin fibula, StW 356 from the 2.6-2.8 mya Member 4 deposits in the Sterkfontain Cave, and OH 35 from 1.85 mya sediments in Olduvai Gorge do not preserve enough of their distal ends to make a judgement about the size of the peroneal muscles.

Other hominin tali, primarily from Sterkfontein cave in South Africa, Olduvai Gorge in Tanzania, and from the Koobi Fora in Kenya, have a strong central keel and high lateral margins. This has been interpreted by some to be an ape-like morphology in which the tibia swings laterally over the talus (Kidd et al., 1996; Hartcourt-Smith, 2002) and is suggestive of their continued use of arboreal habitats (Deloison, 2003). However, when the specimens are oriented relative to the conserved angle between the talocrural joint surface and the axis of rotation present in all African apes and humans (Latimer et al., 1987), these tali do not have high lateral margins, but are striking for their deeply grooved talar surfaces. Most of these tali are absent of any indication for an anterior talofibular ligament. The keeled morphology may have little to do with ape-like arboreal behavior and instead may be a novel manner by which Plio-Pleistocene hominins stabilized their ankles during bipedal locomotion in the absence of an anterior talofibular ligament (Figure 6.12).

Importantly, the four largest tali in the hominin fossil record are the four tali with clear evidence of an anterior talofibular ligament. Using the regression equation from McHenry (1992), the Omo specimen belonged to a 46 kg individual, KNM-ER 813 and 1464 from 52 and 55 kg hominins respectively, and KNM-ER 5428 from a 95 kg individual. An increase in body size, and perhaps the adoption of long distance travel and endurance running in the genus *Homo* (Bramble and Lieberman, 2004), may have resulted in flat tali whether through natural selection or functional adaptation of bone and bone precursors as a result of increased forces. The anterior talofibular ligament is partially responsible for maintaining ankle stability in these ankles for which bony stability has been lost (Figure 6.12).

The chondral modeling theory of bone development (Frost, 1979; Frost; 1999; Hamrick, 1999a) predicts that joints will become flatter with an increase in force across that joint whether from an increase in body mass, or a change in the loading environment. This remodeling assures that the direction of force remains perpendicular to the joint surface, maximizing the compressive component of the force (where bone is strongest), and minimizing shear forces. This model for the adaptation of bone to environmental stimuli hypothesizes that chondrocytes in immature articular cartilage are activated by hydrostatic pressure differences that occur during joint loading. There is experimental evidence for this mechanically-induced activity of chondrocytes (Takahashi et al., 1997; Wong et al., 1997; reviewed in Grodzinsky et al., 2000). Evidence in favor of this model include anteroposterior flattening of the hominoid talus with increased body size (Latimer et al., 1987), a decrease in knee joint curvature with age and size in the marsupial *Didelphis* (Hamrick, 1999b), and an increase in joint surface curvature in the knees of paralyzed humans (Frost, 1999). Although this model was not supported by recent work on the proximal tibia in hominoids and hominins (Organ and Ward, 2006), the flattened distal femur in humans and hominins may ensure that the high forces incurred during bipedality are oriented perpendicular to the axis of the knee (Heiple and Lovejoy, 1971; Organ and Ward, 2006).

An increase in body size notable for *Homo erectus* (McHenry, 1992; Walker and Leakey, 1993; Antón, 2003) would have significantly increased the forces on the talocrural joint, and according to the chondral modeling theory would have resulted in a mediolaterally flatter talocrural joint. However, in addition to an increase in body size, there is evidence that the evolution of *H. erectus* signaled a dramatic change in behavior in Plio-Pleistocene hominins (Wolpoff, 1999; Antón, 2003). Bramble and Lieberman (2004) have presented evidence for the evolution of endurance running in early *Homo* and into *H. erectus*. Studies on modern humans suggest that compared to walking, running results in substantially higher compressive forces on the ankle (Cavanaugh and LaFortune, 1980) approximately five times a runner's body weight (Burdett, 1982; Subotnick, 1985). Thus, the adoption of endurance running in *H. erectus* would have resulted in a substantially greater force regularly incurred on the talocrural joint. An increase in travel distance or speed in *H. erectus* is supported by evidence for an increase in limb length (Wang et al., 2004; Pontzer, 2005; Steudel-Numbers, 2006; Steudel-Numbers, 2007). Furthermore, fossil evidence from the 1.77 mya site of Dmanisi in Georgia (Lordkipanidze et al., 2007), and the 1.5-1.8 mya Indonesian sites of Perning and Sangiran (Antón, 2003) demonstrate that soon after it evolved, *H. erectus* dramatically expanded its geographical range. An increase in body mass and changes in foraging strategies are strong predictors of an increase in home range across primates and *H. erectus* appears to be no different (Antón et al., 2002). Although it was suggested that the Dmanisi hominins were quite small, estimates of body mass based on postcranial remains suggest that these hominins were 40-50 kg, with the tibia D3901 from a 48.6 kg individual (Lordkipanidze et al., 2007). Thus, the Dmanisi hominins are in the size range for some of the larger Plio-Pleistocene hominin tali and tibia from this study (KNM-ER 1481, KNM-ER 813 for example). Thus, in addition to an enlarged body size, an increase in the locomotor activity of early *Homo* and *H. erectus* would have imposed a still greater stress on the talocrural joint, and selected for a mediolaterally flat tibiotalar joint surface. This scenario is supported by fossil evidence measured in this study.

The 1.6 mya KNM-ER 5428 talus, in particular, cannot be easily differentiated from modern human tali in its trochlear shape. A slightly more recent talus, KNM-ER 803 from 1.53 mya deposits in Kenya, is fragmentary, but preserves enough of the lateral aspect of the trochlear surface to tell that it would have an even flatter superior surface than KNM-ER 5428 (Figure 6.13). Additionally, the distal tibia of the *Homo erectus* individual KNM-WT 15000 is also strikingly flat mediolaterally, suggesting that the corresponding talar surface would be flat much like the KNM-ER 5428 and KNM-ER 803 hominins. This morphology is also present in the Kabwe tibia from the Middle Pleistocene and continues into modern humans. This is in contrast to earlier fossil distal tibia, like KNM-ER 1481 and OH 35, which have more keeled midlines. With the evolution of a flat talar surface, *H. erectus* would be susceptible to ankle dislocation during sudden foot inversion. The ankle of *H. erectus* and modern humans may be an example of an evolutionary trade-off in which selection for a flat talar joint surface more efficient at distributing forces through the joint occurs at the expense of joint stability, rendering the ankle joint more susceptible to dislocation. However, the KNM-ER 5428 talus has an obvious tubercle for the anterior talofibular ligament and thus *H. erectus* had evolved the ligamentous support present in modern humans. It cannot be understated how this shift in talocrural morphology, though rendering the ankle susceptible to ligament injury, may have better adapted humans for long distance bipedal travel or running. Osteroarthritis, though common in the human hip and knee, is relatively rare in the ankle (Stauffer et al., 1977; Greenwald, 1983). Stauffer et al. (1977) tested whether this reduction in degenerative joint disease was related to a decrease in forces incurred by the ankle during walking, and instead found that the forces are higher at the ankle than at the

Figure 6.13. Flattening of the talus in hominin evolution.

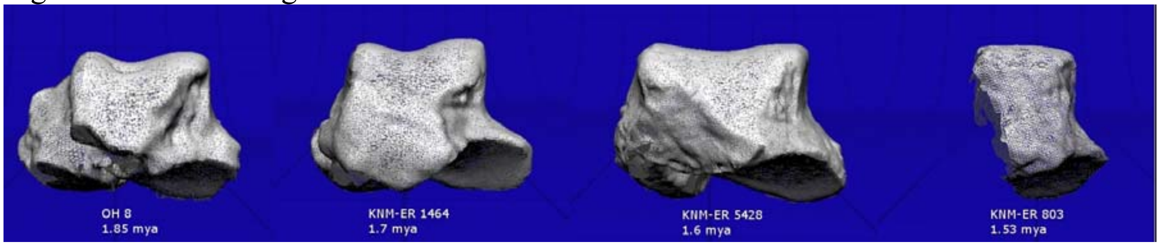


Figure 6.13. 3-D scans from the 1.85 mya talus OH 8 (left), the 1.7 mya talus KNM-ER 1464, the 1.6 mya talus KNM-ER 5428, and the 1.53 mya partial talus KNM-ER 803 in distal view. The specimens have been scaled to approximately the same size, though their actual sizes differ (see Table 6.2). Moving from left to right, the superior aspect of the talar trochlear becomes progressively flatter with time. KNM-ER 1464 and KNM-ER 5248 preserve a tubercle for the anterior talofibular ligament and it is hypothesized that KNM-ER 803 would have possessed this ligament as well (see text for details).

hip or knee. Joint shape may therefore be critical in efficiently distributing these increased forces through the talocrural joint and reducing degenerative disease.

Interestingly, though, there appears to be overlap in these strategies of ankle stability. Two fossil tali (KNM-ER 813 and KNM-ER 1464) that have quite keeled talar surfaces, also have an anterior talofibular ligament tubercle on their talar bodies. This suggests that when selection favored a flat talar surface in large bodied hominins, the presence of an anterior talofibular ligament may have been a feature already variably present in the hominin population and in place to compensate for the loss of bony reinforcement in the ankle.

Testing hypotheses of the pattern of development in the hominin ankle is difficult. The hominin species designations listed in Table 6.2 make clear that few of the tibia and tali measured in this study have been confidently assigned to any one species, and thus it is difficult to follow the evolutionary trajectory of the ankle using hypothesized phylogenies. Because craniodental remains from both *Homo* and robust australopiths have been recovered from Plio-Pleistocene sites in East and South Africa, most of the unassociated fossil tali and tibia listed in Table 6.2 cannot be confidently assigned to either lineage without bias or untested assumptions. The earliest specimens from Kanapoi, Kenya and Hadar, Ethiopia are most likely from *A. anamensis* and *A. afarensis* as indicated.

The Member 4 hominins from Sterkfontein are probably assignable to *A. africanus*, though there may be a second species at this locality (Clarke, 1986; Clarke, 1988; Clarke, 1994; Moggi-Cecchi et al., 1998; Lockwood and Tobias, 2002) and thus care should be taken in assuming these nine fossil tali and tibia are all from the same taxon. Furthermore, there is evidence that the southern Member 4 deposits are of a later age than the northern deposits (Kuman and Clarke, 2002). Thus, the StW 102 talus, from the southern grid X/47, may not be as old as the other tali and tibia. This hypothesis that the Member 4 fossils from Sterkfontein sample either multiple taxa or multiple time periods is consistent with the range of variation found in the morphology of the five tali studied here.

Though it is argued that the KNM-ER 1500 tibia is associated with a robust australopithecine mandible (Grausz et al., 1988), certain identification of the fragmentary KNM-ER 1500 mandible is unclear to some (Wood and Constantino, 2007). The later specimens KNM-ER 803 and KNM-WT 15000 were found with craniodental remains and thus are confidently assigned to *H. erectus*. Suggestions that the OH 8 talus and OH 35 tibia are associated with the craniodental remains of the *H. habilis* type specimen OH 7 (Stern and Susman, 1982) are not supported with more detailed analyses. The OH 8 foot does not have an epiphyseal fusion pattern that matches the development of the teenage OH 7 mandible (pers. obs.) and the OH 8 foot and OH 35 tibia, though similar in size, are not similar enough in morphology to be from the same individual (Aiello et al., 1998; Wood et al., 2000). Thus, these fossils may be from either *P. boisei* or *H. habilis*.

Nevertheless, based on the current evidence, it is suggested that there are two possible scenarios for how the ankle evolved along the direct human lineage (Figure 6.14). The first hypothesis suggests that the earliest hominin ankles were keeled at the tibiotalar junction, as in modern great apes and in the 4.1 mya *A. anamensis* tibia KNM-KP 29285. More committed bipedalism in *A. afarensis* resulted in a mediolaterally flatter talocrural joint present in the Hadar hominins. Strong peroneals were recruited to resist inversion and prevent dislocation of the talocrural joint. The anterior talofibular ligament may have been variably present in *A. afarensis* as well (Lovejoy et al., 1982). In this scenario, *Homo*, as represented by the 2.2 mya, mediolaterally flat talus from Omo, reduced reliance on the peroneal muscles and relied instead on the talofibular ligament to stabilize the ankle against inversion injury. The mediolaterally flat tali KNM-ER 5428, KNM-ER 803, and tibia KNM-WT 15000 are from descendents of this population and are ancestral to the modern human ankle. The keeled morphology present in most other hominin specimens is retained from the keeled *A. anamensis* distal tibia, or is an evolutionary reversal from the *A. afarensis* condition and may represent the robust australopithecine lineage. Adoption of this scenario would necessitate the increase in frequency of the anterior talofibular ligament in populations represented by the later keeled specimens KNM-ER 813 and KNM-ER 1464. This is especially the case if KNM-ER 1464 and other fossils from Ileret 6A area are 1.56-1.6 million years old, as some suggest (Wood and Constantino, 2007), instead of the original suggestion of 1.7 million years old (Feibel et al., 1989).

Figure 6.14. Evolutionary scenarios for origin of anterior talofibular ligament.

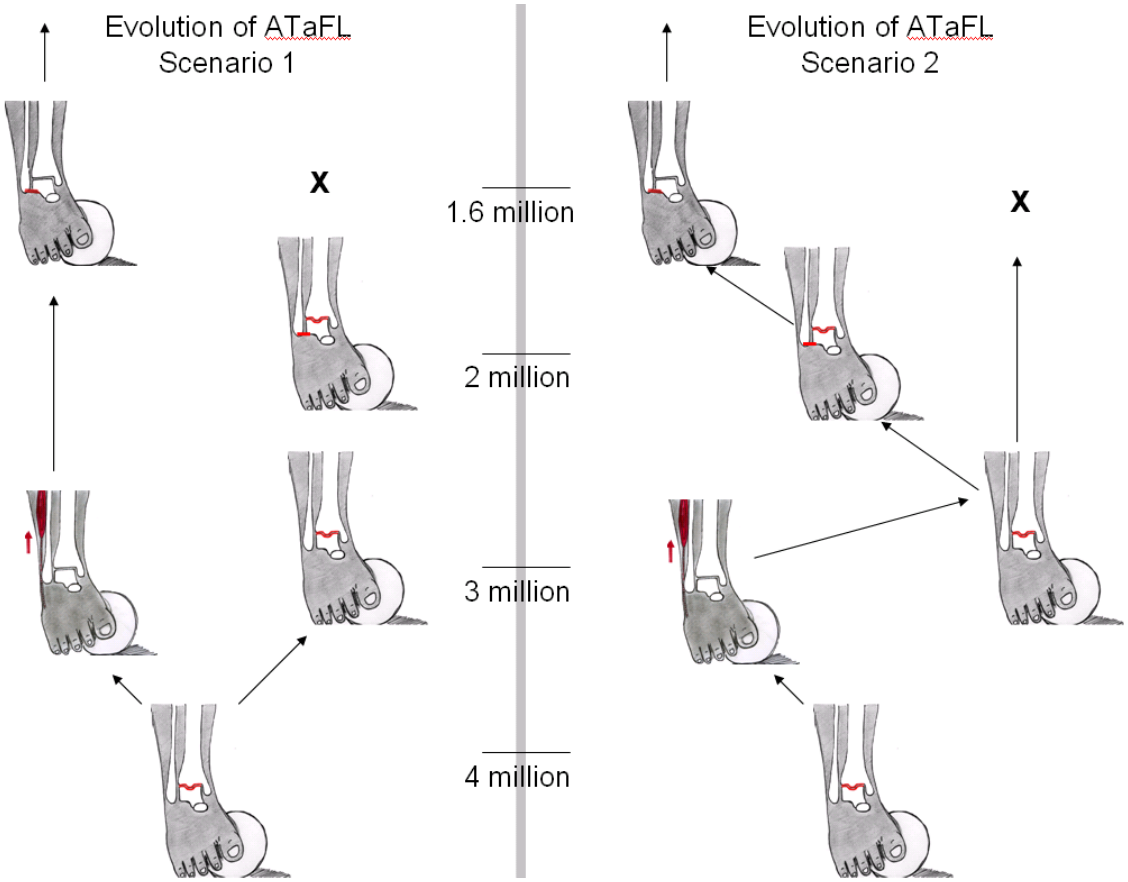


Figure 6.14. Two scenarios for the evolution of the anterior talofibular ligament. Scenario 1 posits the flat surface of the talus as evolving in only one lineage and would imply that the KNM-ER 5428 *Homo erectus* talus descends from the Omo 323-76-898 talus and that the anterior talofibular ligament evolved independently in the keeled tali KNM-ER 813 and KNM-ER 1464. The scenario on the right posits more homoplasy in the hominin talocrural joint and with a variably present anterior talofibular ligament becoming more common first in hominins with keeled tali, and then becoming fixed in later populations with flat talar surfaces (see text for more explanation).

Given the evidence, a phylogenetically less parsimonious scenario than the one presented above may be more likely. The second scenario hypothesizes that the originally keeled talocrural joint morphology, as seen in the KNM-KP 29285 distal tibia evolved into the flat *A. afarensis* talocrural joint by 3.2 million years ago. This morphology evolved back into a joint with a keeled surface to stabilize the ankle in place of strong peroneal musculature in early *Homo* and its immediate ancestors. Peroneal reduction may have been related to the evolution of an enlarged Achilles tendon and a more derived gastrocnemius musculature, which may have occurred in the genus *Homo* (Bramble and Lieberman, 2004). This hypothesis implies that a flat talocrural joint is not a synapomorphy of the genus *Homo*. Only with the evolution of larger body size in *H. erectus* did the talocrural joint evolve a mediolaterally flat morphology once again. The presence of a tubercle for the ATaFL on keeled specimens likely from the genus *Homo*, KNM-ER 813 and KNM-ER 1464, provides evidence for the hypothesis that several evolutionary reversals may characterize the shape of the talocrural joint in the direct human lineage. If this is the case, it will be exceedingly difficult to distinguish robust australopithecine tali and tibia from *Homo* tali and tibia prior to 1.6 mya.

These hypotheses can further be tested with additional discoveries of fossil hominin tibia and tali, including full descriptions of the distal tibia A.L. 545-3 a large talus A.L. 333-147 from *Australopithecus afarensis* (Ward et al., 1998) and the tibia D3901 and talus D4110 from the early *Homo* site of Dmanisi (Lorkipanidze et al., 2007).

Conclusion

There is no evidence that the absence of an anterior talofibular ligament encourages talar tilting in non-human primates. Additionally, the CFL and PTaFL do not compensate for the absence of an ATaFL in a non-human primate. Thus, it is suggested that the angle of the talocrural joint and a keeled trochlear surface provide joint stability in primates lacking an ATaFL. All of the fossil tali and all but one of the fossil tibia studied have a human-like angle between the talocrural joint surface and the ankle axis of rotation. This result implies that the tibia was aligned perpendicular to the talus, and that these hominins necessarily had a valgus knee adapted for bipedalism. This reorientation of the talocrural joint, however, left the ankle susceptible to inversion injuries, and Plio-Pleistocene hominins may have evolved a keeled trochlear morphology to stabilize the joint. Differences between the morphology of fossil hominins and modern humans do not always mean differences in behavior, and may represent instead different solutions to the same evolutionary dilemma. The keeled morphology of hominin tali from the Plio-Pleistocene may be an example of this. The evolution of large body size and forces imposed upon the ankle during long distance running may have selected for flatter talar surfaces, and ligamentous, rather than bony stabilization of the hominin ankle. This trade-off of an ankle morphology equipped to distribute forces more efficiently through the joint at the expense of joint stability occurred in our ancestors roughly 1.6 million years ago, thereby rendering the modern human ankle particularly susceptible to ligament injury.

CHAPTER 7

The evolution of midfoot stability and its relation to vertical climbing. Revisiting the "midtarsal break".

Abstract

The midtarsal break was first described nearly 75 years ago to explain the ability of non-human primates to lift their heel independently of the rest of the foot. Since the initial description of the midtarsal break, the calcaneocuboid joint has been assumed to be the anatomical source of this motion. Recently, two studies have suggested that the midtarsal break may occur between the cuboid and the fifth metatarsal joint, rather than at the calcaneocuboid joint (D'Août et al., 2002; Vereecke et al., 2003). Data compiled from x-rays, dissections, manual manipulation of living primate feet, video of captive and wild anthropoids, EMG of chimpanzees, and osteological specimens concur that the midtarsal break is caused by flexion at both joints with the cuboid-metatarsal joint contributing roughly 2/3 of total midfoot flexion, and the calcaneocuboid joint only about 1/3 of total midfoot flexion. Dorsal expansion of the distal articular surface of the cuboid and the proximal articular surface of metatarsal V, and the curved shape of the proximal articular surface of the fourth and fifth metatarsals and corresponding cuboid facets provide skeletal correlates for the presence of midfoot flexion at the cuboid-metatarsal joint. Study of hominin metatarsals from South Africa (StW 114/115 and StW 485), a fifth metatarsal from Kenya (KNM-ER 803), and the metatarsals and a cuboid from the OH 8 foot show little evidence for flexion at the cuboid-metatarsal joint. These results

suggest that hominins had already evolved a stable midfoot region well adapted for the push-off phase of bipedalism by at least 2.6 million years ago. Study of two 3.2 million year old 5th metatarsals of *Australopithecus afarensis* from Ethiopia are consistent with midfoot stability in this species as well. These data further illuminate the evolution of the longitudinal arch and show further evidence of constraints on the arboreal capacity in early hominins.

Introduction

The primate midfoot is composed of several closely spaced joints that all experience some degree of motion in multiple planes (Figure 7.1). The subtalar joint, formed between the talus and the calcaneus contributes mostly to foot eversion and inversion, though some flexion-extension, and abduction-adduction also occurs at this joint (Wright et al., 1964; Close et al., 1967; Inman, 1976; Siegler et al., 1988; Donatelli, 1990; Scott and Winter, 1991). The midtarsal joint, formed between the cuboid and calcaneus on the lateral side of the foot and the talus and navicular on the medial side of the foot, is also a major source of foot eversion and inversion (Manter, 1941), though abduction/adduction and dorsiflexion/plantarflexion is possible at the midtarsal joint (Czerniecki, 1988; Ouzounian and Shereff, 1989). Finally, the tarsal portion of the foot meets the metatarsals on the lateral side of the foot between the cuboid and 4th and 5th metatarsals, and on the medial side of the foot between the lateral, intermediate, and medial cuneiforms and the 3rd, 2nd, and 1st metatarsals respectively. Movement between the tarsals and metatarsals is primarily dorsiflexion/plantarflexion though some rotation is occurs at this joint (Ouzounian and Shereff, 1989; Blackwood et al., 2005). The anatomy

Figure 7.1. Comparative anatomy of the midfoot in humans (left) and chimpanzees (right).

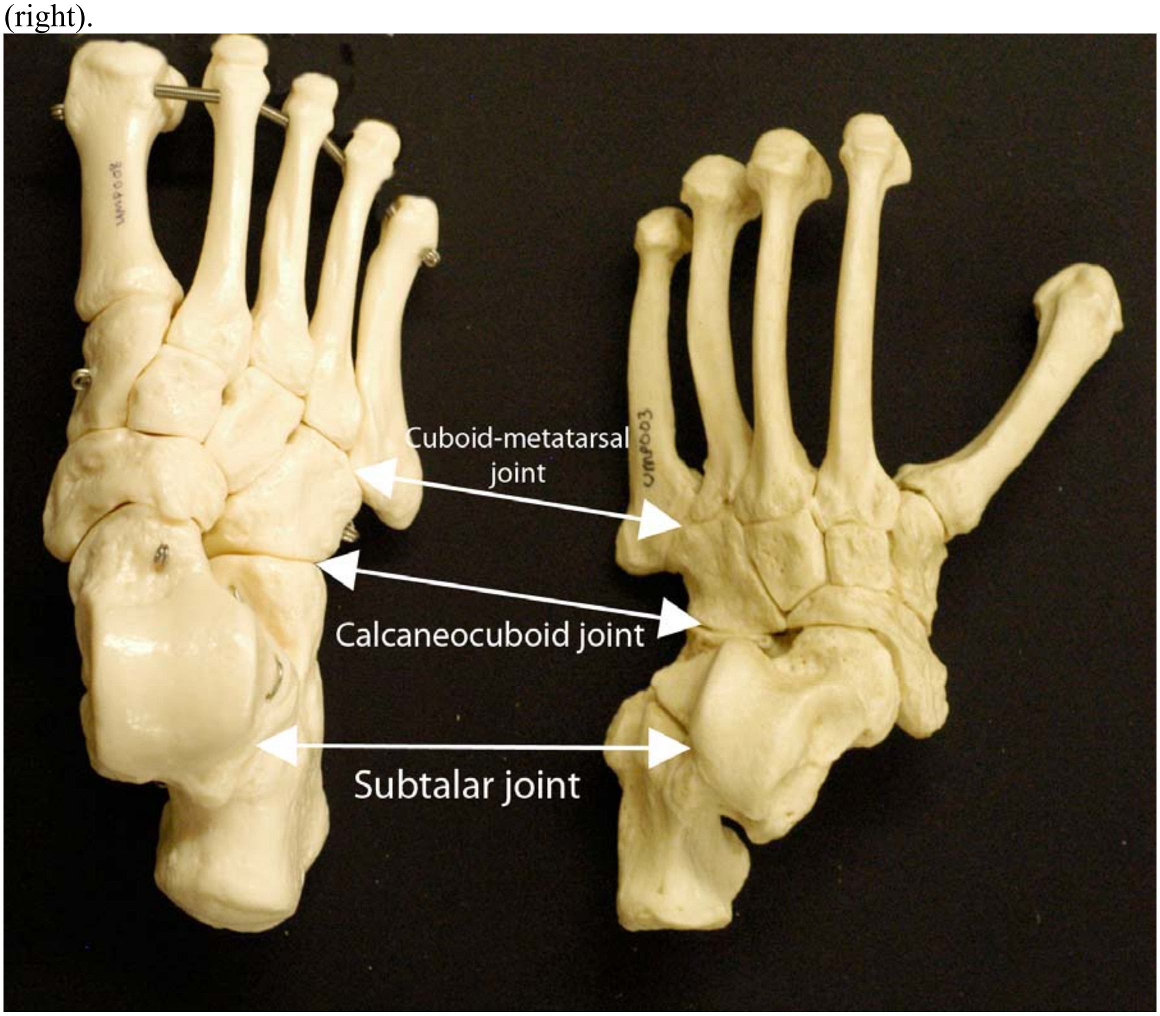


Figure 7.1. Hindfoot and midfoot skeletal elements of human (left) and chimpanzee (right). The subtalar joint is located between the talus and calcaneus. The calcaneocuboid portion of the transverse tarsal joint, and the cuboid-metatarsal portion of the tarsometatarsal joints are both indicated in the image. Note the small proximodistal distance between the calcaneocuboid and cuboid-metatarsal joints. This has made determining the anatomical position of the midtarsal break challenging.

of the tarsal region of the foot and the binding longitudinal arch in humans results in a closed kinetic chain in which movement at a proximal joint necessarily results in movement at a more distal joint, and vice versa (Oatis, 1988; Huson, 2000; Hertel, 2002).

During the initial propulsive stage of human walking, the heel and midfoot simultaneous lift resulting in flexion at the metatarsalphalangeal joint (Close, 1967;

Susman, 1983). However, during terrestrial walking in non-human primates, flexion of the foot occurs first at the midfoot before eventually shifting to the metatarsalphalangeal joint (Figure 7.2). This occurs somewhat among between plantigrade apes, who have heel contact during the contact and early stance phases of walking (Gebo, 1992; Schmitt and Larson, 1995), and cercopithecoids who do not. However, regardless of the role of the heel in walking, the midfoot makes contact with the ground during stance phase in both apes and cercopithecoids. This midtarsal break, also termed a "two stage heel lift" (Kidd, 1993; 1998; 1999), has been observed across a range of non-human anthropoids (Elftman and Manter, 1935; Gebo, 1992; Schmitt and Larson, 1995; Meldrum, 1991; D'Aout et al., 2002; Vereecke et al., 2003). Thus far, humans are the only primate shown to consistently lack a midtarsal break. It is assumed throughout this paper that the midtarsal break occurs in all catarrhines, and that its absence is derived.

Although the midtarsal break has been studied primarily in the context of terrestrial locomotion, it may have significant implications for arboreal activity as well. It has been argued that the midtarsal break is an adaptation that allows climbing primates to have both the grasping forefoot required to hold onto a vertical substrate and the stable hindfoot necessary for propulsion during climbing bouts (Meldrum and Wunderlich, 1998; Meldrum, 2002). Vertical climbing in large bodied primates is most efficiently accomplished by bringing the body close to the vertical substrate, thereby reducing the moment arm produced by a large body at a distance away from the tree (Preuschoft, 1970; Cartmill, 1972; Cartmill, 1985; Preuschoft et al., 1992). Any motion that brings the animal closer to the tree will reduce the moment arm, and thus reduce the muscular force necessary to counteract this moment. For example, extreme dorsiflexion at the talocrural

Figure 7.2. The midtarsal break in chimpanzees and midfoot stability in humans.

a.)

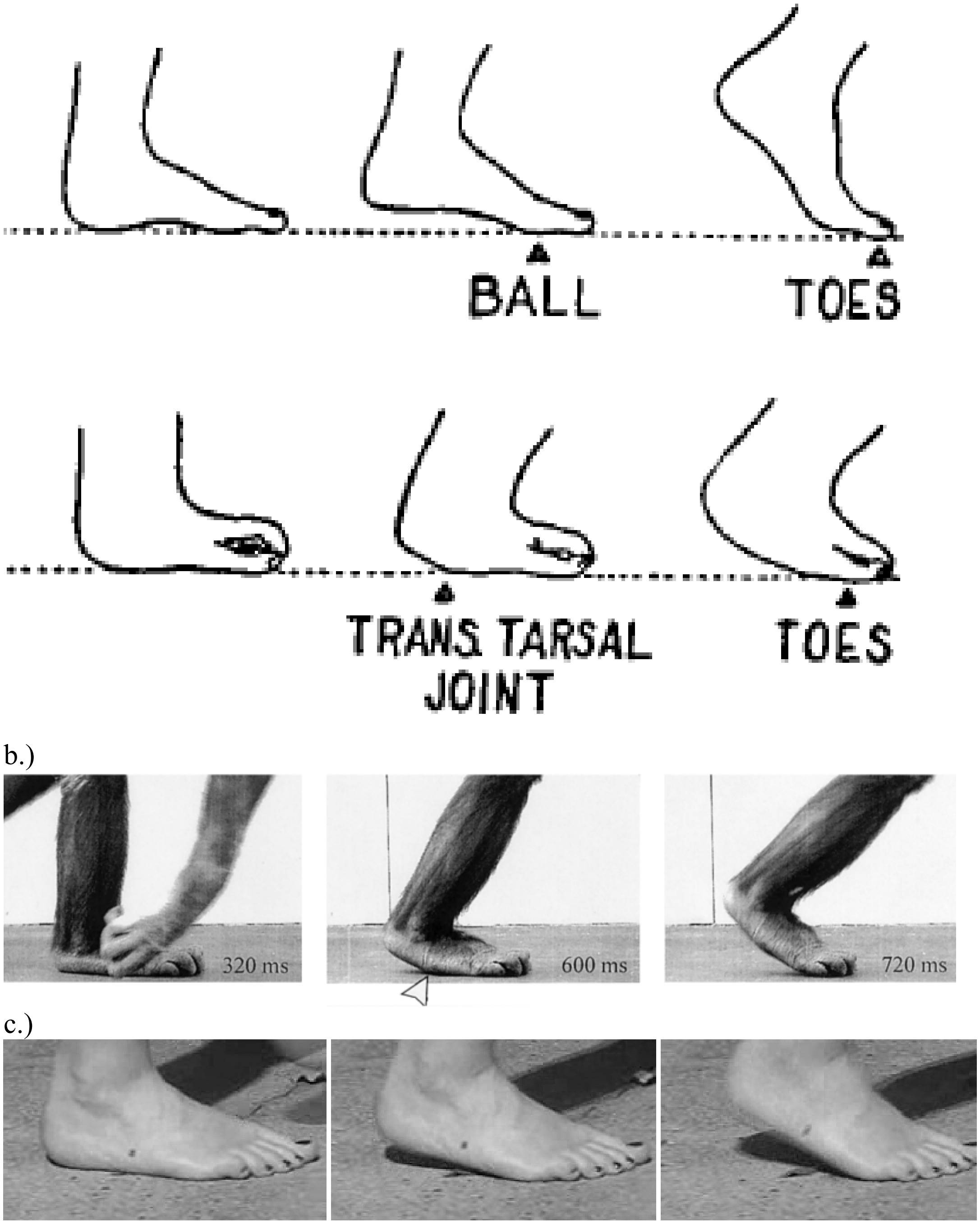


Figure 7.2. Midtarsal break. a.) Drawing from Elftman and Manter (1935) illustrating the repositioning of the fulcrum of the foot from the heel to the metatarsophalangeal joint after initial push-off in humans (top), but an intermediate break at the transtarsal joint in chimpanzees. b.) This is demonstrated more clearly with video of a bonobo (*Pan paniscus*) from D’Août et al. (2002) contrasted with c.) film from a human foot captured for this study. Figures 7.2a and 7.2b reprinted with permission from Wiley-Liss, Inc.Wiley Publishing Inc., a subsidiary of John Wiley & Sons, Inc.

joint is an adaptation found in large-bodied apes in order to bring their bodies closer to the substrate during vertical climbing bouts (Chapter 2). This motion is not as extreme in cercopithecoids (Hirasaki et al., 1993) and is not possible without injury in modern humans (Begeman and Prasad, 1990; Parenteau et al., 1998). Although cercopithecoids do not climb vertically as often as apes do in the wild (Rose, 1977; Hunt, 1989; Hunt, 1991; Gebo, 1996; Hunt, 2004), when they do so, they compensate for minimal dorsiflexion at the ankle by flexing the midfoot. This midtarsal break is present in vertically climbing apes too, though observations of wild chimpanzees suggest that they do not generate flexion in the midfoot until *after* maximum dorsiflexion at the talocrural joint, during the push-off phase of climbing (Chapter 2). Although the primary role of the midtarsal break may involve propulsion, it is hypothesized that the presence of a midtarsal break could assist in vertical climbing as an alternative strategy in species that are unable to hyperdorsiflex at the ankle (Figure 7.3).

This hypothesis has relevance for interpreting the climbing abilities of early hominins. Australopiths were not able to hyperdorsiflex the ankle (Chapters 4 and 5). This, combined with the absence of a divergent toe and limited ability to invert the foot, suggests they were not adapted to vertically climb in the same way that modern apes climb. In the absence of extreme dorsiflexion and inversion, however, australopiths may still have brought their bodies closer to a tree trunk by employing the strategy used by cercopithecoids and flexing at the midfoot during vertical ascents. Furthermore, if australopiths had a midtarsal break, it would not only affect interpretations of their arboreal climbing abilities, but would also impact biomechanical reconstructions of

Figure 7.3. Climbing strategies in apes and monkeys.

Figure 7.3. The two images on the left are stills from video taken of wild chimpanzees vertically climbing in the Kibale National Forest. An adult male is on the left, an adult female on the right. Notice the dorsiflexion at the talocrural joint in the chimpanzees and the absence of a midtarsal break. In contrast, the image on the right is from a vertically climbing cercopithecoid monkey from the Toledo Zoo. Note the weak dorsiflexion and the presence of a midtarsal break. All three images were taken during push-off of the opposite foot.

terrestrial bipedal walking. Interpretation of this motion in extant and extinct anthropoids, however, relies on accurately assessing the joints where this motion actually occurs.

The midtarsal break was initially described by Elftman and Manter (1935) in the first paper to assess the stress distribution under the chimpanzee foot during bipedal and quadrupedal walking (Figure 7.2a). Based on footprints, these authors noted that chimpanzees exert pressure on the navicular, first cuneiform, and base of the fifth metatarsal during walking, whereas humans, equipped with a longitudinal arch, do not experience contact between the midfoot and the ground. In addition to the absence of an arch, chimpanzees also have a more mobile midfoot. Elftman and Manter (1935) suggested that when the chimpanzee heel lifts off the ground, the midfoot remains in contact with the ground. Although Elftman and Manter (1935) observed that when the chimpanzee heel lifts off the ground, there is increased stress under the 5th metatarsal, they suggested that this was a result of motion at the transverse tarsal joint and made no mention of the tarsometatarsal joint. A pilot study of chimpanzee and human locomotion using video data and radiographs of the feet of anesthetized chimpanzees suggested that midtarsal flexion in the ape occurs at the talonavicular joint on the medial side of the foot and that this flexion exceeded that possible at the calcaneocuboid joint (Meldrum and Wunderlich, 1998).

Important skeletal differences are present in the human and the chimpanzee transverse tarsal joint. Elftman (1960) demonstrated that the axes of the transverse tarsal joint in humans, though aligned during pronation, became incongruent during supination, thus locking the transverse tarsal joint and preventing movement. This converts the human midfoot into a rigid lever that is biomechanically more efficient and more stable during the initial push-off phase of walking than is a foot with a mobile midfoot region (Sammarco, 1989). Chimpanzees, however, have a transverse tarsal region with aligned axes whether the foot is in supination or pronation, resulting in constant midtarsal mobility (Close, 1967; Langdon et al., 1991).

The stability of the midtarsal region is partially achieved in humans by a pronounced flange of the cuboid that is located more plantarly and medially than the case in non-human primates. This projection of bone locks into a corresponding facet on the calcaneus during supination in humans. No such locking mechanism occurs in non-human primates (Bojsen-Moller, 1979; Lewis, 1980; Susman, 1983; Kidd, 1998; Harcourt-Smith, 2002).

Ligaments and the soft tissue components of the longitudinal arch have also been implicated in the differing degrees of mobility at the midtarsal region in humans and non-human primates. Bojsen-Møller (1979) noted that the long plantar ligament and plantar aponeurosis both restrict motion in the human midfoot, but are absent from the non-human primate foot. Additionally, after the plantar calcaneonavicular ligaments, long and short plantar ligaments and bifurcate ligaments were cut in human cadavers, the transverse tarsal joint had a greater range of motion, including dorsiflexion (Manter, 1941). Motion was especially freed when the calcaneo-navicular portion of the bifurcate ligament was severed. Gomberg (1985) found that the posterior portion of the long plantar ligament, present in humans but not the great apes, prevents dorsiflexion at the transverse tarsal joint.

Recently, the hypothesis that the midtarsal break occurs at transverse tarsal and more specifically the calcaneocuboid joint, has been challenged. In a study of joint kinematics in captive bonobos (*Pan paniscus*) D'Aout et al. (2002) suggested that the midtarsal break may be occurring at the more distal tarsometatarsal joint rather than the transverse tarsal. Vereecke et al. (2003) also challenged the idea that the midtarsal break occurs between the cuboid and the calcaneus using plantar pressure data on captive bonobos. Based on both the presence of pressure under the 5th metatarsal after initial heel lift, and the manipulation of osteological specimens, Vereecke et al. (2003) suggested that it was more likely that this midfoot motion occurs at the tarsometatarsal joint than at the transverse tarsal.

Determining the exact anatomical location of the midtarsal break has implications for understanding the biomechanics of terrestrial and arboreal locomotion both in extant primates, and also extinct apes and hominins. Although it has been suggested that australopiths had more midtarsal mobility than modern humans (Sarmiento, 1991; Gomberg and Latimer, 1984; Harcourt-Smith, 2002), this would not necessarily imply the presence of a midtarsal break if, in fact, the midtarsal break occurs at the tarsometatarsal joint and not the transverse tarsal joint. Yet, finding evidence for a midtarsal break in australopiths would have important ramifications for interpreting both their bipedal biomechanics and their climbing capacity.

Here, I attempt to determine precisely where the midtarsal break occurs in non-human primates. I test the hypothesis that the midtarsal break occurs exclusively at the calcaneocuboid joint on the lateral side of the foot in non-human primates with data obtained from radiographs, dissections, video of ape and cercopithecoid feet with a mark on the tuberosity of the 5th metatarsal, EMG data obtained from chimpanzee subjects, and skeletal specimens. Using skeletal correlates of this foot motion, I will also investigate whether extinct hominins were capable of midfoot flexion.

Materials and Methods

X-rays

Both lower limbs were obtained from ten sub-adult olive baboons (*Papio anubis*) which had completed a research protocol approved by the University of Michigan's Institutional Animal Care and Use Committee. These animals were between two-three years old, and thus still had unfused epiphyses on the distal fibula and tibia. The animals weighed an average of seven kg (range 6.0- 8.4 kg). A foot from an adult male gorilla who had died during a veterinary procedure was also x-rayed. The feet were positioned in lateral view and xrays were taken using a MinXray HF 100/30 at 50 kVDC for 0.3mAs. Radiographs were taken of the right foot of each individual in a neutral position with the most plantar aspect of the foot forming a ninety degree angle with the long axis of the tibia. Radiographs were then taken of the same feet with the heel elevated to approximately 20 degrees from the horizontal plane of the plantar aspect of the foot. This was achieved by manually exerting a tensile force on the proximal tibia (thus lifting the calcaneus) while simultaneously holding the metatarsophalangeal joint to prevent movement there. Two approaches were employed: one consisted of manually holding the metatarsophalangeal joint, and the other bound the toes to a wooden board using plastic tie wraps. The two methods produced similar results. Importantly, these methods did not appear to influence whether the calcaneocuboid or tarsometatarsal joint was more involved in flexing the midfoot. The gorilla foot could not be flexed to 20 degrees and instead was flexed to only about 5 degrees. This may have been due in part to the inability of this author to produce the 500 lbs. of pressure that would have been applied to the gorilla foot in life.

Dissections

Ten, right baboon feet and the right gorilla foot were dissected. The 5th metatarsal was felt through the skin on the lateral side of the foot and a small area of the skin removed to reveal the peroneal tendons. With the feet held to a horizontal surface, the tibia was slowly elevated and 2 digital photographs were taken in lateral view. The first photograph captured the maximum dorsiflexion at the calcaneocuboid joint and the second the maximum total flexion of the midtarsal region of the baboon foot. Angles relative to the horizontal plantar aspect of the foot were measured using the angle tool in the program Image J.

The tendons of peroneal brevis and longus were then cut and the calcaneocuboid articulation and the cuboid-metatarsal V articulations were isolated without removing any ligamentous tissue. Photographs were again taken, imported into Image J, and angles were measured at both the calcaneocuboid and the cuboid-metatarsal V joints. These did not differ from the angles taken with the peroneal tendons still attached (t-test paired two sample for means : t=0.34, p=0.74).

Video analysis

Articulated osteological specimens of chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), and a cercopithecoid (*Papio anubis*) were used to predict where the midtarsal break should be observed if it occurred at the calcaneocuboid joint and where it should be observed if it occurred at the more distal tarsometatarsal joint. The lateral aspect of the cuboid tapers to a very narrow area of bone in the non-human hominoids and cercopithecoids causing the calcaneocuboid and cuboid-metatarsal V joints to be quite close to one another in lateral view (Figure 7.4). This anatomy is partially why it has been challenging to determine precisely where the mid-tarsal break motion occurs in non-human primates. However, it can be predicted from these osteological specimens that foot flexion proximal to the tuberosity of the 5th metatarsal implies movement at the calcaneocuboid joint whereas flexion distally to the tuberosity implies the involvement of the tarsometatarsal joint.

Primates were videotaped with a Canon GL2 digital video recorder. The video captured frames every 70 msec. The film was imported into Windows Movie Maker and examined frame by frame to assess where the midtarsal break occurs relative to the position of the tuberosity of the 5th metatarsal.

Figure 7.4. Chimpanzee foot indicating close position between calcaneocuboid joint and cuboid-metatarsal joint on lateral side of foot.

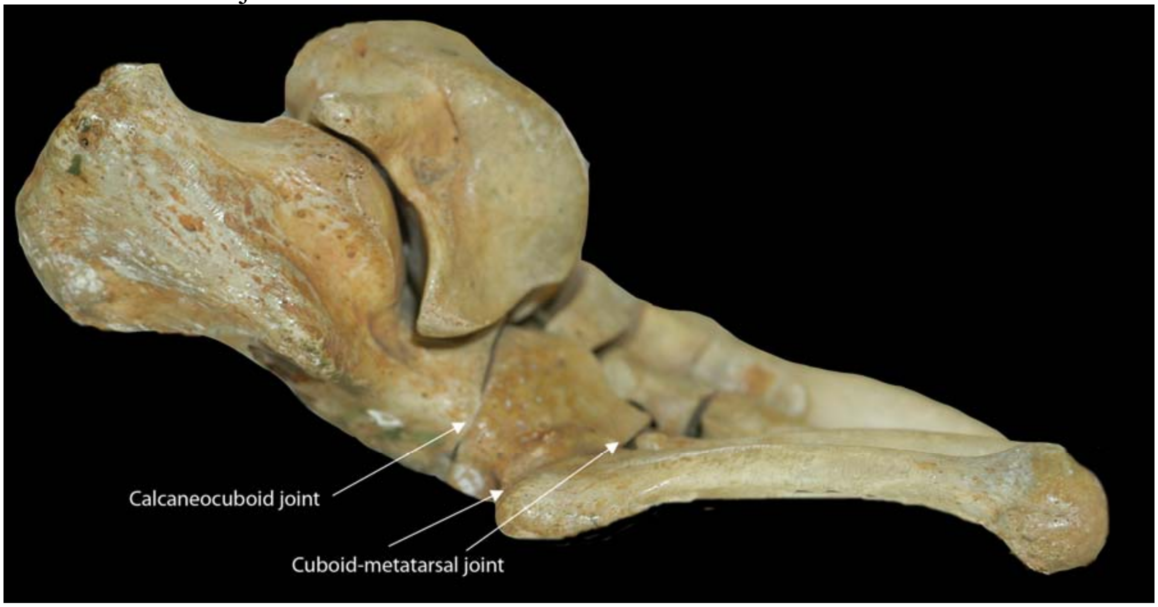


Figure 7.4. Chimpanzee foot in lateral view positioned to model the midtarsal break if it occurred at the cuboid-metatarsal joint. Notice that flexion at the calcaneocuboid joint would be proximal to the tuberosity of the 5th metatarsal whereas flexion at the cuboid-metatarsal joint would be distal to the tuberosity.

In one protocol, wild chimpanzees were filmed at the Ngogo study site in the Kibale National Forest, Uganda. Twenty-five sequences of walking were video recorded. These were mostly of adult male chimpanzees walking in lateral, posterolateral, and posterior view. Because the position of the tuberosity of the 5th metatarsal could only be estimated on the wild chimpanzees, only qualitative observations were made on these data.

In the second protocol, several captive primates were analyzed. The right feet of a male and female adult chimpanzee (*Pan troglodytes*), a male and female adult lowland gorilla (*Gorilla gorilla gorilla*), two adult female mandrills (*Mandrillus sphinx*), and three adult lion-tailed macaques (*Macaca silenus*) at the Detroit Zoo were measured while the animals were under anesthesia. The tuberosity of the 5th metatarsal was felt through the skin on the lateral side of the foot and the ratio of the total foot length that was composed of the calcaneus and cuboid was measured. Manipulation of the foot was attempted to ascertain whether flexion occurred in the region of the metatarsal V tuberosity or more proximally at the calcaneocuboid joint. Finally, a circular white mark was placed directly on the skin overlaying the tuberosity of the 5th metatarsal. After the animals awoke, video was captured in lateral view of the chimpanzees, gorillas, mandrills, and macaques engaging in quadrupedal locomotion.

Ligaments, musculoskeletal anatomy, and EMG

The effect of muscles and ligaments on the midtarsal break was assessed based on data from the literature and on the results of gross dissections of the ten baboon feet, the dissections of a male gorilla from the Cincinnati Zoo and a chimpanzee of unknown provenience at the Museum of Comparative Zoology at Harvard University, and five human cadavers from the Department of Anatomy at Wayne State University in Detroit, MI. These data were supplemented with Museum osteological specimens from the Harvard Museum of Comparative Zoology and the Cleveland Museum of Natural History in which the ligamentous tissue was still present and was still holding the foot bones in their anatomical positions.

Muscle activity patterns during quadrupedal walking in chimpanzees were obtained from raw EMG data provided by Dr. Jack Stern at the State University of New York, Stony Brook. The experimental protocol for obtaining EMG data on the lower limbs of captive chimpanzees can be found in Jungers et al. (1983) and Jungers et al. (1993). The video produces simultaneous footage of locomotion of the chimpanzee with raw EMG activity from four electrode channels superimposed on the screen. Video was viewed frame by frame to assess muscle activity prior to, during, and after heel lift in quadrupedally walking chimpanzees. Activity of the tibialis posterior muscle was analyzed from data collected on a young male chimpanzee on June 4, 1981. Gastrocnemius/soleus activity was assessed from two young male chimpanzees studied in July of 1997. Activity of the peroneus longus muscle was taken from published results from EMG studies of chimpanzees at SUNY Stony Brook (Stern and Susman, 1983; Reeser et al., 1983).

Skeletal and fossil specimens

The calcaneus, cuboid, and 4th and 5th metatarsals of *Pan troglodytes* (n=33) and *Gorilla gorilla* (n=29) were studied at the Cleveland Museum of Natural History. The Libben Paleoindian collection housed at Kent State University and the Todd-Hamman collection at the Cleveland Museum of Natural History served as the *Homo sapiens* comparative sample (n=31). Fossil cuboids and metatarsals of the hominoids *Proconsul nyanzae* (KNM-RU 5872) and *Nacholapithecus kerioi* (KNM-BG 35250) were studied at the Kenya National Museum, as was a *Homo erectus* 5th metatarsal (KNM-ER 803). Fossil casts of the 5th metatarsals of *Australopithecus afarensis* (A.L. 333-13, and A.L. 333-78) were made available for study by the Cleveland Museum of Natural History and the Harvard Peabody Museum. Original hominin 4th (StW 485) and 5th metatarsals (StW 114/115) from Sterkfontein were studied at the University of Witwatersrand in Johannesburg, South Africa. The calcaneus, cuboid, and 4th and 5th metatarsals of OH 8 individual were studied at the Tanzania National Museum and House of Culture, Dar es Salaam.

The length and width of the cuboid articular facets for the 4th and 5th metatarsals were measured with digital calipers to the nearest 0.1 mm. This was done for the cuboid articular facet on the proximal surface of the 4th and 5th metatarsals as well. Additionally, the shape of the joint surfaces was assessed using a carpenter's contour guide. The joint surfaces of the 4th and 5th metatarsals and cuboid were pressed into the carpenter's contour guide, and the guide was photographed with a Nikon D100 digital camera. The images were then imported into the program Image J and the shape of the articular surface quantified as a ratio of the height or depth of the articular surface relative to the overall dorsoplantar height of the joint facet. Fossils were not measured using the carpenter's contour guide. Instead, 3D models of the fossils were obtained by scanning the specimens with a NextEngine 3D laser scanner. The 3D fossil models were oriented using the program ScanStudio and then cropped so that the height or depth of the articular surface could be isolated in the same plane that the extant specimens were measured with the carpenter's contour guide. A still frame of the isolated articular surface was taken and imported into Image J where the height and depth of the articular surface was measured relative to the overall dorsoplantar height of the joint surface. Four human and chimpanzee 4th and 5th metatarsals were measured using both the carpenter's contour guide and the 3D scanner method and the results obtained were statistically identical (t-test paired sample for means test: t=0.38, p=0.71).

The dorsal surfaces of the cuboid and the 5th metatarsal were also examined closely to assess whether the articular surface between these two bones extended superiorly onto the dorsal surface of the bone. Categories established were “no”, “yes”, and “slightly” if it appeared that the articular surface bent onto the dorsal surface, but not in an obvious manner.

Significance was assessed using Fisher’s least squares difference (LSD) test for planned comparisons, after first performing a one-way analysis of variance (ANOVA) test.

Results

X-rays of baboons and gorilla

The ten X-rays of baboon feet flexed at the midfoot all consistently demonstrated that relative to the neutral position, the majority of movement during the “midtarsal break” occurred at the cuboid-metatarsal joint, though some motion did occur at the calcaneocuboid joint as well (Figure 7.5a). The calcaneus moved to a position slightly more superiorly relative to the cuboid when the midfoot was elevated; however, the majority of the midfoot motion occurred by the cuboid shifting to a significantly more superior position relative to the 5th metatarsal. This pattern occurred in all 10 X-rayed baboon feet.

The X-ray of the gorilla foot is more difficult to interpret. In lateral view, it is not clear whether the cuboid or the proximal metatarsals moved dorsally. In superior view, the cuboid overlays the metatarsals in neutral position but a small amount of flexion (about 5 degrees) at the midfoot caused the cuboid and the metatarsals to become more aligned (Figure 7.5b). It is unknown whether a greater applied force would have resulted

Figure 7.5a. Radiographs of baboon feet before and after midfoot flexion.

Figure 7.5b. Radiographs of gorilla feet before and after midfoot flexion.

Figure 7.5. a.) X-rays of baboon (*Papio anubus*) foot in lateral view in neutral position (top) and during midfoot flexion (bottom). The straight arrows indicate the calcaneocuboid joint while the diamond-shaped arrows indicate the cuboid-metatarsal joint. Note the movement of the cuboid onto the superior surface of the 5th metatarsal in the baboon during midfoot flexion. b.) X-rays of gorilla foot in superior view in neutral position (top) and during midfoot flexion (bottom).

Figure 7.6. Dissection of baboon foot indicating location of midtarsal break.

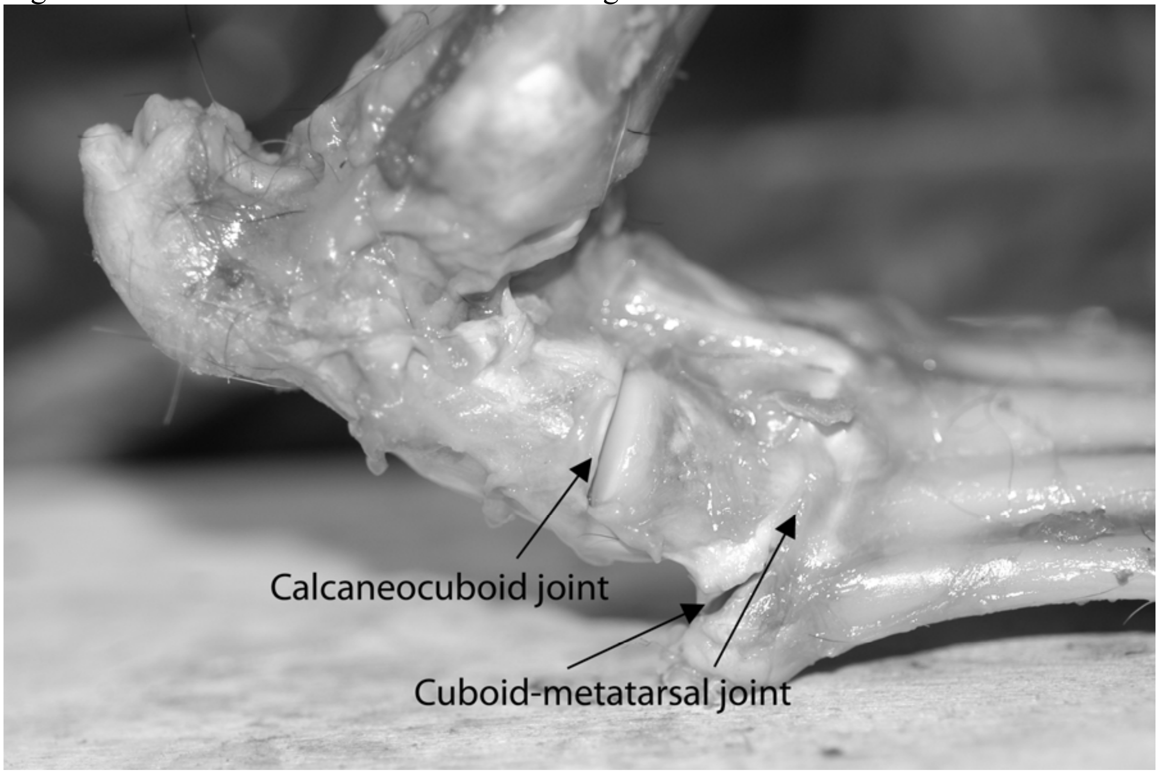


Figure 7.6. Dissected baboon (*Papio anubus*) foot in lateral view with the tibia being manually lifted. The tuberosity of the fifth metatarsal is in contact with the tabletop, with the majority of midfoot flexion happening at the cuboid-metatarsal joint, rather than the calcaneocuboid joint.

in more flexion and if this flexion would have occurred more proximally at the calcaneocuboid joint, or the cuboid-metatarsal joint.

Dissections of baboon feet

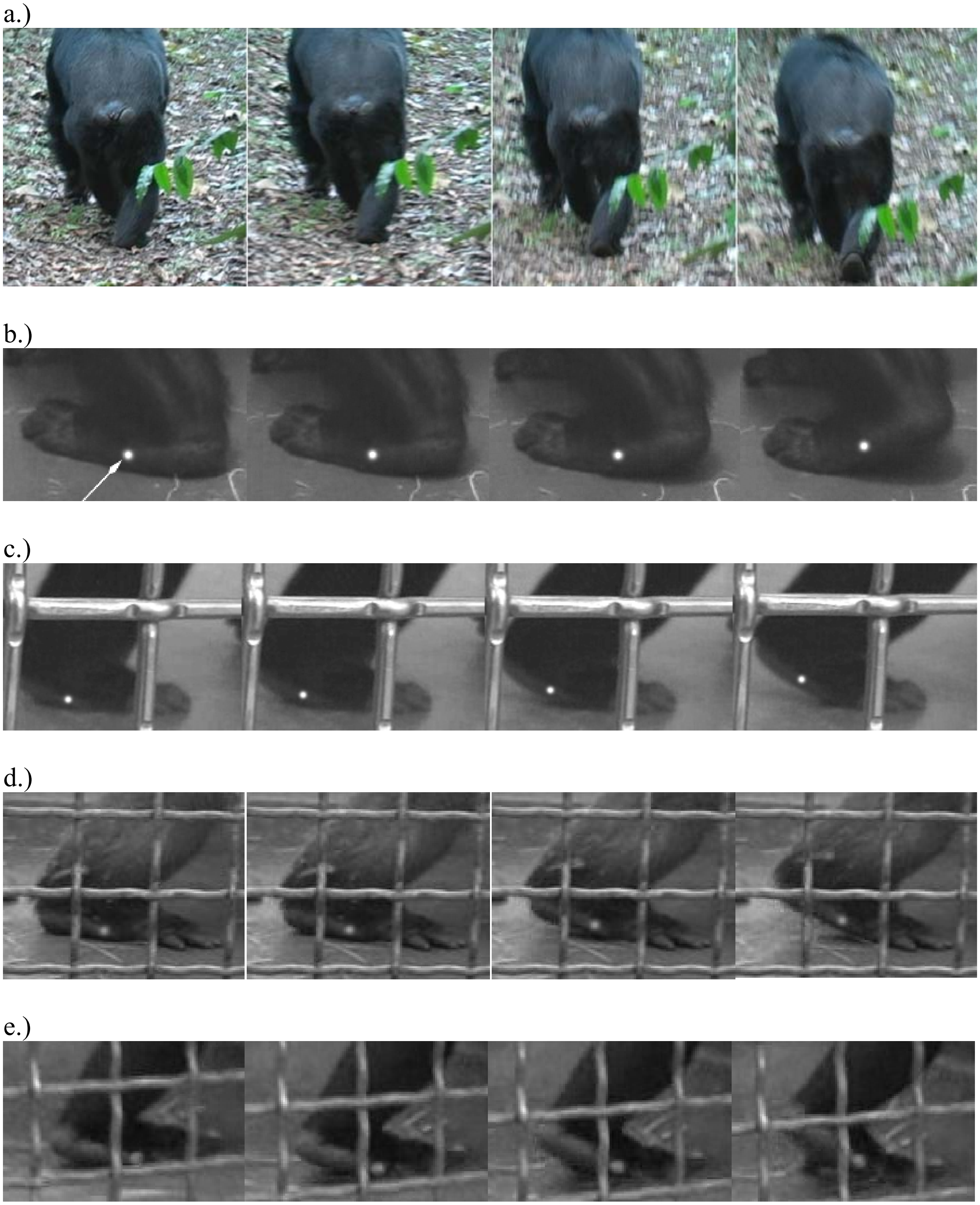
Dissections of right feet of the baboons also suggest that both joints may be involved in producing the cumulative midfoot flexion. When tension was applied to the proximal tibia and the calcaneus lifted off a horizontal surface, flexion occurred first at the calcaneocuboid joint with a magnitude of 9.2˚ ± 1.5˚. When tension continued to be applied to the tibia and the calcaneus further lifted from the horizontal surface, flexion shifted from the calcaneocuboid joint to the cuboid-metatarsal joint and become significantly more pronounced. Flexion at the cuboid-metatarsal joint amounted to 20.6° ± 2.3°, or 69.1% of the total flexion at the midfoot (Figure 7.6).

The baboon feet used in this study were on average 162.1 ± 13.3 mm from the heel to the tip of the longest toe. The average distance to the calcaneocuboid joint was 45.6 ± 3.3 mm, or 28.2% ± 1.5% of the total foot length. The average distance to the cuboid-metatarsal joint was 56.6 ± 3.8 mm, or 35.0% ± 1.9% of the total foot length. There was no overlap between the percentage of foot length to the calcaneocuboid and cuboid-metatarsal joints among the different baboons. Thus, the shortest percent of total foot length to the cuboid-metatarsal joint in any of the baboons was still longer than the longest percent of total foot length to the calcaneocuboid joint. Unfortunately, few data on terrestrial walking in baboons exist to compare these results. Using six stills taken of two different baboons by Muybridge (1957), the midtarsal break occurs between roughly 32-42% of the total foot length, although initial foot flexion can be detected in a region about 25% of the total foot length. This result is consistent with initial slight movement occurring at the calcaneocuboid joint, and subsequently shifting to the more distally located tarsometatarsal joint. Some care should be taken, however, in interpreting these results as the dissected baboons were sub-adult *Papio anubis* while the baboons photographed by Muybridge (1957) were adult chacma baboons (*Papio ursinus*).

Study of live chimpanzee and gorilla feet

Unobscured video of terrestrially knuckle-walking wild chimpanzees was difficult to obtain. The Kibale forest is dense with underbrush and it was not possible to obtain a clear sequence of terrestrial walking in lateral view. However, video analysis of

Figure 7.7. Location of midtarsal break in terrestrially walking cercopithecoids, apes and human



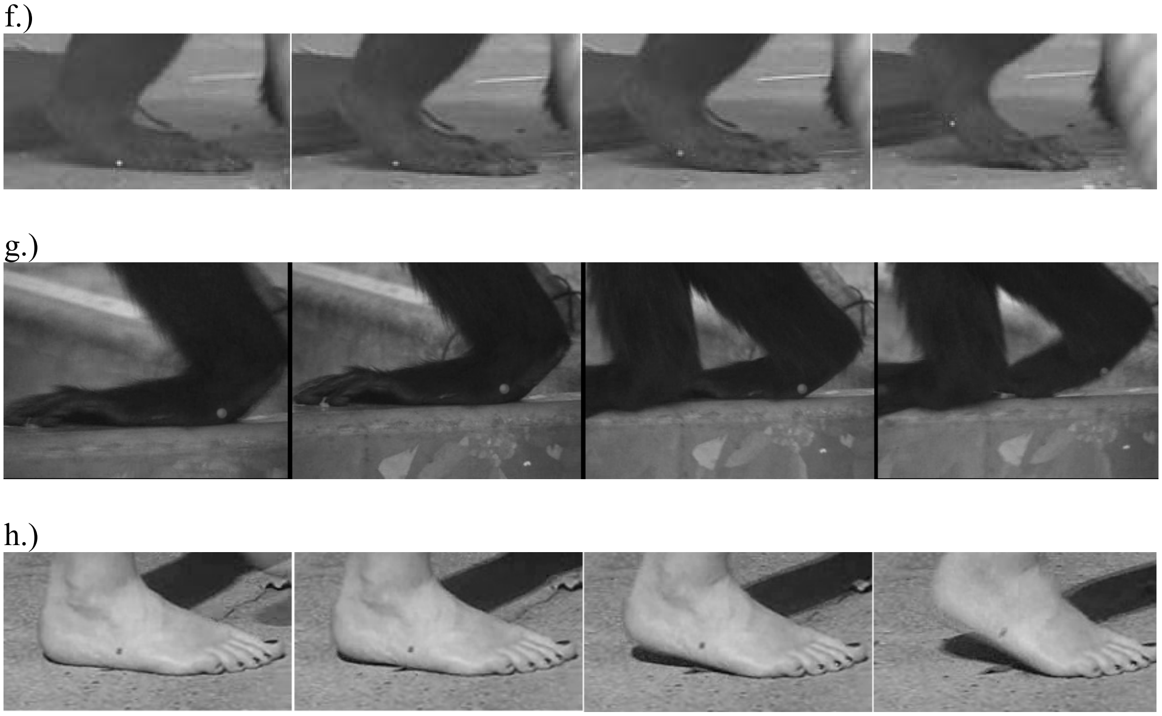


Figure 7.7. Stills of video taken of terrestrial walking in wild and captive primates. For all of the images, the first frame is stance phase, the second is initial heel lift, the third is continued heel lift, and the final frame is push-off. The frames are in sequence with 70 msec between each. a.) Adult male chimpanzee walking in Ngogo study area of Kibale National Park. b.-e.) Adult male chimpanzee, adult female chimpanzee, and adult male and female gorillas at Detroit Zoo with 5th metatarsal tuberosity marked. f.) Adult female *Mandrillus* and g.) Adult female *Macaca silenus* both from the Detroit Zoo and the 5th metatarsal tuberosity marked. h.) Adult female human with tuberosity of 5th metatarsal marked. Frames 1, 2, and 4 do not differ between the apes and the human. However, in frame 3 midfoot flexion is clear in the apes but not the human. Notice that the midfoot flexion generally occurs on or distally to the white spot indicating the position of the tuberosity of the 5th metatarsal in the chimpanzees and gorilla. This suggests motion at the cuboid-metatarsal joint. Likewise in the cercopithecoids, digitigrades postures and midfoot flexion during push-off phase of walking appear to be a function of both calcaneocuboid and cuboid-metatarsal flexion.

chimpanzees in posterolateral and posterior view did reveal that wild chimpanzees have a midtarsal break while walking. It is also apparent from the video data that during initial heel lift, there is a proximally placed midtarsal break of minimal magnitude. This midfoot flexion then shifts slightly distally and is more pronounced as the chimpanzee enters the later stages of stance phase (Figure 7.7a). This observation appears to be consistent with the hypothesis that the midtarsal break begins with slight dorsiflexion at the transverse tarsal joint, but then shifts distally to the tarsometatarsal joint where more flexion is possible.

The tuberosity of the 5th metatarsal could be easily palpated through the skin on the lateral aspect of both feet of the male and female chimpanzees and gorillas, the two female mandrills and three female macaques from the Detroit Zoo. The approximate length of the foot from heel to the tip of the 5th digit was 20 cm for the female chimpanzee and 21 cm for the male chimpanzee (Table 7.1). This same measurement was 22 cm for the female gorilla and 29 cm for the male gorilla. The lateral aspect of the female mandrill feet were both 16 cm, and the three female macaque feet were 14 cm, 13 cm, and 13 cm respectively. The tuberosity of the 5th metatarsal was located 7 cm from the heel in the female chimpanzee; 7.5 cm from the heel in the male chimpanzee; 9 cm from the heel in the female gorilla and 12 cm from the heel in the male gorilla; 5 cm in one mandrill and 5.5 cm in the other; 5 cm in the larger macaque and 4 cm in the two smaller macaques. Thus, of the total length of the foot, the tuberosity of the fifth metatarsal is located 35.7% and 35% in male and female chimpanzees respectively, in male and female gorillas 41.4% and 40.9% respectively, 31.3% and 34.4% in the two female mandrills, and 35.7%, 30.8% and 30.8% in the three macaques. Manually, the foot of both chimpanzees and gorillas could be moderately flexed in a region only a few millimeters distal to the location of the tuberosity of the 5th metatarsal whereas the region proximal to the tuberosity was more rigid. The mandrill and macaque feet were more mobile than the ape feet at both the calcaneocuboid and cuboid-metatarsal joints.

Table 7.1. Proportions of lateral column of the primate foot.

Species	Sex	Length of lateral side of foot (cm)	Distance from heel to 5th MT tuberosity (mm)	% of foot length to 5th MT tuberosity
Pan troglodytes	Male	21	7.5	35.7%
Pan troglodytes	Female	20	7	35.0%
Gorilla gorilla gorilla	Male	29	12	41.4%
Gorilla gorilla gorilla	Female	22	9	40.9%
Mandrillus sphinx	Female (n=2)	16	5.3	32.9% ± 2.2%
Macaca silenus	Female (n=3)	13.3	4.3	32.4% ± 2.8%
Papio anubis (dissections)	Mixed (n=10)	16.2 ± 1.3	5.7 ± 0.3	35.0% ± 1.9%

Four sequences of quadrupedal walking in chimpanzees (two from the male, two from the female), two sequences of walking in both male and female gorillas, two sequences of walking in the female mandrills, and two sequences in the macaques were captured in which the white spot indicating the position of the tuberosity of the 5th metatarsal was visible, the foot was in lateral orientation, and the primates had undergone a fully weight-bearing stance phase complete with a midtarsal break. Instead of moving directly from a heel-flat, plantigrade position to flexion at the midfoot, the chimpanzee foot appeared to "roll" during heel lift through push-off phase of walking with an initial slight flexion occurring proximally to the tuberosity of the 5th metatarsal (calcaneocuboid joint) and then smoothly transitioning to a more pronounced flexion in a position more distal to the tuberosity mark (tarsometarsal joint). The transition from this joint to the metatarsalphalangeal joint was also done in a fluid manner (Figure 7.7b-c). The gorilla feet (7d-e) appeared to undergo the same series of midfoot motions as the chimpanzee foot during quadrupedal walking. As with the baboon, it is clear from the chimpanzee and gorilla walking sequences that the midtarsal break is initiated with slight (~10˚) flexion first at the calcaneocuboid joint and then augmented with a higher magnitude of flexion (~20˚) at the tarsometatarsal joint. The mandrill and macaque heel begins in a more elevated position than what is observed in African apes and this appears to occur primarily at the calcaneocuboid joint (Figure 7.7f-g). However, as seen in the ape feet, the midtarsal break shifts to the more distal cuboid-metatarsal joint as motion continues. Motion observed in gorilla, chimpanzee, mandrill and macaque feet contrasts with that shown by the human foot (Figure 7.7h), which establishes a fulcrum at the metatarsophalangeal joint just after heel lift, by-passing the midfoot flexion seen in the ape feet.

Ligaments

Ligaments crossing either the calcaneocuboid joint or the tarsometatarsal joint on the plantar aspect of the foot would limit flexion at either joint. Therefore, the presence or absence of particular ligaments in this region of the foot may provide additional evidence for the location of the majority of flexion during the midtarsal break. Soft tissue that crosses the calcaneocuboid joint in humans includes the plantar aponeurosis, long plantar ligament, and short plantar ligament. Of these, only the short plantar ligament is present in non-human primates; however, this ligament is particularly strong in chimpanzees, gorillas, and orangutans (Gomberg, 1985) and was also strong in the dissected baboon and gorilla feet from this study. Lewis (1980) described this ligament as "massive" in chimpanzees. Given the size, strength, and location of this ligament, it is difficult to conceive that this ligament would permit 30˚ of flexion between the calcaneus and the cuboid. In fact, Grand (1967) suggested that the presence of this ligament in the foot of the slow loris would inhibit flexion of the midfoot at the calcaneocuboid joint. Furthermore, manual manipulation of the dissected baboon, chimpanzee, and gorilla feet suggests that the short plantar ligament restricts hyperflexion of the calcaneocuboid joint. The long plantar ligament in humans continues distally and attaches to the base of the metatarsals, preventing flexion at the tarsometatarsal joint. The long plantar ligament does not extend this far distally in non-human primates (Gomberg, 1985; pers. obs.), and would not restrict movement at the cuboid-metatarsal joint. The tarsometatarsal joint is reinforced on the plantar aspect of the foot only with the small and more pliable tarsometatarsal ligaments. Manual manipulation of dissected non-human primate feet suggests that this ligament is not a strong deterrent to hyperflexion of the midfoot at the tarsometatarsal joint.

Musculoskeletal anatomy and EMG results

Muscles crossing either the calcaneocuboid or cuboid-metatarsal joints can assist or restrict movement at these joints as well. Because the midtarsal break is observed during heel lift, it is probable that the gastrocnemius/soleus complex is active. However, additional lower limb muscle activity can influence the timing and location of midfoot flexion if the tendon of the muscle in question is in the extensor compartment and thus enhances midfoot flexion upon activation, or in the flexor compartment and thus inhibits midfoot flexion. An ideal muscle to study would cross the calcaneocuboid joint but not the cuboid-metatarsal joint.

Data from the literature (Swindler and Wood, 1982; Aiello and Dean, 1990) and dissection of the muscles and tendons of the lower limb of baboons, humans, a chimpanzee, and a gorilla demonstrate that most lower limb muscles cross both the calcaneocuboid and cuboid-metatarsal joints and/or the regions of the foot that contain these joints. These include the following extensor compartment muscles: anterior tibialis, extensor digitorum longus, extensor digitorum brevis, peroneus tertius, peroneus brevis and the following flexor compartment muscles: flexor digitorum longus, flexor digitorum brevis, abductor digiti minimi, and quadratus plantae. The peroneus tertius and peroneus brevis muscles attach to the base of the 5th metatarsal and thus would enhance cuboid-metatarsal motion, but because the tendons also cross the calcaneocuboid joint, activity of these muscles would promote flexion at this joint as well.

Only the peroneus longus and the posterior tibialis cross the calcaneocuboid joint but not the cuboid-metatarsal joint in any substantial manner. The peroneus longus muscle originates on the proximal portion of the lateral fibula, its tendon curls around the peroneal groove of the fibula, and inserts on the plantar aspect of the medial cuneiform and first metatarsal via a groove in the plantar cuboid. It is a major everter of the foot (Aiello and Dean, 1990) and contributes to adduction of the hallux during the push-off phase of walking (Reeser et al., 1983; Susman and Stern, 1984). Because the peroneus longus inserts plantarly, simultaneous contraction of the gastrocnemius/soleus complex and the peroneus longus would inhibit flexion at the calcaneocuboid joint. Likewise, the tendons of the posterior tibialis are located on the plantar aspect of the foot and thus activity of this muscle with the gastrocnemius/soleus would inhibit flexion of the calcaneocuboid joint. The posterior tibialis originates on the proximal aspect of the posterior tibia, interosseous membrane, and fibula. The tendon enters the foot via the malleolar groove of the tibia and inserts primarily on the navicular tuberosity, all three cuneiforms and the cuboid. Fibers can extend distally to the bases of the lateral four metatarsals, though this comprises a relatively small component of the insertion area for the posterior tibialis.

In humans, all three muscles are active during the late stance phase into the early heel off phase of walking (Reeser, et al., 1983) though with more resolution it appears that the peroneus longus is active only moments prior to the tibialis posterior and gastrocnemius/soleus (Suzuki, et al., 1985) during the late stance phase. In chimpanzees, the peroneus longus muscle is not active at all during terrestrial locomotion (Stern and Susman, 1983). Although no EMG data is available on the tibialis posterior and gastrocnemius/soleus in the same animal, analysis of EMG on two different chimpanzees reveals that the triceps surae is active during stance phase and into the initial phase of heel off (Figure 7.8). The posterior tibialis is also active during late stance phase into heel off thus providing evidence that the two muscles are simultaneously active during quadrupedal walking in chimpanzees (Figure 7.8). Importantly, this simultaneous muscle activity occurs precisely when the midtarsal break is observed in lateral view. Given that simultaneous activity of these muscles would restrict flexion of the midfoot at the calcaneocuboid joint, but not the tarsometatarsal joint, this EMG data provides additional evidence that the midtarsal break occurs primarily at the tarsometatarsal joint.

Skeletal specimens

Estimation of joint mobility from osteological specimens suggested that the tarsal region of non-human primates facilitated more flexion and extension than the same

Figure 7.8. EMG of chimpanzees indicating activity of triceps surae and posterior tibialis during push-off phase of quadrupedal walking.

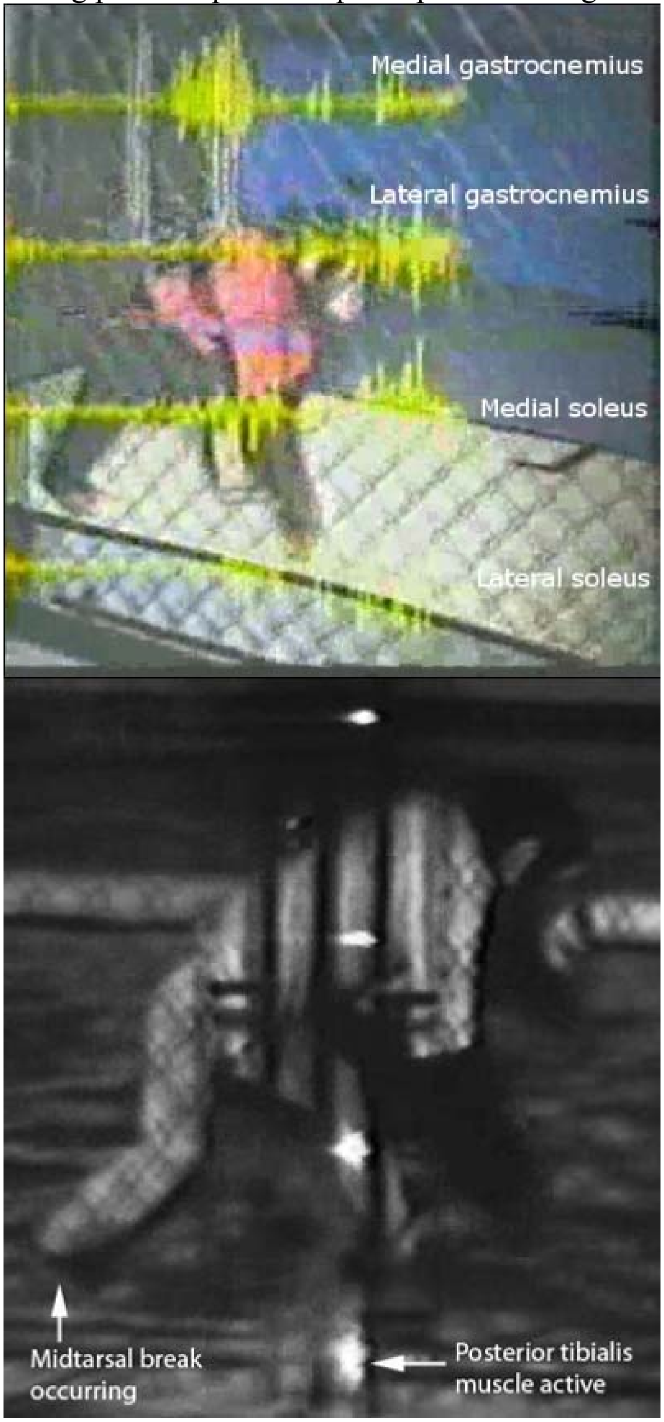


Figure 7.8. Stills from EMG video of chimpanzees terrestrially walking at SUNY Stony Brook. Frames were selected because midfoot flexion is occurring for the right foot in both chimpanzees. The chimpanzee at the top has activity in all 4 EMG electrodes, indicating that the triceps surae is active during push-off. The chimpanzee at the bottom has activity in the bottom two electrodes, indicating maximum activity of the posterior tibialis muscle.

region in human bones, and more flexion was possible between the cuboid and metatarsals than between the cuboid and the calcaneus for all primate feet studied. A skeletal correlate of the movement between the cuboid and metatarsals is the extension of the articular surface onto the dorsal surface of the 5th metatarsal and the cuboid. These were found in many non-human primate specimens. This articular extension can be described as a lip of bone that curls from the most superior aspect of the joint onto either the cuboid or the fifth metatarsal. Often, it is simply an extension of an already convex joint surface. The joint extension does not extend very far proximally (on the 5th metatarsal) or distally (on the cuboid), but the presence of this articular extension permits a considerable amount of flexion between these bones during manipulation of prepared specimens. It is important, however, to note that there is variation in the presence and degree of development of the articular extension, and this feature can occur in human specimens. For the cuboid, this extension was present in 94% of chimpanzees (n=33), 72% of gorillas (n=29), and 45% of humans (n=31). On the 5th metatarsal, a dorsally located articular extension was present on 73% of chimpanzee bones, 79% of gorillas, and 26% of humans.

Gorillas and chimpanzees are statistically identical for the shape of the articular surface of the 4th metatarsal ($p=0.42$). This articular facet is strongly convex in chimpanzees and gorillas, extending 16.2% ± 4.4% and 17.2% ± 4.9% of the total height of the facet respectively (Figure 7.9). This measure is only 5.2% ± 5.3% in modern humans, which is significantly flatter than the 4th metatarsal facet in African apes ($p<0.001$).

Figure 7.9. Shape of the cuboid facet on the proximal 4th metatarsal

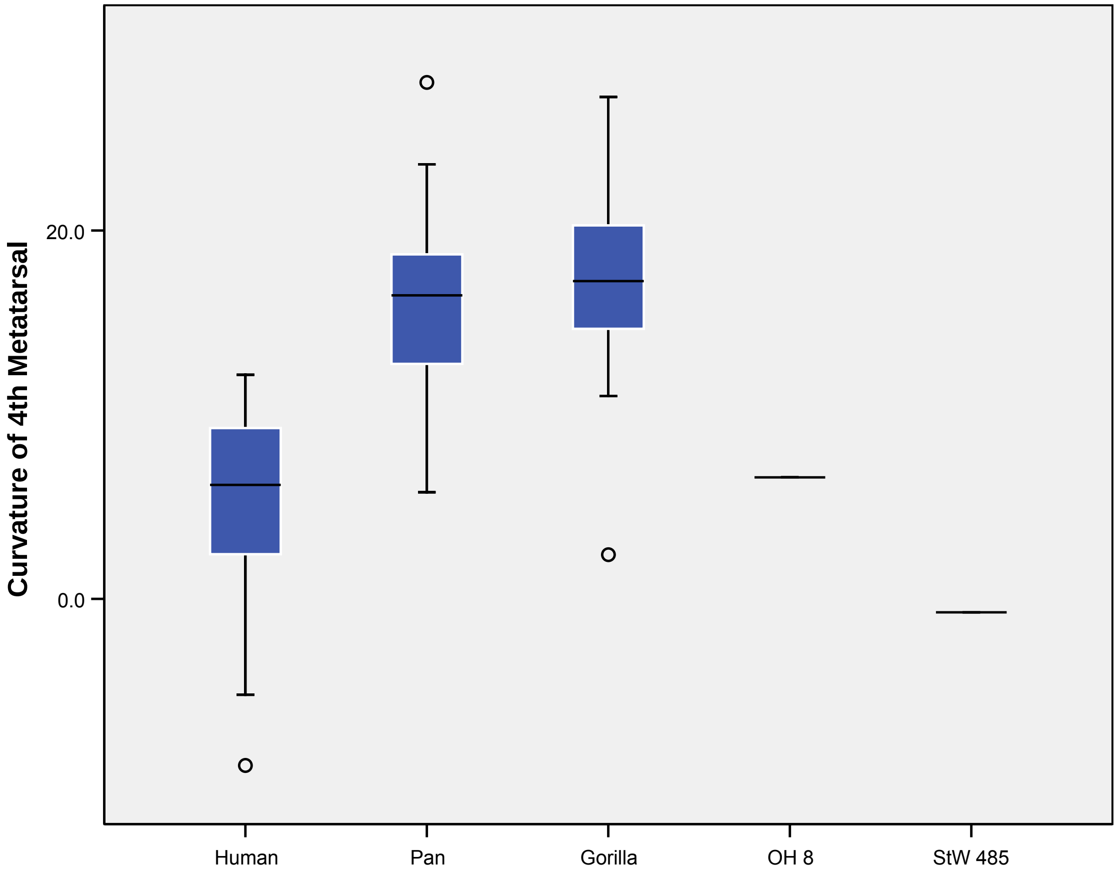


Figure 7.9. The y-axis is the ratio of the height or depth of the proximal metatarsal facet relative to its dorsoplantar width. A positive value is convex, a negative is concave. Boxplots show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Humans tend to have flatter cuboid facets on the 4th metatarsal, whereas chimpanzees and gorillas have more convex facets. The OH 8 and StW 485 4th metatarsals have flat human-like proximal facets.

Likewise, chimpanzees and gorillas have 5th metatarsal facets that are statistically indistinguishable in convexity 10.6% ± 5.4% and 8.4% ± 5.5% of the width of the facet respectively (p=0.11). In humans, the 5th metatarsal base is significantly flatter (p=0.001) measuring 3.9% ± 4.6% of the total height of the facet (Figure 7.10).

Figure 7.10. Shape of the cuboid facet on the proximal 5th metatarsal

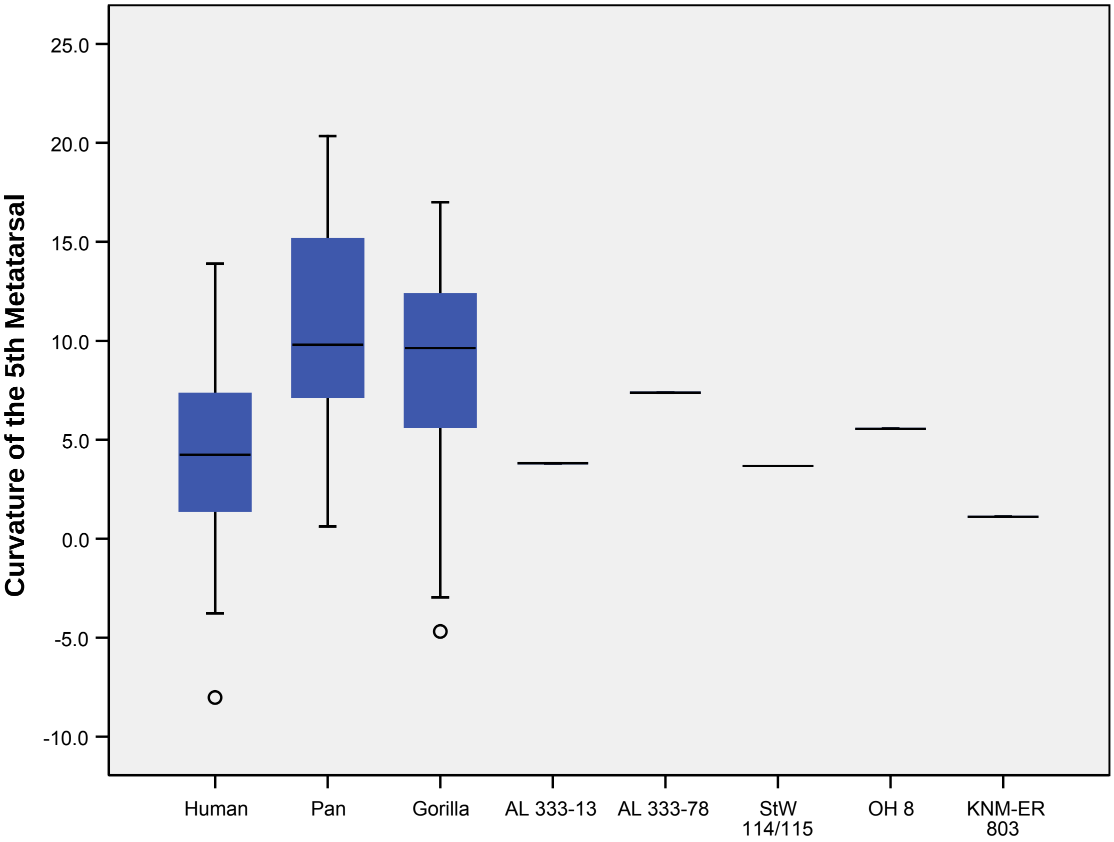


Figure 7.10. The y-axis is the ratio of the height or depth of the proximal metatarsal facet relative to its dorsoplantar width. A positive value is convex, a negative is concave. Boxplots show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Although there is some overlap, humans tend to have flatter cuboid facets on the 5th metatarsal, whereas chimpanzees and gorillas have more convex facets. The KNM-ER 803, OH 8, StW 114/115, and A.L. 333-13 5th metatarsals have flat human-like proximal facets, whereas the A.L. 333-78 *A. afarensis* metatarsal falls between the human and ape distributions.

The 4th metatarsal facet of the cuboid is slightly flatter in chimpanzees, 11.0% ± 4.5% than in gorillas, 14.0% ± 3.2% (p=0.02) (Figure 7.11). Humans have articular surfaces that are 4.5% ± 5.4%, statistically flatter than African ape cuboid 4th metatarsal facets (p< 0.01).

Figure 7.11. Shape of the 4th metatarsal facet on the cuboid.

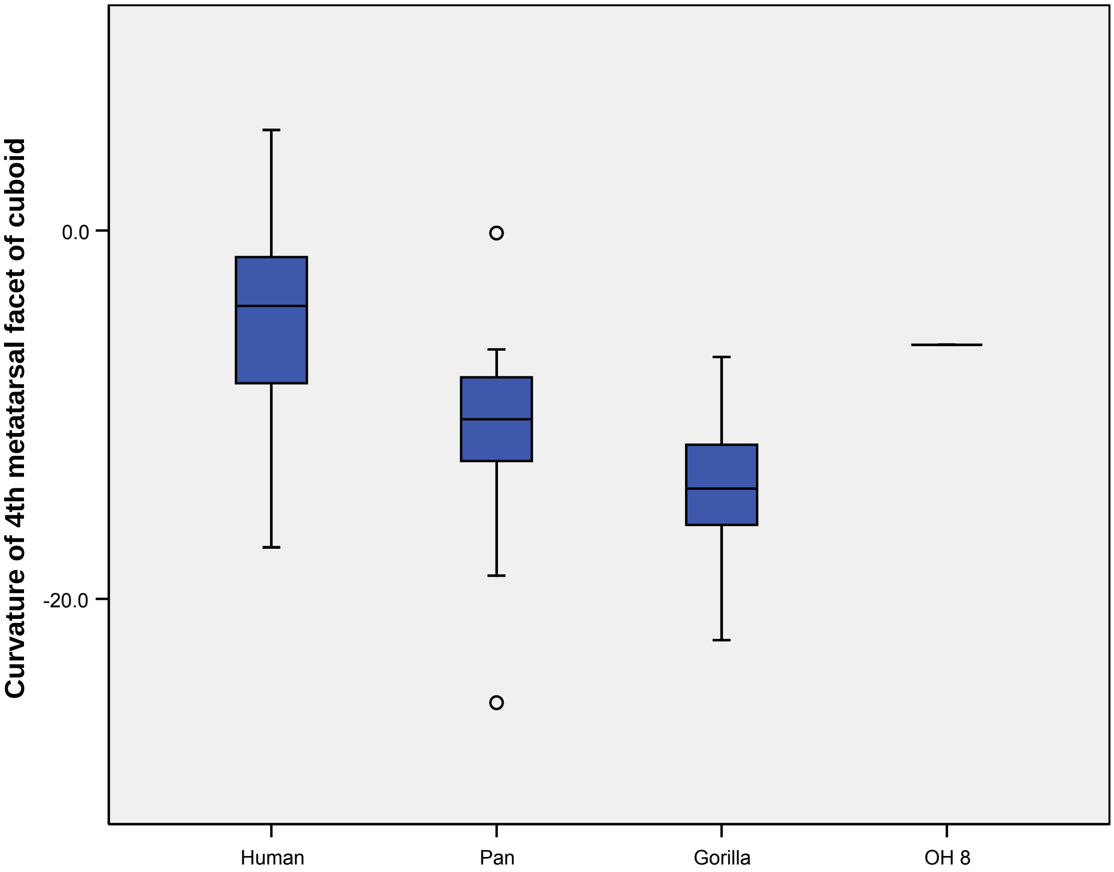


Figure 7.11. The y-axis is the ratio of the height or depth of the cuboid facet relative to its dorsoplantar width. A positive value is convex, a negative is concave. Boxplots show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Although there is some overlap, humans tend to have flatter 4th metatarsal facets on the cuboid, whereas chimpanzees and gorillas have more concave facets. The OH 8 cuboid has a flat human-like facet for the 4th metatarsal.

The 5th metatarsal facet of the cuboid is slightly flatter in chimpanzees than in gorillas, (p=0.02); however, each of the African apes is statistically identical to humans for this measure (*Gorilla*, p=0.55; *Pan*, p=0.06) (Figure 7.12).

Figure 7.12. Shape of the 5th metatarsal facet on the cuboid.

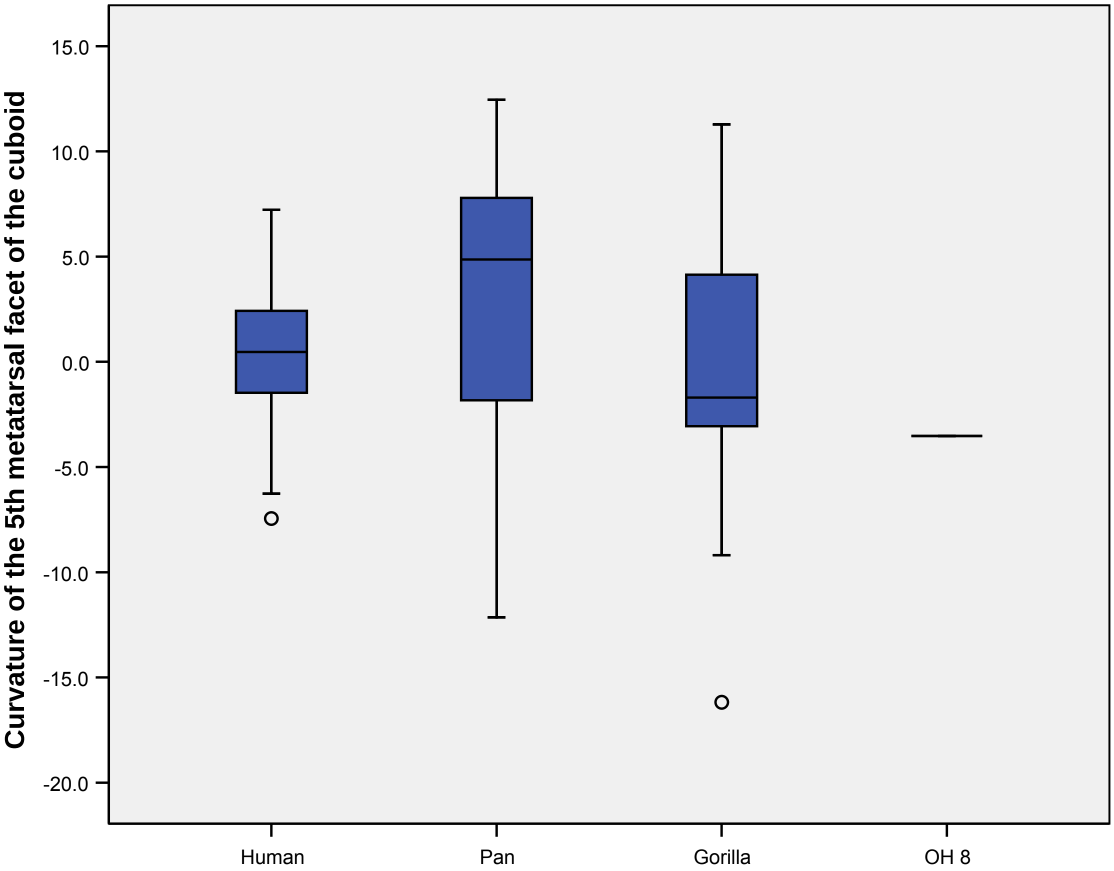


Figure 7.12. The y-axis is the ratio of the height or depth of the cuboid facet relative to its dorsoplantar width. A positive value is convex, a negative is concave. Boxplots show the median (black bar), interquartile ranges (blue/gray), and overall ranges of the data. Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Human and African ape cuboids cannot be differentiated based on the shape of the facet for the 5th metatarsal.

Fossils

The cuboid and lateral metatarsals of *Proconsul nyanzae* (KNM-RU 5872) (Figure 7.13) and the lateral metatarsals of the *Nacholapithecus kerioi* (KNM-BG 35250) (Figure 7.14) hominoid skeletons preserved evidence of a midtarsal break.

The cuboid of *P. nyanzae* is 24.9 mm proximodistally and 18.1 mm mediolaterally. The facet for the 5th metatarsal is slightly concave and 8.2 mm dorsoplantarly whereas and 4th metatarsal facet is strongly concave. This facet extends

Figure 7.13. Lateral aspect of *Proconsul nyanzae* (KNM-RU 5872) midfoot.

Figure 7.13. Articulated cuboid, and 5th and 4th metatarsals from the *Proconsul nyanzae* foot KNM-RU 5872 in dorsal view. Notice the extension of the articular surface onto the dorsal surface of both metatarsals and the cuboid indicative of midfoot flexion in this Miocene ape.

superiorly onto the dorsal surface of the cuboid. The 5th metatarsal, which preserves 66.6 mm of its entire length, also has an expansion of the cuboid articular facet onto the dorsal surface. The cuboid facet is 7.9 mm and convex in the dorsoplantar direction and 6.6 mm and flat mediolaterally. The fourth metatarsal of *P. nyanzae* preserves 65.1 mm of its

Figure 7.14. Lateral metatarsals of *Nacholapithecus kerioi* (KNM-BG 35250).

Figure 7.14. Articulated 5th and 4th metatarsals from the *Nacholapithecus kerioi* skeleton KNM-BG 35250 in dorsal view. Notice the extension of the articular surface for the cuboid onto the dorsal surface of the 5th metatarsal and the markedly convex shape of the cuboid facet of the 4th metatarsal.

length. The cuboid facet is strongly convex and is 12.8 mm dorsoplantarly and 7.8 mm mediolaterally.

The 5th metatarsal of *Nacholapithecus* preserves 61.3 mm of its total length. The cuboid facet is 7.8 mm dorsoplantarly and is convex (21.1% of total height), extending onto the superior surface of the bone. The fourth metatarsal is very convex in a dorsoplantar direction (21.7% of total height), though this bone has been distorted during fossilization and is artificially compressed mediolaterally.

The hominin cuboid-metatarsal region is poorly represented in the fossil record (Table 7.2). Only the OH 8 cuboid, and an undescribed potential *P. robustus* cuboid from Kromdraai (Thackeray et al., 2001) are known from the Plio-Pleistocene. Only nine

Table 7.2. Fossil hominin cuboids, 4th metatarsals and 5th metatarsals.

Element	Accession number	Geological age	Taxon	Studied for this paper
Cuboid	OH 8	1.8 mya	*Homo habilis?* *Paranthropus boisei?*	Yes
	KB 3133	1.7-2.0	*Paranthropus robustus?*	No (in Thackeray, 2003)
Fourth Metatarsal	A.L. 333-160	3.2 mya	*Australopithecus afarensis*	No (unpublished)
	StW 485	2.6-2.8 mya	*Australopithecus africanus?*	Yes
	StW 596	2.6-2.8 mya	*Australopithecus africanus?*	No (in Deloison, 2003)
	OH 8	1.8 mya	*Homo habilis?* *Paranthropus boisei?*	Yes
	D4165	1.77 mya	*Homo* sp.	No (in Lordkipanidze et al., 2007)
	D2669	1.77 mya	*Homo* sp.	No (in Lordkipanidze et al., 2007)
Fifth metatarsal	A.L. 333-13	3.2 mya	*Australopithecus afarensis*	Yes (cast)
	A.L. 333-78	3.2 mya	*Australopithecus afarensis*	Yes (cast)
	StW 114/115	2.4-2.8 mya? 1.5-2.0 mya?	*A. africanus?* *Homo* sp.*?* *Paranthropus* sp.*?*	Yes
	OH 8	1.8 mya	*Homo habilis?* *Paranthropus boisei?*	Yes
	D4508	1.77 mya	*Homo* sp.	No (in Lordkipanidze et al., 2007)
	KNM-ER 803f	1.53 mya	*Homo erectus*	Yes

lateral metatarsals were known until the recently described postcranial remains from Dmanisi increased that number to twelve (Lordkipanidze et al., 2007).

A.L 333-78 and A.L. 333-13 are left fifth metatarsals from *Australopithecus afarensis* dated to approximately 3.2 million years old (Walter, 1994). These bones have been previously described by Latimer et al. (1982). The cuboid facet of A.L. 333-78 is 10.8 mm and slightly convex in the dorsoplantar direction, and 10.2 mm and flat mediolaterally. This facet in A.L. 333-13 is a slightly larger 12.0 mm and flat in the dorsoplantar direction, and 10.7 mm and slightly concave mediolaterally. The articular surface for the cuboid angles proximomedially to distolaterally and is continuous with the articulation for the 4th metatarsal in both fossils. There is no evidence for extension of the cuboid articular surface onto the dorsal aspect of either bone, like the condition found in most human fifth metatarsals (74%) and fewer ape 5th metatarsals (24%). The slightly convex shape to the cuboid facet measured to be 7.4% the height of the facet dorsoplantarly falls in between the ranges observed for humans and African apes (Figure 7.10). A.L. 333-13 is almost identical to the modern human mean for this measure, having a dorsoplantar convexity 3.8% of the height of the cuboid facet (Figure 7.10).

Sterkfontein, South Africa has yielded two 4th metatarsals (StW 485 and StW 596) from Member 4. Only StW 485 was measured for this study, though Deloison (2003) has described these two bones as having very similar morphology. These *Australopithecus africanus* specimens are dated to approximately 2.6-2.8 mya (Kuman and Clarke, 2000) though Berger et al. (2002) have suggested a later date of 1.5-2.5 mya for the Member 4 hominins. Additionally, a single 5th metatarsal (StW 114/115) has been recovered from the southerly located W/45 grid of Member 4, which may have been deposited more recently than the more northerly Member 4 sediments, but still is regarded by most as *A. africanus* (Kuman and Clarke, 2000).

Figure 7.15. Lateral view of South African hominin 4th metatarsal (StW 485) compared to chimpanzee (left) and human (right).

Figure 7.15. The shape of the cuboid articular surface of the 4th metatarsal is convex in African apes (chimpanzee on left) and flat in modern humans (right). Note also that the curvature of the chimpanzee 4th metatarsal base extends dorsally (to the left in the image) indicating that the convex surface enhances dorsiflexion at the cuboid-4th metatarsal joint. South African hominin StW 485 has a human-like flat articular surface, suggestive of a stable midfoot. These metatarsals are all in lateral view.

StW 485 is a right fourth metatarsal, broken 26.8 mm from the base (Figure 7.15). The articulation with the cuboid is slightly concave mediolaterally and dorsoplantarly it is very slightly concave with a depth 0.7% of the total dorsoplanar height of the facet. The flat dorsoplantar cuboid facet on the proximal end of this bone is quite unlike the convex surface of the cuboid facet in apes (Figure 7.9). The dimensions of this articulation are 14.3 mm (PD) and 9.3 mm (ML). There is no evidence that the articular surface for the cuboid extends superiorly whatsoever. Deloison (2003) describes the cuboid facet of StW 596 as “sinueuse”, with a convex central part and a concave plantar aspect. Images of this fossil from Deloison (2003) are clear that while there is undulation to the cuboid facet, overall it is flat like modern humans, and dissimilar to the convex condition of apes and monkeys.

StW114/115 is the earliest complete hominin 5th metatarsal. It is 60.7 mm from the tip of the lateral tuberosity to the most distal point on the metatarsal head. The articular surface for the cuboid angles only slightly proximomedially to distolaterally and is continuous with the articulation for the 4th metatarsal. The cuboid articulation is mediolaterally convex and dorsoplantarly only slightly convex, 3.7% of the dorsoplantar height of the facet. This is almost identical to the human mean for this measure (3.9% ± 4.6%) (Figure 7.10). This articulation measures 12.9 mm mediolaterally, 10.6 mm dorsoplantarly on the lateral aspect of the cuboid articulation, and 8.1 mm dorsoplantarly on the medial aspect. The superior aspect of the base of the metatarsal is roughened and has no evidence for a superior expansion of the tarsometatarsal joint surface.

KNM-ER 803 is a partial skeleton of the genus *Homo* (Day and Leakey, 1974) from the 1.53 mya Okote Member on the east side of Lake Turkana (Feibel et al., 1989). The left 5th metatarsal (KNM-ER 803f) preserves only the most proximal 32.4 mm, including the base, which angles strongly from proximomedially to distolaterally. The articulation for the cuboid is flat mediolaterally. Dorsoplantarly the facet is slightly convex, with a height only 1.1% of the dorsoplantar length, in the low part of the human range (Figure 7.10). It measures 15.2 mm mediolaterally, 12.1 mm dorsoplantarly on the lateral side and tapers to 8.1 mm dorsoplantarly on the medial aspect of the cuboid articulation. There is no continuation of the cuboid facet to the superior aspect of the base of the 5th metatarsal.

The OH 8 foot preserves the cuboid, 4th, and 5th metatarsals from the same individual (Figure 7.14). This 1.8 million year old specimen is considered by many to be

Figure 7.16. Lateral aspect of the OH 8 foot.

Figure 7.16. Articulated cuboid, and 5th and 4th metatarsals from the OH 8 foot in dorsal view. Notice the absence of any extension of the articular surfaces onto the dorsum of the cuboid or 5th metatarsal. Also note the pathological growths along medial aspect of both the 5th and 4th metatarsals and the reduced 5th metatarsal tuberosity.

Homo habilis (Leakey et al., 1964; Susman and Stern, 1982) and by others (Wood, 1974; Grausz et al., 1988; Gebo and Schwartz, 2006) to be from *Paranthropus boisei*.

The cuboid is quite small, measuring 28.0 mm proximodistally, 20.4 mm mediolaterally, and 18.7 mm dorsoplantarly. Dorsoplantarly, the facet for the 5th metatarsal is slightly concave, 3.5% of its total height, and mediolaterally slightly concave, though this measure does not discriminate modern humans and African apes (Figure 7.12). The 5th metatarsal facet measures 9.3 mm mediolaterally, 10.7 mm dorsoplantarly on the medial aspect and tapers to 9.3 mm laterally. The facet for the 4th metatarsal is slightly concave dorsoplantarly (6.2% of total height) and mediolaterally flat. It is quite distinct from the African ape condition for this measure (Figure 7.11). The 4th metatarsal facet measures 13.2 mm dorsoplantarly and 9.1 mm mediolaterally. These articular facets end abruptly at the junction of the dorsal surface of the cuboid.

The 5th metatarsal preserves a proximal section 48.3 mm in length but is broken prior to the metatarsal head. The lateral aspect of the bone is poorly developed and may be the result of an unfused lateral tuberosity, consistent with the specimen's hypothesized juvenile status (Stern and Susman, 1982). Alternatively, the absence of the styloid of the 5th metatarsal may be pathological and the result of arthritis (Day and Napier, 1964). A pathological ridge of bone on the medial aspect of the metatarsal is quite salient and projects plantarmedially to a corresponding "facet" of osteophytic bone growth on the lateral aspect of the 4th metatarsal. The articulation with the cuboid is slightly convex dorsoplantarly (5.5% of total height) and convex mediolaterally. It measures 9.4 mm dorsoplantarly and 7.7 mm mediolaterally.

The 4th metatarsal preserves the most proximal 40.6 mm. The articular facet for the cuboid is slightly convex dorsoplantarly (6.6% of total height) and mediolaterally. The slight convexity of the cuboid facets of the 4th and 5th metatarsals is strikingly human-like and distinct from the African ape condition (Figures 7.9 and 7.10). The 5th metatarsal base measures 15.4 mm dorsoplantarly and 9.3 mm mediolaterally. There is no superior extension of the cuboid articular facet on either the 4th or the 5th metatarsals.

Discussion

It is clear that a single line of evidence would not be sufficient to convincingly demonstrate that the midtarsal break occurs primarily at the tarsometatarsal joint rather than the transverse tarsal joint. However, results obtained from x-rays, dissections, video data from live chimpanzees and gorillas, EMG results from chimpanzees, and skeletal comparisons all point to the same conclusion. It can thus be reasonably argued that D'Août et al. (2002) and Vereecke et al. (2003) were correct in suggesting that the primary location of the midtarsal break is the cuboid-metatarsal joint. Although it was found that the calcaneocuboid joint does contribute approximately one-third of the total midtarsal flexion in macaques, baboons, mandrills, chimpanzees, and gorillas, the majority of this motion happens more distally at the tarsometatarsal joint. It is recommended here that this motion be referred to as the "midfoot" break rather than the "midtarsal" break. Additional work using cineradiography could continue to test this hypothesis, and more precisely resolve the relative contributions of the calcaneocuboid and cuboidmetatarsal joints to the midfoot break.

X-rays of baboon feet in lateral view demonstrate that relative to a neutral position, the cuboid shifted superiorly on the fifth metatarsal during midfoot flexion. Although there is movement at the calcaneocuboid joint that would also contribute to midfoot flexion, the majority occurs at the tarsometatarsal joint. A similar result is obtained on the one gorilla foot x-rayed, with a plantarflexed neutral position between the cuboid and metatarsals becoming more aligned with midfoot flexion. Unfortunately, the X-ray protocol which involves human manipulation of the primate feet was not able to generate the enormouns force on the gorilla foot that the adult male would have been capable of during normal quadrupedal walking, and thus the midfoot flexion was minimal.

The X-rays were consistent with the results obtained from the dissections, and video data of live primates. Although some flexion was generated at the calcaneocuboid joint during initial heel lift (about 10 degrees), the majority (another 20 degrees) occurred more distally at the tarsometatarsal joint. These data are consistent with stills from terrestrially walking baboons (Muybridge, 1957) in which heel elevation is followed by more distally located flexion before toe-off.

Perhaps the most compelling evidence for the anatomical location of the midfoot break comes from video data of walking apes and mandrills with the tuberosity of their 5th metatarsal marked. Initial heel lift in chimpanzees, gorillas, mandrills, and macaques slightly flexes the midfoot in a region proximal to the tuberosity of the 5th metatarsal, almost certainly the calcaneocuboid joint. However, flexion then shifts to a position located distally to the tuberosity of the 5th metatarsal, consistent with flexion at the tarsometatarsal joint. Furthermore, the magnitude of foot flexion is greater at the tarsometataral joint than at the calcaneocuboid joint. These data are consistent with EMG results that indicate simultaneous activity of the gastrocnemius/soleus and the posterior tibialis during the midfoot break in terrestrially walking chimpanzees. The broad insertion of the posterior tibialis tendons across the navicular, cuboid, and three cuneiforms would restrict transverse tarsal flexion during activity of this muscle. Instead, given these data, it is more likely that the majority of midfoot flexion occurs at the tarsometatarsal region.

In humans, the midfoot break is prevented by components of the longitudinal arch of the foot: the plantar ligaments (short plantar ligament, long plantar ligament, calcaneonavicular ligament) and the plantar aponeurosis. Kidd (1993) has also suggested that the midfoot break is possible only because of an absence of an arch in non-human primates. Apes and monkeys have a strong short plantar ligament between the calcaneus and cuboid, providing additional soft tissue evidence that the majority of midfoot flexion does not occur at this joint. However, the absence of the other components of a longitudinal arch, such as the long plantar ligament and the calcaneonavicular ligament, give non-human primates a flat-foot with increased mobility at the tarsometatarsal region.

Role of the calcaneocuboid joint in the midfoot break

Elftman and Manter (1935) were the first to recognize the important and considerable differences in the calcaneocuboid joint between humans and non-human primates. Many studies of the primate midfoot have followed (Bojsen-Møller, 1979; Lewis, 1980; Langdon et al., 1991; Kidd et al., 1996; Kidd, 1998; Hartcourt-Smith, 2002) and it is now widely accepted that a variety of ligamentous and osteological changes in the human calcaneocuboid joint render the human midfoot more stable than that of non-human primates. This study does not question that non-human primates have a more mobile transverse tarsal joint than humans and are capable of greater ranges of supination and pronation. Instead, it was tested whether the calcaneocuboid joint was the anatomical site of the approximately 30° of flexion necessary to account for the midtarsal break.

Plio-Pleistocene hominin foot fossils have been examined to assess whether australopiths and other early human ancestors had more mobile midfeet, or had already evolved a stable lever during push-off phase of walking (Lewis, 1980; Stern and Susman, 1982; Susman, 1983; Gomberg and Latimer, 1984; White and Suwa, 1987; Langdon et al., 1991; Kidd et al., 1996; Kidd, 1998). These studies looked primarily at the calcaneocuboid joint to make this determination. This is a critical area for determining whether the midtarsal joint locking mechanism is in place even if most of the midfoot flexion is not actually occurring in this region. During the push-off phase of human walking, the hindfoot inverts, the cuboid and calcaneus lock together, and the longitudinal arch lowers and tenses. These events all significantly reduce the mobility of the midfoot and transform the foot into a rigid lever well adapted for efficient push-off (Sarrafian et al., 1987). Although in humans flexion of about ten degrees can occur between the cuboid and metatarsals (Ouzounian et al., 1989), this flexion is significantly reduced when the calcaneus is inverted during the pushoff phase of walking (Blackwood et al., 2006). Thus, the locking of the calcaneocuboid joint, and perhaps more critically the presence of a binding longitudinal arch that tenses during hindfoot inversion, prevent a midfoot break in humans. Interestingly though, Blackwood et al. (2006) did not find that flexion between the calcaneus and cuboid was more prominent during hindfoot eversion than when the hindfoot is inverted. This insight further supports the hypothesis that although the locking between the calcaneus and the cuboid helps stabilize the midfoot and prevent the midfoot break, it is not the primary anatomical source of it.

Evolution of the stable midfoot.

It is quite useful for paleoanthropologists to locate skeletal correlates for particular joint motions to assess the timing of and circumstances behind locomotor evolution in the fossil record. Because the locking of the calcaneocuboid joint is a critical component of midfoot stability, this region has featured prominently in discussions of human locomotor evolution. This study reveals that there is another joint, and potentially three more joint surfaces that can be studied to assess how stable the midfoot is in extinct hominins: the distal cuboid, and proximal articular surfaces of the fourth and fifth metatarsals. These data are useful because of both the scant fossil record, and the conflicting interpretations of the available fossil evidence.

A study of the cuboid, fifth and fourth metatarsal joint surfaces suggest that these joint surfaces in humans and African apes are statistically distinguishable. African apes studied here have dorsal expansion of the cuboid and 5th metatarsal joint surfaces, although this condition can also occur in human feet and is perhaps in part the result of humans occasionally having midfoot flexion (Vereecke et al., 2003). It will be important to test whether midfoot flexion in humans is correlated with the occurrence of flat-footedness in humans. The 4th and 5th metatarsal bases of chimpanzees and gorillas are statistically more convex than these articular facets on modern human metatarsals. The difference between the human and ape cuboid-metatarsal joint can be found in the cuboid-4th metatarsal joint shape. The 4th metatarsal facet on the cuboid of humans is significantly flatter than the more concave facet in African apes. The convex morphology of the 4th and 5th metatarsal bases and corresponding concave facet on the cuboid in African apes is argued to be related to midfoot flexion, and not to general grasping abilities, for two reasons. One, the convexity of the cuboid facet on the 4th metatarsal extends dorsally, consistent with increased dorsiflexion rather than plantarflexion at the tarsometatarsal joint. Two, the metatarsal-cuneiform facets of apes are flat. If these joint surfaces were convex and concave respectively, it could be argued that the cuboid-4th metatarsal joint morphology was like the rest of the distal ape midfoot in being adapted for grasping plantarflexion. Furthermore, these features indicative of midfoot flexion are preserved in the fossil record as demonstrated by the cuboid and lateral metatarsals of the Miocene hominoids *Proconsul nyanzae* and *Nacholapithecus kerioi*.

Australopithecus afarensis

There is not yet any pedal evidence for hominins earlier than 3.5 million years that could address midfoot stability and the possible presence of the longitudinal arch. Studies on the oldest hominin feet, attributed to *A. afarensis*, have produced mixed results. Calceneocuboid joint morphology in *A. afarensis* has been assessed based on a fragmentary cuboid that has not been formally described. Preliminarily, though, it has been suggested that the calcaneocuboid joint may allow more mobility than that found in modern humans (Gomberg and Latimer, 1984; White and Suwa, 1987). This is consistent with studies that have suggested that *A. afarensis* did not have a longitudinal arch. This conclusion has been based on the dorsal inclination of facets of the foot (Sarmiento, 1991; Berillon, 2003), and evidence for weight bearing on the navicular (Harcourt-Smith, 2002; Harcourt Smith and Aiello, 2004).

However, others have suggested that *A. afarensis* may have had an arch. There is a distinct impression on the talar heads of both A.L. 288-1, and A.L. 333-75 for the calcaneonavicular ligament (Lamy, 1986). Furthermore, the inferior navicular bones of *A. afarensis* (A.L. 333-36 and A.L. 333-47) have broad insertion areas for the cubonavicular ligament, also important in stabilizing the arch (Stern and Susman, 1983; Lamy, 1986; Gebo, 1992). Finally, the Laetoli footprints demonstrate that at 3.5 million years ago, a hominin species had evolved a longitudinal arch (White, 1980; White and Suwa, 1987). Unless *A. afarensis* did not make the Laetoli footprints as argued by some (Tuttle et al., 1990; Harcourt-Smith, 2004), these footprints are strong evidence that *A. afarensis* had an arched foot.

The 5th metatarsals A.L. 333-13 and A.L. 333-78 do not conclusively indicate whether *A. afarensis* had midfoot flexion and was absent of a longitudinal arch, or had midfoot stability and thus had a longitudinal arch (Figure 7.17). However, the fossils are consistent with the latter scenario. The cuboid surface of A.L. 333-78 is more convex than most modern human 5th metatarsals, though within a standard deviation of the human mean for this measure. Likewise, the cuboid surface of this fossil is flatter than most African ape 5th metatarsals, though also within a standard deviation of the ape mean for this measure. The A.L. 333-13 fossil is almost identical to the human mean for this measure, though ape 5th metatarsals can be found with this morphology. There is no indication that the cuboid ever moved superiorly onto the dorsum of the 5th metatarsal in either of these individuals. Because the fourth metatarsal may be a better skeletal

Figure 7.17. Fossil hominin 5th metatarsals.

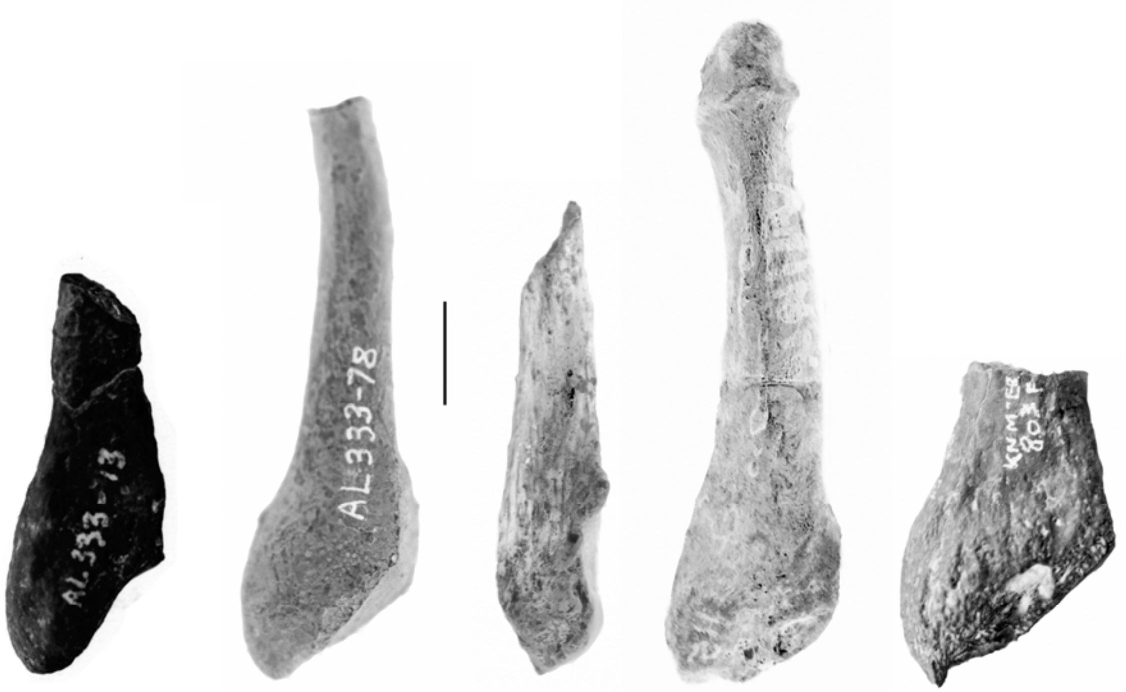


Figure 7.17. Fossil hominin 5th metatarsals in dorsal view. From left to right: A.L. 333-13 (cast), A.L. 333-78 (cast), and original fossils of OH 8, StW 114/115, and KNM-ER 803. Scale bar is 10 mm. The fossils have been inverted to all represent the left side.

indicator of midfoot flexion, the morphology of the currently unpublished *A. afarensis* fourth metatarsal A.L. 333-160 from Hadar (Kimbel et al., 2004) will be critical for assessing midfoot stability in this species.

Sterkfontein. cf. *Australopithecus africanus*

Based on the non-weight bearing navicular of "Little Foot" StW 573, it has been suggested that *A. africanus* had at least a minimal longitudinal arch (Harcourt-Smith, 2002). If the three metatarsals from Member 4 represent the same taxon, the results of this study agree. The cuboid facet on the 4th metatarsals StW 485 and StW 596 are both flat, like modern human and distinctly unlike the convex facet of non-human primates

Figure 7.18. Fossil hominin 4th metatarsals.

Figure 7.18. Fossil hominin 4th metatarsals in dorsal view. StW 485 (left) and OH 8 (right). Scale bar is 10 mm.

with midfoot flexion (Figure 7.9; Figure 7.18). Additionally, the fifth metatarsal from Member 4 in Sterkfontein StW 114/115 is human-like in lacking dorsal expansion of the cuboid articular surface, and the curvature of the cuboid facet is almost identical to the modern human mean (Figure 7.17). These data suggest limited midfoot flexion, and may constitute evidence for the presence of a longitudinal arch in *A. africanus*.

East and South African hominins circa 2.4-1.5 mya

It is difficult to assign postcranial specimens to particular hominin taxa unless they are associated with craniodental remains. Thus the following discussion pertains to fossils that could be early members of the genus *Homo*, or from the robust australopithecine genus *Paranthropus*. Regardless of taxa, the evidence is strong that known hominins from this time period had a longitudinal arch, and limited flexion at the midfoot.

Stability at the calcaneocuboid joint is human-like for the 2.36 million year old calcaneus from Omo (33-74-896) (Langdon et al., 1991; Gebo and Schwartz, 2006), and thus this hominin may have had a longitudinal arch (Gebo and Schwartz, 2006). Interpretations of the OH 8 foot have been more contentious. Multiple studies agree that the morphology of the calcaneocuboid joint in the OH 8 foot would produce a stable lever during push-off (Lewis, 1980; Stern and Susman, 1982; Susman, 1983; Langton et al., 1991; Kidd et al., 1996; Kidd, 1998). Additionally, many have argued that the morphology of the OH 8 foot preserves evidence for a longitudinal arch by 1.8 million year ago (Napier, 1965; Susman, 1983; Lamy, 1986; Berillon, 2003). However, others (Oxnard and Lisowski, 1980; Kidd et al., 1996; Kidd, 1998) have argued that the OH 8 foot has a divergent first ray, and a divergent hallux and longitudinal arch cannot coexist in the same foot (Lisowski, 1967). The argument for an abducted hallux in the OH 8 foot is based on a high neck angle in the talus which would shift the whole medial column of the foot, the navicular, medial cuneiform and first metatarsal, in a position of abduction relative to the rest of the foot (Kidd et al., 1996; Kidd, 1998). But, others have argued that the talus is three joint surfaces away from the first metatarsal and thus may not be the best skeletal indicator of a divergent big toe (Lovejoy, 1975; Harcourt-Smith, 2002). Furthermore, because the neck angle is statistically identical in humans, macaques, baboons, and orangutans (Barnett, 1955), there is no relationship between this measure and a divergent great toe. Instead, the high neck angle of the talus may indicate the presence of a particularly high arch, rather than an absent arch, as this would reduce bending forces on the medial aspect of the foot (Preuschoft, 1971).

The morphology of the cuboid, fourth and fifth metatarsals in the OH 8 foot are strongly suggestive of midfoot stability in this hominin species. The shape of the joint facets, and the absence of any dorsal expansion of the articular surface on the cuboid or fifth metatarsal are evidence that the OH 8 individual did not experience midfoot flexion, and thus probably had the structural components of a longitudinal arch. The articular facets on the cuboid, 4th metatarsal and 5th metatarsal are distinctly human-like in having a flat joint shape (Figures 7.9, 7.10, 7.16, 7.17, 7.18, 7.19).

The fifth metatarsal from the Koobi Fora assigned to *Homo* KNM-ER 803 is indistinguishable from modern humans and provides further evidence for midfoot stability in Early Pleistocene hominins (Figure 7.17). Finally, two fourth metatarsals and a fifth metatarsal from the 1.77 million year old site of Dmanisi have been recently published (Lordkipanidze et al., 2007). Although the joint morphology of these specimens is not described in detail, a human-like, flat facet for the cuboid can be seen from the images of these bones suggesting midfoot stability and the likelihood for the presence of a longitudinal arch in the Dmanisi hominins (Lordkipanidze et al., 2007).

Figure 7.19. 3-D model of 4th metatarsal of the OH 8 foot compared to chimpanzee and human.

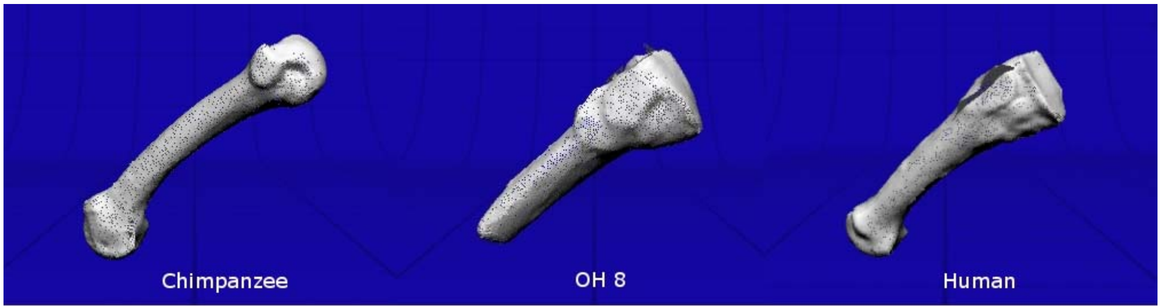


Figure 7.19. 3D models obtained by scanning the 4th metatarsals of a chimpanzee (left), human (right) and the OH 8 foot (middle) using a portable NextEngine laser scanner from. Each bone is oriented with the distal metatarsal head to the lower left and the proximal metatarsal base to the upper right. Notice the convex base to the ape metatarsal, and the flattened proximal base on the human and OH 8 metatarsals.

The midfoot break, longitudinal arch and climbing adaptations in the midfoot.

The climbing abilities of early hominins must be considered in the context of them as terrestrial bipeds. For example, climbing in modern apes is strongly facilitated by a divergent big toe. A divergent hallux has been suggested for an early South African australopithecine (Clarke and Tobias, 1995), for *Australopithecus afarensis* (Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004) and for the OH 8 foot (Kidd et al., 1996; Kidd, 1998). However, a reanalysis of these specimens has recently suggested that a divergent toe was probably not present in any of these hominin species (McHenry and Jones, 2006). If early hominins had already evolved an adducted hallux, and they were climbing often, they would have to have evolved even more obvious and exaggerated musculoskeletal features related to climbing in other regions of the body (i.e. stronger arms and hands relative to body size than modern apes) to compensate for the absence of a divergent toe (Coffing, 1998; Ward, 2002). Additional adaptations for bipedalism in the foot that restrict arboreality would further place a selection pressure on the arm, hip, and knee. A debate has raged for 25 years now whether the adaptations for bipedality preclude climbing in early hominins (Latimer et al., 1987; Latimer, 1991), or whether some of the primitive skeletal features of early hominins are evidence that these animals were both bipedal and arboreal (Susman et al., 1984). The data presented in this paper provide yet more fodder for this discussion.

During the early stance phase of bipedal walking, the foot is pronated, i.e. the calcaneus is everted (Sammarco, 1989; Donatelli, 1990). This position of hindfoot eversion raises the longitudinal arch, relaxes the aponeurosis and long plantar ligament, and allows for some midfoot mobility (Hicks, 1953; Inman, 1976; Sarrafian et al., 1987). However, during the later stance phase of walking, the tibia swings over the foot at the talocrural joint and internally rotates. The calcaneus inverts and locks at the calcaneocuboid joint, and this position of the hindfoot lowers the longitudinal arch, tensing the aponeurosis and long plantar ligament (Hicks, 1953; Inman, 1976; Sarrafian et al., 1987; Donatelli, 1990). This tension remains as the foot lifts off the ground at the heel and the toes extend at the metatarsophalangeal joint (Sarrafian et al., 1987). Tension in the longitudinal arch provides a rigid lever arm through the late stance phase and push-off phase of walking.

What is critical for the relationship between midfoot flexibility and climbing is the recognition that dorsiflexion at the talocrural joint, and the corresponding foot abduction, both lower the longitudinal arch and place this structure under maximum tension. During vertical climbing, chimpanzees place their foot in a position of abduction against the tree, and engage in extreme dorsiflexion at the talocrural joint (Chapter 2; Figure 7.3). They are in this position during push-off of the opposite foot and hand, meaning that they are supporting much of their body weight on a single grasping foot and ipsilateral hand. If chimpanzees had a longitudinal arch, dorsiflexion and adduction would tense the arch, and limit midfoot mobility and grasping capacity precisely during the time when they would require it most. Based on this logic, it is difficult to imagine that once an early hominin had evolved a longitudinal arch, it could climb in the manner of a modern chimpanzee. It has been suggested that the grasping midfoot of climbing apes may have preadapted hominins for a longitudinal arch (Oxnard and Lisowski, 1980; Pickford, 2006). Although the presumed grasping midfoot of the hominin last common ancestor may have provided the structural raw material for the evolution of the longitudinal arch, it is suggested here that the evolution of one necessarily replaces the other.

However, Old World monkeys may provide another model for climbing in early hominins and this will be examined briefly. Preliminary kinematic data on climbing in Old World monkeys suggest that they may climb differently than modern apes (Hirasaki et al., 1993; Isler, 2005). Old World monkeys grasp the vertical substrate with their heel lifted and thus the midfoot break helps to reduce the climbing moment arm, rather than extreme dorsiflexion at the talocrural joint. This differs from climbing chimpanzees who engage in a midfoot break only during the push-off phase of climbing, in much the same way that they use this motion terrestrially. If early hominins were climbing more like cercopithecoids rather than apes, they would require a midfoot break to ascend a vertical substrate. Once again, the presence of a longitudinal arch would be the limiting factor. As demonstrated above, the structural components of the longitudinal arch prohibit midfoot flexion, and thus once the arch evolves, early hominins would not have been able to climb in the manner of either a modern ape, or a modern cercopithecoid.

These data suggest that the evolution of the arch and the resulting stability of the midfoot would preclude any kind of arboreal climbing in hominins that resembles that of any extant anthropoid. If hominins with a longitudinal arch did climb, they would have to do so in a manner kinematically different from modern apes or cercopithecoids. Thus, if hominins climbed, the splayed leg strategy of climbing practiced by some modern humans may have roots in the Plio-Pleistocene, or early hominins may have climbed in a manner without any modern analogues. Climbing with the legs splayed laterally would impose shearing forces on both the ankle and the knee of the hominin. If this mode of locomotion was practiced frequently by hominins, adaptations in the knee and the ankle may evolve to counteract these forces. Predictions from this biomechanical model should be tested with skeletal remains of populations known to climb trees in this manner and compared to the lower limb fossils of hominins.

Based on the results of this study and the results from other studies examining midfoot stability and the longitudinal arch, it is doubtful that any known Plio-Pleistocene hominin had a foot capable of vertical ascent in an ape-like manner. If the Plio-Pleistocene hominins represented by StW 485, StW 114/115, OH 8, and ER 803 did climb, they may have used a kinematically different strategy than apes employ today. Given the current pedal evidence, it is suggested that *A. afarensis* also had a foot poorly adapted for ape-like vertical climbing. These data are consistent with evidence from the ankle (Latimer et al., 1987; Chapter 4) and metatarsophalangeal joint (Latimer and Lovejoy, 1990) that suggest that *A. afarensis* had evolved lower limb morphology maladapted for climbing. Additional fossil evidence should shed light on this question.

Conclusions

Although the morphology of the calcaneocuboid joint may facilitate midtarsal mobility, the anatomical site for the midtarsal break is primarily at the tarsometatarsal joint. Midfoot flexion in humans is inhibited by the presence of the longitudinal arch. In addition to the calcaneus and the proximal cuboid, the distal facets of the cuboid and the articular surface of the proximal fourth and fifth metatarsals can provide evidence for midfoot stability in hominins. Data from the midfoot fossils of *A. afarensis* are currently inconclusive though consistent with the hypothesis that this species had evolved a stable midfoot and longitudinal arch. By the Pleistocene, known hominins had almost certainly evolved a longitudinal arch and were devoid of any midfoot flexion. This would severely restrict their ability to vertically climb trees in a manner kinematically similar to modern chimpanzees.

CHAPTER 8

Conclusions and future research

This dissertation investigated whether the skeletal and ligamentous morphology of the primate ankle and midfoot was adapted for bouts of vertical climbing in hominoids and some atelines. I employed a multifaceted approach that addressed questions of ankle functional morphology using evidence from the following:

- Kinematic data on wild and captive catarrhines.
- Radiographs and dissections of primate lower limbs.
- EMG data on muscle activity during climbing and terrestrial walking in chimpanzees.
- Biomechanical assessment of the ankle ligaments of a baboon.
- Linear and angular study of the distal tibia and talus in extant anthropoid primates.
- Quantification of the surface topography of the anthropoid talocrural joint and cuboid-metatarsal joint using a 3D laser scanner.

This dissertation provides the first kinematic data on vertical climbing in chimpanzees, and is the first to describe the kinematics of climbing in any completely wild hominoid species. In addition, this dissertation presents data for the first time on the biomechanics of the ligaments of the ankle in any non-human primate. Both of these contributions have important ramifications for future studies of primate functional morphology. Using this multifaceted approach, it was found that in contrast to cercopithecoids, hominoids and atelines vertically climb often enough and in a kinematically distinct manner to result in specific skeletal morphologies of the talocrural joint. These include a mediolaterally wide anterior aspect of the distal tibia, a mediolaterally expanded metaphysis of the distal tibia and a mediolaterally thickened medial malleolus. These skeletal morphologies are functionally related to foot dorsiflexion and inversion and loading of the ankle in these joint positions. In addition, hominoids and ateline primates have a weakly developed intercollicular groove and may have a poorly developed posterior tibiotalar ligament. This ligament is an important dorsiflexion inhibitor in the ankle of modern humans and cercopithecoid monkeys.

Application of these results to the early Miocene catarrhine fossil record suggest that the majority of purported hominoid species known from this time were above branch arboreal quadrupeds poorly adapted for bouts of modern hominoid and ateline-like vertical climbing. However, four tali from *Rangwapithecus* have a morphology consistent with the hypothesis that this species may have vertically climbed like modern atelines and *Pongo*. In addition, the distal tibia of *Proconsul major* has a modern ape-like morphology functionally correlated with loading of the talocrural joint in dorsiflexion and inversion- joint positions important during vertical climbing.

In contrast, data on 30 hominin fossil tibiae and tali from the Plio-Pleistocene suggest that the known hominins lack adaptations for vertical climbing. In fact, it is argued that adaptations for bipedality result in a talocrural morphology maladapted for ape-like vertical climbing. Hominins distribute bone on the posterior and lateral aspect of the talocrural joint, which necessarily reduces the relative amount of bone in the anterior and medial aspects of the joint, rendering the joint maladapted for positions of dorsiflexion and inversion. In addition, a varus ankle positions both the feet and knees directly under the center of gravity in hominins. This ankle morphology prevents the lower limb from obtaining positions of foot inversion critical for successful ascents of a vertical substrate. Only extreme dorsiflexion beyond what is observed in modern hominoids would compensate for this joint morphology, and strong attachments for the posterior tibiotalar ligament on the distal tibia of Plio-Pleistocene hominins demonstrate that this was not the case. Arguments that many Plio-Pleistocene tali possess an inverted set are unfounded. Instead, the unique talar morphology found in many Plio-Pleistocene tali may be a mechanism by which small hominins stabilized the ankle in the absence of an anterior talofibular ligament. Thus, the keeled talar surface and strong peroneal muscles that have been argued as evidence for arboreality can be explained as mechanisms of stabilizing the ankle in a fully bipedal hominin that had not yet evolved the anterior talofibular ligament. Furthermore, the morphology of the cuboid-metatarsal joint suggests that lateral midfoot stability, perhaps in the form of a longitudinal arch, was present in hominins by 3.2 million years ago. The presence of a longitudinal arch would restrict midfoot grasping and would severely restrict arboreal capacity in early hominins.

In science, the answer to one question results in many more new questions. This study is no exception. What follows below is a list of potentially new research questions that have surfaced as a result of this dissertation organized by the Chapter that inspired them.

- Chapter 2:
    - Results from Chapter 2 suggest that kinematic data on locomotion in wild primates can complement data collected in more controlled captive settings. To address questions regarding vertical climbing in hominoids, additional observations of wild lowland gorillas and gibbons are sorely needed. Specifically, we require more data on how often they climb and climbing kinematics.
    - Kinematic analyses of hominoid and ateline vertical climbing can also be extended from the ankle to the more proximal lower limb joints of the knee, hip, elbow and shoulder. These results can be applied to provide more thorough tests of the hypothesis that vertical climbing was practiced by Miocene catarrhines and Plio-Pleistocene hominins.
    - Finally, the hypothesis supported in this dissertation, that vertical climbing in hominoids and atelines is kinematically different from vertical climbing in cercopithecoids, requires more systematic testing. Analyses of climbing bouts in the Old World monkeys and of joints other than just the ankle would furnish two means to do so.
- Chapter 3:
    - Results from Chapter 3 tentatively suggest that there may be more locomotor diversity in the early Miocene than previously suggested. The tali from Songhor suggest that *Rangwapithecus* may include vertical climbing into its locomotor repertoire. Other potential *Rangwapithecus* postcrania should be reexamined. Because the similarly sized *P. africanus*

is also present at Songhor, it is not easy to assign postcrania to these two taxa, and as a consequence, it may be difficult to test this hypothesis.

- In addition, the functional anatomy of *Proconsul major* should be reassessed. It is suggested here that *P. major* is not a size-scaled version of *P. nyanzae* or *P. heseloni* and may be better adapted for below branch suspensory behaviors, orthogrady, and vertical climbing than the other *Proconsul* species. A study of the postcrania of *P. major* may have important implications for *Proconsul* taxonomy and hominoid phylogenetics.
- The role that body size may have in selecting for postcranial adaptations related to forelimb-dominated suspension, orthogrady, and vertical climbing needs to be studied in greater detail. It is likely that at a certain body mass, primates either must become fully terrestrial or evolve postcranial adaptations that better distribute the large mass of the primate across many arboreal substrates. Tests of these hypotheses may involve a study of the postcranial remains of the large bodied (~40-50 kg) Pleistocene cercopithecoids *Rhinocolobus*, *Paracolobus*, and *Theropithecus*. Preliminary examination of the *Rhinocolobus* remains suggest that this cercopithecoid had evolved hominoid-like adaptations in the ankle, shoulder, and elbow to better navigate its arboreal setting. This study would have important implications for assessing how much homoplasy can evolve in the primate postcranium, thereby informing phylogenetic hypotheses.

  - It was not possible to study the distal tibia of *Dryopithecus* or the tali known from the later Miocene hominoid *Oreopithecus*. Applying the results of this dissertation to the ankle of these hominoids would provide valuable insights into the locomotion of later Miocene apes and test hypotheses of homoplasy in the hominoid postcranial skeleton.
- Chapter 4:
  - Chapter 4 asked specifically whether the hominin talocrural joint was adapted for bouts of vertical climbing. It may also be important to ask the same question of the hominin knee and hip joint, and test whether hominins were climbing using kinematic data obtained at these more proximal lower limb joints in wild chimpanzees.
  - Based on the results from the ankle and work done by many other researchers, it is unlikely that the knee or hip would reveal that hominins were adapted for vertical climbing bouts. Given the morphology of the lower limb, the upper limb of a purported climbing hominin should therefore possess even more strongly exaggerated features related to arboreality than the similarly sized chimpanzee. The upper limb of early hominins should be reassessed based on a biomechanical model that shifts a majority of the propulsive and grasping responsibilities to the upper limb and hand. In addition, the question needs to be asked how vertical climbing and arboreality would produce strains on the upper limb bones that would be distinct from other upper limb activities such as carrying and throwing.

- The results of this study strongly suggest that if hominins were climbing, they were doing so in a manner kinematically distinct from both modern apes and modern cercopithecoids. There is another modern analogue to test: climbing humans. Variation of climbing in modern human populations such as the Ache, Efe, or Hadza should be assessed. A biomechanical model of pulse climbing by a bipedal hominin should be developed and predictions for how the ankle and knee should adapt to the shear forces that would be produced should be tested on a skeletal population known from the ethnographic record to engage in frequent bouts of climbing. If there is a skeletal signature of climbing, these data could be used to test whether australopithecines climbed in a manner similar to some modern human populations.
- There are other, indirect ways to test for climbing in early hominins. As discussed in Chapter 4, I hypothesize that if hominins were frequently arboreal, then they would follow the pattern known from the skeletal remains of every other extant hominoid: they would frequently fall and break bones. In fact, one may expect even more broken bones from hominins as it is likely that they were more poorly adapted to an arboreal environment than modern apes. First, a comparative study of the pathology known from the modern human Libben collection, and studies of healed fractures in extant hominoids should be undertaken to test whether an arboreal signature can be obtained from the pattern of bone

pathology. A resampling approach could then be applied to the hominin fossil record.

  - Finally, there is an increasing tendency in the paleoanthropological literature to apply multivariate and geometric morphometric approaches to the hominin fossil record and to *a posteriori* assign more nonhuman ape-like behavior to fossils that fall in the morphospace between humans and extant African apes. Instead, I suggest *a priori* predictions of what differences one might expect to see in morphology based on biomechanical models. These predictions can then be employed to interpret the results of geometric morphometric studies of hominin fossils.
- Chapter 5:
  - This study assumes that the size and position of the posterior tibiotalar ligament affects the range of dorsiflexion. An orthopaedic study that uses x-ray or CT data to measure the size and position of the PTTL could be used to test the relative roles of the PTTL, the Achilles tendon, and the morphology of the talocrural joint itself on dorsiflexion in the human ankle.
  - This study also assumed that the type of mechanoreceptors in the PTTL were the same across primates. This may not be true. A histological study that examines the types and frequencies of mechanoreceptors in the PTTL of various primate species should be undertaken to test whether the assumption made in this chapter is correct.
- Chapter 6:

    - Results from this chapter on the evolution of the anterior talofibular ligament lead to specific predictions about ankle stability in modern humans. If there is a trade-off between bony and ligamentous stability directly related to body size, then within humans, a mismatch between these two variables may result in chronic ankle instability or ankle degeneration. For example, a large-bodied individual with a more keeled talocrural joint may be predicted to be less efficient at distributing forces through the joint and may ultimately suffer more frequently from joint damage and degeneration.
    - The absence or rarity of the anterior talofibular ligament in non-human primates is based on very few dissected primate ankles. More data assessing whether the anterior talofibular ligament is always absent from the non-human primate ankle, or variably present in certain species (*Hylobates*, and *Gorilla* in particular) is sorely needed.
    - The timing and pattern of the evolution of the anterior talofibular ligament is difficult to assess because of the scant fossil record. Two fossil tali from *A. afarensis* (A.L. 333-147) and *Homo* sp. from Dmanisi (D4110) will be important specimens to examine in order to test the hypotheses presented in this chapter.
- Chapter 7:
    - The midtarsal break, or midfoot flexion, is a complex movement involving rotation of the calcaneus and subsequent motion of the cuboid, talus, and navicular. Although this dissertation examined only the dorsiflexion

component of this motion at only the calcaneocuboid and cuboid-metatarsal joints, a cineradiography study that captures precisely how and where the different primate tarsals move during heel lift will help better understand midfoot mobility. These data will help assess how mobile the foot of early hominins may have been. In addition, this approach would help determine where on the medial side of the foot midfoot flexion is occurring. The morphology of ape 2nd and 3rd metatarsals strongly suggests that flexion is not occurring at the cuboid-metatarsal joint on the medial side, and thus the medial and lateral sides of the foot may be decoupled in primates.

- A prediction from this study is that humans with relatively low lateral arches would possess more mobility at the cuboid-metatarsal joint. Given that mobility at this joint can be assessed by marking the tuberosity of the 5th metatarsal, a kinematic study on modern human feet and the hypothesis of a correlation between arch development and cuboid-metatarsal dorsiflexion should be tested.
- Given that hominoids are more plantigrade than cercopithecoids, I hypothesize that Old World monkeys possess even greater cuboid-metatarsal curvature than hominoids. These data could be used to interpret the foot position in Miocene hominoids.
- Finally, the results in this study strongly suggest that hominins had a stable lateral side of the foot, consistent with the presence of, at the very least, a long plantar ligament and at most, a completely developed

longitudinal arch. Although the 5th metatarsal curvature of two *Australopithecus afarensis* specimens was within the interquartile range of modern humans, the two specimens were also within the full range of modern ape morphology, and thus the hypothesis that *A. afarensis* had nonhuman ape-like midfoot mobility could not be refuted. Because the 4th metatarsal is a better skeletal indicator of midfoot stability, it will be important to apply the results of this dissertation to the currently unpublished 4th metatarsal from Hadar A.L. 333-160 when it is possible to study this fossil.

BIBLIOGRAPHY

Aiello, L., Dean, C. 2002. An Introduction to Human Evolutionary Anatomy. San Diego: Elsevier Academic Press.

Aiello, L., Wood, B., Key, C., Wood, C. 1998. Laser scanning and paleoanthropology. An example from Olduvai Gorge, Tanzania. In: Strasser, E., Fleagle, J., Rosenberger, A., McHenry, H. (eds.). Primate Locomotion. Recent Advances. New York: Plenum Press. pp. 223-236.

Alemseged, Z., Spoor, F., Kimbel, W.H., Bobe, R., Geraads, D., Reed, D., Wynn, G.G. 2006. A juvenile early hominin skeleton from Dikika, Ethiopia. Nature. 443: 296-301.

Alexander, R. McN., Bennett, M.B. 1987. Some principles of ligament function, with examples from the tarsal joints of the sheep (*Ovis aries*). Journal of Zoology, London. 211: 487-504.

Andrews, P. 1974. New species of *Dryopithecus* from Kenya. Nature. 249: 188-190.

Andrews, P., Cronin J.E. 1982. The relationship of *Sivapithecus* and *Ramapithecus* and the evolution of the orang-utan. Nature. 297: 541-546.

Andrews, P., Harrison, T. 2006. The last common ancestor of apes and humans. In: Lieberman, D.E., Smith, R.J., Kelly, J. (eds). Interpreting the Past: Essays on Human, Primate, and Mammal Evolution. Boston: Brill Academic Publishers. pp. 103-122.

Ankel-Simons, F. 2000. Primate Anatomy. An Introduction. San Diego: Academic Press.

Antón, S.C., Leonard, W.R., Robertson, M.L. 2002. An ecomorphological model of the initial hominid dispersal from Africa. Journal of Human Evolution. 43: 773-785.

Antón, S.C. 2003. Natural history of *Homo erectus*. Yearbook of Physical Anthropology. 122: 126-170.

Appleton, A.B. 1913. Note on a variable feature of the astragalus. Journal of Anatomy and Physiology. 47: 123-142.

Asfaw, B., Gilbert, W.H., Beyene, Y., Hart, W.K., Renne, P.R., WoldeGabriel, G., Vrba, E.S., White, T.D. 2002. Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia. Nature. 416: 317-320.

Attarian, D.E., McCrackin, H.J., DeVito, D.P., McElhaney, J.H., Garrett, W.E. 1985. Biomechanical characteristics of human ankle ligaments. Foot and Ankle. 6: 54-58.

Autumn, K., Hsieh, S.T., Dudek, D.M., Chen, J., Chitaphan, C., Full, R.J. 2006. Dynamics of geckos running vertically. The Journal of Experimental Biology. 209: 260-272.

Avis, V. 1962. Brachiation: the crucial issue for man's ancestry. Southwest Journal of Anthropology. 18: 119-148.

Barnett, C.H. 1955. Some factors influencing the angulation of the neck of the mammalian talus. Journal of Anatomy. 89: 225-230.

Barnett, C.H., Napier, J.R. 1952. The axis of rotation at the ankle joint in man. Its influence upon the form of the talus and the mobility of the fibula. Journal of Anatomy. 86: 1-9.

Barnett, C.H., Napier, J.R. 1953. The rotatory mobility of the fibula in eutherian mammals. Journal of Anatomy. 87: 11-21.

Beau, A. 1939. Recherches sur le developpement et la constitution morphlogiques de l'articulation du cou-de-pied chez l'homme. Archives d'anatomie, d'histologie et d'embryologie. 27: 203-258.

Begeman, P.C., Prasad, P. 1990. Human ankle impact response in dorsiflexion. Proceedings of the 34th Stapp Car Crash Conference. No. 902308: 39-54.

Begun, D.R., Ward, C.V., Rose, M.D. 1997. Events in hominoid evolution. In Begun, D.R., Ward, C.V., Rose, M.D. (eds). Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press. pp. 389-416.

Begun, D.R, Ward, C.V. 2005. Comment on "*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain". Science. 308: 203.

Begun, D.R, Ward, C.V., Deana, A.S., Kivell, T.L., Nargolwalla, M.C., Taylor, N.D. 2006. Stem hominine or hominid? The phylogeny and functional anatomy of *Pierolapithecus catalaunicus*. American Journal of Physical Anthropology. (Suppl). 41: 63.

Berger, L.R. 2006. Brief communication: predatory bird damage to the Taung type-skull of *Australopithecus africanus* Dart 1925. American Journal of Physical Anthropology. 131: 166-168.

Berger, L.R., Tobias, P.V. 1996. A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for the interpretation of bipedalism in *Australopithecus africanus*. Journal of Human Evolution. 30: 343-348.

Berger, L.R., Lacruz, R., DeRuiter, D.J. 2002. Revised age estimates of *Australopithecus*-bearing deposits at Sterkfontein, South Africa. American Journal of Physical Anthropology. 119: 192-197.

Berillon, G. 2003. Assessing the longitudinal structure of the early hominin foot: a two-dimensional architecture analysis. Human Evolution. 18: 113-122.

Bernhardt, D.B. 1988. Prenatal and postnatal growth and development of the foot and ankle. Physical Therapy. 68: 1831-1839.

Beumer, A., van Hemert, W.L.W., Swierstra, B.A., Jasper, L.E., Belkoff, S.M. 2003. A biomechanical evaluation of the tibiofibular and tibiotalar ligaments of the ankle. Foot and Ankle International. 24: 426-429.

Beynnon, B.D., Renström, P.A., Alosa, D.M., Baumhauer, J.F., Vacek, P.M. 2001. Ankle ligament injury risk factors: a prospective study of college athletes. Journal of Orthopaedic Research. 19: 213-220.

Bishop, W.W., Miller, J.A., Fitch, F.J. 1969. New potassium-argon age determinations relevant to the Miocene fossil mammal sequences in East Africa. American Journal of Science. 267: 669-699.

Blackwood, C.B., Yuen, T.J., Sangeorzan, B.J., Ledoux, W.R. 2005. The midtarsal joint locking mechanism. Foot and Ankle International. 26: 1074-1080.

Bock, W.M., Winkler, H. 1978. Mechanical analysis of the external forces on climbing mammals. Zoomorphologie. 91: 49-61.

Bohonak, A.J. 2002. RMA: software for reduced major axis regression.

[http://www.bio.sdsu.edu/pub/andy/BohonakCV.html].

Bojsen-Møller, F. 1979. Calcaneocuboid joint and stability of the longitudinal arch of the foot at high and low gear push off. Journal of Anatomy. 129: 165-176.

Boss, A.P., Hintermann, B. 2002. Anatomical study of the medial ankle ligament complex. Foot and Ankle International. 23: 547-553.

Bramble, D.M., Lieberman, D.E. 2004. Endurance running and the evolution of *Homo*. Nature. 432: 345-352.

Brain, C.K. 1969. The probably role of leopards as predators of the Swartkrans australopithecines. South African Archaeological Bulletin. 24: 170-171.

Bremer, S.W. 1985. The unstable ankle mortise- functional ankle varus. The Journal of Foot Surgery. 24: 313-317.

Brenner, E., Piegger, J., Platzer, W. 2003. The trapezoid form of the trochlea tali. Surgical and Radiological Anatomy. 25: 216-225.

Burdett, R.G. 1982. Forces predicted at the ankle during running. Medicine and Science in Sports and Exercise. 14: 308-316.

Burks, R.T., Morgan, J. 1994. Anatomy of the lateral ligaments. The American Journal of Sports Medicine. 22: 72-77.

Butler, A.M., Walsh, W.R. 2004. Mechanical responses of ankle ligaments at low loads. Foot and Ankle International. 25: 8-12.

Calhoun, J.H., Eng, M., Li, F., Ledbetter, B.R., Viegas, S.F. 1994. A comprehensive study of pressure distribution in the ankle joint with inversion and eversion. Foot and Ankle. 15: 125-133.

Cant, J.G.H. 1987. Positional behavior of female bornean orangutans (*Pongo pygmaeus*). American Journal of Primatology. 12: 71-90.

Cant, J.G.H., Youlatos, D., Rose, M.D. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuní National Park, Ecuador: general patterns and nonsuspensory modes. Journal of Human Evolution. 41: 141-166.

Carrier, D. 2007. The short legs of great apes: evidence for aggressive behavior in australopiths. Evolution. 61: 596-605.

Carter, M.L., Pontzer, H., Wrangham, R.W., Peterhans, J.K. 2008. Skeletal pathology in *Pan troglodytes schweinfurthii* in Kibale National Park, Uganda. American Jouurnal of Physical Anthropology. In press.

Cartmill, M. 1972. Pads and claws in arboreal locomotion. In: Jenkins, F.A. (ed.). Primate Locomotion. New York: Academic Press. pp. 45-83.

Cartmill, M. 1985. Climbing. In: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, B.D. (eds.). Functional vertebrate morphology. Cambridge: Harvard University Press. pp. 73-88.

Cartmill, M., Milton, K. 1977. The lorisiform wrist and the evolution of “brachiating” adaptations in the Hominoidea. American Journal of Physical Anthropology. 47: 249-272.

Cass, J.R., Settles, H. 1994. Ankle instability: In vitro kinematics in response to axial load. Foot and Ankle. 15: 134-140.

Cavanaugh, P.R., LaFortune, M.A. 1980. Ground reaction forces in distance running. Journal of Biomechanics. 13: 397-406.

Chen, J., Siegler, S., Schneck, C.D. 1988. The three-dimensional kinematics and flexibility characteristics of the human ankle and subtalar joint – part II: flexibility characteristics. Journal of Biomechanical Engineering. 110: 374-385.

Christie, P.W. 1990. Mathematical representation and analysis of articular surfaces: application to the functional anatomy and palaeoanthropology of the ankle joint. Ph.D. Thesis. University of Witwatersrand.

Clarke, R.J. 1986. Early acheulean with *Homo habilis* at Sterkfontein. In Tobias, P.V. (ed.). Hominid Evolution: Past, Present, Future. New York: Alan R. Liss Inc. pp. 287-298.

Clarke, R.J. 1988. A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. In Grine, F.E. (ed.). Evolutionary History of the "Robust" Australopithecines. New York: Aldine de Gruyter. pp. 285-292.

Clarke, R.J. 1994. Advances in understanding the craniofacial anatomy of South African early hominids. In Corrucini, R.S., Ciochon, R.L. (eds.) Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell. New York: Prentice–Hall. pp. 205-222.

Clarke, R.J., Tobias, P.T. 1995. Sterkfontein Member 2 foot bones of the oldest South African hominid. Science. 269: 521-524.

Close, J.R. 1956. Some applications of the functional anatomy of the ankle joint. Journal of Bone and Joint Surgery. 38A: 761-781.

Close, J.R., Inman, V.T., Poor, P.M., Todd, F.N. 1967. The function of the subtalar joint. Clinical Orthopaedics and Related Research. 50: 159-179.

Coffing, K.E. 1998. The metacarpals of *Australopithecus afarensis*: locomotor and behavioral implications of cross-sectional geometry. Ph.D. Thesis. Johns Hopkins University.

Conroy, G.C., Rose, M.D. 1983. The evolution of the primate foot from the earliest primates to the Miocene hominoids. Foot and Ankle. 3: 342-364.

Corazza, F., Stagni, R., Castelli, V.P., Leardini, A. 2005. Articular contact at the tibiotalar joint in passive flexion. Journal of Biomechanics. 38: 1205-1212.

Costa, M.L., Logan, K., Heylings, D., Donell, S.T., Tucker, K. 2006. The effect of Achilles tendon lengthening on ankle dorsiflexion: a cadaver study. Foot and Ankle International. 27: 414-417.

Cox, J.S., Hewes, T.F. 1979. "Normal" talar tilt angle. Clinical Orthopaedics and Related Research. 140: 37-41.

Crompton, R.H., Thorpe, S., Weijie, W., Yu, L., Payne, R., Savage, R., Carey, T., Aerts, P., Van Elsacker, L., Hofstetter, A., Günther, M., Richardson, J. 2003. The biomechanical evolution of erect bipedality. Courier Forschunginstitut Senckenberg. 243: 135-146.

Curnoe, D., Tobias, P. 2006. Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. Journal of Human Evolution. 70: 36-77.

Currey, J.D. 2002. Bones. Structure and Mechanics. Princeton: Princeton University Press.

Czerniecki, J.M. 1988. Foot and ankle biomechanics in walking and running. A review. American Journal of Physical Medicine and Rehabilitation. 67: 246-252.

D'Août, K., Aerts, P., De Clercq, D., De Meester, K., Van Elsacker, L. 2002. Segment and joint angles of hind limb during bepedal and quadrupedal walking of the bonobo (*Pan paniscus*). American Journal of Physical Anthropology. 119: 37-51.

Darroch, J.N., Mosimann, J.E. 1985. Canonical and principal components of shape. Biometrika. 72: 241-252.

Day, M.H., Napier, J.R. 1964. Fossil foot bones. Nature. 201: 967-970.

Day, M.H., Leakey, R.E.F. 1974. New evidence of the genus *Homo* from East Rudolf, Kenya (III). American Journal of Physical Anthropology. 41: 367-380.

Day, M.H., Leakey, R.E.F., Walker, A.C., Wood, B.A. 1975. New hominids from East Rudolf, Kenya. American Journal of Physical Anthropology. 42: 461-476.

Day, M.H., Leakey, R.E.F., Walker, A.C., Wood, B.A. 1976. New hominids from East Turkana, Kenya. American Journal of Physical Anthropology. 45: 369-436.

Day, R.W., Quinn, G.P. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs. 59: 433-463.

Deloison, Y., 1986. Description d'un calcanéum fossile de primate et sa comparaison avec des calcanéum de Pongidés, d'Australopithèques et d'*Homo*. Comptes Rendus Academie of Sciences (IIA). 302: 257-262.

Deloison, Y., 1997. Description d'un astragale fossile de primate et comparaison avec des astragales de chimpanzés, d'*Homo sapiens* et d'hominoidés fossils: Australopithèques et *Homo habilis*. Comptes Rendus Academie of Sciences (IIA). 324: 685-692.

Deloison, Y. 2003. Anatomie des os fossils de pieds des hominids d'Afrique du sud dates entre 2,4 et 3,5 millions d'annés. Interprétation quant à leur mode de locomotion. Biométrie Humaine et Anthropologie. 21: 189-230.

DeSilva, J.M., Shoreman, E., MacLatchy, L. 2006. A fossil hominoid proximal femur from Kikongogo Crater, southwestern Uganda. Journal of Human Evolution. 50: 687-695.

Devine, J. 1985. The versatility of human locomotion. American Anthropologist. 87: 550-570.

Donatelli, R. 1990. The Biomechanics of the Foot and Ankle. Philadelphia: F.A. Davis Company.

Doran, D.M. 1993. Sex differences in adult chimpanzee positional behavior: the influence of body size on locomotion and posture. American Journal of Physical Anthropology. 91: 99-115.

Doran, D.M. 1993. The comparative locomotor behavior of chimpanzees and bonobos: the influence of morphology on locomotion. American Journal of Physical Anthropology. 89: 85-99.

Doran, D.M., Hunt, K.D. 1994. Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In: Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., Heltne, P.G. Chimpanzee Cultures. Cambridge: Harvard University Press. pp. 93-108.

Doran, D.M. 1996. Comparative positional behavior of the African apes. In: McGraw, W.C., Marchant, L.F., Nishida, T. (eds.) Great Ape Societies. Cambridge: Cambridge University Press. pp. 213-224.

Doran, D.M. 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. Journal of Human Evolution. 32: 323-344.

Drake, R.E., van Couvering, J.A., Pickford, M.H., Curtis, G.H., Harris, J.A. 1988. New chronology for the Early Miocene mammalian faunas of Kisingiri, Western Kenya. Journal of the Geological Society, London. 145: 479-491.

Drapeau, M.S.M., Ward, C.V., Kimbel, W.H., Johanson, D.C., Rak, Y. 2005. Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. Journal of Human Evolution. 48: 593-642.

Driscoll, H.L., Christensen, J.C., Tencer, A.F. 1994. Contact characteristics of the ankle joint. Part 1. The normal joint. Journal of the American Podiatric Medical Association. 84: 491-498.

Earll, M., Wayne, J., Brodrick, C., Vokshoor, A., Adelaar, R. 1996. Contribution of the deltoid ligament to ankle joint contact characteristics: a cadaver study. Foot and Ankle. 17: 317-324.

Elftman, H. 1960. The transverse tarsal joint and its control. Clinical Orthopaedics. 16: 41-45.

Elftman, H., Manter, J. 1935. Chimpanzee and human feet in bipedal walking. American Journal of Physical Anthropology. 20: 69-79.

Erikson, G.E. 1963. Brachiation in New World monkeys and in anthropoid apes. Symposium of the Zoological Society of London. 10: 135-164.

Feibel, C.S., Brown, F.H., McDougall, I. 1989. Stratigraphic context of fossil hominins from the Omo group deposits: Northern Turkana basin, Kenya and Ethiopia. American Journal of Physical Anthropology. 78: 595-622.

Feibel, C.S., Brown, F.H. 1991. Age of the primate-bearing deposits on Maboko Island, Kenya. Journal of Human Evolution. 21: 221-225.

Finarelli, J.A., Clyde, W.C. 2004. Reassessing hominoid phylogeny: evaluating congruence in the morphological and temporal data. Paleobiology. 30: 614-651.

Fisk, G.R., Macho, G.A. 1992. Evidence of a healed compression fracture in a Plio-Pleistocene hominid talus from Sterkfontein, South Africa. International Journal of Osteoarchaeology. 2: 325-332.

Fleagle, J.G. 1976. Locomotion and posture of the Malayan Siamang and implications for hominoid evolution. Folia Primatologica. 26: 245-269.

Fleagle, J.G. 1999. Primate Adaptation and Evolution. San Diego: Academic Press.

Fleagle, J.G., Stern, J.T. Jr., Jungers, W.L., Susman, R.L., Vangor, A.K., Wells, J.P. 1981. Climbing: a biomechanical link with brachiation and with bipedalism. Symposium of the Zoological Society of London. 48: 359-375.

Freeman, M.A.R., Wyke, B. 1967. The innervation of the ankle joint. An anatomical and histological study in the cat. Acta Anatomica. 68: 321-333.

Frost, H.M. 1979. A chondral modeling theory. Calcified Tissue International. 28: 181-2000.

Frost, H.M. 1999. Joint anatomy, design and arthroses: insights of the Utah paradigm. Anatomical Record. 255: 162-174.

Garrick, J.G. 1982. Epidemiological perspective. Clinical Journal of Sports Medicine. 1: 13-18.

Gebo, D.L. 1992. Plantigrady and foot adaptation in African apes: implications for hominin origins. American Journal of Physical Anthropology. 89: 29-58.

Gebo, D.L. 1993. Functional morphology of the foot in primates. In Gebo, D.L. (ed.). Postcranial Adaptation in Nonhuman Primates. DeKalb, Illinois: Northern Illinois Press. pp. 175-196.

Gebo, D.L. 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominin bipedalism. American Journal of Physical Anthropology. 101: 55-92.

Gebo, D.L., MacLatchy, L.M., Kityo, R., Deino, A., Kingston, J., Pilbeam, D. 1997. A hominoid genus from the early Miocene of Uganda. Science. 276: 401-404.

Gebo, D.L., Schwartz, G.T. 2006. Foot bones from Omo: implications for human evolution. American Journal of Physical Anthropology. 129: 499-511.

Gibson, V., Prieskorn, D. 2007. The valgus ankle. Foot and Ankle Clinics of North America. 12: 15-27.

Gittins, S.P. 1983. Use of the forest canopy by the agile gibbon. Folia Primatologica. 40: 134-144.

Golanó, P., Vega, J., Pérez-Carro, L., Götzens, V. 2006. Ankle anatomy for the arthroscopist. Part II: Role of the ankle ligmaments in soft tissue impingement. Foot and Ankle Clinics of North America. 11: 275-296.

Gomberg, D.N. 1981. Form and function of the hominoid foot. Ph.D. Thesis. University of Massachusetts, Amherst.

Gomberg, D.N., Latimer, B. 1984. Observations on the transverse tarsal joint of *A. afarensis*, and some comments on the interpretation of behaviour from morphology. American Journal of Physical Anthropology. 63: 164.

Gomberg, D.N. 1985. Functional difference of three ligaments of the transverse tarsal joint in hominoids. Journal of Human Evolution. 14: 553-562.

Gommery, D., Senut, B., Pickford, M. 1998. Nouveaux restes postcrâniens d'Hominoidea du Miocène inférieur de Napak, Ouganda. Annales de Palèontologie. 84: 287-306.

Gommery D, Senut, B., Pickford, M., Musiime, E. 2002. Les nouveaux restes du squelette d'*Ugandapithecus major* (Miocene inferieur de Napak, Ouganda. Annales de Paléontologie. 88: 167-186.

Gommery, D., Senut, B. 2006. The terminal thumb phalanx of *Orrorin tugenensis* (Upper Miocene of Kenya). Geobios. 39: 372-384.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behavior. Cambridge: Belknap Press of Harvard University Press.

Grand, T.I. 1967. The functional anatomy of the ankle and foot of the slow loris (*Nycticebus coucang*). American Journal of Physical Anthropology. 26: 207-218.

Grausz, H.M., Leakey, R.E., Walker, A.C., Ward, C.V. 1988. Associated cranial and postcranial bones of *Australopithecus boisei*. In Grine, F.E. (ed.). Evolutionary History of the "Robust" Australopithecines. New York: Aldine de Gruyter. pp. 127-132.

Green, D.J., Gordon, A.D., Richmond, B.G. 2007. Limb-size proportions in *Australopithecus afarensis* and *Australopithecus africanus*. Journal of Human Evolution. 52: 187-200.

Greenwald, A.S. 1983. Ankle Joint Mechanics. In: Yablon, I.G., Segal, D., Leach, R.E. (eds.). Ankle Injuries. New York: Churchill Livingstone. pp. 253-264.

Grodinskiy, A.J., Levenston, M.E., Jin, M., Frank, E.H. 2000. Cartilage tissue remodeling in response to mechanical forces. Annual Review of Biomedical Engineering. 2: 691-713.

Guillot, D., Youlatos, D., Lawler, R., MacLatchy, L. 2008. Patterns of positional behavior among ateline primates: a comparative study of *Alouatta seniculus*, *Lagothrix poeppigii*, *Ateles belzebuth*. Journal of Human Evolution. In press.

Haeusler, M., McHenry, H.M. 2007. Evolutionary reversals of limb proportions in early hominids? Evidence from KNM-ER 3735 (*Homo habilis*). Journal of Human Evolution. 53: 383-405.

Hamrick, M.W. 1999a. A chondral modeling theory revisited. Journal of Theoretical Biology. 201: 201-208.

Hamrick, M.W. 1999b. Development of the epiphyseal structure and function in *Didelphis virginiana* (Marsupiala, Didelphidae). Journal of Morphology. 239: 283-296.

Harcourt-Smith, W. 2002. Form and function in the hominoid tarsal skeleton. Ph.D. thesis. University College London.

Harcourt-Smith, W. 2004. Did *Australopithecus afarensis* make the Laetoli footprint trail? New insights into an old problem. American Journal of Physical Anthropology (Suppl.). 123: 112.

Harcourt-Smith, W., Aiello, L.C. 2004. Fossils, feet and the evolution of human bipedal locomotion. Journal of Anatomy. 204: 403-416.

Harper, M.C. 1987. Deltoid ligament: an anatomical evaluation of function. Foot and Ankle. 8: 19-22.

Harper, M.C. 1990. Talar shift. The stabilizing role of the medial, lateral, and posterior ankle structures. Clinical Orthopaedics and Related Research. 257: 177-183.

Harrington, K.D. 1979. Degenerative arthritis of the ankle secondary to long-standing lateral ligament instability. Journal of Bone and Joint Surgery. 61A: 354-361.

Harrison, T. 1982. Small-bodied apes from the Miocene of East Africa. Ph.D. Thesis. University of London.

Harrison, T. 1986. New fossil anthropoids from the middle Miocene of East Africa and their bearing on the origin of the Orepithecidae. American Journal of Physical Anthropology. 71: 265-284.

Harrison, T. 1987. A reassessment of the phylogenetic relationships of *Oreopithecus bambolii* Gervais. Journal of Human Evolution. 15: 541-583.

Harrison, T. 1987. The phylogenetic relationship of the early catarrhine primates: a review of the current evidence. Journal of Human Evolution. 16: 41-80.

Harrison, T. 1989. New postcranial remains of *Victoriapithecus* from the Middle Miocene of Kenya. Journal of Human Evolution. 18: 3-54.

Harrison, T. 2002. Late Oligocene to middle Miocene catarrhines from Afro-Arabia. In: Hartwig, W. (Ed.). The Primate Fossil Record. Cambridge: Cambridge University Press. pp. 311-338.

Harrison, T., Rook, L. 1997. Enigmatic anthropoid or misunderstood ape? The phylogenetic status of *Oreopithecus bambolii* reconsidered. In Begun, D.R., Ward, C.V., Rose, M.D. (eds.). Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press. pp. 327-361.

Hartwig-Scherer, S., Martin, R.D. 1991. Was "Lucy" more human than her "child"? Observations on early hominid postcranial skeletons. Journal of Human Evolution. 21: 439-449.

Heinrich, R.E., Rose, M.D., Leakey, R.E., Walker, A.C. 1993. Hominid radius from the middle Pliocene of Lake Turkana, Kenya. American Journal of Physical Anthropology. 92: 139-148.

Heiple, K.G., Lovejoy, C.O. 1971. The distal femoral anatomy of *Australopithecus*. American Journal of Physical Anthropology. 35: 75-84.

Hertel, J. 2002. Functional anatomy, pathomechanics, and pathophysiology of lateral ankle instability. Journal of Athletic Training. 37: 364-375.

Hicks, J.H. 1953. The mechanics of the foot. I. The joints. Journal of Anatomy. 83: 345-357.

Hill, W.C.O. 1953. Primates, Comparative Anatomy and Taxonomy. Volume 4. Cebidae. Part A. New York: Interscience Publishers.

Hill, W.C.O. 1953. Primates, Comparative Anatomy and Taxonomy. Volume 6. Catarrhini and Cercopithecoidea. New York: Interscience Publishers.

Hildebrand, M. 1985. Walking and running. In: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B. (eds.). Functional Vertebrate Morphology. Cambridge: Harvard University Press. pp. 38-57.

Hintermann, B. 2002. Biomechanics of ligaments in ankle instability. In: Nyska, M., Mann, G. (eds.). The Unstable Ankle. Champaign, Illinois: Human Kinetics. pp. 27-35.

Hirasaki, E., Kumakura, H., Matano, S. 1993. Kinesiological characteristics of vertical climbing in *Ateles geoffroyi* and *Macaca fuscata*. Folia Primatologica. 61: 148-156.

Hirasaki, E., Kumakura, H., Matano, S. 2000. Biomechanical analysis of vertical climbing in the spider monkey and the Japanese macaque. American Journal of Physical Anthropology. 113: 455-472.

Hubbard, T.J., Kramer, L.C., Denegar, C.R., Hertel, J. 2007. Contributing factors to chronic ankle instability. Foot and Ankle International. 28: 343-354.

Hunt, K.D. 1989. Positional behavior in *Pan troglodytes* at the Mahale Mountains and the Gombe Stream National Parks, Tanzania. Ph.D. Thesis. University of Michigan.

Hunt, K.D. 1991. Positional behavior in the Hominoidea. International Journal of Primatology. 12: 95-118.

Hunt, K.D. 1992. Positional behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. American Journal of Physical Anthropology. 87: 83-105.

Hunt, K.D. 1994. The evolution of human bipedality: ecology and functional morphology. Journal of Human Evolution. 26: 183-202.

Hunt, K.D., Cant, J.G.H., Gebo, D.L., Rose, M.D., Walker, S.E., Youlatos, D. 1996. Standardized descriptions of primate locomotor and postural modes. Primates. 37: 363-387.

Hunt, K.D. 1998. Ecological morphology of *Australopithecus afarensis*. In: Strasser, E., Fleagle, J., Rosenberger, A., McHenry, H. (eds.). Primate Locomotion. Recent Advances. New York: Plenum Press. pp. 397-418.

Hunt, K.D. 2004. The special demands of great ape locomotion and posture. In: Russon, A.E., Begun, D.R. (eds.). The Evolution of Thought. Cambridge: Cambridge University Press. pp. 172-189.

Huson, A. 2000. Biomechanics of the tarsal mechanism. A key to the function of the normal human foot. Journal of the American Podiatric Medical Association. 90: 12-17.

Inman, V.T. 1976. The Joints of the Ankle. Baltimore: Williams and Wilkins.

Ishida, H., Kunimatsu, Y., Nakatsukasa, M., Nakano, Y. 1999. New hominoid genus from the Middle Miocene of Nachola, Kenya. Anthropological Sciences. 107: 189-191.

Ishida, H., Kunimatsu, Y., Takano, T., Takano, Y., Nakatsukasa, M. 2004. *Nacholapithecus* skeleton from the Middle Miocene of Kenya. Journal of Human Evolution. 46: 69-103.

Isler, K. 2002. Characteristics of vertical climbing in the African apes. Senckenbergiana lethaea. 82: 115-124.

Isler, K. 2003. 3D-kinematics of vertical climbing in hominoids. Ph.D. Thesis. University of Zürich.

Isler, K. 2004. Footfall Patterns, Stride Length and Speed of Vertical Climbing in Spider Monkeys (*Ateles fusciceps robustus*) and Woolly Monkeys (*Lagothrix lagotricha*). Folia Primatologica. 75: 133-149.

Isler, K. 2005. 3-D kinematics of vertical climbing in hominoids. American Journal of Physical Anthropology. 126: 66-82.

Isler, K., Thorpe, S.K.S. 2003. Gait parameters in vertical climbing of captive, rehabilitant and wild Sumatran orang-utans (*Pongo pygmaeus abelii*). Journal of Experimental Biology. 206: 4081-4096.

Jenkins, F. 1972. Chimpanzee bipedalism: cineradiographic analysis and implications for the evolution of gait. Science. 178: 877-879.

Johanson, D.C., Lovejoy, C.O., Kimbel, W.H., White, T.D., Ward, S.C., Bush, M.E., Latimer, B.M., Coppens, Y. 1982. Morphology of the Pliocene partial hominid skeleton (A.L. 288-1) from the Hadar formation, Ethiopia. American Journal of Physical Anthropology. 57: 403-451.

Johnson, E.E., Markolf, K.L. 1983. The contribution of the anterior talofibular ligament to ankle laxity. J. Bone Joint Surg. 65A: 81-88.

Jungers, W.L. 1982. Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. Nature. 297: 676-678.

Jungers, W.L. 1984. Scaling of the hominoid locomotor skeleton with special reference to the lesser apes. In: Preuschoft, H. Chivers, D. Brockelman, W. Creel, N. (eds.). The Lesser Apes. Edinburgh: Edinburgh University Press. pp. 146-169.

Jungers, W.L. 1987. Body size and morphometric affinities of the appendicular skeleton of *Oreopithecus bambolii* (IGF 11778). Journal of Human Evolution. 16: 445-456.

Jungers, W.L., Stern, J.T., Jr., Jouffroy, F.K. 1983. Functional morphology of the quadriceps femoris in primates: a comparative anatomical and experimental analysis. Annales des Sciences Naturelles. Zoologie et Biologie Animale. 1: 147-155.

Jungers, W.L., Meldrum, J.D., Stern, J.T., Jr. 1993. The functional and evolutionary significance of the human peroneus tertius muscle. Journal of Human Evolution. 25: 377-386.

Kano, T. 1983. An ecological study of the pygmy chimpanzee (*Pan paniscus*) of Yalosidi, Republic of Zaire. International Journal of Primatology. 4: 1-31.

Keith, A. 1893-1894. The ligaments of the catarrhine monkeys, with references to the corresponding structures in man. Journal of Anatomy and Physiology. 28: 149-168.

Keith, A. 1923. Man's posture: its evolution and disorders. 2. The evolution of the orthograde spine. British Medical Journal. 1: 499-502.

Keith, A. 1928. The history of the human foot and its bearing on orthopaedic practice. Journal of Bone and Joint Surgery. 11: 10-32.

Kelley, J. 1997. Paleobiological and phylogenetic significance of life history in Miocene hominoids. In Begun, D.R., Ward, C.V., Rose, M.D. (eds). Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press. pp. 173-208.

Kennedy, G.E. 1983. A morphometric and taxonomic assessment of a hominine femur from the lower member, Koobi Fora, Lake Turkana. American Journal of Physical Anthropology. 61: 429-436.

Khin-Myo-Hla, Ishii, T., Sakane, M., Hayashi, K. 1999. Effect of anesthesia of the sinus tarsi on peroneal reaction time in patients with functional instability of the ankle. Foot and Ankle International. 20: 554-559.

Kidd, R. 1993. Gradualistic evolution as expressed in the hominoid talus. Journal of British Podiatric Medicine. November: 171-174.

Kidd, R. 1993. The long arch: new thoughts on the evolution of an old structure. Australian Podiatrist. June: 35-43.

Kidd, R.S., O'Higgins, P., Oxnard, C.E. 1996. The OH 8 foot: a reappraisal of the functional morphology of the hindfoot utilizing a multivariate analysis. Journal of Human Evolution. 31: 269-291.

Kidd, R. 1998. The past is key to the present: thoughts on the origins of human foot structure, function and dysfunction as seen from the fossil record. The Foot. 8: 75-84.

Kidd, R., Oxnard, C. 2005. Little foot and big thoughts- a re-evaluation of the StW 573 foot from Sterkfontein, South Africa. Homo. 55: 189-212.

Kimbel, W.H., Rak, Y., Johanson, D.C. 2004. The Skull of *Australopithecus afarensis*. Oxford: Oxford University Press.

Klein, M.A. 1994. MR Imaging of the ankle: normal and abnormal findings in the medial collateral ligament. American Journal of Roentgenology. 162: 377-383.

Konradsen, L., Ravn, J.B. 1990. Ankle instability caused by prolonged peroneal reaction time. Acta Orthopaedica Scandinavia. 61: 388-390.

Konradsen, L., Højsgaard, C. 1993. Pre-heel-strike peroneal muscle activity during walking and running with and without an external ankle support. Scandinavian Journal of Medicine and Science in Sports. 3: 99-103.

Konradsen, L., Voigt, M., Højsgaard, C. 1997. Ankle inversion injuries. The role of the dynamic defense mechanism. American Journal of Sports Medicine. 25: 54-58.

Konradsen, L. 2002. Sensori-motor control of the uninjured and injured human ankle. Journal of Electromyography and Kinesiology. 12: 199-203.

Kordos, L., Begun, D.R. 2001. Primates from Rudabánya: allocation of specimens to individuals, sex and age categories. Journal of Human Evolution. 40: 17-39.

Krentz, H.B. 1993. Postcranial anatomy of extant and extinct species of *Theropithecus*. In Jablonski, N. (ed.) Theropithecus: the rise and fall of a primate genus. Cambridge: Cambridge University Press. pp. 383-424.

Kuman, K., Clarke, R.J. 2000. Stratigraphy, artifact industries and hominin associations for Sterkfontein, Member 5. Journal of Human Evolution. 38: 827-847.

Kumai, T., Takakura, Y., Rufai, A., Milz, S., Benjamin, M. 2002. The functional anatomy of the human anterior talofibular ligament in relation to ankle sprains. Journal of Anatomy. 200: 457-465.

Kunimatsu, Y. 1992. A revision of the hypodigm of *Nyanzapithecus vancouveringi*. African Study Monographs. 13: 231-235.

Kura, H., Kitaoka, H.B., Luo, Z.-P., An, K.-N. 1998. Measurement of surface contact area of the ankle joint. Clinical Biomechanics. 13: 365-370.

Kuroda, S., Nishihara, T., Suzuki, S., Oko, R.A. 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In: McGraw, W.C., Marchant, L.F., Nishida, T. (eds.) Great Ape Societies. Cambridge: Cambridge University Press. pp. 71-81.

Lamy, P. 1986. The settlement of the longitudinal plantar arch of some African Plio-Pleistocene hominins: a morphological study. Journal of Human Evolution. 15: 31-46.

Langdon, J.H. 1985. Fossils and the origin of bipedalism. Journal of Human Evolution. 14: 615-635.

Langdon, J.H. 1986. Functional Morphology of the Miocene Hominoid Foot. Contributions to Primatology. Volume 22. New York: Karger.

Langdon, J.H., Bruckner, J., Baker, H.H. 1991. Pedal mechanics and bipedalism in early hominins. In: Coppens, Y., Senut, B. (eds.). Origine(s) de la Bipédie chez les Homininés. Paris: Centre National de la Recherche Scientifique. pp. 159-167.

Larson, S. 1998. Parallel evolution in the hominoid trunk and forelimb. Evolutionary Anthropology. 6: 87-99.

Latimer, B. 1991. Locomotion adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Coppens, Y., Senut, B. (eds.). Origine(s) de la Bipédie chez les Homininés. Paris: Centre National de la Recherche Scientifique. pp. 169-176.

Latimer, B.M., Lovejoy, C.O., Johanson, D.C., Coppens, Y. 1982. Hominin tarsal, metatarsal, and phalangeal bones recovered from the Hadar Formation: 1974-1977 collections. American Journal of Physical Anthropology. 57: 701-719.

Latimer, B., Ohman, J.C., Lovejoy, C.O. 1987. Talocrural joint in African hominoids: implications for *Australopithecus afarensis*. American Journal of Physical Anthropology. 74: 155-175.

Latimer, B., Lovejoy, C.O. 1989. The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. American Journal of Physical Anthropology. 78: 369-386.

Latimer, B., Lovejoy, C.O. 1990. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. American Journal of Physical Anthropology. 82: 125-133.

Latimer, B., Lovejoy, C.O. 1990. Metatarsophalangeal joints of *Australopithecus afarensis*. American Journal of Physical Anthropology. 83: 13-23.

Lauge-Pedersen, H., Aspenberg, P., Ryd, L., Tanner, K.E. 2002. Arch-shaped versus flat arthodesis of the ankle joint: strength measurements using synthetic cancellous bone. Proceedings of the Institution of Mechanical Engineers. 216: 43-49.

Leakey, L.S.B., Tobias, P.V., Napier, J.R. 1964. A new species of genus *Homo* from Olduvai Gorge. Nature. 202: 7-9.

Leakey, M.D. 1971. Olduvai Gorge. Excavations in Beds I and II. 1960-1963. Cambridge: Cambridge University Press.

Leakey, M.G. 1982. Extinct large colobines from the Plio-Pleistocene of Africa. American Journal of Physical Anthropology. 58: 153-172.

Leakey, M.G., Feibel, C.S., McDougall, I., Walker, A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature. 376: 565-571.

Leakey, M.G., Feibel, C.S., McDougall, I., Ward, C., Walker, A. 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. Nature. 393: 62-66.

Leakey, M.G., Ungar P.S., Walker A.C. 1995. A new genus of large primate from the Late Oligocene of Lothikok, Turkana District, Kenya. Journal of Human Evolution. 28: 519-531.

Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N., McDougall, I. 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. Nature. 410: 433-440.

Leakey, R.E.F., Mungai, J.M., Walker, A.C. 1972. New australopithecines from East Rudolf, Kenya (II). American Journal of Physical Anthropology. 36: 235-251.

Leakey, R.E.F. 1973. Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1972. Nature. 242: 170-173.

Leakey, R.E.F., Walker, A. 1985. Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. American Journal of Physical Anthropology. 67: 135-163.

Leakey, R.E.F., Leakey, M.G. 1986. A new Miocene hominoid from Kenya. Nature. 324: 143-146.

Leakey, R.E.F., Leakey, M.G. 1987. A new Miocene small-bodied ape from Kenya. Nature. 16: 369-387.

Leakey, R.E.F., Leakey, M.G., Walker A.C. 1988. Morphology of *Afropithecus turkanensis* from Kenya. American Journal of Physical Anthropology. 76: 289-307.

Leakey, R.E.F., Walker, A.C., Ward, C.V., Grausz, H.M. 1989. A partial skeleton of a gracile hominid from the Upper Burgi Member of the Koobi Fora Formation, East Lake Turkana, Kenya. In: Giacobini, G. (ed.). Hominidae, Proceedings of the 2nd International Congress of Human Paleontology, Turin. Milano: Jaca Books. pp. 167-173.

Leardini, A., O'Connor, J.J., Catani, F., Giannini, S. 1999. Kinematics of the human ankle complex in passive flexion; a single degree of freedom system. Journal of Biomechanics. 32: 111-118.

Leardini, A., O'Connor, J.J, Catani, F., Giannini, S. 2000. The role of the passive structures in the mobility and stability of the human ankle joint: A literature review. Foot and Ankle. 21: 602-615.

Lentell, G., Baas, B., Lopez, D., McGuire, L., Sarrels, M., Snyder, P. 1995. The contributions of proprioceptive deficits, muscle function, and anatomic laxity to functional instability of the ankle. Journal of Orthopaedic and Sports Physical Therapy. 21: 206-215.

Le Gros Clark, W.E. 1947. Observations on the anatomy of the fossil Australopithecinae. Journal of Anatomy. 81: 300-333.

Le Gros Clark, W.E. 1952. Report on fossil material collected by the British-Kenya Miocene Expedition, 1949-1951. Proceedings of the Zoological Society of London. 122: 273-286.

Lewis, O.J. 1980. The joints of the evolving foot. Part II. The intrinsic joints. Journal of Anatomy. 130: 833-857.

Lewis, O.J. 1980. The joints of the evolving foot. Part III. The fossil evidence. Journal of Anatomy. 131: 275-298.

Lisowski, F.P., Albrecht, G.H., Oxnard, C.E. 1974. The form of the talus in some higher primates: a multivariate study. American Journal of Physical Anthropology. 41: 191-216.

Liu, S.H., Jason, W.J. 1994. Lateral ankle sprains and instability problems. Foot and Ankle Injuries. 13: 793-809.

Lockwood, C.A., Tobias, P.V. 2002. Morphology and affinities of new hominin cranial remains from Member 4 of the Sterkfontein Formation, Gauteng Province, South Africa. Journal of Human Evolution. 42: 389-350.

Lordkipanidze, D., Jashashville, T., Vekua, A., Ponce de Léon, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L. 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. Nature. 449: 305-310.

Lovejoy, C.O. 1978. A biomechanical review of the locomotor diversity of early hominids. In: Jolly, C.E. (ed). Early Hominids of Africa. London: Duckworth. pp. 403-429

Lovejoy, C.O. 2005a. The natural history of human gait and posture. Part 1. Spine and pelvis. Gait and Posture. 21: 95-112.

Lovejoy, C.O. 2005b. The natural history of human gait and posture. Part 2. Hip and thigh. Gait and Posture. 21: 113-124.

Lovejoy, C.O. 2007. The natural history of gait and posture. Part 3. The knee. Gait and Posture. 25: 325-341.

Lovejoy, C.O., Heiple, K.G. 1972. Proximal femoral anatomy of *Australopithecus*. Nature. 235: 175-176.

Lovejoy, C.O., Meindl, R.S., Pryzbeck, T.R., Barton, T.S., Heiple, K.G., Kotting, D. 1977. Paleodemography of the Libben Site, Ottawa County, Ohio. Science. 198: 291-293.

Lovejoy, C.O., Johanson, D.C., Coppens, Y. 1982. Hominid lower limb bones recovered from the Hadar formation: 1974-1977 Collections. American Journal of Physical Anthropology. 57: 679-700.

Lovejoy, C.O., Cohn, M.J., White, T.D. 1999. Morphological analysis of the mammalian postcranium: a developmental perspective. Proceedings of the National Academy of Sciences. 96: 13247-13252.

Lovejoy, C.O., Meindl, R.S., Ohman, J.C., Heiple, K.G., White, T.D. 2002. The Maka femur and its bearing on the antiquity of human walking: applying contemporary concepts of morphogenesis to the human fossil record. American Journal of Physical Anthropology. 119: 97-133.

Lundberg, A., Svensson, O.K., Németh, G., Selvik, G. 1989. The axis of rotation of the ankle joint. Journal of Bone and Joint Surgery [Br]. 71B: 94-99.

Lundberg, A., Goldie, I., Kalin, B., Selvik, G. 1989. Kinematics of the ankle/foot complex: plantarflexion and dorsiflexion. Foot and Ankle. 9: 194-200.

Luo, Z-P., Kitaoka, H.B., Hsu, H-C., Kura, H., An, K-N. 1997. Physiological elongation of ligamentous complex surrounding the hindfoot joints: In vitro biomechanical study. Foot and Ankle International. 18: 277-283.

MacInnes, D.G. 1943. Notes on the East African Miocene primates. Journal of the East African Uganda Natural History Society Nairobi. 17: 141-181.

MacLatchy, L.M. 1996. Another look at the australopithecine hip. Journal of Human Evolution. 31: 455-476.

MacLatchy, L.M., Gebo, D., Kityo, R., Pilbeam, D. 2000. Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. Journal of Human Evolution. 39: 159-183.

MacLatchy L.M. 2004. The oldest ape. Evolutionary Anthropology. 13: 90-103.

MacLatchy L.M., Rossie J.B. 2005. The Napak hominoid: still *Proconsul major*. In: Lieberman, D.E., Smith, R.J., Kelly, J. (eds). Interpreting the Past: Essays on Human, Primate, and Mammal Evolution. Boston: Brill Academic Publishers. pp. 15-28.

MacLatchy, L.M., Deino, A., Kingston, J. 2006. An updated chronology for the early Miocene of NE Uganda. Journal of Vertebrate Paleontology (Suppl.). A26: 93.

MacLatchy, L.M., Cote, S., Kingston, J., Rossie, J., Winkler, A. 2007. New early Miocene localities at Napak, Uganda. Journal of Vertebrate Paleontology (Suppl.). 27: 109A.

Madar, S.I., Rose, M.D., Kelley, J., MacLatchy, L., Pilbeam, D. 2002. New *Sivapithecus* postcranial specimens from the Siwaliks of Pakistan. Journal of Human Evolution. 42: 705-752.

MacKinnon, J. 1974. The behavior and ecology of wild orang-utans (*Pongo pygmaeus*). Animal Behavior. 22: 3-74.

Manter, J.T. 1941. Movements of the subtalar and transverse tarsal joints. The Anatomical Record. 80: 397-410.

McBrearty, S., Brooks, A.S. 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. Journal of Human Evolution. 39: 453-563.

McHenry, H.M. 1991. First steps? Analysis of the postcranium of early hominids. In: Coppens, Y. Senut, B. (eds.). Origine(s) de las Bipedie chez les Hominides. Paris: Editions du Centre National de la Recherche Scientifique. pp 133-141.

McHenry, H.M. 1992. Body size and proportions in early hominids. American Journal of Physical Anthropology. 87: 407-431.

McHenry, H.M. 1994. Early hominid postcrania. In: Corruccini, R.S., Ciochon, R.L. (eds.). Integrative Paths to the Past. Englewood Cliffs, NJ: Prentice Hall. pp. 251-268.

McHenry, H.M., Berger, L. 1998. Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. Journal of Human Evolution. 35: 1-22.

McHenry, H.M., Jones, A.L. 2006. Hallucial convergence in early hominins. Journal of Human Evolution. 50: 534-539.

McKee, J.K. Thackeray, J.F., Berger, L.R. 1995. Faunal assemblage seriation of sourthern African Pliocene and Pleistocene fossil deposits. American Journal of Physical Anthropology. 96: 235-250.

Meldrum, D.J. 1991. Kinematics of the cercopithecine foot on arboreal and terrestrial substrates with implications for the interpretation of hominin terrestrial adaptations. American Journal of Physical Anthropology. 84: 273-289.

Meldrum, D.J., Wunderlich, R.E. 1998. Midfoot flexibility in ape foot dynamics, early hominid footprints and bipedalism. American Journal of Physical Anthropology (Suppl). 26: 161.

Meldrum, D.J. 2002. Midfoot flexibility and the evolution of bipedalism. American Journal of Physical Anthropology (Suppl). 34: 111-112.

Michelson, J.D., Helgemo, S.L. 1995. Kinematics of the axially loaded ankle. Foot and Ankle International. 16: 577-582.

Michelson, J.D., Hutchins, C. 1995. Mechanoreceptors in human ankle ligaments. Journal of Bone and Joint Surgery. 77B: 219-224.

Michelson, J.D., Checcone, M., Kuhn, T., Varner, K. 2001. Intra-articular load distribution in the human ankle joint during motion. Foot and Ankle International. 22: 226-233.

Millard, A.R. 2008. A critique of the chronometric evidence for hominid fossils: I. African and the Near East 500-50 ka. Journal of Human Evolution. In press.

Milner, C.E., Soames, R.W. 1997. Anatomical variations of the anterior talofibular ligament of the human ankle joints. Journal of Anatomy. 191: 457-458.

Milner, C.E., Soames, R.W. 1998. The medial collateral ligaments of the human ankle joint: anatomical variations. Foot and Ankle International. 19: 289-292.

Milner, C.E., Soames, R.W. 1998. Anatomy of the collateral ligaments of the human ankle joint. Foot and Ankle International. 19: 757-760.

Minetti, A.E., Saibene, F., Ardigo, L.P., Atchou, G., Schena, F., Ferretti, G. 1994. Pygmy locomotion. European Journal of Applied Physiology. 68: 285-290.

Mkandawire, C., Ledoux, W.R., Sangeorzan, B.J., Ching, R.P. 2005. Foot and ankle ligament morphometry. Journal of Rehabilitation Research and Development. 42: 809-820.

Moggi-Cecchi, J., Tobias, P.V., Beynon, A.D. 1998. The mixed dentition and associated skull fragments of a juvenile fossil hominid from Sterkfontein, South Africa. American Journal of Physical Anthropology. 106: 425-465.

Morbeck, M.E. 1983. Miocene hominoid discoveries from Rudabánya. Implications from the postcranial skeleton. In: Ciochon, R.L. (ed.). New Interpretations of Human and Ape Ancestry. New York: Plenum Press. pp. 369-404.

Moyà-Solà, S, Köhler, M. 1996. A *Dryopithecus* skeleton and the origins of great-ape locomotion. Nature. 379: 156-159.

Moyà-Solà, S, Köhler, M., Alba, D., Casanovas-Vilar, I., Galindo, J. 2004. *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science. 306: 1339-1344.

Muybridge, E. 1957. Animals in Motion. New York: Dover Publications.

Nengo, I.O., Rae, T.C. 1992. New hominoid fossils from the early Miocene site of Songhor, Kenya. Journal of Human Evolution. 23: 423-429.

Nigg, B.M., Skarvan, G., Frank, C.B., Yeadon, M.R. 1990. Elongation and forces of ankle ligaments in a physiological range of motion. Foot and Ankle. 11: 30-40.

Njau, J., Blumenschine, R. 2007. Crocodilian predation risk for Plio-Pleistocene hominins at Olduvai Gorge, Tanzania. Paleoanthropology. A21.

Oatis, C.A. 1988. Biomechanics of the foot and ankle under static conditions. Physical Therapy. 68: 1815-1821.

Organ, J.M., Ward, C.V. 2006. Contours of the hominoid lateral tibial condyle with implications for *Australopithecus*. Journal of Human Evolution. 51: 113-127.

Ouzounian, T.J., Shereff, M.J. 1989. In vitro determination of midfoot motion. Foot and Ankle International. 10: 140-146.

Oxnard, C.E., Lisowski, F.P. 1980. Functional articulation of some hominoid foot bones: implications for the Olduvai (hominin 8) foot. American Journal of Physical Anthropology. 52: 107-117.

Owen, J. 2007. Odd fossil skeletons show both apelike and human traits. National Geographic News. September 19.

Pankovich, A.R., Shivaram, M.S. 1979. Anatomical basis of variability in injuries of the medial malleolus and the deltoid ligament. Acta Orthopaedica Scandinavica. 50: 217-223.

Parenteau, C.S., Viano, D.C., Petit, P.Y. 1998. Biomechanical properties of human cadaveric ankle-subtalar joints in quasi-static loading. Journal of Biomechanical Engineering. 120: 105-111.

Parsons, F.G. 1899. The joints of mammals compared with those of man. Journal of Anatomy. 34: 302-323.

Payne, R. 2001. Musculoskeletal adaptations for climbing in hominoids and their role as exaptations for the acquisition of bipedalism. Ph.D. Thesis. The University of Liverpool.

Pearson, C.M., Lieberman, D.E. 2004. The aging of Wolff's "Law": ontogeny and responses to mechanical loading in cortical bone. Yearbook of Physical Anthropology. 47: 63-99.

Pickering, T.R., Clarke, R.J., Moggi-Cecchi, J. 2004. Role of carnivores in the accumulation of the Sterkfontein Member 4 hominid assemblage: A taphonomic reassessment of the complete hominid fossil sample (1936-1999). American Journal of Physical Anthropology. 125: 1-15.

Pickford, M. 2006. Paleoenvironments, paleoecology, adaptations, and the origins of bipedalism in homininae. In: Ishida, H., Tuttle, R., Pickford, M., Ogihara, N., Nakatsukasa, M. (eds.). Human Origins and Environmental Backgrounds. New York: Springer. pp. 175-198.

Pickford, M., Andrews, P. 1981. The Tinderet Miocene sequence. Journal of Human Evolution. 10: 11-33.

Pickford, M., Senut, B., Gommery, D., Treil, J. 2002. Bipedalism in *Orrorin tugenensis* revealed by its femora. Comptes Rendus Palevol. 1: 191-203.

Pilbeam, D.R. 1969. Possible identity of Miocene tali from Kenya. Nature. 223: 648.

Pilbeam, DR. 1982. New hominoid skull material from the Miocene of Pakistan. Nature. 295: 232-234.

Pilbeam, D.R. 1996. Genetic and morphological records of the hominoidea and hominid origins: a synthesis. Molecular Phylogenetics and Evolution. 5: 155-168.

Pilbeam, D.R., Rose, M.D., Badgley, C., Lipschutz, B. 1980. Miocene hominoids from Pakistan. Postilla. 181: 1-94.

Pilbeam, D.R., Rose M.D., Barry J.C., Ibrahim Shah S.M. 1990. New *Sivapithecus* humeri from Pakistan and the relationship between *Sivapithecus* and *Pongo*. Nature. 348: 237-239.

Pilbeam, D.R., Young, N.M. 2004. Hominoid evolution: synthesizing disparate data. Comptes Rendus Palevol. 3: 305-321.

Pontzer, H., Wrangham, R.W. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotion evolution. Journal of Human Evolution. 46: 317-335.

Pontzer, H. 2005. A new model predicting locomotor cost from limb length *via* force production. Journal of Experimental Biology. 208: 1513-1524.

Preuschoft, H. 1970. Functional anatomy of the lower extremity. In: Bourne, G.H. (ed.). The Chimpanzee. Vol. 3. Basel: Karger. pp. 221-294.

Preuschoft, H. 1971. Body posture and mode of locomotion in early Pleistocene hominins. Folia Primatologica. 14: 209-240.

Preuschoft, H., Witte, H. 1991. Biomechanical reasons for the evolution of hominid body shape. In: Coppens, Y., Senut, B. (eds.). Origine(s) de la Bipédie chez les Hominidés. Paris: Centre National de la Recherche Scientifique. pp. 59-77.

Preuschoft, H., Witte, H., Demes, B. 1992. Biomechanical factors that influence overall body shape of large apes and humans. In: Matano, S., Tuttle, R.H., Ishida, H., Goodman, M. (eds.). Topics in Primatology, Evolutionary Biology, Reproductive Endocrinology and Virology. Vol. 3. Tokyo: University of Tokyo Press. pp. 259-289.

Prost, J.H. 1977. Positional behavior in chimpanzees. Yearbook of Physical Anthropology. 20: 454-465.

Pruetz, J.D., Fulton, S.J., Marchant, L.F., McGrew, M.C., Schiel, M., Waller, M. 2007. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in Southeastern Senegal. American Journal of Primatology. 70: 1-9.

Rae T.C. 1999. Mosaic evolution in the origin of the hominoidea. Folia Primatologica. 70: 125-135.

Rafferty, K.L., Walker, A.C., Ruff, C.B., Rose, M.D., Andrews, P.J. 1995. Postcranial estimates of body weight in *Proconsul*, with a note on a distal tibia from Napak, Uganda. American Journal of Physical Anthropology. 97: 391-402.

Rasmussen, O., Kromann-Anderson, C., Boe, S. 1983. Deltoid ligament. Functional analysis of the medial collateral ligamentous apparatus of the ankle joint. Acta Orthopaedica Scandinavica. 54: 36-44.

Rasmussen, O. 1985. Stability of the ankle joint. Acta Orthopaedica Scandinavica. S. 211. 56: 1-75.

Reeser, L.A., Susman, R.L., Stern, J.T. 1983. Electromyographic studies of the human foot: experimental approaches to hominin evolution. Foot and Ankle. 3: 391-407.

Remis, M.J. 1995. Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. American Journal of Physical Anthropology. 97: 413-433.

Remis, M.J. 1999. Tree structure and sex differences in arboreality among Western lowland gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. Primates. 40: 383-396.

Reno, P.L., DeGusta, D., Serrat, M.A., Meindl, R.S., White, T.D., Eckhardt, R.B., Kuperavage, A.J., Galik, K., Lovejoy, C.O. 2005. Plio-Pleistocene hominid limb proportions. Current Anthropology. 46: 575-588.

Richmond, B.G., Jungers, W.L. 1995. Size variations and sexual dimorphism in *Australopithecus afarensis* and living hominoids. Journal of Human Evolution. 29: 229-245.

Richmond, B.G., Begun, D.R., Strait, D.S. 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. Yearbook of Physical Anthropology. 44: 70-105.

Richmond, B.G., Jungers, W.L. 2008. *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. Science. 319: 162-1665.

Rightmire, G.P. 1998. Human evolution in the middle Pleistocene: the role of *Homo heidelbergensis*. Evolutionary Anthropology. 6: 218-227.

Rodman, P.S., Mitani, J.C. 1987. Orangutan: sexual dimorphism in a solitary species. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Stuhsaker, T.T. (eds.) Primate Societies. Chicago: University of Chicago Press. pp. 146-154.

Rome, K. 1996. Ankle joint dorsiflexion measurement studies. A review of the literature. Journal of the American Podiatric Medical Association. 86: 205-211.

Rose, M.D. 1977. Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. Primates. 18: 59-116.

Rose, M.D. 1983. Miocene hominoid postcranial morphology: monkey-like, ape-like, neither, or both? In Ciochon, R.L., Corruccini, R.S. (eds). New Interpretations of Ape and Human Ancestry. New York: Plenum Press. pp. 405-417.

Rose, M.D. 1991. The process of bipedalization in hominids. In: Coppens, Y., Senut, B. (eds.). Origine(s) de la Bipédie chez les Hominidés. Paris: Centre National de la Recherche Scientifique. pp. 37-48.

Rose, M.D. 1992. Postcranial specimens of *Simiolus enjiessi* and other primitive catarrhines from the early Miocene of Lake Turkana, Kenya. Journal of Human Evolution. 22: 171-237.

Rose, M.D. 1993. Locomotor anatomy of Miocene hominoids. In Gebo, D.L. (ed.). Postcranial Adaptation in Nonhuman Primates. Dekalb, Illinois: Northern Illinois University Press. pp. 70-95.

Rose, M.D. 1994. Quadrupedalism in some Miocene catarrhines. Journal of Human Evolution. 26: 387-411.

Rose, M.D. 1997. Functional and phylogenetic features of the forelimb in Miocene hominoids. In: Begun, D.R., Ward, C.V., Rose, M.D. (eds.). Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press. pp. 79-100.

Rose, M.D., Nakano, Y., Ishida, H. 1996. *Kenyapithecus* postcranial specimens from Nachola, Kenya. African Study Monographs, Suppl. 24: 3-56.

Ruff, C., Holt, B., Trinkaus, E. 2006. Who's afraid of the big bad Wolff? "Wolff's Law" and bone functional adaptation. American Journal of Physical Anthropology. 129: 484-498.

Sammarco, G.J. 1989. Biomechanics of the Foot. In: Nordin, M., Frankel, V.H. (eds.). Basic biomechanics of the musculoskeletal system. Philadelphia: Lippincott Williams & Wilkins. pp. 163-181.

Sanders, W.J., Bodenbender, B.E. 1994. Morphometric analysis of lumbar vertebra UMP 67-28: implications for the spinal function and phylogeny of the Miocene Moroto hominoid. Journal of Human Evolution. 26: 203-237.

Sanders, W.J. 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. Journal of Human Evolution. 34: 249-302.

Sarmiento, E. 1991. Functional and phylogenetic implications of the differences in the pedal skeleton of australopithecines. American Journal of Physical Anthropology (Suppl.). 12: 157-158.

Sarrafian, S.K. 1987. Functional characteristics of the foot and plantar aponeurosis under tibiotalar loading. Foot and Ankle. 8: 4-18.

Sarrafian, S.K. 1993. Anatomy of the Foot and Ankle: Descriptive, Topographic, Functional, Philadelphia: J.B.Lippincott Co.

Sawada, Y., Pickford, M., Itaya, T., Makinouchi, T., Tateishi, M., Kabeto, K., Ishida, S., Ishida, H. 1998. K-Ar ages of Miocene hominoidea (*Kenyapithecus* and *Samburupithecus*) from Samburu Hills, northern Kenya. Comptes Rendus Academie of Sciences, Paris. 326: 445-451.

Sawyer, K., Lovejoy, C.O. 2008. The chimpanzee has no clothes. A critical examination of *Pan troglodytes* in models of human evolution. Current Anthropology 49: 87-114.

Schmitt, D., Larson, S.G. 1995. Heel contact as a function of substrate type and speed in primates. American Journal of Physical Anthropology. 96: 39-50.

Schultz, A.H. 1927. Studies on the growth of the gorilla and of other higher primates, with special reference to a fetus of gorilla preserved in the Carnegie Museum. Memoirs of the Carnegie Museum. 11: 1-87.

Schultz, A.H. 1930. The skeleton of the trunk and limbs of higher primates. Human Biology. 2: 303-438.

Schultz, A.H. 1934. Some distinguishing characters of the mountain gorilla. Journal of Mammalogy. 15: 51-61.

Schultz, A.H. 1963. Relations between the lengths of the main parts of the foot skeleton in primates. Folia Primatologica. 1: 150-171.

Scott, S.H., Winter, D.A. 1991. Talocrural and talocalcaneal joint kinematics and kinetics during the stance phase of walking. Journal of Biomechanics. 24: 743-752.

Seiffert, E.R., Simons, E.L. 2001. Astragalar morphology of late Eocene anthropoids from the Fayum Depression (Egypt) and the origin of catarrhine primates. Journal of Human Evolution. 41: 577-606.

Semaw, S., Simpson, S.W., Quade, J., Renne, P.R., Butler, R.F., McIntosh, W.C., Levin, N., Dominguez-Rodrigo, M., Rogers, M.J. 2005. Early Pliocene hominids from Gona, Ethiopia. Nature. 433: 301-305.

Senut, B. 1988. Climbing as a crucial preadaptation for human bipedalism. International Journal of Skeletal Research. 14: 35-44.

Senut, B., Pickford, M., Gommery, D., Kunimatsu, Y. 2000. Un nouveau genre d'hominoide du Miocene inferieur d'Afrique orientale: *Ugandapithecus major* (Le Gros Clark & Leakey, 1950). Comptes Rendus Academie of Sciences, Paris. 331: 227-233.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., Coppens, Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). Comptes Rendus Academie of Sciences, Paris, Sciences de la Terre et des Planets. 332: 137-144.

Senut, B., Nakatsukasa, M., Kunimatsu, Y., Nakano, Y., Takano, T., Tsujikawa, H., Shimizu, D., Kagaya, M., Ishida, H. 2004. Preliminary analysis of *Nacholapithecus* scapula and clavicle from Nachola, Kenya. Primates. 45: 97-104.

Siegler, S., Chen, J., Schneck, C.D. 1988. The three-dimensional kinematics and flexibility characteristics of the human ankle and subtalar joints- part I: kinematics. Journal of Biomechanical Engineering. 110: 364-373.

Siegler, S., Block, J., Schneck, C.D. 1988. The mechanical characteristics of the collateral ligaments of the human ankle joint. Foot and Ankle. 8: 234-242.

Skie, M., Woldenberg, L., Ebraheim, N., Jackson, W.T. 1989. Assessment of collicular fractures of the medial malleolus. Foot and Ankle. 10: 118-123.

Smith, R.J., Jungers, W.L. 1997. Body mass in comparative primatology. Journal of Human Evolution. 32: 523-559.

Sokal, R.R., Rohlf, F.J. 2001. Biometry. New York: W.H. Freeman and Co.

Solomonow, M., Lewis, J. 2002. Reflex from the ankle ligaments of the feline. Journal of Electromyography and Kinesiology. 12: 193-198.

Stagni, R., Leardini, A., Ensini, A. 2004. Ligament fibre recruitment at the human ankle joint complex in passive flexion. Journal of Biomechanics. 37: 1823-1829.

Stauffer, R.N., Chao, E.Y.S., Brewster, R.C. 1977. Force and motion analysis of the normal, diseased, and prosthetic ankle joint. Clinical Orthopaedics and Related Research. 189-196.

Stern, J.T., Susman, R.L. 1981. Electromyography of gluteal muscles in *Hylobates*, *Pongo*, and *Pan*: Implications for the evolution of hominid bipedality. American Journal of Physical Anthropology. 55: 153-166.

Stern, J.T., Susman, R.L. 1983. The locomotor anatomy of *Australopithecus afarensis*. American Journal of Physcial Anthropology. 60: 279-317.

Stern, J.T., Jr. 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. Evolutionary Anthropology. 9: 113-133.

Steudel, K.L. 1990. The work and energetic cost of locomotion: the effects of limb mass distribution in quadrupeds. Journal of Experimental Biology. 154: 273-285.

Steudel-Numbers, K.L. 2006. Energetics in *Homo erectus* and other early hominins: the consequences of increased lower-limb length. Journal of Human Evolution. 51: 445-453.

Steudel-Numbers, K.L., Weaver, T.D., Wall-Scheffler, C.M. 2007. The evolution of human running: effects of changes in lower limb length on locomotor economy. Journal of Human Evolution. 53: 191-196.

Stormont, D.M., Morrey, B.F., An, K-N, Cass, J.R. 1985. Stability of the loaded ankle. The American Journal of Sports Medicine. 13: 295-300.

Straus, W.L., Jr. 1926. The development of the human foot and its phylogenetic significance. American Journal of Physical Anthropology. 9: 427-438.

Subotnick, S.I. 1985. The biomechanics of running. Implications for the prevention of foot injuries. Sports Medicine. 2: 144-153.

Sugardjito, J., van Hooff, J.A.. 1986. Age-sex class differences in the positional behaviour of the Sumatran orang-utan (*Pongo pygmaeus abelii*) in the Gunung Leuser National Park, Indonesia. Folia Primatologica. 47: 14-25.

Sugimoto, K., Samoto, N., Takakura, Y., Tamai, S. 1997. Varus tilt of the tibial plafond as a factor in chronic ligament instability of the ankle. Foot and Ankle International. 18: 402-405.

Susman, R.L. 1983. Evolution of the human foot: evidence from Plio-Pleistocene hominins. Foot and Ankle. 3: 365-376.

Susman, R.L. 1984. The locomotor behavior of *Pan paniscus* in the Lomako Forest. In: Susman, R.L. (ed.). Pygmy Chimpanzee. New York: Plenum Press. pp. 369-393

Susman, R.L., Stern, J.T. 1982. Functional morphology of *Homo habilis*. Science. 217: 931-934.

Susman, R.L., Stern, J.T., Jungers, W.L. 1984. Arboreality and bipedality in the Hadar hominins. Folia Primatologica. 43: 113-156.

Susman, R.L., de Ruiter, D.J., Brain, C.K. 2001. Recently identified post-cranial remains of *Paranthropus* and early *Homo* from Swartkrans Cave, South Africa. Journal of Human Evolution. 41: 607-629.

Swindler, D.R., Wood, C.D. 1982. Atlas of Primate Gross Anatomy. New York: Krieger Publishing Company.

Szalay, F.S., Langdon, J.H. 1987. The foot of *Oreopithecus*: an evolutionary assessment. Journal of Human Evolution. 15: 585-621.

Takahashi, K., Kubo, T., Kobayashi, K., Imanishi, J., Takigawa, M., Arai, Y., Hirasawa, Y. 1997. Hydrostatic pressure influences mRNA expression of transforming growth factor-beta 1 and heat shock protein 70 in chondrocyte-like cell line. Journal of Orthopaedic Research. 15: 150-158.

Tardieu, C. 1999. Ontogeny and phylogeny of femoro-tibial characters in humans and hominid fossils: functional influence and genetic determinism. American Journal of Physical Anthropology. 110: 365-377.

Taser, F., Shafiq, Q., Ebraheim, NA. 2006. Anatomy of the lateral ankle ligaments and their relationship to bony landmarks. Surgical and Radiological Anatomy. 28: 391-397.

Taylor, A.B. 1997. Scapula form and biomechanics in gorillas. Journal of Human Evolution. 33: 529-553.

Temerin, L.A., Cant, J.G.H. 1983. The evolutionary divergence of Old World monkeys and apes. The American Naturalist. 122: 335-351.

Thackeray, J.F., de Ruiter, D.J., Berger, L.R., van de Merwe, N. 2001. Hominid fossils from Kromdraai: a revised list of specimens discovered since 1938. Annals of the Transvaal Museum 38: 158-169.

Thorpe, S.K.S., Crompton, R.H. 2006. Orangutan positional behavior and the nature of arboreal locomotion in hominoidea. American Journal of Physical Anthropology. 131: 384-401.

Thorpe, S.K.S., Holder, R.H., Crompton, R.H. 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science. 316: 1328-1331.

Tobias, P.V. 1965. New discoveries in Tanganyika: their bearing on hominin evolution. Current Anthropology. 6: 391-411.

Tochigi, Y., Rudert, M.J., Amendola, A., Brown, T.D., Saltzman, C.L. 2005. Tensile engagement of the peri-ankle ligaments in stance phase. Foot and Ankle International. 26: 1067-1073.

Tochigi, Y., Rudert, M.J., Saltzman, C.L., Amendola, A., Brown, T.D. 2006. Contribution of the articular surface geometry to ankle stabilization. Journal of Bone and Joint Surgery (Am). 88: 2704-2713.

Trinkaus, E. 1984. Does KNM-ER 1481A establish *Homo erectus* at 2.0 myr BP? American Journal of Physical Anthropology. 64: 137-139.

Tutin, C.E.G. 1996. Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. In: McGraw, W.C., Marchant, L.F., Nishida, T. (eds.). Great Ape Societies. Cambridge: Cambridge University Press. pp. 58-70.

Tuttle, R.H. 1975. Parallelism, brachiation and hominoid phylogeny. In: Luckett, W.P., Szalay, F.S. (eds). Phylogeny of the Primates. New York: Plenum Press. pp. 447-480.

Tuttle, R.H., Rogers, C.M. 1966. Genetic and selective factors in reduction of the hallux in *Pongo pygmaeus*. American Journal of Physical Anthropology. 24: 191-198.

Tuttle, R.H., Basmajian, J.V. 1974. Electromyography of brachial muscles in *Pan gorilla* and hominoid evolution. American Journal of Physical Anthropology. 41: 71-90.

Tuttle, R.H., Watts, D.P. 1985. The positional behavior and adaptive complexes of *Pan gorilla*. In: Kondo, S., Ishida, S., Okada, M., Kimura, T. & Yamazaki, M. (eds.). Primate Morphophysiology, Locomotor Analyses and Human Bipedalism. Tokyo: Tokyo University Press. pp. 261-288.

Tuttle, R.H. 1985. Ape footprints and Laetoli impressions: A response to the SUNY claims. In: Tobias, P.V. (ed.). Hominid Evolution: Past, Present and Future. New York: Alan R. Liss. pp. 129-133.

Vančata, V. 1985. Morphological trends in the lower limb skeleton of the recent Hominoidea: analysis of the femur and tibia. In: Herrmann, J., Ullrich, H. (eds.). Menschwerdung- biotischer und gesellschaftlicher Entwicklungsprozeß. Berlin: Akademie Verlag.

Vangor, A.K. 1977. Functional pre-adaptation to bipedality in non-human primates. American Journal of Physical Anthropology. 47:164-165.

Vangor, A.K., Wells, J.P. 1983. Muscle recruitment and the evolution of bipedality: evidence from telemetered electromyography of spider, woolly and patas monkeys. Annales des Sciences Naturelles, Zoologie, Paris. 5: 125-135.

Vereecke, E., D'Août, K., De Clercq, D., Van Elsacker, L., Aerts, P. 2003. Dynamic plantar pressure distribution during terrestrial locomotion in bonobos (*Pan paniscus*). American Journal of Physical Anthropology. 120: 373-383.

Vilensky, J.A., Gankiewicz, E. 1990. Effects of growth and speed on hindlimb joint angular displacement patterns in Vervet Monkeys (*Cercopithecus aethiops*). American Journal of Physical Anthropology. 81: 441-449.

Walker, A.C. 1994. Early *Homo* from 1.8-1.5 million year deposits at Lake Turkana, Kenya. In Franzen, J.F. (ed.), 100 years of *Pithecanthropus*; the *Homo erectus* problem. Frankfurt am Main: Courier Forschunginstitut Senckenberg. pp. 167-173.

Walker AC. 1997. *Proconsul*: function and phylogeny. In Begun, D.R., Ward, C.V., Rose, M.D. (eds.). Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press. pp. 209-224.

Walker, A.C., Pickford, M. 1983. New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In: Ciochon, R.L. (ed.). New Interpretations of Human and Ape Ancestry. New York: Plenum Press. pp. 325-351.

Walker, A., Leakey, R.E. 1993. The Nariokotome *Homo erectus* skeleton. Cambridge: Harvard University Press.

Walmsley, T. 1933. The vertical axes of the femur and their relations. A contribution to the study of the erect posture. Journal of Anatomy. 67: 284-300.

Walter, R.C. 1994. Age of Lucy and the First Family: laser ^{40}Ar/^{39}Ar dating of the Denen Dora member of the Hadar Formation. Geology. 22: 6-10.

Wang, W., Crompton, R.H., Carey, T.S., Günther, M.M., Yi, L., Savage, R., Sellers, W.I. 2004. Comparison of inverse-dynamics musculo-skeletal models of AL 288-1 *Australopithecus afarensis* and KNM-WT 15000 *Homo ergaster* to modern humans, with implications for the evolution of bipedalism. Journal of Human Evolution. 47: 453-478.

Ward, C.V. 1997. Functional anatomy and phyletic implications of the hominoid trunk and hindlimb. In: Begun, D.R., Ward, C.V., Rose, M.D. (eds.). Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. New York: Plenum Press. pp. 101-130.

Ward, C.V. 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: Where do we stand? Yearbook of Physical Anthropology. 119: 185-215.

Ward, C.V., Drapeau, M.S., Kimbel, W.H., Johanson, D.C. 1998. New postcranial fossils of *Australopithecus afarensis* from Hadar, Ethiopia. American Journal of Physical Anthropology (Suppl.). 26: 225-226.

Ward, C.V., Leakey, M.G., Walker, A. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. Journal of Human Evolution. 41: 255-368.

Wheatley, B.P. 1987. The evolution of large body size in orang-utans: a model for hominoid divergence. American Journal of Primatology. 13: 313-324.

White, T.D. 1980. Evolutionary implications of Pliocene hominid footprints. Science. 208: 175-176.

White, T.D. Suwa, G. 1987. Hominid footprints at Laetoli: facts and interpretations. American Journal of Physical Anthropology. 72: 485-514.

White, T.D., Suwa, G., Asfaw, B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature. 371: 306-312.

White, T.D. 2003. Early hominids- diversity or distortion? Science. 299: 1994-1997.

White, T.D., WoldeGabriel, G., Asfaw, B., Ambrose, S., Beyene, Y., Bernor R.L., Boisserie, J.-R., Currie, B., Gilbert, H., Haile-Selassie, Y., Hart, W.K., Hlusko, L.J., Howell, F.C., Kono, R.T., Lehmann, T., Louchart, A., Lovejoy, O., Renne, P.R., Saegusa, H., Vrba, E.S., Wesselman, H., Suwa, G. 2006. Asa Issie, Aramis and the origin of *Australopithecus*. Nature. 440: 883-889.

Wiltse, L.L. 1972. Valgus deformity of the ankle: a sequel to acquired or congenital abnormalities of the fibula. Journal of Bone and Joint Surgery (Am). 54: 595-606.

Wolf, P. 2006. Tarsal kinematics. Ph.D. Thesis. Swiss Federal Institute of Technology: Zurich.

Wolpoff, M.H. 1996. *Australopithecus*: a new look at an old ancestor. General Anthropology. 3: 1-7.

Wolpoff, M.H. 1999. Paleoanthropology. Boston: McGraw-Hill.

Wong, M., Wuethrich, P., Buschmann, M., Eggli, P., Hunziker, E. 1997. Chondrocyte biosynthesis correlates with local tissue strain in statically compressed adult articular cartilage. Journal of Orthopaedic Research. 15: 189-196.

Wood, B.A. 1974. Olduvai Bed I post-cranial fossils: a reassessment. Journal of Human Evolution. 3: 373-378.

Wood, B.A. 1974. Evidence on the locomotor pattern of *Homo* from early Pleistocene of Kenya. Nature. 251: 135-136.

Wood, B., Aiello, L., Wood, C., Kay, C. 1998. A technique for establishing the identity of ‘isolated’ fossil hominin limb bones. Journal of Anatomy. 193: 61-72.

Wood, B.A., Constantino, P. 2007. *Paranthropus boisei*: Fifty years of evidence and analysis. Yearbook of Physical Anthropology. 50: 106-132.

Wrangham, R.W., Pilbeam, D. 2001. African apes as time machines. In Galdikas, B., Briggs, N., Sheeran, L., Shapiro, G., Goodall, J. (eds.). All Apes Great and Small Volume 1. African Apes. New York: Kluwer Academic Publishers. pp. 5-17.

Wright, D.G., Desai, M.E., Henderson, W.H. 1964. Action of the subtalar and ankle-joint complex during the stance phase of walking. The Journal of Bone and Joint Surgery. 46A: 361-382.

Wunderlich, R. 1999. Pedal form and plantar pressure distribution in anthropoid primates. Ph.D. Thesis. State University of New York at Stony Brook.

Wyke, B. 1972. Articular neurology: a review. Physiotherapy. 58: 94-99.

Yamazaki, N., Ishida, H., Okada, M., Kimura, T., Kondo, S. 1983. Biomechanical evaluation of evolutionary models for pre-habitual bipedalism. Annales des Sciences Naturelles, Zoologie, Paris. 5: 159-168.

Yamazaki, N., Ishida, H. 1984. A biomechanical study of vertical climbing and bipedal walking in gibbons. Journal of Human Evolution. 13: 563-571.

Young, N.M. 2003. A reanalysis of variability in the hominoid postcranium: implications for ape evolution. Journal of Human Evolution. 45: 441-464.

Young, N.M., MacLatchy, L.M. 2004. The phylogenetic position of *Morotopithecus*. Journal of Human Evolution. 46: 163-184.

Zimny, M.I. 1988. Mechanoreceptors in articular tissues. American Journal of Anatomy. 182: 16-32.