

Revisiting the “Midtarsal Break”

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KEY WORDS foot evolution; bipedalism; hominin locomotion; longitudinal arch

ABSTRACT Themidtarsal break was first described in this journal 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 themidtarsal break, the calcaneocuboid joint has been assumed to be the anatomical source of this motion. Recently, however, it has been suggested that themidtarsal break may occur at the cuboid-metatarsal joint, rather than at the calcaneocuboid joint. Data compiled from X-rays, dissections, manual manipulation of living primate feet, video of captive catarrhines, and osteological specimens concur that themidtarsal break is a complex motion caused by dorsiflexion at both joints with the cuboid-metatarsal joint contributing roughly 2/3 of total midfoot dorsiflexion, and the calcaneocuboid joint only about 1/3 of total midfoot dorsiflex-

ion. The convexity of the proximal articular surface of the fourth and fifth metatarsals and corresponding concave cuboid facets provide skeletal correlates for the presence of midfoot dorsiflexion at the cuboid-metatarsal joint. Study of hominin metatarsals from *Australopithecus afarensis*, *A. africanus*, *Homo erectus*, and the metatarsals and a cuboid from the OH 8 foot show little capacity for dorsiflexion at the cuboid-metatarsal joint. These results suggest that hominins may have already evolved a stable midfoot region well adapted for the push-off phase of bipedalism by at least 3.2 million years ago. These data illuminate the evolution of the longitudinal arch and show further evidence of constraints on the arboreal capacity in early hominins. *Am J Phys Anthropol* 141:245–258, 2010. © 2009 Wiley-Liss, Inc.

During the initial propulsive stage of human walking, the heel and midfoot simultaneously lift resulting in dorsiflexion at the metatarsophalangeal joint (Close et al., 1967; Susman, 1983). However, during terrestrial walking in non-human primates, dorsiflexion¹ of the foot occurs first at the midfoot before eventually shifting to the metatarsophalangeal joint. This occurs both in planigrade apes, who have heel contact during the early stance phases of walking, and cercopithecoids who do not (Gebo, 1992; Schmitt and Larson, 1995). Regardless of the role of the heel in walking, the midfoot makes contact with the ground during stance phase in both apes and cercopithecoids. Thismidtarsal break, also termed a “two-stage heel lift” (Kidd, 1998, 1999), has been observed across a range of non-human primates (Elftman and Manter, 1935; Meldrum, 1991; Gebo, 1992; Schmitt and Larson, 1995; D’Aouit et al., 2002; Vereecke et al., 2003; Vereecke and Aerts, 2008). Thus far, humans are the only primate shown to consistently lack amidtarsal break. Accordingly, it is assumed throughout this article that themidtarsal break is primitive and occurs in all primates, and that its absence is derived.

Themidtarsal break was initially described by Elftman and Manter (1935) in the first article to assess the stress distribution under the chimpanzee foot during bipedal and quadrupedal walking (Fig. 1A). 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. Although Elftman and Manter (1935) observed that when the chimpanzee heel lifts off the ground, there is increased stress under the fifth metatarsal, they suggested that

this was a result of motion at the transverse tarsal joint and made no mention of the tarsometatarsal joint. Meldrum and Wunderlich (1998), who studied chimpanzee and human locomotion using video data and radiographs of the feet of anesthetized chimpanzees suggested thatmidtarsal dorsiflexion in the ape occurs at the talonavicular joint on the medial side of the foot, and that this motion exceeded what is possible at the calcaneocuboid joint.

Important skeletal differences are present in the human and the chimpanzee transverse tarsal joint and are partially responsible for themidtarsal break. 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 when the foot is supinated or pronated, resulting in continuousmidtarsal mobility (Close et al., 1967; Langdon et al., 1991). The stability of themidtarsal region is

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¹Motion at the midfoot region during themidtarsal break will be referred to as “dorsiflexion” in this article.

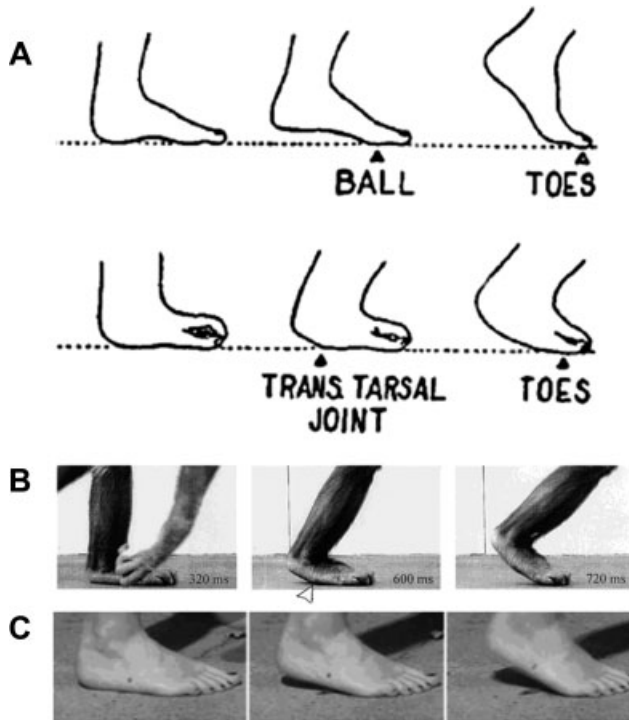


Fig. 1. Midtarsal break. (A) Drawing from Elftman and Manter (1935) illustrating the repositioning of the fulcrum of the foot from the heel to the metatarsophalangeal joint after initial push-off in humans (top), but an intermediate break at the midfoot in chimpanzees. (B) This is demonstrated more clearly 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. The triangle in B represents the position of the midtarsal break.

partially achieved in humans by a pronounced flange of the cuboid that is eccentrically located more inferomedially than the case in non-human primates (Aiello and Dean, 1990). 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-Møller, 1979; Lewis, 1980a; 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 restricts motion in the human midfoot, but is absent in the non-human primate foot. Gomberg (1981, 1985) also 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. Additionally, Manter (1941) noted that 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.

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'Août 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 fifth 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 joint. More recently, Vereecke and Aerts (2008) found that the gibbon foot dorsiflexes on average 38° at the tarsometatarsal joint during bipedal locomotion. This work on the gibbon foot demonstrates that even an ape with midfoot mobility can still store elastic energy during bipedal walking, and raises the intriguing hypothesis that the earliest hominins may have possessed a midtarsal break to successfully navigate both an arboreal and terrestrial environment (Vereecke and Aerts, 2008). Skeletal correlates of this midfoot mobility are thus of critical importance in determining precisely when the hominin foot transitioned from a mobile, grasping organ to a stable lever.

Testing locomotor hypotheses in the earliest hominins requires a more precise determination of the exact anatomical location, and skeletal correlates, of the midtarsal 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, 1980a; Langdon et al., 1991; Kidd et al., 1996; Kidd, 1998; Harcourt-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. Data collected from these studies have been used to assess Pliocene hominin foot bones in addressing 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, 1980b; Susman and Stern, 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. However, the calcaneocuboid joint is poorly preserved in the fossil record and these studies on hominin midfoot stability have produced mixed results. If the midtarsal break occurs at the tarsometatarsal joint, the morphology of the distal cuboid and lateral metatarsals could also be used to assess midfoot mobility in early hominins. Identifying fossil evidence for a midtarsal break in early hominins would have important implications for understanding both the evolution of bipedalism and the arboreal nature of our ancestors.

The goals of this study are twofold. 1) The hypothesis that the midtarsal break in non-human primates occurs exclusively at the calcaneocuboid joint on the lateral side of the foot is tested with data from osteological and soft-tissue specimens, radiographs, and kinematics. 2) Skeletal correlates of mobility at the cuboid-metatarsal joint are identified using a comparative skeletal sample consisting of modern humans, apes, and cercopithecoids. The hypothesis that early hominins lacked a midtarsal break is tested by comparing fossil hominin cuboids and lateral metatarsals to this comparative sample.

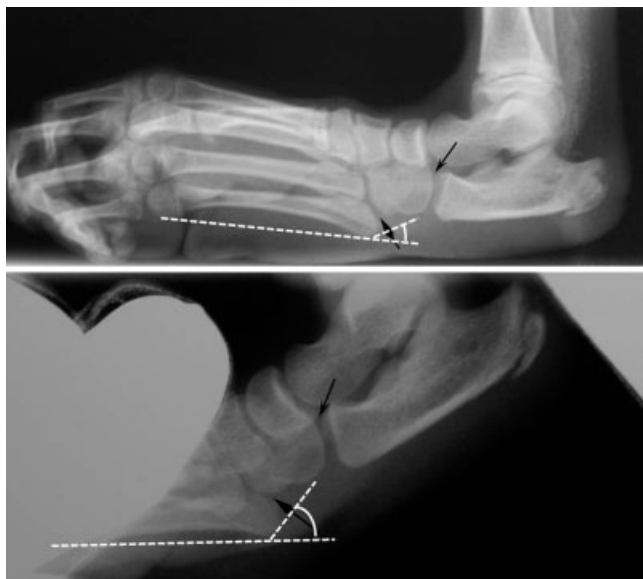


Fig. 2. X-rays of baboon (*Papio anubis*) foot in lateral view in neutral position (top) and during midfoot dorsiflexion (bottom). The straight arrows indicate the calcaneocuboid joint, while the diamond-shaped arrows indicate the cuboid-metatarsal joint. Notice that relative to neutral position, the angle (dotted white lines) formed between the plantar aspect of the fifth metatarsal and the cuboid during the “midtarsal break” is considerably larger. In contrast, there is only moderate dorsiflexion at the calcaneocuboid joint during the “midtarsal break.”

MATERIALS AND METHODS

X-rays and dissections

Both lower limbs were obtained from 10 subadult 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 2- and 3-years-old, and thus still had unfused epiphyses on the distal fibula and tibia. The animals weighed an average of 7 kg (range 6.0–8.4 kg). The feet were positioned in lateral view and X-rays were taken using a MinXray, HF 100/30 at 50 kVDC for 0.3 mAs. The X-ray source was located ~3 feet from the baboon limbs. Radiographs were taken of the right foot of each individual in a neutral position with the most plantar aspect of the foot forming a 90 degree angle with the long axis of the tibia. Although baboons are digitigrade, the foot was initially placed in a plantigrade position to ascertain whether the elevated heel was a product of dorsiflexion at the calcaneocuboid joint, the cuboid-metatarsal joint, or a combination of both. Radiographs were then taken of the same feet with the heel elevated to ~20–30 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 dorsiflexing the midfoot.

The X-rays were imported into the program Image J to quantify the relative amount of dorsiflexion between the cuboid and the calcaneus proximally and the fifth metatarsal distally. To quantify dorsiflexion between the cuboid and the fifth metatarsal, an angle was taken between a straight line drawn along the plantar aspect of the fifth metatarsal and the line connecting the plantar aspect of the fifth metatarsal base and the most proximal part of the plantar aspect of the cuboid (see Fig. 2). To quantify dorsiflexion between the cuboid and the calcaneus, an angle was taken between a straight line drawn along the plantar aspect of the cuboid and the line connecting the plantar aspect of the proximal cuboid and the most distal aspect of the plantar calcaneus. These angles were taken first on the radiograph of the neutrally positioned baboon foot, and subtracted from the angles obtained from the radiographs of the same foot experiencing midfoot dorsiflexion.

The same 10, right baboon feet were also dissected. Both X-rays and dissections were performed on the same baboon feet for two reasons. First, employing multiple techniques to assess the location of the midfoot break may be useful for future studies that are restricted to either X-rays (especially if the animal is still alive) or dissections. Second, there may be a rotational component to midfoot dorsiflexion that is more easily accounted for in the dissection than the X-rays. The fifth metatarsal was palpated 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 manually held to a horizontal surface, the tibia was slowly elevated and two digital photographs were taken in lateral view. The first photograph captured the maximum dorsiflexion at the calcaneocuboid joint and the second the maximum dorsiflexion 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. An angle was measured between a line drawn along the plantar aspect of the fifth metatarsal and a line drawn along the plantar aspect of the elevated heel (see Fig. 3).

Video analysis

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. A single adult human female was analyzed as well. The tuberosity of the fifth metatarsal was palpated through the skin on the lateral side of the foot, and manual manipulation of the foot was used to ascertain whether dorsiflexion occurred in the region of the metatarsal V tuberosity or more proximally at the calcaneocuboid joint. It can be predicted from osteological specimens (see Fig. 4) that foot dorsiflexion proximal to the tuberosity of the fifth metatarsal implies movement at the calcaneocuboid joint, whereas dorsiflexion distally to the tuberosity implies the involvement of the tarsometatarsal joint. A circular white mark was placed directly on the skin overlying the tuberosity of the fifth metatarsal. Video was captured in lateral view of the primates engaging in slow quadrupedal locomotion on a flat, concrete substrate after they awoke. Primates were videotaped with a Canon GL2 digital video recorder. The video captured frames every 70 ms. The film was imported into

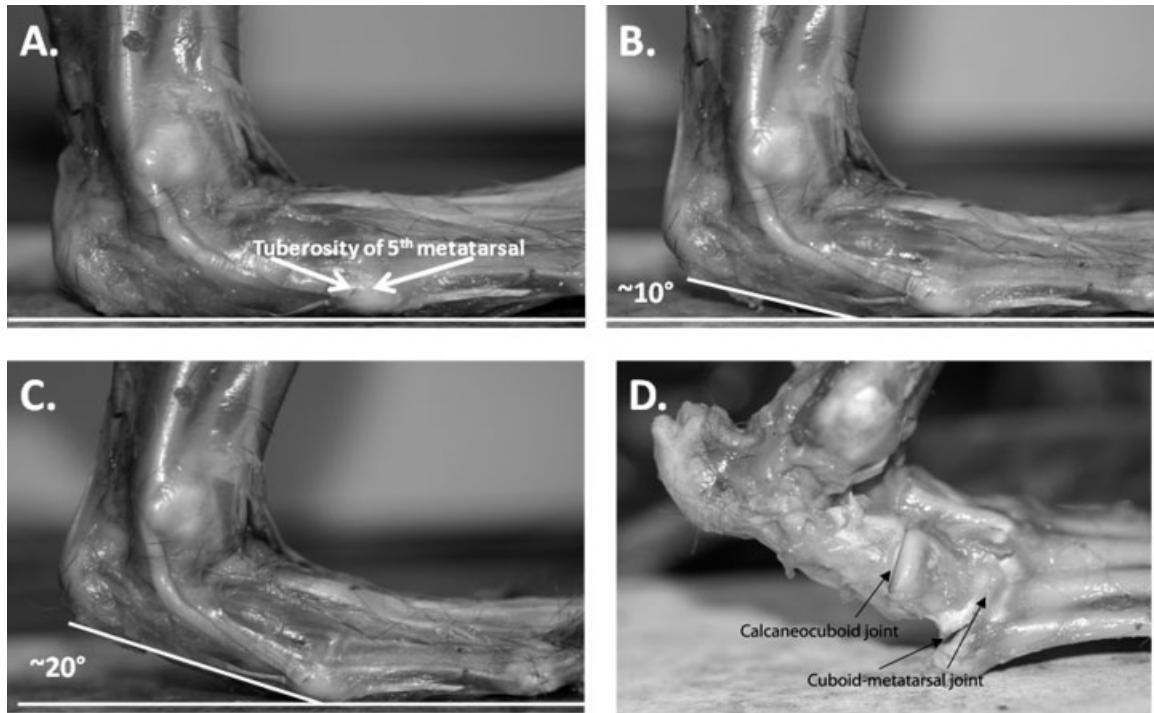


Fig. 3. Dissected baboon (*Papio anubis*) foot in lateral view with the tibia being manually lifted. (A) The foot is in a plantigrade position with the tuberosity of the fifth metatarsal in contact with the tabletop. (B) Slight tension on the tibia initially elevates the heel ($\sim 10^\circ$) at a position proximal to the tuberosity of the fifth metatarsal, presumably the calcaneocuboid joint. (C) Addition tension on the tibia shifts the position of the midtarsal break distally to the cuboid-metatarsal joint ($\sim 20^\circ$). (D) With the soft tissue removed, it is clearer that midfoot dorsiflexion is pronounced at the cuboid-metatarsal joint.

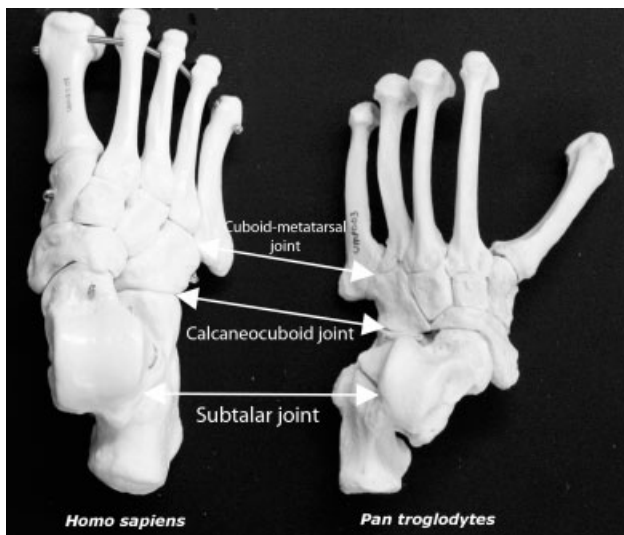


Fig. 4. Hindfoot and midfoot skeletal elements of a right human foot (left) and a left chimpanzee foot (right). The subtalar joint is located between the talus and calcaneus. The calcaneocuboid portion of the transverse tarsal joint, and the cuboid-metatarsal portion of the tarsometatarsal joints are both indicated in the image. Note that dorsiflexion proximally to the tuberosity of the fifth metatarsal would indicate movement at the calcaneocuboid joint, whereas dorsiflexion distally to the tuberosity would indicate movement at the tarsometatarsal joint.

Windows Movie Maker and examined frame by frame to assess where the midtarsal break occurs relative to the position of the white mark demarcating the tuberosity of

the fifth metatarsal. Ten sequences of quadrupedal walking in chimpanzees (5 male, 5 female), nine sequences of walking in gorillas (6 male, 3 female), six sequences of walking in the female mandrills, and nine sequences in the macaques were captured in which the white spot indicating the position of the tuberosity of the fifth metatarsal was visible, the foot was roughly in lateral orientation, and the primates had undergone a fully weight-bearing stance phase complete with a midtarsal break. The amount of dorsiflexion occurring during the midtarsal break was quantified in the following manner. Video was analyzed frame by frame and still-image photographs of the primate video were captured when the maximum midfoot dorsiflexion was achieved, indicated by the moment the heel is most elevated but prior to weight transfer to the metatarsal heads. These still-image photographs were imported into the program Image J. As the analysis proceeded, it became clear that the midfoot dorsiflexed in two locations: proximally to the white mark demarcating the tuberosity of the fifth metatarsal and distal to this mark. At these two anatomical positions, two angles were taken between a line drawn along the lateral plantar aspect of the foot and a line drawn along the plantar aspect of the elevated heel during periods of maximum dorsiflexion first at a position proximal to the tuberosity of the fifth metatarsal (presumably the calcaneocuboid joint), and next a position more distal to the tuberosity (presumably the tarsometatarsal joint).

Skeletal and fossil specimens

The cuboid, and fourth and fifth metatarsals of wild-shot adult *Pan troglodytes* ($n = 33$) and *Gorilla gorilla*

TABLE 1. Fossil hominin cuboids, fourth metatarsals and fifth metatarsals from Plio-Pleistocene

Element	Accession number	Geological age (mya)	Taxon	Studied for this article
Cuboid	OH 8	1.8	<i>Homo habilis?</i>	Yes
			<i>Paranthropus boisei?</i>	
Fourth metatarsal	KB 3133	1.7–2.0	<i>P. robustus?</i>	No (listed in Thackeray et al., 2001)
	A.L. 333–160	3.2	<i>Australopithecus afarensis</i>	No (listed in Kimbel et al., 2004)
	StW 485	2.6–2.8	<i>A. africanus</i>	Yes
	StW 596	2.6–2.8	<i>A. africanus</i>	No (described in Deloison, 2003)
	OH 8	1.8	<i>H. habilis?</i>	Yes
			<i>P. boisei?</i>	
		D4165	1.77	<i>Homo</i> sp.
Fifth metatarsal	D2669	1.77	<i>Homo</i> sp.	No (in Lordkipanidze et al., 2007)
	A.L. 333–13	3.2	<i>A. afarensis</i>	Yes (cast)
	A.L. 333–78	3.2	<i>A. afarensis</i>	Yes (cast)
	StW 114/115	2.4–2.8	<i>A. africanus</i>	Yes
	OH 8	1.8	<i>H. habilis?</i>	Yes
			<i>P. boisei?</i>	
		D4508	1.77	<i>Homo</i> sp.
	KNM-ER 803f	1.53	<i>H. erectus</i>	Yes

($n = 29$) were studied at the Cleveland Museum of Natural History. The Libben Paleoindian collection housed at Kent State University and the Hamann-Todd collection at the Cleveland Museum of Natural History served as the *Homo sapiens* comparative sample ($n = 31$ adults). The cuboid, and lateral metatarsals of a small sample of wild-shot adult *Mandrillus sphinx* ($n = 5$), *Papio* spp. ($n = 6$), *Macaca* spp. ($n = 8$), and *Hylobates lar* ($n = 10$) were studied at the Harvard Museum of Comparative Zoology. There was a roughly equal representation of males and females in the comparative sample.

Original hominin material from Sterkfontein was studied at the University of Witwatersrand in Johannesburg, South Africa (Table 1). Member 4 deposits in Sterkfontein Cave, South Africa have yielded two fourth metatarsals (StW 485 and StW 596). 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 ~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 fifth metatarsal (StW 114/115) recovered from the southerly located W/45 grid of Member 4 was studied. Although this bone may have been deposited more recently than the more northerly Member 4 remains, it is still regarded by most as belonging to *A. africanus* (Kuman and Clarke, 2000; Zipfel et al., 2009).

The OH 8 foot, which preserves the cuboid, fourth, and fifth metatarsals from the same individual, was studied at the Tanzania National Museum and House of Culture, Dar es Salaam (Table 1). This 1.8-million-year-old specimen is considered by many to be *Homo habilis* (Leakey et al., 1964; Susman and Stern, 1982; Susman, 2008) and by others (Wood, 1974; Grausz et al., 1988; Gebo and Schwartz, 2006) to be from *Paranthropus boisei*. KNM-ER 803 is a partial skeleton of *Homo erectus* (Day and Leakey, 1974) from the 1.53 mya Okote Member on the east side of Lake Turkana (Feibel et al., 1989). The fifth metatarsal (KNM-ER 803f) was studied at the Kenya National Museum.

Fossil casts of the fifth 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 (Table 1). A.L. 333-13 and A.L. 333-78 are left fifth metatarsals from *Australopithecus afarensis* dated to ~3.2-million-

years-old (Walter, 1994). These bones have been previously described by Latimer et al. (1982).

The dorsoplantar height of the cuboid articular facets for the fourth and fifth metatarsals was measured with digital calipers to the nearest 0.1 mm. This was done for the cuboid articular facet on the proximal surface of the fourth and fifth metatarsals as well. Additionally, the extent of convexity/concavity of the joint surfaces was assessed using a carpenter's contour guide. The joint surfaces of the fourth and fifth metatarsals and cuboid were pressed into the carpenter's contour guide, and the impressions were photographed with a Nikon D100 digital camera. The images were then imported into the program Image J and the extent of convexity/concavity of the articular surface quantified as a ratio of the proximo-distal depth of the articular surface relative to the overall dorsoplantar height of the joint facet (see Fig. 5). Because an increase in the convexity of the “male” joint surface is correlated with joint mobility (Hamrick, 1996), it is hypothesized that more convex proximal fourth and fifth metatarsal bases will be correlated with increased tarsometatarsal joint mobility and a midtarsal break. Primates possessing a midtarsal break are hypothesized to possess a correspondingly concave cuboid facet, which would help stabilize a tarsometatarsal joint that is incurring a loading force throughout a wide range of motion (Hamrick, 1996). In contrast, a flatter cuboid-metatarsal joint surface may restrict midfoot mobility and is hypothesized to characterize the modern human foot. Qualitative observations were made on the lateral metatarsals to assess whether the articular surface extends dorsally or plantarly.

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 depth of the articular surface was measured relative to the overall dorsoplantar height of the joint surface. Four human and chimpanzee fourth and fifth metatarsals were measured using both the carpenter's contour guide and the 3D scanner method, and the results obtained were statisti-

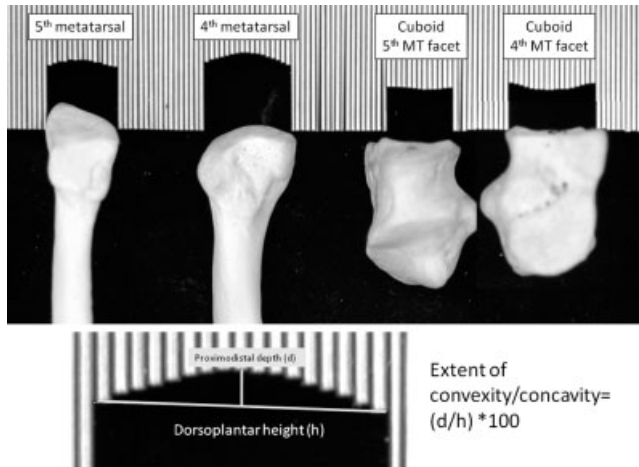


Fig. 5. Method for estimating the extent of convexity/concavity of the cuboid-metatarsal joint surface. The dorsal surface is on the left of each bone whereas the plantar surface is on the right except for the cuboid fourth metatarsal facet for which these positions are reversed. The bases of the fifth and fourth metatarsals were depressed into a carpenter's contour guide as shown in this example from *Pan troglodytes* (left). Impressions of the fifth and fourth metatarsal facets on the cuboid are also shown (right). The proximodistal depth of the impression was divided by the dorsoplantar height and multiplied by 100 to quantify the extent of convexity/concavity of the joint surface. Details are provided in the text.

cally identical (*t*-test paired sample for means test: $t = 0.38$, $P = 0.71$).

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

RESULTS

X-rays and dissections of baboon feet

The 10 X-rays of baboon feet 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 (see Fig. 2). The calcaneus moved to a position slightly more superiorly relative to the cuboid when the midfoot was elevated, on average $5.7^\circ \pm 4.2^\circ$. The majority of the midfoot motion occurred as a result of the cuboid shifting to a more superior position relative to the fourth and fifth metatarsals, $16.7^\circ \pm 2.4^\circ$. The goal of the X-rays was to assess where midfoot mobility was occurring, rather than precisely quantifying it. Therefore, the variation in the angle formed between the foot bones from one baboon to another occurred in part because the amount of tensile force being exerted on the tibiae was not perfectly standardized. Nevertheless, the pattern of more dorsiflexion occurring between the cuboid and the metatarsals rather than the cuboid and calcaneus consistently occurred in all 10 X-rayed baboon feet.

Dissections of right feet of the baboons also suggest that both joints may be involved in producing the cumulative midfoot dorsiflexion. When tension was applied to the proximal tibia and the calcaneus lifted off a horizontal surface, dorsiflexion occurred first at the calcaneocuboid joint with a magnitude of $9.2^\circ \pm 1.5^\circ$.

When tension continued to be applied to the tibia and the calcaneus further lifted from the horizontal surface, dorsiflexion shifted from the calcaneocuboid joint to the cuboid-metatarsal joint and become significantly more pronounced. Dorsiflexion at the cuboid-metatarsal joint amounted to $20.6^\circ \pm 2.3^\circ$ (Table 2).

Study of live primate feet

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 fifth 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.

Instead of moving directly from a heel-flat, plantigrade position to dorsiflexion at the midfoot, the chimpanzee foot appeared to "roll" during heel lift through push-off phase of walking with an initial slight flexion ($16.1^\circ \pm 4.3^\circ$) occurring proximally to the tuberosity of the fifth metatarsal (calcaneocuboid joint) and then smoothly transitioning to a more pronounced dorsiflexion ($26.5^\circ \pm 4.4^\circ$) in a position more distal to the tuberosity mark (tarsometatarsal joint). The transition from this joint to the metatarsophalangeal joint was also done in a fluid manner (Fig. 6A,B). The gorilla feet (Fig. 6C,D) appeared to undergo the same series of midfoot motions as the chimpanzee foot during quadrupedal walking, though the magnitude of midfoot dorsiflexion was slightly less, with $14.1^\circ \pm 5.3^\circ$ occurring at the calcaneocuboid joint and $21.1^\circ \pm 3.8^\circ$ of dorsiflexion at the tarsometatarsal joint. Nevertheless, it is clear from the chimpanzee and gorilla walking sequences that the midtarsal break is initiated with dorsiflexion first at the calcaneocuboid joint and then augmented with a higher magnitude of dorsiflexion at the more distal tarsometatarsal joint. Mandrills and macaques are digitigrades primates and do not experience heel strike. Instead, the heel begins in a more elevated position than what is observed in African apes ($28.2^\circ \pm 6.0^\circ$ in *Mandrillus* and $28.0^\circ \pm 7.8^\circ$ in *Macaca*), and this appears to occur primarily at the calcaneocuboid joint (Fig. 6E,F). However, as seen in the ape feet, the midtarsal break shifts to the more distal cuboid-metatarsal joint as motion continues and increases in magnitude ($42.1^\circ \pm 4.6^\circ$ in *Mandrillus* and $40.4^\circ \pm 8.0^\circ$ in *Macaca*). Motion observed in gorilla, chimpanzee, mandrill and macaque feet contrasts with that shown by the human foot (Fig. 6G), which establishes a fulcrum at the metatarsophalangeal joint just after heel lift, by-passing the midfoot dorsiflexion seen in the non-human primate feet.

Skeletal specimens

Gorillas and chimpanzees are statistically identical for the convexity of the articular surface of the fourth metatarsal ($P = 0.42$). This articular facet is strongly convex in chimpanzees and gorillas, extending $16.2\% \pm 4.4\%$ and $17.2\% \pm 4.9\%$ of the total height of the facet, respectively (see Fig. 7). This measure is only $5.2\% \pm 5.3\%$ in modern humans, which is significantly flatter than the fourth metatarsal facet in African apes ($P < 0.001$). Likewise, chimpanzees and gorillas have fifth metatarsal facets that are statistically indistinguishable in convexity: $10.6\% \pm 5.4\%$ and $8.4\% \pm 5.5\%$ of the height of the

TABLE 2. Dorsiflexion at the tarsometatarsal joint and the shape of this joint in primates

Taxa	Dorsiflexion at TMT joint	Source	n	^a Mean shape of the tarsometatarsal joint (Depth/Dorsoplantar height) × 100			
				Proximal fourth MT facet	Proximal fifth MT facet	Cuboid fourth MT facet	Cuboid fifth MT facet
<i>Mandrillus sphinx</i>	42.1° (n = 6)	Kinematic analysis. This study.	5	17.1 ± 3.9	11.3 ± 4.1	-8.1 ± 1.7	-4.5 ± 2.1
<i>Papio</i> spp.	^b 16.7° ^b 20.6° (n = 10)	X-ray Dissection. This study.	6	12.2 ± 3.8	12.7 ± 3.0	-7.7 ± 1.9	-2.7 ± 2.6
<i>Macaca</i> spp.	40.4° (n = 9)	Kinematic analysis. This study.	8	12.6 ± 2.9	8.7 ± 2.3	-7.1 ± 1.2	-3.9 ± 1.8
<i>Hylobates lar</i>	38.0° (n = 8)	Vereecke and Aerts, 2008	10	15.6 ± 2.5	14.2 ± 3.7	-9.2 ± 2.7	-1.4 ± 4.0
<i>Gorilla gorilla</i>	21.1° (n = 9)	Kinematic analysis. This study.	29	17.2 ± 4.9	8.4 ± 5.5	-13.9 ± 3.2	-0.4 ± 5.9
<i>Pan</i> spp.	~30° (n = 1)	D'Août et al., 2002 (Fig. 7)	33	16.2 ± 4.4	10.6 ± 5.4	-10.8 ± 4.5	3.1 ± 6.2
<i>Homo sapiens</i>	26.5° (n = 10)	Kinematic analysis. This study.					
	~5° (n = 19)	Ouzounian and Shereff, 1989; Blackwood et al., 2005	31	5.2 ± 5.2	3.9 ± 4.6	-4.5 ± 5.4	0.5 ± 3.6
A.L. 333-13				-	3.8	-	-
A.L. 333-78				-	7.4	-	-
StW 485				-0.7	-	-	-
StW 114/115				-	3.7	-	-
OH 8				6.6	5.5	-6.2	-3.5
KNM-ER 803				-	1.1	-	-

^a Negative values indicate a concave surface; 0 indicates a flat surface; positive values a convex surface.

^b The lower values for *Papio* spp. compared to other cercopithecoids may be the result of both the different method (X-ray) employed to quantify dorsiflexion at the tarsometatarsal joint, and the fact that these animals were not alive. The *Homo sapiens* estimates are reported here as one-half the total range of sagittal motion between the cuboid and lateral metatarsals on human cadavers from the cited studies and assume an equal amount of dorsiflexion and plantarflexion.

facet, respectively ($P = 0.11$). In humans, the fifth metatarsal base is significantly flatter ($P = 0.001$) measuring $3.9\% \pm 4.6\%$ of the total height of the facet (see Fig. 8). The small sample of cercopithecoids and *Hylobates* examined possess convex bases on the lateral metatarsals, similar to what is observed in the African apes, and quite distinct from the flattened condition of human lateral metatarsal bases (Table 2).

The fourth metatarsal facet of the cuboid is slightly flatter in chimpanzees, $11.0\% \pm 4.5\%$ than in gorillas, $14.0\% \pm 3.2\%$ ($P = 0.02$) (see Fig. 9). Humans have articular surfaces that are $4.5\% \pm 5.4\%$, statistically flatter than African ape cuboid fourth metatarsal facets ($P < 0.01$). Like the African apes, the small sample of cercopithecoids and *Hylobates* measured had a concave facet on the cuboid for the base of the fourth metatarsal (Table 2). The fifth 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*, $P = 0.06$) (see Fig. 10). The cercopithecoids measured in this study possess a more concave cuboid facet for the base of the fifth metatarsal than what is typically found in apes (Table 2).

It is important to note that “flatness” can be achieved either by decreasing the magnitude of the concavity/convexity of the joint surface, or by increasing the dorsoplantar height. The dorsoplantar height of the proximal fourth and fifth metatarsal bases and the cuboid facets are statistically identical between humans and gorillas (MT IV: $t = 0.44$, $P = -0.66$, $df = 56$; MT V: $t = 0.11$, $P = 0.91$, $df = 58$; Cuboid IV MT facet: $t = 0.55$, $P = 0.58$, $df = 57$; Cuboid V MT facet: $t = 0.21$, $P = 0.83$, $df = 57$). Chimpanzee fourth and fifth metatarsal dimensions are size-reduced versions of the gorilla morphology. Therefore, the difference in the extent of convexity/concavity between humans and the African apes is most likely a function of the shallowness of the joint depth

and not an expansion of the dorsoplantar height in humans.

Hominin fossils

The hominin cuboid-metatarsal region is poorly represented in the fossil record (Table 1). Only the OH 8 cuboid, and an undescribed, possibly *P. robustus*, cuboid from Kromdraai (Thackeray et al., 2001) are known from the Plio-Pleistocene. Only nine lateral metatarsals were known until the recently discovered postcranial remains from Dmanisi increased that number to twelve (Lordkipanidze et al., 2007).

StW 485 is a right fourth metatarsal, broken 26.8 mm from the base. The articulation with the cuboid is slightly concave mediolaterally and dorsoplantarly it is flat with a depth only 0.7% of the total dorsoplantar 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 (see Fig. 7). Deloison (2003) describes the cuboid facet of StW 596 as “sinuouse,” 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.

A.L. 333-78 possesses a slightly convex cuboid facet of the fifth metatarsal—7.4% the height of the facet—a value that falls within the range for both humans and African apes (see Fig. 8). A.L. 333-13 is almost identical to the modern human median for this measure, having a dorsoplantar convexity 3.8% of the height of the cuboid facet (see Fig. 8).

StW114/115 is the earliest complete hominin fifth metatarsal (Zipfel et al., 2009). It is 60.7 mm from the tip of the lateral tuberosity to the most distal point on the metatarsal head. The cuboid articulation is mediolaterally convex and dorsoplantarly only slightly convex,

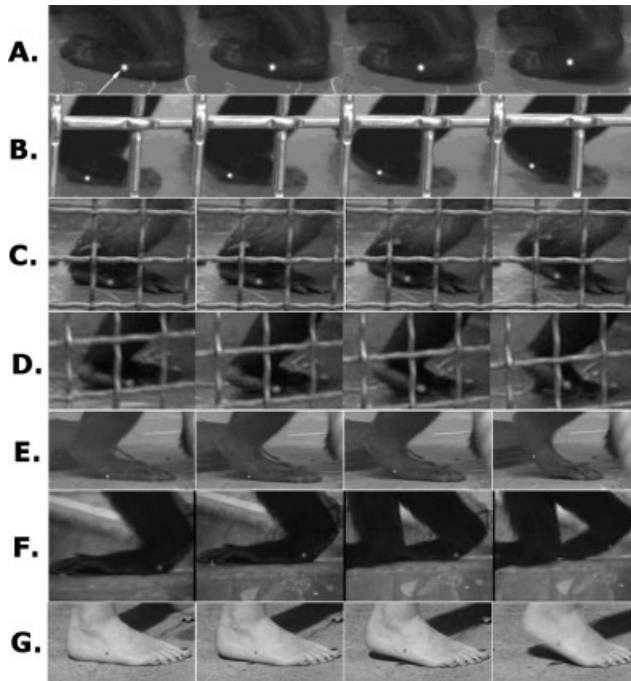


Fig. 6. Stills of video taken of terrestrial walking in captive primates. For all of the images, the first frame is stance phase, the second is initial heel lift, the third is continued heel lift, and the final frame is push-off. The frames are in sequence with 70 ms between each. (A–D) Adult male chimpanzee, adult female chimpanzee, and adult male and female gorillas at Detroit Zoo with fifth metatarsal tuberosity marked. (E) Adult female *Mandrillus* and (F) Adult female *Macaca silenus* both from the Detroit Zoo and the fifth metatarsal tuberosity marked. (G) Adult female human with tuberosity of fifth metatarsal marked. Frames 1 and 4 do not differ between the apes and the human. However, in frames 2 and 3, midfoot dorsiflexion is clear in the apes but not the human. Notice that in frame 3, the midfoot dorsiflexion generally occurs on or distally to the white spot indicating the position of the tuberosity of the fifth metatarsal in the chimpanzees and gorilla. This suggests motion at the cuboid-metatarsal joint. Likewise in the cercopithecoids, digitigrade postures and midfoot dorsiflexion during push-off phase of walking appear to be a function of both calcaneocuboid and cuboid-metatarsal dorsiflexion.

3.7% of the dorsoplantar height of the facet. This is almost identical to the human mean for this measure ($3.9\% \pm 4.6\%$) (see Fig. 8).

The left fifth metatarsal (KNM-ER 803f) preserves only the most proximal 32.4 mm, including the base. The articulation for the cuboid is relatively flat, with a height only 1.1% of the dorsoplantar height, in the low part of the human range (see Fig. 8).

The fifth metatarsal of the OH 8 foot preserves a proximal section 48.3 mm in length, but is broken prior to the metatarsal head. The articulation with the cuboid is slightly convex dorsoplantarly (5.5% of total height) and convex mediolaterally. The fourth metatarsal preserves the most proximal 40.6 mm. The articular facet for the cuboid is slightly convex dorsoplantarly (6.6% of total height). The slight convexity of the cuboid facets of the fourth and fifth metatarsals is strikingly human-like and distinct from the African ape condition (Figs. 7 and 8). The cuboid of OH 8 is quite small, measuring 28.0 mm proximodistally, 20.4 mm mediolaterally, and 18.7 mm dorsoplantarly. The facet for the fourth metatarsal is

Shape of the cuboid facet of the 4th metatarsal in African apes, humans and hominins.

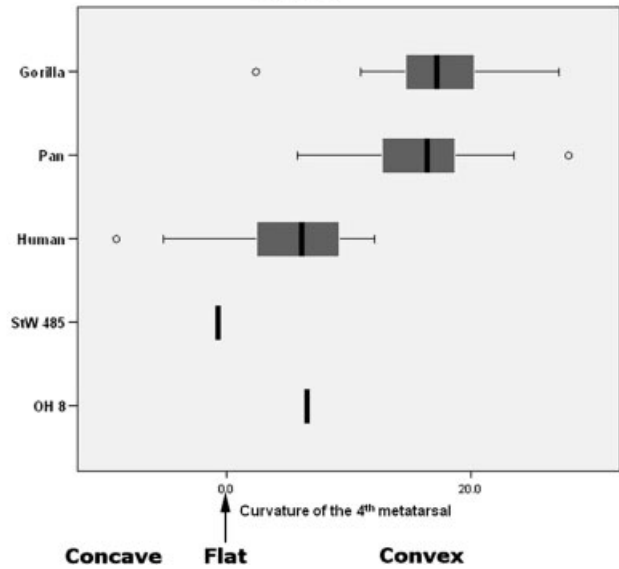


Fig. 7. The x-axis is the ratio of the proximodistal depth of the proximal fourth metatarsal facet relative to its dorsoplantar height. A positive value is convex, a negative is concave. Box-plots show the median (black bar), interquartile ranges (gray box), and overall ranges of the data (whiskers). Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Humans have dorsoplantarly flat fourth metatarsal bases, whereas chimpanzees and gorillas have more convex fourth metatarsal bases. The OH 8 and StW 485 fourth metatarsals have flat, human-like, proximal facets.

Shape of the cuboid facet of the 5th metatarsal in African apes, humans and hominins.

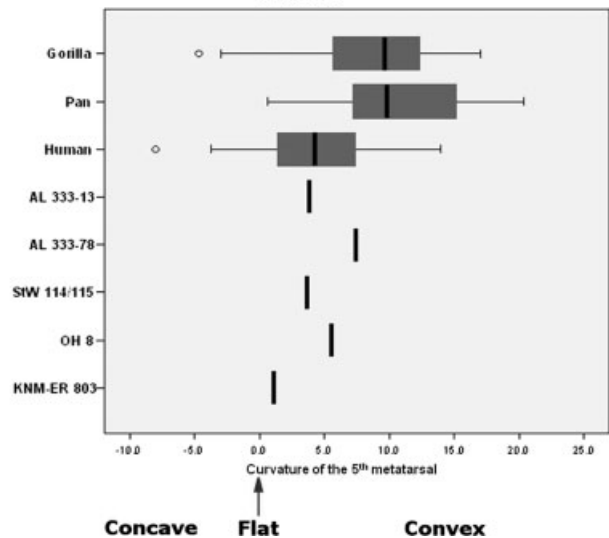


Fig. 8. The x-axis is the ratio of the proximodistal depth of the proximal fifth metatarsal facet relative to its dorsoplantar height. A positive value is convex, a negative is concave. Box-plots show the median (black bar), interquartile ranges (gray), and overall ranges of the data (whiskers). Outliers defined as greater than 1.5 times the interquartile range are shown as circles. Although there is some overlap, humans tend to have flatter fifth metatarsal bases, whereas chimpanzees and gorillas have more convex fifth metatarsal bases. The KNM-ER 803f, 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.

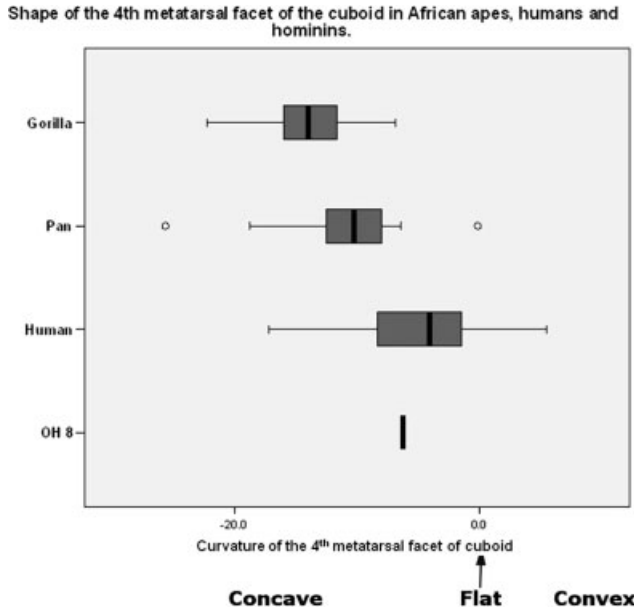


Fig. 9. The x-axis is the ratio of the proximodistal depth of the cuboid facet for the fourth metatarsal relative to its dorsoplantar height. A positive value is convex, a negative is concave. Boxplots show the median (black bar), interquartile ranges (gray), and overall ranges of the data (whiskers). 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 fourth 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 fourth metatarsal.

slightly concave dorsoplantarly (6.2% of total height) and mediolaterally flat. It is quite distinct from the African ape condition for this measure (see Fig. 9). Dorsoplantarly, the facet for the fifth metatarsal is slightly concave, 3.5% of its total height, though this measure does not discriminate modern humans and African apes (see Fig. 10).

DISCUSSION

It is clear that a single line of evidence would not be sufficient to convincingly demonstrate that on the lateral side of the foot the midtarsal break occurs primarily at the tarsometatarsal joint rather than the calcaneocuboid joint. However, results obtained from X-rays, dissections, video data from live catarrhines, and skeletal comparisons all point to the same general conclusion. It can thus be reasonably argued that D’Aouët 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 the calcaneocuboid joint does contribute to midtarsal dorsiflexion in macaques, baboons, mandrills, chimpanzees, and gorillas, the majority of this motion appears to happen more distally at the tarsometatarsal joint. It is therefore 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 cuboid-metatarsal joints to the midfoot break. An important caveat is that this study only examined dorsiflexion at the midfoot.

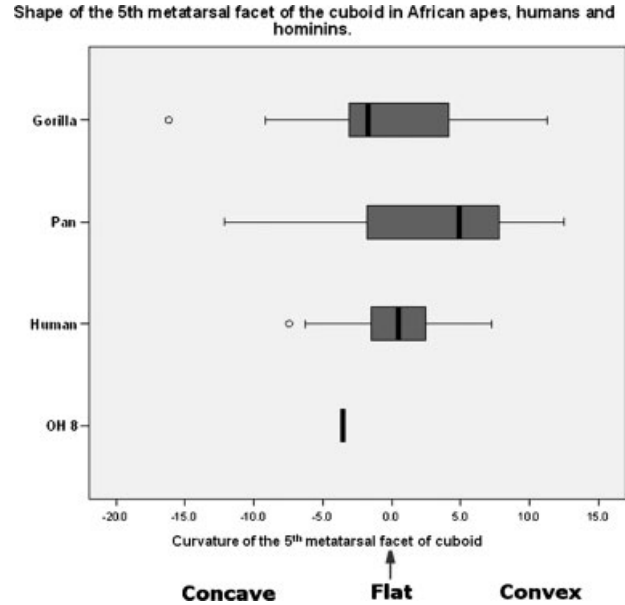


Fig. 10. The x-axis is the ratio of the proximodistal depth of the cuboid facet for the fifth metatarsal relative to its dorsoplantar height. A positive value is convex, a negative is concave. Boxplots show the median (black bar), interquartile ranges (gray), and overall ranges of the data (whiskers). 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 extent of convexity/concavity of the facet for the fifth metatarsal.

However, the midfoot break probably involves a rotational component as well that could be better understood with cineradiography. Additionally, these results are in part based on a kinematic analysis of only 34 individual strides from 4 different species of non-human primate. It may thus be premature to state that all non-human primates share the exact same pattern of joint movements at the transverse tarsal and tarsometatarsal joints during the midfoot break. This hypothesis could be tested with additional kinematic data from a more diverse sample of anthropoid 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 is questioned whether the calcaneocuboid joint was the sole anatomical site of the midfoot break. The results of this study suggest that both the calcaneocuboid joint and the tarsometatarsal joint contribute to midfoot dorsiflexion, with the more distal joint perhaps having a greater range of dorsiflexion capacity. Nevertheless, the calcaneocuboid joint is a critical area for assessing whether the midtarsal joint locking mechanism is in place even if most of the midfoot flexion is not 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 (Sarraffian, 1987). Although in humans total foot flexion of about 10 degrees can occur between the cuboid and metatarsals (Ouzounian and Shereff, 1989), this flexion is significantly reduced when the calcaneus is inverted during

the push-off phase of walking (Blackwood et al., 2005). Interestingly though, Blackwood et al. (2005) did not find that dorsiflexion 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 prevents the midfoot break, it is not the primary anatomical source of it. Nevertheless, the locking of the calcaneocuboid joint, and perhaps more critically the presence of a binding longitudinal arch that tenses during hindfoot inversion help prevent a midfoot break in humans.

This study therefore has implications for understanding the evolution of a lateral longitudinal arch itself. 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 the absence of an arch in non-human primates. Apes and monkeys have a strong short plantar ligament between the calcaneus and cuboid, perhaps providing additional soft tissue evidence that the majority of midfoot dorsiflexion 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. If the structural components of the longitudinal arch are the primary inhibitors of midfoot dorsiflexion in humans, then it follows that identifying skeletal correlates of midfoot stability in early hominins may provide indirect evidence for the evolution of the structural components of the longitudinal arch. At the very least, it would provide evidence for the evolution of a stiff midfoot acting as a rigid lever during the push-off phase of bipedal locomotion.

Evolution of the stable midfoot

It is quite useful for paleoanthropologists to identify skeletal correlates of 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 examined to assess how stable the midfoot was 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, and functionally related to midfoot mobility. The fourth and fifth metatarsal bases of chimpanzees and gorillas are significantly more convex than these articular facets on modern human metatarsals. Additionally, the fourth metatarsal facet on the human cuboid is significantly flatter than the more concave facet in African ape cuboids, though no statistically significant difference was found in the extent of concavity of the fifth metatarsal facet on the cuboid of humans and African apes. The convex morphology of the fourth and fifth metatarsal bases and

corresponding concave facet on the cuboid in African apes is argued to be related to midfoot dorsiflexion, and not to general grasping abilities, for three reasons. One, the convexity of the cuboid facet on the fourth metatarsal extends dorsally, consistent with increased dorsiflexion rather than plantarflexion at the tarsometatarsal joint. Two, the metatarsal-cuneiform facets of apes are moderately flat. If these joint surfaces were convex and concave respectively, it could be argued that the cuboid-fourth metatarsal joint morphology was like the rest of the distal ape midfoot in being adapted for mobility and grasping. Three, a preliminary assessment of the cuboids and lateral metatarsals of *Hylobates* and three cercopithecoid genera are consistent with kinematic, dissection, and X-ray data demonstrating that significant dorsiflexion occurs at the tarsometatarsal joint in the foot of these primates. These results strongly suggest that the morphology of the lateral tarsometatarsal joint is an indicator of midfoot stability across primates and can be used to interpret the functional morphology of fossil hominins.

The morphology of a joint surface is functionally related to both joint mobility and the loading environment. Hamrick (1996) has found that relatively flat joint surfaces on both the "male" and "female" ends of a joint imply limited mobility and unidirectional loading environments. This appears to be the case for the relatively immobile human tarsometatarsal joint (Figs. 7–10). However, it is important to note that curvature of a joint surface is not always a simple indicator of joint mobility. For example, the glenoid cavity of the hominoid scapula is *less* curved in the craniocaudal direction than what is found in cercopithecoids, despite the observation that apes have a larger range of motion at the shoulder joint (MacLatchy et al., 2000). However, it is the humeral head, considered the "male" aspect of the shoulder joint that is significantly more curved in the hominoids and helps facilitate a greater range of motion (Larson, 1993). As Hamrick (1996) observed, a highly curved "male" surface of a joint implies high angular excursions regardless of the shape of the "female" joint surface, which is functionally related to the loading environment. This may help explain why humans and non-humans primates possess lateral metatarsal joint surfaces with such a different extent of convexity (Figs. 7 and 8), but share relatively similar distal cuboid joint surfaces (Figs. 9 and 10). Thus, the convexity of the proximal surfaces of the lateral metatarsals may be more informative than the extent of concavity of the proximal cuboid surface in gauging mobility at the tarsometatarsal joint.

The midfoot of *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. Calcaneocuboid 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). Some studies have also 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

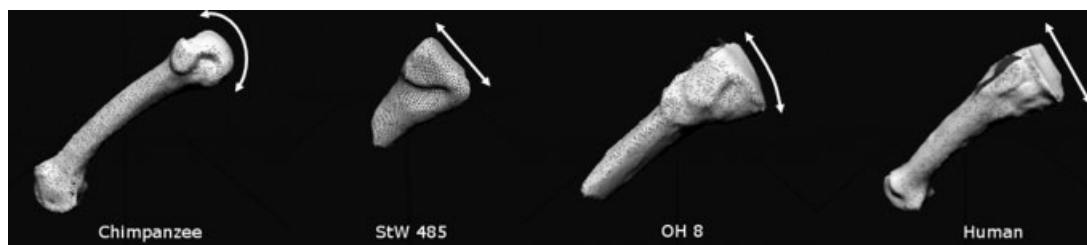


Fig. 11. 3D models obtained by scanning the fourth metatarsals of a chimpanzee (left), human (right), StW 485 (middle left), and the OH 8 foot (middle right) using a portable NextEngine laser scanner. Each bone is oriented with the distal metatarsal head to the lower left and the proximal metatarsal base to the upper right. Notice the convex base to the ape metatarsal, and the flattened proximal base on the human, StW 485, and OH 8 metatarsals.

(Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004).

However, others have suggested that *A. afarensis* may have had an arch and a stable, stiff midfoot. 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., 1991; Harcourt-Smith and Hilton, 2005), these footprints are evidence that *A. afarensis* had an arched foot. Such an arched foot would have limited midfoot mobility (Kidd, 1993).

The fifth metatarsals of A.L. 333-13 and A.L. 333-78 do not conclusively indicate whether *A. afarensis* had a more mobile midfoot than what modern humans possess (see Fig. 8). The cuboid surface of A.L. 333-78 is more convex than most modern human fifth 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 fifth 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 some ape fifth metatarsals can be found with this morphology. Because the fourth metatarsal may be a better skeletal indicator of midfoot mobility, the morphology of the currently unpublished *A. afarensis* fourth metatarsal A.L. 333-160 from Hadar (Kimbel et al., 2004) may be critical for assessing midfoot stability in this species.

The midfoot of *Australopithecus africanus*. Based on the nonweight 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 fourth metatarsals of StW 485 and StW 596 are both flat, like modern humans and distinctly unlike the convex facet of African apes with midfoot mobility (Figs. 7 and 11). Additionally, the extent of convexity of the cuboid facet on the fifth metatarsal from Member 4 in Sterkfontein StW 114/115 is almost identical to the modern human mean (see Fig. 8). These data suggest that *A. africanus* possessed a stiff midfoot with limited

midfoot mobility, and perhaps even had the soft tissue components of a lateral longitudinal arch.

The midfoot of East African hominins circa 1.8–1.5 mya. It is difficult to assign postcranial specimens from this time period 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 genus *Paranthropus*. Regardless of taxa, the evidence is strong that known hominins from this time period had a stiff foot with limited range of dorsiflexion at the midfoot, and possibly a lateral longitudinal arch.

Multiple studies agree that the morphology of the calcaneocuboid joint in the OH 8 foot would produce a stable lever during push-off (Lewis, 1980b; Stern and Susman, 1983; Susman, 1983; Langdon 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 years ago (Day and Napier, 1964; Susman, 1983; Lamy, 1986; Berillon, 2003). However, others (Oxnard and Lisowski, 1980; Kidd et al., 1996; Kidd, 1998) have disagreed, and have suggested that the OH 8 foot did not possess a fully developed longitudinal arch.

This study finds that the morphology of the cuboid, fourth and fifth metatarsals in the OH 8 foot are strongly suggestive of midfoot stability in this hominin. The articular facets on the cuboid, fourth metatarsal and fifth metatarsal are distinctly human-like in having a flat joint (Figs. 7–11). The extent of convexity/concavity of the joint facets are thus consistent with the OH 8 individual being unable to produce midfoot dorsiflexion, and perhaps then possessing the structural components of a lateral longitudinal arch.

The fifth metatarsal from Koobi Fora assigned to *Homo erectus* KNM-ER 803f is indistinguishable from that of modern humans and provides further evidence for midfoot stability in early Pleistocene hominins (see Fig. 9). This assessment of the *H. erectus* midfoot is consistent with recently discovered footprints from the 1.52 mya site of Ileret (Bennett et al., 2009). 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 is predicted based on the interpretation of Lordkipanidze et al. (2007) that the Dmanisi hominins had a longitudinal arch.

The midfoot break, longitudinal arch, and climbing capacity of early hominins

A debate has raged for at least 25 years now whether the adaptations for bipedality preclude climbing in early hominins (e.g., Latimer, 1991), or whether some of the primitive skeletal features of early hominins are evidence that these animals were both bipedal and arboreal (e.g., Susman et al., 1984). The data presented in this article provide more insight into the study of early hominin locomotion.

During the early stance phase of bipedal walking, the foot is pronated, that is, the calcaneus is everted (Samarco, 1989; Donatelli, 1990). This position of hindfoot eversion raises the longitudinal arch, relaxes the plantar aponeurosis and long plantar ligament, and allows for some midfoot mobility (Hicks, 1953; Inman, 1976; Sarrafian, 1987). However, during the later stance phase of walking, the tibia swings over the foot at the talocrural joint, dorsiflexes, and internally rotates. The calcaneus inverts and locks at the calcaneocuboid joint, and this position of the hindfoot lowers the longitudinal arch, tensing the plantar aponeurosis and long plantar ligament (Hicks, 1953; Inman, 1976; Sarrafian, 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, 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 (DeSilva, 2008, 2009). 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 during climbing bouts. If chimpanzees had a longitudinal arch, or even a flat but stiff midfoot, dorsiflexion and adduction would tense the midfoot region, and limit mobility precisely during the time when they would require it most. Meldrum and Wunderlich (1998) have suggested that midfoot flexion may allow climbing primates to have both a grasping forefoot required to hold onto a vertical substrate and a stable hindfoot necessary for propulsion. The absence of a midfoot break or midfoot mobility would therefore severely compromise a climbing primate's ability to efficiently and safely navigate in an arboreal environment. The evolution of a stiff midfoot, perhaps even with the structural components of a longitudinal arch, produces an efficient lever during the push-off phase of bipedal locomotion. But, this foot morphology would be maladaptive for climbing in a modern ape-like manner. These data suggest that if hominins with a stiff midfoot did climb, they would have to do so in a kinematically unique manner.

CONCLUSIONS

Although the morphology of the calcaneocuboid joint facilitates midtarsal mobility, the primary anatomical site for the midtarsal break is at the tarsometatarsal joint. Midfoot dorsiflexion in modern humans is inhibited by the structural components 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. Midfoot fossils of *A. afarensis* appear more human-like, but are not conclusive due to the overlap in morphology between humans and African apes. By the Pleistocene, known hominins were devoid of any midfoot dorsiflexion and may have possessed a well-developed longitudinal arch. The presence of a stable midfoot may have restricted their ability to vertically climb trees in a manner kinematically similar to modern chimpanzees.

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