



A complete second metatarsal (StW 89) from Sterkfontein Member 4, South Africa

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ABSTRACT

The functional anatomy of the hominin foot has played a crucial role in studies of locomotor evolution in human ancestors and extinct relatives. However, foot fossils are rare, often isolated, and fragmentary. Here, we describe a complete hominin second metatarsal (StW 89) from the 2.0–2.6 million year old deposits of Member 4, Sterkfontein Cave, South Africa. Like many other fossil foot bones, it displays a mosaic of derived human-like features and primitive ape-like features. StW 89 possesses a domed metatarsal head with a prominent sulcus, indicating dorsiflexion at the metatarsophalangeal joint during bipedal walking. However, while the range of motion at the metatarsophalangeal joint is human-like in dorsiflexion, it is ape-like in plantarflexion. Furthermore, StW 89 possesses internal torsion of the head, an anatomy decidedly unlike that found in humans today. Unlike other hominin second metatarsals, StW 89 has a dorsoplantarly gracile base, perhaps suggesting more midfoot laxity. In these latter two anatomies, the StW 89 second metatarsal is quite similar to the recently described second metatarsal of the partial foot from Burtele, Ethiopia. We interpret this combination of anatomies as evidence for a low medial longitudinal arch in a foot engaged in both bipedal locomotion, but also some degree of pedal, and perhaps even hallucal, grasping. Additional fossil evidence will be required to determine if differences between this bone and other second metatarsals from Sterkfontein reflect normal variation in an evolving lineage, or taxonomic diversity.

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Introduction and provenience

Complete metatarsals are extremely rare in the hominin fossil record, yet they can reveal a tremendous amount of information regarding general foot anatomy and function (e.g., Zipfel et al., 2010; Ward et al., 2011). Currently, there are only seven complete lateral metatarsals known from early hominins (Table 1). Here, we describe a complete second metatarsal from Sterkfontein Member 4, South Africa, and use this bone to evaluate the medial column of the foot in early hominins and to address variation in the Sterkfontein fossil assemblage.

StW 89 is a well preserved complete left second metatarsal from Member 4, Sterkfontein Cave, South Africa (Fig. 1). It was recovered by Alan Hughes in 1980, in grid S/59 at a depth of 12'0"–13'4" (3.7–4.1 m), and is first referenced in the scientific literature by Clarke (1985). Though the anatomy was not described at all, Clarke (1985) suggested that StW 89 may have derived from Sterkfontein

Member 5, and notes that flaked artifacts were found in proximity to this metatarsal. Given its apparent association with these stone tools, StW 89 was provisionally assigned to *Homo habilis* (Clarke, 1985). However, reexamination of the Sterkfontein stratigraphy led Kuman and Clarke (2000) to reposition the StW 89 metatarsal within the older deposits of Member 4, now thought to be between 2.0 and 2.6 Ma (millions of years ago) (Pickering and Kramers, 2010). In preliminary descriptions of the foot bones from Sterkfontein, Deloison (2003) discusses StW 89. The anatomy of the bone is briefly described and basic metrics provided, but comparative data are lacking and the functional anatomy is categorized only as "indéterminés". In this paper, we expand on these important preliminary observations by Deloison (2003) and re-evaluate StW 89 in the context of more recent discoveries, including the partial foot from the Burtele locality at Woranso-Mille, Ethiopia (Haile-Selassie et al., 2012).

A talus, StW 88 (R/59; 12'3"–13'3"), and a proximal foot phalanx, StW 355 (T/59 10'7"–11'7"), were found in close proximity to this metatarsal, though the stratigraphy at Sterkfontein is exceedingly complex (Clarke, 2006) and proximity may not necessarily imply any association. Nevertheless, StW 355 has

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Table 1
Table of complete non-hallucal metatarsals in the early hominin fossil record.

Metatarsal	Species	Accession number	Age (Ma)	Reference
2	<i>Australopithecus africanus</i> ?	StW 89	2.0–2.6	This study
2	Hominin indet.	BRT-VP-2/73b	3.4	Haile-Selassie et al., 2012
3	<i>Ardipithecus ramidus</i>	ARA-VP-6/505	4.4	Lovejoy et al., 2009
4	Hominin indet.	BRT-VP-2/73a	3.4	Haile-Selassie et al., 2012
4	<i>Australopithecus afarensis</i>	A.L. 333-160	3.2	Ward et al., 2011
4	Early <i>Homo</i>	D2669	1.78	Pontzer et al., 2010
5	<i>Australopithecus africanus</i>	StW 114/115	2.0–2.6	Zipfel et al., 2009

a strikingly similar patina and may belong with StW 89 as has been suggested elsewhere (Kuman and Clarke, 2000). The implications of the possible association between StW 89 and 355 are discussed later. No craniodental remains have been described from this precise area of the Sterkfontein grid, though S/59 is now thought to be part of Member 4 (Kuman and Clarke, 2000), and *Australopithecus africanus* is the only species of hominin currently recognized from these 2.0–2.6 Ma (Pickering and Kramers, 2010) deposits of Sterkfontein cave. It is notable, however, that Clarke (1988, 2008) has long held that Sterkfontein Member 4 is a mixed assemblage containing two species of hominin. Schwartz and Tattersall (2005) also identify several distinct morphs in the Sterkfontein Member 4 assemblage. Furthermore, the recent description of the 3.4 Ma foot from the Burtele locality of the Woronso-Mille study area, Ethiopia, demonstrates that there were two distinct foot morphs during the Late Pliocene (Haile-Selassie et al., 2012). If two locomotor anatomies evolved in the East African Pliocene, it is not unreasonable to suppose that the same locomotor diversity existed in South Africa in the years that followed. Here we provide a functional description of StW 89, and use this specimen to test locomotor and taxonomic hypotheses regarding the medial column of the hominin foot.

Materials and methods

StW 89 was compared with second metatarsals from modern humans and extant apes. In addition, the fossil was compared with fragmentary fossil hominin second metatarsals listed in Table 2. The South African material was studied at the University of the Witwatersrand in Johannesburg. The original OH 8 foot was studied at the Tanzania National Museum and House of Culture, Dar es Salaam. Casts of the Hadar metatarsals were studied at the Harvard

Peabody Museum. All measurements were made with digital calipers. These included the maximum length from the most proximal projection of the base to the most distal point of the head, the maximum mediolateral width of the midshaft and the maximum dorsoplantar height taken perpendicular to the mediolateral width of the midshaft, the dorsoplantar and mediolateral height and width of the metatarsal head (following Latimer and Lovejoy, 1990), the maximum dorsoplantar height and mediolateral width of the base of the metatarsal, and the maximum dorsoplantar height and mediolateral width of only the articular portion of the base of the metatarsal. Torsion was measured as described by Pontzer et al. (2010).

A bootstrapping approach was utilized to test whether the ratio of the second metatarsal head area to first metatarsal head area in the Sterkfontein Member 4 assemblage could be best sampled from a human or African ape population. This approach assumes that StW 89 and the first metatarsals StW 562 and StW 595 are from the same species (but see Zipfel et al., 2010), though it does not assume that they are from the same individual. The area of the metatarsal heads was calculated as the product of the dorsoplantar height and the mediolateral width of the heads (not including the cornua) following Latimer and Lovejoy (1990) for chimpanzees ($n = 33$), gorillas ($n = 20$) and humans ($n = 39$). Though a simple by-product of the mediolateral and dorsoplantar dimensions is a crude method for measuring the surface area, it effectively discriminates between apes and humans (see below). All of these extant data were collected at the Cleveland Museum of Natural History. For each species, a first metatarsal head area was selected at random and paired with a randomly selected second metatarsal head area, and a ratio of these areas was calculated. This process was repeated 1000 times for each species. The ratio of the area of the head of StW 89 to the area of the heads of StW 562 and 595 was then compared to the distribution of ratios obtained by resampling from the modern populations. This same procedure was also done on *Australopithecus afarensis* second metatarsal heads (A.L. 333-115B and A.L. 333-72) and first metatarsal heads (A.L. 333-115A, A.L. 333-21) using published measurements (Latimer et al., 1982; Latimer and Lovejoy, 1990), and measurements made from casts.

A second bootstrapping approach was used to test the likelihood of sampling second metatarsals from a modern population with base depths as different as StW 89 and another second metatarsal from Sterkfontein Member 4, StW 377 (discussed more below). The ratio of the base dorsoplantar height to bone length was calculated for chimpanzees ($n = 43$), gorillas ($n = 35$), and humans ($n = 22$). The extant ape data were measured at the Cleveland Museum of Natural History, American Museum of Natural History (NY), and the Harvard Museum of Comparative Zoology. The human samples are from the 15th and 16th century Mistihalj collection (Montenegro) housed at the Harvard Peabody Museum. Two chimpanzee second metatarsals were selected at random, and the difference between the base height to bone length ratios was calculated. This process was repeated 1000 times to generate a likelihood distribution of sampling at random



Figure 1. StW 89. Second metatarsal from Sterkfontein Member 4 in dorsal (far left) and plantar (far right) views. In middle: medial (top), lateral (middle), proximal (bottom left), and distal (bottom right) views. Scale bar is 1 cm.

Table 2

Comparative measurements on fossil hominin second metatarsals.

Fossil	Age (Ma)	Taxa	Length	Midshaft ML	Midshaft DP	Head ML	Head DP	Base ML Max	Base DP Max	Base A ML	Base A DP
BRT-VP-73b ^a	3.4	Hominin indet.	66.9	6.1	7.4	9.8	11.2	–	–	12.8	14.2
A.L. 333-72	3.2	<i>Au. afarensis</i>	–	–	–	9.7	12.8	–	–	–	–
A.L. 333-115	3.2	<i>Au. afarensis</i>	–	–	–	9.9	11.8	–	–	–	–
StW 573	2.6–2.8	<i>Australopithecus</i> sp.	–	7.5	8.5	–	–	13.5	15.1	11.8	14.7
StW 89	2.0–2.6	<i>Au. africanus?</i>	61.6	5.6	7.7	8.3	11.9	11.0	12.8	10.6	11.8
StW 377	2.0–2.6	<i>Au. africanus</i>	54.9 (est.)	6.1	7.2	–	–	13.2	14.9	11.7	14.7
OH 8	1.85	<i>H. habilis?</i> <i>P. boisei?</i>	54.4 (est.)	6.3	7.2	–	–	11.2	14.4	10.1	13.7

^a From Haile-Selassie et al., 2012. ML = mediolateral; DP = dorsoplantar; A = articular surface.

bones with the relative base depths found in StW 89 and StW 377. This process was repeated with the gorilla second metatarsals and finally with the human sample. StW 377 is not a complete second metatarsal and is broken just distal to the dorsal sulcus. The total length of this bone was estimated by superimposing the head of StW 89 onto the shaft of StW 377 and overlapping the preserved dorsal sulci and plantar cornua. Given that StW 89 is a longer bone, this method is conservative in producing most likely a maximum length for StW 377.

Two further analyses were done to compare linear dimensions of StW 89 with habitually shod *Homo* ($n = 34$), unshod *Homo* ($n = 31$), *Gorilla* ($n = 32$), and *Pan* ($n = 30$). The habitually shod *Homo* sample was collected from the Hamann-Todd collection at the Cleveland Museum of Natural History and the human osteology collection in the Department of Anthropology at the University of Iowa. The unshod sample was collected at the National Museum, Bloemfontein, and the South African Museum in Cape Town, South Africa. All unshod specimens are from pre-pastoral populations from several different South African localities. Some specimens have absolute dates, most in the range of 2000–5000 BP (before present), but many do not have dates due to the collection methods in obtaining them (Sealy, 2006). The South African sample presumably represents habitually unshod people, as they are pre-pastoral with behavior of Late Stone Age people (Hausman, 1982; Roberts, 1989; Sealy and Pfeifer, 2000; Stock and Pfeiffer, 2001). The *Pan* and *Gorilla* samples were collected at the Cleveland Museum of Natural History.

One analysis includes nine measurements, using Mosimann shape variables by dividing the raw data variables by the geometric mean for each specimen. The second analysis used four variables, also using Mosimann shape variables. This second analysis was conducted with fewer variables to examine the proximal morphology of several incomplete fossil specimens. Geometric means were calculated separately for each analysis to account for the different number of variables. The shape variables from these analyses were subjected to a principle components analysis (PCA). See Table 3 for a list of measures entered into the PCA.

Table 3

Measures entered into principal components analysis.

PCA measures
Maximum length
Mediolateral (ML) maximum base breadth ^a
Dorsoplantar (DP) maximum base height ^a
Mediolateral (ML) head diameter
Dorsoplantar (DP) head diameter
Mediolateral (ML) midshaft diameter
Dorsoplantar (DP) midshaft diameter
Mediolateral (ML) proximal articular surface maximum width ^a
Dorsoplantar (DP) proximal articular surface maximum height ^a

^a These variables are used in the second analysis of four variables.

Anatomical description and results of comparative analyses

From the most distal end of the head to the most proximal tip of the base, StW 89 measures 61.6 mm. The fossil is cracked and repaired roughly two-thirds of the way down the shaft, but otherwise is in remarkable condition. At midshaft, the dimensions of the bone are 7.7 mm dorsoplantarly and 5.6 mm mediolaterally. StW 89 has medial (internal) torsion of head relative to the base of -19.7° , completely outside the range of both modern humans, which exhibit less torsion, and chimpanzees, which exhibit more torsion (Fig. 2). The head is 11.9 mm in the dorsoplantar direction and 8.3 mm mediolaterally. It is expanded dorsally (domed) such that the articular surface projects above the diaphysis of the bone, which is a human-like feature. There is a dorsal sulcus proximal to the head, and a raised ridge of bone proximal to the sulcus that terminates both medially and laterally in small tubercles for the attachment of the collateral ligaments. These morphologies suggest that dorsiflexion at the metatarsophalangeal joint was occurring during bipedal toe-off. The head is widest plantarly and tapers dorsally, unlike the condition in modern humans, which have a mediolaterally wide dorsal aspect of the metatarsal head. The StW 89 anatomy is similar to the morphology found in other *Australopithecus* and *Paranthropus* metatarsals (Susman et al., 1984; Susman and Brain, 1988; Susman and de Ruiter, 2004).

When viewed dorsally, the articular surface of the metatarsal head is angled from a proximolateral to distomedial direction. This orientation, measured by following the most distal aspect of the articular surface of the head proximally, is angled approximately

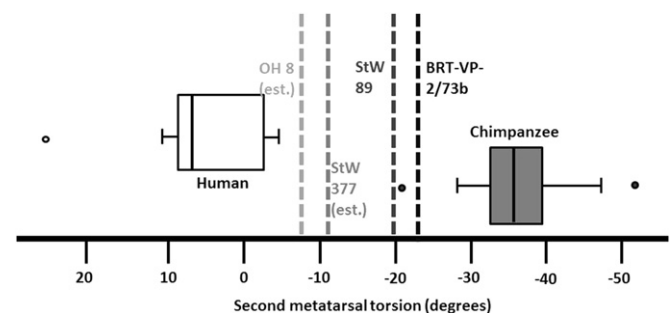


Figure 2. Torsion of the second metatarsal head is quite different between humans (white box) and chimpanzees (gray box). Chimpanzees have an internal torsion of the head that places the second metatarsal in opposition with the first metatarsal. Humans have a second metatarsal head without torsion, or, with some external torsion. StW 89 has internal torsion of nearly 20° , outside the range of chimpanzees, but far more torsion than what is present in modern humans. It is similar to the torsion values reported for the second metatarsal of the Burtel foot (BRT-VP-2/73b). The OH 8 second metatarsal is damaged distally, but has been estimated to have torsion near the human condition. The boxplots have been redrawn with permission from Pontzer et al. (2010), and illustrate the median value (solid lines), 25th and 75th percentiles (boxes), and range of values (whiskers). Outliers are illustrated as circles.

45° relative to the long axis of the shaft. This orientation is quite unlike the condition found in modern human second metatarsals, which more often have a dorsal articular surface of the metatarsal head perpendicularly oriented relative to the metatarsal shaft. Plantarly, the metatarsal head terminates in medial and lateral plantar cornua separated by a small m-shaped sulcus. The medial cornu extends slightly more proximally than the lateral cornu, opposite to the condition found in most modern human second metatarsals, and similar to ape and *Au. afarensis* second metatarsals. Both the oblique orientation of the articular surface of the head dorsally, and the relative positioning of the cornua may be related to the medial torsion of the head. Viewed laterally or medially, the subchondral surface of the metatarsal head appears plantarly extended. The articular set of the metatarsal head was calculated following Duncan et al. (1994). In lateral view, the shaft is bisected 40% of the distance from the tip of the head and a line bisecting the shaft into equal dorsal and plantar proportions is drawn. Another line bisecting the most proximal extent of the articular surface of the head is drawn, and is then bisected with a perpendicular line extending to the tip of the metatarsal head. The angle between these lines reaching the end of the metatarsal head is calculated, and we estimate an articular set of 3° for the StW 89 head, within the range of both modern humans and chimpanzees, and similar to *Au. afarensis*. Because StW 355 may be an associated second proximal phalanx, we also employed the technique of Latimer and Lovejoy (1990) in which the proximal phalanx is manually positioned in maximum dorsiflexion and maximum plantarflexion with the articular surfaces still in contact with one another. Using this technique, we found that the angle of dorsiflexion in StW 89/355 is 78°, within the range of modern humans and similar to *Au.*

afarensis. However, the angle of plantarflexion is 72°, within the range of chimpanzees and gorillas, and quite different from humans and *Au. afarensis* (Fig. 3). Direct comparisons between StW 89 and casts of A.L. 333-115 and A.L. 333-72, second metatarsal heads from *Au. afarensis*, confirm that the Sterkfontein fossil has a more proximally extensive plantar surface than the Hadar fossils. This is consistent with the 72° angle for plantarflexion measured for StW 89/StW 355 and the only 45° of plantarflexion measured for A.L. 333-115 (Latimer and Lovejoy, 1990). The maximum proximodistal length of StW 355 is 24.8 mm. If associated with StW 89, the proximal phalanx would be 40.3% the length of the second metatarsal. Jungers et al. (2009) show a human range of between 32% and a bit under 39%, and an African ape range of between 43% and 61%. As others have reported for australopiths (Susman et al., 1984; Latimer and Lovejoy, 1990), the relative phalangeal length for StW 89/355 is between that found in the extant apes, and in modern humans.

The base is strikingly gracile relative to the length of the bone: 11.0 mm mediolateral, and only 12.8 mm dorsoplantar. It thus falls well outside the modern human range, and instead is more ape-like (Fig. 4). Another second metatarsal from Sterkfontein Member 4, StW 377, is more human-like in its base robusticity (Fig. 5). The gracility of the base in StW 89 may be evidence for lax plantar ligaments, as has been argued for the second metatarsal in the Burtele foot (Haile-Selassie et al., 2012). In lateral view, the base of StW 89 is angled proximodorsally to distoplantarly. The facet for the intermediate cuneiform is flat dorsoplantarly and moderately concave mediolaterally. This facet is triangular in shape with weakly formed indentation on the lateral side that narrows the base at the dorsoplantar midpoint to 6.1 mm mediolaterally. This is

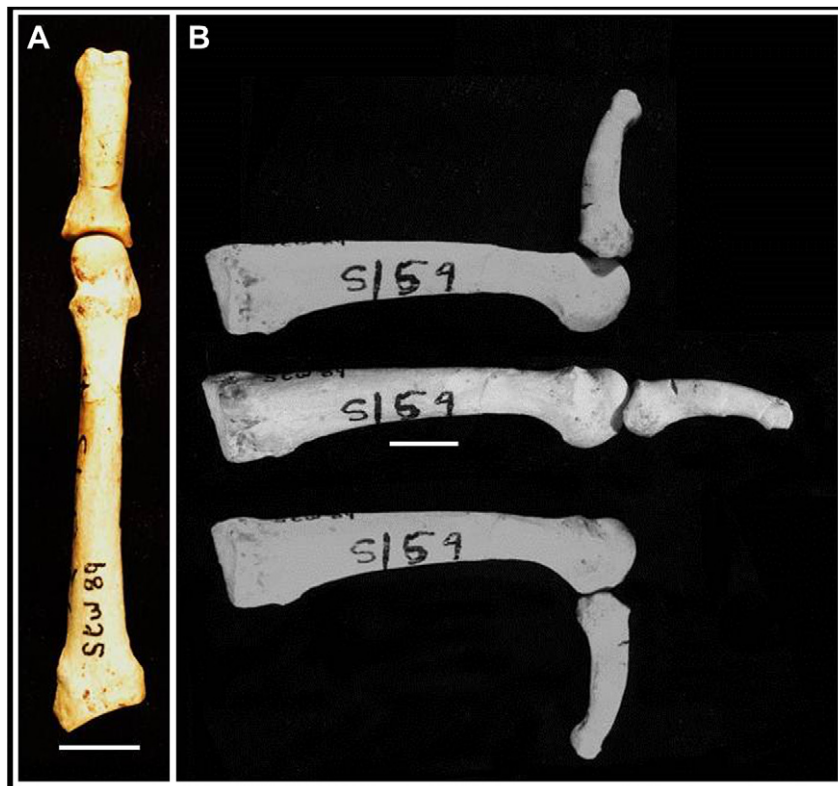


Figure 3. StW 89 and possibly associated second proximal phalanx StW 355. As shown in the color image on the left, these two bones articulate quite well and have a similar patina. At right, StW 355 in maximum dorsiflexion (top), neutral position (middle), and maximum plantarflexion (bottom). The range of dorsiflexion is similar to that seen in modern humans and fossil *Australopithecus*. However, StW 355 possesses an ape-like range of plantarflexion, quite unlike that found in the associated foot bones of *Au. afarensis*. If these two bones are associated, more advanced pedal grasping abilities is hypothesized for this Sterkfontein hominin than for the East African australopiths.

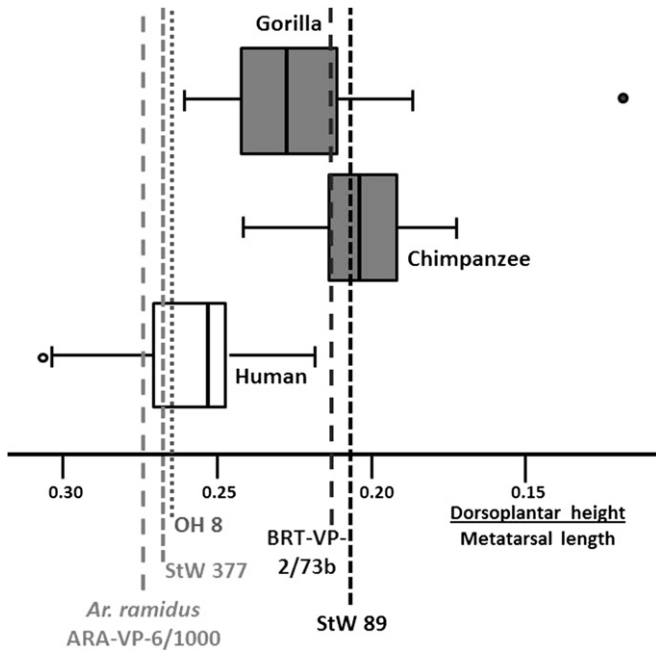


Figure 4. Base robusticity is measured as the dorsoplantar height of the base divided by the maximum length of the bone. Humans (white box) have considerably deeper dorsoplantar bases of the second metatarsal than what is found in chimpanzees or gorillas (gray box). This base robusticity may be indicative of plantar ligaments that provide midfoot rigidity in the human foot. Fossil second metatarsals from *Ardipithecus ramidus*, OH 8, and another Sterkfontein second metatarsal (StW 377) are all damaged distally, but their lengths can be estimated. All of these fossils fall within the modern human range. Surprisingly, StW 89 does not, and instead has base robusticity within the range of modern chimpanzees and gorillas, and close to the value reported for the second metatarsal of the Burtele, Ethiopia foot (BRT-VP-2/73b). The boxplots have been redrawn with permission from Lovejoy et al. (2009), and illustrate the median value (solid lines), 25th and 75th percentiles (boxes), and range of values (whiskers). Outliers are illustrated as circles.

unlike the extreme narrowing of the base found in modern chimpanzees. Dorsally, the base is angled from the proximolateral to distomedial direction 23° relative to a plane perpendicular to the long axis of the metatarsal shaft, similar to angled human metatarsal bases, though this angle is quite variable in modern humans.



Figure 5. StW 377 and StW 89. To the left are dorsal views of these two Sterkfontein Member 4 second metatarsals (StW 377 to left; StW 89 to right). To the right are these same bones in lateral view (StW 89 on top; StW 377 on bottom). The shaded head of StW 89 has been superimposed on the broken distal end of StW 377 to estimate how long StW 377 could have been. Notice that despite being shorter in length, StW 377 possesses a more human-like dorsoplantar tall base. Scale bar is 1 cm.

Laterally, there are facets for the proximal third metatarsal and distal lateral cuneiform. The dorsal facet for the third metatarsal is 5.2 mm and flat dorsoplantarly, and 4.6 mm and concave proximodistally. It is separated from the facet for the lateral cuneiform by a palpable, raised ridge of bone. The dorsal facet for the lateral cuneiform is 5.2 mm and slightly concave dorsoplantarly, and 3.4 mm and flat proximodistally. This is a relatively large facet proximodistally, suggesting that the StW 89 metatarsal was recessed within the cuneiforms as in modern humans. There is a second, plantar facet that is somewhat eroded, and difficult to measure with certainty. The plantar facet for the lateral cuneiform is roughly 4 mm proximodistally and 3.9 mm in the dorsoplantar direction. Distal to this facet is a small articular region presumably for the third metatarsal. There is some damage here that extends plantarly to the base of the metatarsal, but we do not think that it artificially truncates the base. Medially, there is a flat facet that is 4.6 mm dorsoplantarly and 4.3 mm proximodistally for the medial cuneiform. There is a roughened region, located plantarly and distally to the medial cuneiform facet, which may be evidence for contact with the first metatarsal, and suggestive of a smaller angle between the first and second metatarsal than is found in the ape foot. Evidence for contact with the first metatarsal in the form of a smooth facet or roughened area were found in 69% of human second metatarsals in one study (Singh, 1960) and 70% in another (Zipfel, 2004). This raised and roughened area on the StW 89 metatarsal has defined borders and is 4.8 mm dorsoplantarly and 3.9 mm proximodistally. Plantarly, the base tapers to a rugose point roughly 9.0 mm in proximodistal length for the attachment of plantar ligaments, and a slip of the tibialis posterior tendon.

The head area of StW 89 is 53.1% the area of the first metatarsal StW 562 and 77.7% the area of StW 595 (Fig. 6). The former value reflects the condition found in most humans. However, the ratio between StW 89 and StW 595 (77.7%) is an extremely unlikely value to sample from a human population ($p = 0.001$). Instead, this ratio between the first and second metatarsal heads can be more easily sampled from a chimpanzee or gorilla distribution (Fig. 6). Importantly, the values for the Sterkfontein metatarsals are more ape-like than those generated from the Hadar *Au. afarensis* metatarsals

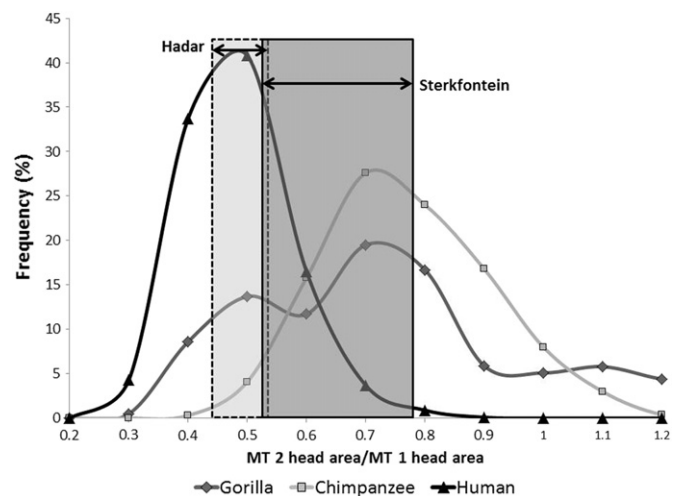


Figure 6. A resampling technique was used (see Materials and methods section) to create a range of ratios of the second metatarsal head area to first metatarsal head area in humans, African apes, and fossil hominins. Humans have a larger first metatarsal head area (to left on graph). African apes have a relatively smaller first metatarsal head area (to right on graph). Combinations of male first metatarsal heads and female second metatarsal heads and vice versa yield the bimodal bell curve distribution in gorillas. Metatarsal heads from Hadar fall well within the human range. However, the metatarsals from Sterkfontein are considerably more ape-like in these proportions.

(44.5–54.2%), which have been interpreted elsewhere as being quite human-like in the relative size of the metatarsal heads (Latimer and Lovejoy, 1990). We caution that this analysis assumes that the metatarsals from Sterkfontein Member 4 are all from the same species, which may not be the case.

We also tested the likelihood of drawing two second metatarsals with such distinct values for the dorsoplantar base/length as seen in StW 89 and StW 377 (Fig. 5) from a modern collection. Our resampling procedure produced mixed results. The likelihood of sampling such distinct morphologies from a modern human collection was exceedingly small ($p = 0.003$). However, one could sample this variation in dorsoplantar depth relative to length from a chimpanzee ($p = 0.07$) or more likely a gorilla ($p = 0.11$) collection.

In the analysis of linear measurements using nine shape variables, factor 1 accounts for 38% of the variation and is the most important factor separating human and ape groups. The mediolateral and dorsoplantar dimensions of the metatarsal base are most heavily loaded on factor 1, in addition to the dorsoplantar midshaft diameter and dorsoplantar proximal articular surface height. The human groups have a higher dorsoplantar proximal articular surface relative to the mediolateral width compared with apes, and the same is true for the overall dimensions of the proximal metatarsal. StW 89 shows affiliation with *Pan* (Fig. 7). The dorsoplantar head diameter tends to be larger in relation to the mediolateral head diameter in human groups compared with ape groups. Factor 2 accounts for 18% of the variation. The most important loadings for factor 2 are the maximum length, dorsoplantar proximal height, the mediolateral and dorsoplantar head diameter, and the mediolateral midshaft diameter. *Gorilla* groups further on the positive side of the factor 2 axis, with *Pan* on the opposite extreme and both human groups plotted in an intermediate position relative to the ape groups. Factor 2 differentiates *Gorilla* and *Pan*, showing that *Pan* has a relatively longer second metatarsal and smaller head, and a narrower mediolateral midshaft relative to *Gorilla* (Table 4 and Fig. 7). Factor 3 accounts for 14% of the variance, but did not provide any additional insight in differentiating between the apes and humans.

In a PCA, there is always a concern that some variables are correlated with one another, introducing redundancy into the analysis. This is particularly the case for the multiple measurements of the metatarsal base. Maximum dorsoplantar base height is

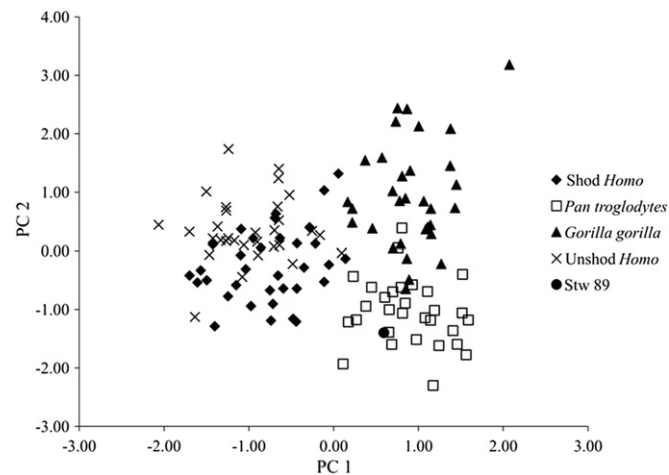


Figure 7. Principal components analysis using nine size-standardized variables. Factor 1 (x-axis) explains 38% of the variation, and clearly separates humans (to left) from the African apes (to right). This factor is being driven by dimensions of the metatarsal base, and the dorsoplantar height of the metatarsal head. StW 89 falls well within the chimpanzee distribution, and outside the range of modern humans.

Table 4

Factor loadings for nine size adjusted measurements.

Variables	Factor 1 (38%)	Factor 2 (18%)
Maximum length	0.12	-0.63
ML base breadth	0.61	0.07
DP base height	-0.82	0.43
ML head diameter	0.47	-0.53
DP head diameter	-0.51	-0.63
ML midshaft diameter	0.43	0.59
DP midshaft diameter	0.71	0.06
ML proximal articular surface maximum width	0.55	0.14
DP proximal articular surface maximum height	-0.95	0.07

ML = mediolateral; DP = dorsoplantar.

highly correlated with maximum dorsoplantar articular surface height ($r = 0.78$). However, maximum mediolateral base width is only moderately correlated with the maximum mediolateral articular surface width ($r = 0.50$). Excluding the maximum articular surface measurements from the nine-variable analysis did not appreciably alter the results of the analysis. It is an important observation that the mediolateral dimensions are less correlated, indicating that overall mediolateral robusticity is only somewhat correlated to the overall width of the proximal articular surface.

Four shape variables of the proximal metatarsal showed a high degree of factor loading for each variable, with factor 1 accounting for 80% of the variation (Table 5). In the plot of factor 1, humans and apes are well distinguished, though there is some overlap (Fig. 8). Humans overlap with *Gorilla* more than *Pan*. The fossil specimens StW 595c and StW 89 group with apes, and Little Foot (StW 573d) and StW 377 occupy an area where humans and apes overlap. Since the dorsoplantar measurements are quite correlated (see above), the analysis was also conducted with three variables, subtracting the dorsoplantar articular surface measurement. The results were not appreciatively different compared with using the four variables.

Discussion and functional interpretation

StW 89 displays a mosaic of human-like, and African ape-like features (Fig. 9). Like human second metatarsals, the dorsal head is domed, and there is a prominent dorsal sulcus just proximal to the metatarsal head, indicative of phalangeal dorsiflexion during the toe-off phase of bipedal locomotion. The range of motion in dorsiflexion appears human-like, and unlike the more abbreviated metatarsophalangeal dorsiflexion found in the ape foot (Griffin et al., 2010). Additionally, like in humans, the base in dorsal view is angled proximolaterally to distomedially, and does not possess the mediolateral concavity found in African ape second metatarsals. A raised and well-defined rugosity on the medioplantar aspect of the base indicates contact with what may have been an adducted first metatarsal.

However, this bone also possesses many presumably more primitive ape-like features. Multivariate analyses show that the biggest differences between humans and apes are the relative proximal and distal dimensions. In these dimensions, StW 89 clusters with the modern apes (Figs. 7 and 8). Additionally, the base

Table 5

Factor loadings for four size adjusted measurements.

Variables	Factor 1 (80%)	Factor 2 (11%)
ML proximal breadth	0.90	-0.29
DP proximal height	-0.88	-0.38
ML proximal articular surface maximum width	0.89	0.29
DP proximal articular surface maximum height	-0.90	0.36

ML = mediolateral; DP = dorsoplantar.

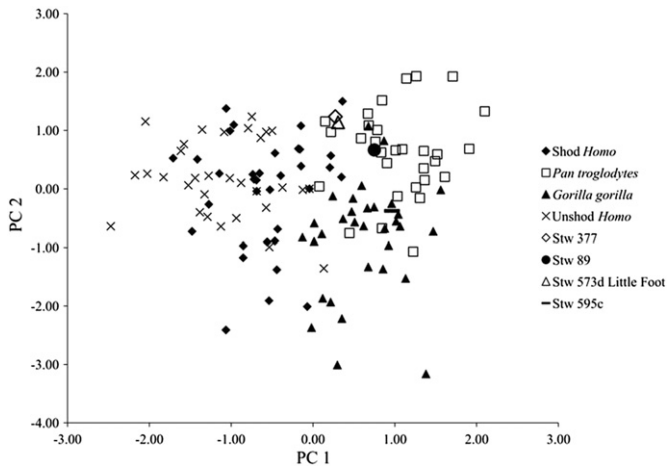


Figure 8. Principal components analysis using four size-standardized measures of the second metatarsal base. Factor 1 (x-axis) accounts for 80% of the variation. Along this axis, humans (to left) are separated from the African apes (right), though there is overlap. The four Sterkfontein metatarsals cluster in the same general area, though Stw 377 and Stw 573 are more human-like than Stw 595 and Stw 89, which fall within the ape range.

of StW 89 is quite *Gorilla*-like in overall shape (Proctor, 2010a). The metatarsal base and articular surface are dorsoplantarly deeper relative to the mediolateral width in humans compared with apes, partly due to plantar expansion for attachment of the plantar ligaments in humans. The base of StW 89 lacks the dorsoplantar depth typical for human second metatarsals. In fact, compared with the length of the bone, the depth of the base falls within the range of chimpanzees and gorillas, and entirely outside the range of humans, including fossils StW 377, OH 8, and even the *Ardipithecus ramidus* second metatarsal (Fig. 4, from Lovejoy et al., 2009). Lovejoy et al. (2009) suggest that a robust metatarsal base is an important adaptation to stiffen the midfoot and limit midfoot laxity during the propulsive phase of bipedalism. The relatively gracile base in StW 89 is surprising, given the robusticity of the base found in hominins as primitive as *Ardipithecus*. Nevertheless, the variation seen between StW 89 and StW 377 does not necessarily imply taxonomic diversity, as two bones with such distinct morphologies can be sampled from a chimpanzee ($p = 0.07$) or gorilla ($p = 0.11$)

population. The likelihood of drawing such distinct morphologies from a human population is much lower ($p = 0.003$). These distinct base morphologies in StW 377 and StW 89 may suggest either more variation in early hominins, or an overall less rigid midtarsal region in *Au. africanus* which would shift the range of variation to the ape side of Fig. 4. This latter hypothesis may indicate more laxity of the plantar ligaments than is found in the modern human foot and in this regard StW 89 is quite similar to the second metatarsal of the Burtele foot (Haile-Selassie et al., 2012).

Perhaps most functionally salient, the metatarsal head of StW 89 exhibits internal torsion of nearly 20°, similar to the 23° of internal torsion in the second metatarsal from the Burtele, Ethiopia foot (Haile-Selassie et al., 2012). Although the torsion is not as extreme as that present in modern apes, the medial twisting of the head is beyond the range found in modern humans (Fig. 2). StW 89 is thus a puzzling bone, in many ways littered with inconsistencies. There is internal torsion of the head, a morphology that has been argued to be functionally related to a grasping hallux (Morton, 1922), and yet the roughened area on the medial aspect of the bone suggests a more adducted, not abducted, hallux. Below, we attempt to synthesize some of these seemingly contradictory anatomies.

Explaining the internal torsion of the metatarsal head

Internal torsion of the second metatarsal functionally places the second digit in opposition to the first, and is a critical adaptation for climbing in the apes (Morton, 1922). It is possible that the internal torsion of StW 89 implies a divergent hallux and ape-like grasping ability, and therefore a considerable degree of arboreality in *Au. africanus*. *A. ramidus* has internal torsion of the second metatarsal and a grasping hallux (Lovejoy et al., 2009). The presence of a grasping hallux has also been suggested for the 3.4 Ma foot from Burtele, Ethiopia (Haile-Selassie et al., 2012). Though a divergent, grasping hallux was originally proposed for StW 573 ‘Little Foot’ (Clarke and Tobias, 1995), others have found little support for this interpretation (Harcourt-Smith, 2002; Kidd and Oxnard, 2005; McHenry and Jones, 2006; Lovejoy et al., 2009). Nevertheless, there are postcranial data suggesting that the postcranial skeleton of *Au. africanus* was adapted for some arboreality, and perhaps was even better adapted for climbing than *Au. afarensis* (McHenry and Berger, 1998; Green et al., 2007). Certainly our finding that plantarflexion at the metatarsophalangeal joint in StW 89 and StW 355 exceeds

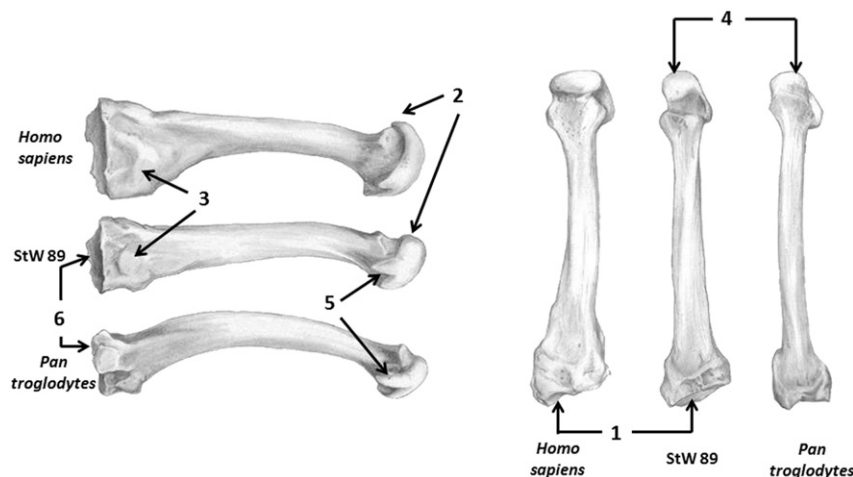


Figure 9. Illustrations of (left top to bottom) human, StW 89, and chimpanzee second metatarsals in medial view. Right (left to right) illustrations of human, StW 89, and chimpanzee in dorsal view. Salient features are labeled as follows: as in humans, StW 89 has an angled base (1); a domed head (2); and a rugosity perhaps indicating contact with an adducted first metatarsal (3). As in non-human apes, StW 89 possesses a proximolateral to distomedial angulation of the head (4); internal, or medial, torsion of the head (5); and a dorsoplantarly truncated base (6). Illustrations by Daniel Valerio.

that found in humans and *Au. afarensis*, lends some support to this hypothesis (assuming that StW 355 and StW 89 are in fact from the same individual or same species). Pedal grasping abilities may also have been advantageous for large infants to cling onto their bipedal mothers (DeSilva, 2011). Undoubtedly though, a grasping hallux would solidly place *Au. africanus* in trees during much of their daily life. Unfortunately, a medial cuneiform has never been recovered from Sterkfontein Member 4 (StW 573 ‘Little Foot’) has a medial cuneiform but is from Sterkfontein Member 2). Nevertheless, it remains possible that StW 89 belongs to a foot with a more mobile, grasping hallux. However, below we propose an alternative hypothesis to explain the internal torsion of this second metatarsal.

Opposition between the first and second digits in the apes is possible not only because of the internal torsion of the second metatarsal, but also the external torsion of the first metatarsal. First metatarsal torsion differs significantly between humans and the apes (Morton, 1922; Pontzer et al., 2010). Though StW 595, and especially StW 562, display some internal torsion, both are within the range of modern humans and similar to the range seen in early *Homo* from Dmanisi first metatarsals (Pontzer et al., 2010). This observation of course assumes that StW 89 is the same species as StW 562 and StW 595. Regardless, StW 89 possesses a raised and well-defined roughened region on the plantomedial aspect of the bone. This rugosity, present in around 70% of humans, is generally associated with an adducted hallux (Singh, 1960; Zipfel, 2004). In fact, it has been found that there is more mobility in the hallux tarsometatarsal joint in modern humans without a facet between the first and second metatarsals (Fritz and Prieskorn, 1995). It is possible that this roughened area on StW 89 is for the attachment of the Lisfranc ligament, which connects the medial cuneiform and the base of the second metatarsal in both humans and the African apes and can leave a small ligamentous tuberosity (Lewis, 1980; Clarke and Tobias, 1995). However, we suggest that the rugosity is too distal and dorsal for it to be the insertion of the Lisfranc ligament. We examined 15 chimpanzee and gorilla second metatarsals to look specifically for this rugosity and found it present in ten. However, in all cases, the rugosity was positioned more plantarly and proximally than the one in question on the StW 89 metatarsal. Furthermore, a raised rugosity on the OH 8 second metatarsal, which clearly articulates with a facet on the adducted OH 8 first metatarsal, is in the exact same position as the rugosity on the StW 89 specimen. We therefore find it likely that this anatomy indicates contact with a more adducted first metatarsal. This raises the question: how can a second metatarsal with internal torsion exist in a foot with a non-grasping hallux?

External torsion of the second metatarsal in modern humans is a product of two things: the non-grasping hallux, and the high transverse and medial longitudinal arch (Pontzer et al., 2010). To maximize the contact between the plantar aspect of the head and the ground, the metatarsal head in humans must have torsion near zero. However, if the pinnacle of the transverse arch is under the third metatarsal head, the second metatarsal would be positioned more plantarly. In other words, in a foot that has a higher transverse arch than an ape but a lower one than in modern humans, the medial aspect of the foot may be more plantarly positioned as illustrated in Fig. 10. Given a plantar deviation of the second metatarsal, the only way to place the head flush against the substrate would be to internally rotate the bone, as is found in StW 89 (Fig. 10). This idea, that internal torsion of the second metatarsal could be found in a non-grasping, but low-arched foot, was developed with significant and important intellectual input from Michelle Drapeau (Université de Montréal).

There are important implications for the internal torsion of StW 89: either the foot of StW 89 possessed a divergent hallux, or a low medial arch. If the former is correct, then a Sterkfontein

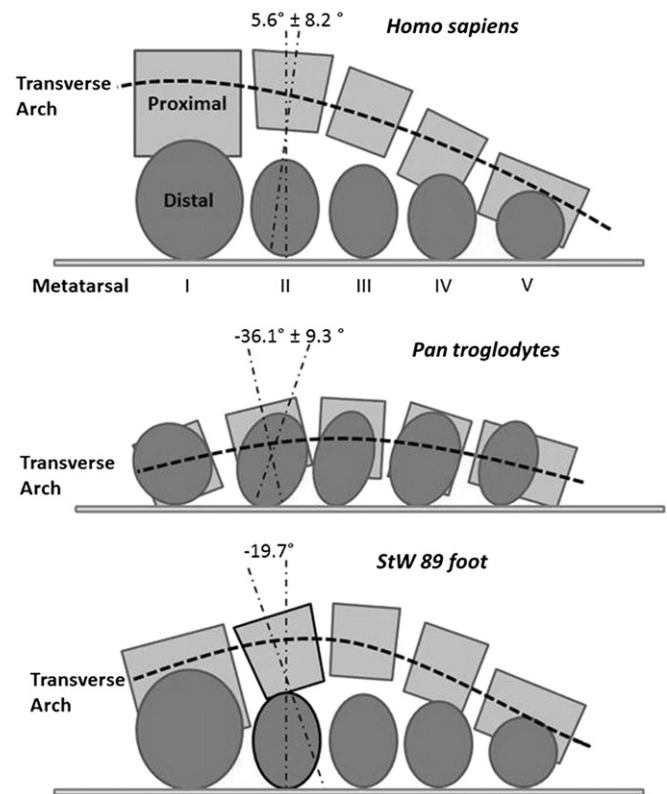


Figure 10. Models of hominoid feet in distal view (redrawn from Pontzer et al., 2010 and Ward et al., 2011). The gray boxes represent the metatarsal bases, and the darker circles the metatarsal heads. Humans (top image) possess a high transverse arch and considerably higher longitudinal arch on the medial side of the foot than the lateral side. Human second metatarsal heads possess little to no torsion to keep the plantar aspect of the head in contact with the substrate. Chimpanzees and other apes do possess a transverse arch, but it is not as elevated as in humans and there is no longitudinal arching. They possess considerable internal torsion of the metatarsal to position the head in opposition with the first metatarsal. The StW 89 second metatarsal possesses internal torsion. This may be the result of hallux grasping. Alternatively, as modeled here, a bipedal foot with a low transverse arch, without the high medial aspect of the longitudinal arch would have to have internal torsion of the bone to keep the plantar aspect of the head in maximal contact with the ground. Thus, the StW 89 metatarsal belonged either in a foot with a grasping hallux, or a low medial arch.

australopith was particularly skilled in an arboreal environment. If the latter is correct, then some South African australopiths, while possessing a rigid lateral foot and lateral longitudinal arch (DeSilva, 2010), would have a lower and less developed medial longitudinal arch. This reconstruction of the foot would be consistent with seemingly contradictory studies finding evidence for an arch in australopiths using bones found in the lateral column (e.g., DeSilva, 2010; Ward et al., 2011), but the absence of an arch in the medial column (e.g., Berillon, 2003; Harcourt-Smith and Aiello, 2004). However, we caution about over-generalizing the arch given the range of variation in arch development in humans today and evidence that such variation may have existed in australopiths as well (DeSilva and Throckmorton, 2010). Thus, the low medial arch may characterize the foot of StW 89, but not necessarily australopiths in general.

Taxonomy

All of these primitive morphologies must be considered in the context of another second metatarsal from Sterkfontein Member 4: StW 377. Although this specimen is lacking a head, it is complete

enough to get an estimate of total length. Unlike StW 89, StW 377 has a relatively robust base dorsoplantarly, within the range of humans and quite similar to OH 8 (Fig. 4). Though the head is not preserved, torsion is estimated to be -11° , similar to, but more human-like than StW 89 (Drapeau and Harmon, in press). The likelihood of sampling bones with these differences from the same population is certainly possible, as we have found in this study, though it is quite unlikely to have been sampled from a human population. The differences between these two bones are therefore of importance (Fig. 5). There are three ways to interpret these differences. First, StW 89 and StW 377 may be the two endpoints of an evolving lineage. Member 4 spans 2.0–2.6 Ma (Pickering and Kramers, 2010), and thus it is reasonable to hypothesize that considerable foot evolution may have occurred in one lineage during this time. Within this interpretation, one might expect that the morphology exhibited by StW 377 evolved from a foot represented by StW 89. The problem with such an interpretation is that it is more likely that StW 89 is in the younger Member 4 deposits, since it was initially interpreted as deriving from Member 5, and even was preliminarily suggested to be associated with stone tools (Clarke, 1985).

The second interpretation is that these two bones simply represent endpoints of a highly variable and polymorphic population of hominins (presumably *Au. africanus*). Additional fossils will be necessary to test this hypothesis. The third interpretation is that StW 377 and StW 89 are from different species. The second species hypothesis for Sterkfontein Member 4 has been most clearly advocated by Clarke (1988, 2008). Others have indicated that there is considerable phenotypic diversity in the Sterkfontein assemblage, both cranially (Kimbel and White, 1988; Lockwood and Tobias, 2002; Schwartz and Tattersall, 2005; Fornai, 2010) and postcranially (Berger and Tobias, 1996; Deloison, 2003; Partridge et al., 2003; Zipfel and Berger, 2009; Zipfel et al., 2010), and have hinted at the possibility of taxonomic diversity. The distinct anatomies of StW 89 and StW 377 make this third possibility worth examining in more detail. In fact, it is worth noting that StW 89 and the first metatarsal StW 595 are quite similar to the anatomies described in the 3.4 Ma foot from Burtele, Ethiopia, with StW 595 lacking the dorsal doming characteristic of *Australopithecus* first metatarsals (Haile-Selassie et al., 2012). However, simultaneously present at Sterkfontein are first and second metatarsals StW 562 and StW 377, which are similar in many ways to the anatomy described for the Hadar *Au. afarensis* foot, including pronounced dorsal doming of the StW 562 first metatarsal and a robust second metatarsal base in StW 377.

If StW 89 represents a distinct hominin species, then what is it? Given that bones of the foot (Harcourt-Smith, 2002; Zipfel et al., 2009), ankle (DeSilva, 2009), knee (Heiple and Lovejoy, 1970), and pelvis (Häusler and Berger, 2001; Häusler, 2002) of material assigned to *Au. africanus* are derived in many ways, we find it compelling that StW 377 is a better fit for *Au. africanus* than is StW 89. This raises several possibilities. StW 89 may be from Member 5, may belong to *Paranthropus robustus* and may support the hypothesis that the foot of this robust hominin is more ape-like, with some degree of hallux grasping (Proctor, 2010b). Alternatively, StW 89 may be from the second, unnamed (pre-*Paranthropus*) species from Member 4 discussed by Clarke (2008) in the context of StW 573 or 'Little Foot'. Unfortunately, the StW 573 second metatarsal (Deloison, 2003) is too fragmentary to assess the base robusticity, head torsion, or head articular surface morphology. However, one of us (DP) found that the base morphology of StW 573 is more human-like than the base morphology of StW 89 (Proctor, 2010a). Finally, we must consider the possibility that StW 89 is one of a very few *Au. sediba* fossils that could be mixed into the Sterkfontein Member 4 assemblage,

especially given the near overlap in ages between the Malapa locality (Pickering et al., 2011) and the upper deposits of Member 4 (Pickering and Kramers, 2010). This hypothesis is particularly intriguing given the remarkably primitive morphology of the foot bones from the Malapa hominins (Zipfel et al., 2011). However, the Burtele-like anatomy of StW 562 and StW 89 are not what we would predict for the medial column of the foot of *Au. sediba* (DeSilva et al., 2012). Nevertheless, the known foot bones of *Au. sediba* provide an important lesson that bones in isolation should be treated with great caution. The talus and calcaneus of the MH 2 *Au. sediba* skeleton do not look as though they should belong to the same species, and yet they were cemented together in the same foot. We thus suggest that a full understanding of the functional anatomy of StW 89, and testing hypotheses of locomotor diversity in Plio-Pleistocene hominins from South Africa will require not only additional fossil remains, but more complete and associated fossil material from Sterkfontein, Malapa, and other hominin-bearing localities.

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References

- 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*. *J. Hum. Evol.* 30, 343–348.
- Berillon, G., 2003. Assessing the longitudinal structure of the early hominin foot: a two-dimensional architecture analysis. *Hum. Evol.* 18, 113–122.
- Clarke, R.J., 1985. Early Acheulean with *Homo habilis* at Sterkfontein. In: Tobias, P.V. (Ed.), *Hominid Evolution: Past, Present, Future*. Alan R. Liss Inc., New York, 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*. Aldine de Gruyter, New York, pp. 285–292.
- Clarke, R.J., 2006. A deeper understanding of the stratigraphy of Sterkfontein fossil hominid site. *Trans. R. Soc. S. Afr.* 61, 111–120.
- Clarke, R.J., 2008. Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*. *S. Afr. J. Sci.* 104, 443–449.
- Clarke, R.J., Tobias, P.V., 1995. Sterkfontein Member 2 foot bones of the oldest South African hominid. *Science* 269, 521–524.
- Deloison, Y., 2003. Anatomie des os fossils de pieds des hominides d'Afrique du sud dates entre 2,4 et 3,5 millions d'années. Interprétation quant à leur mode de locomotion. *Biométrie Hum. Anthropol.* 21, 189–230.
- DeSilva, J.M., 2009. Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proc. Natl. Acad. Sci.* 106, 6567–6572.

- DeSilva, J.M., 2010. Revisiting the 'midtarsal break'. *Am. J. Phys. Anthropol.* 141, 245–258.
- DeSilva, J.M., 2011. A shift toward birthing relatively large infants early in human evolution. *Proc. Natl. Acad. Sci.* 108, 1022–1027.
- DeSilva, J.M., Throckmorton, Z.J., 2010. Lucy's flat feet: the relationship between the ankle and rearfoot arching in early hominins. *Plos One* 5, e14432.
- DeSilva, J.M., Zipfel, B., Kidd, R.S., Carlson, K.J., Churchill, S.E., Berger, L.R., 2012. The primitive aspects of the foot and ankle of *Australopithecus sediba*. *Am. J. Phys. Anthropol. Suppl.* 147, 129.
- Drapeau, M.S.M., Harmon, E.H., Metatarsal head torsion in monkeys, apes, humans and australopithecids. *J. Hum. Evol. in press*.
- Duncan, A.S., Kappelman, J., Shapiro, L.J., 1994. Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 93, 67–81.
- Fornai, C., 2010. Testing the second australopithecine species hypothesis for the South African site of Sterkfontein: geometric morphometric analysis of maxillary molar teeth. Ph.D. Dissertation, University of the Witwatersrand.
- Fritz, G.R., Prieskorn, D., 1995. First metatarsocuneiform motion: a radiographic and statistical analysis. *Foot Ankle Int.* 16, 117–123.
- Green, D.J., Gordon, A.D., Richmond, B.G., 2007. Limb-size proportions in *Australopithecus afarensis* and *Australopithecus africanus*. *J. Hum. Evol.* 52, 187–200.
- Griffin, N.L., D'Août, K., Richmond, B., Gordon, A., Aerts, P., 2010. Comparative in vivo forefoot kinematics of *Homo sapiens* and *Pan paniscus*. *J. Hum. Evol.* 59, 608–619.
- Haile-Selassie, Y., Saylor, B.Z., Deino, A., Levin, N.E., Alene, M., Latimer, B.M., 2012. A new hominin foot from Ethiopia shows multiple Pliocene bipedal adaptations. *Nature* 483, 565–569.
- Harcourt-Smith, W.E.H., 2002. Form and function in the hominoid tarsal skeleton. Ph.D. Dissertation, University College London.
- Harcourt-Smith, W.E.H., Aiello, L.C., 2004. Fossils, feet and the evolution of human bipedal locomotion. *J. Anat.* 204, 403–416.
- Häusler, M., 2002. New insights into the locomotion of *Australopithecus africanus* based on the pelvis. *Evol. Anthropol.* 13, 53–57.
- Häusler, M., Berger, L.R., 2001. StW 441/465: a new fragmentary ilium of a small-bodied *Australopithecus africanus* from Sterkfontein, South Africa. *J. Hum. Evol.* 40, 411–417.
- Hausman, A.J., 1982. The biocultural evolution of Khoisan populations of southern Africa. *Am. J. Phys. Anthropol.* 58, 315–330.
- Heiple, K.G., Lovejoy, C.O., 1970. The distal femoral anatomy of *Australopithecus*. *Am. J. Phys. Anthropol.* 35, 75–84.
- Jungers, W.L., Harcourt-Smith, W.E.H., Wunderlich, R.E., Tocheri, M.W., Larson, S.G., Sutikna, T., Awe Due, R., Morwood, M.J., 2009. The foot of *Homo floresiensis*. *Nature* 459, 81–84.
- Kidd, R.S., Oxnard, C., 2005. Little foot and big thoughts – a re-evaluation of the StW 573 foot from Sterkfontein, South Africa. *J. Comp. Hum. Biol.* 55, 189–212.
- Kimbel, W.H., White, T.D., 1988. Variation, sexual dimorphism, and taxonomy of *Australopithecus*. In: Grine, F.E. (Ed.), *Evolutionary History of the 'Robust' Australopithecines*. Aldine de Gruyter, New York, pp. 175–192.
- Kuman, K., Clarke, R.J., 2000. Stratigraphy, artifact industries and hominin associations for Sterkfontein, Member 5. *J. Hum. Evol.* 38, 827–847.
- Latimer, B.M., Lovejoy, C.O., 1990. Metatarsophalangeal joints of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 83, 13–23.
- 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. *Am. J. Phys. Anthropol.* 57, 701–719.
- Lewis, O.J., 1980. The joints of the evolving foot. Part III. The fossil evidence. *J. Anat.* 131, 275–298.
- 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. *J. Hum. Evol.* 42, 389–450.
- Lovejoy, C.O., Latimer, B., Suwa, G., Asfaw, B., White, T.D., 2009. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. *Science* 326, 72e1–72e8.
- McHenry, H.M., Berger, L.R., 1998. Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. *J. Hum. Evol.* 35, 1–22.
- McHenry, H.M., Jones, A.L., 2006. Hallucial convergence in early hominins. *J. Hum. Evol.* 50, 534–539.
- Morton, D.J., 1922. Evolution of the human foot. *Am. J. Phys. Anthropol.* 5, 305–336.
- Partridge, T.C., Granger, D.E., Caffee, M.W., Clarke, R.J., 2003. Lower Pliocene hominin remains from Sterkfontein. *Science* 300, 607–612.
- Pickering, R., Dirks, P.H.G.M., Jinnah, Z., de Ruiter, D.J., Churchill, S.E., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C., Berger, L.R., 2011. *Australopithecus sediba* at 1.977 Ma and implications for the origins of the genus *Homo*. *Science* 333, 1421–1423.
- Pickering, R., Kramers, J.D., 2010. Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa. *J. Hum. Evol.* 59, 70–86.
- Pontzer, H., Rolian, C., Rightmire, G.P., Jashashvili, T., Ponce de León, M.S., Lordkipanidze, D., Zollikofer, C.P.E., 2010. Locomotor anatomy and biomechanics of the Dmanisi hominins. *J. Hum. Evol.* 58, 492–504.
- Proctor, D.J., 2010a. Three-dimensional morphometrics of the proximal metatarsal articular surfaces of Gorilla, Pan, Hylobates, and shod and unshod humans. Ph.D. Dissertation, University of Iowa.
- Proctor, D.J., 2010b. Brief communication: shape analysis of the MT 1 proximal articular surface in fossil hominins and shod and unshod *Homo*. *Am. J. Phys. Anthropol.* 143, 631–637.
- Roberts, N., 1989. *The Holocene – An Environmental History*. Basil Blackwell Inc., Oxford.
- Schwartz, J.H., Tattersall, I., 2005. The Human Fossil Record. In: *Craniodental Morphology of Early Hominids (Genera Australopithecus, Paranthropus, Orrorin) and Overview*, vol. 4. John Wiley and Sons, New Jersey.
- Sealy, J., 2006. Diet, mobility, and settlement pattern among Holocene hunter-gatherers in southernmost Africa. *Curr. Anthropol.* 47, 569–595.
- Sealy, J., Pfeifer, S., 2000. Diet, body size, and landscape use among Holocene people in the Southern Cape, South Africa. *Curr. Anthropol.* 41, 642–655.
- Singh, I., 1960. Variations in the metatarsal bones. *J. Anat.* 94, 345–350.
- Stock, J., Pfeiffer, S., 2001. Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the southern African Later Stone Age and the Andaman Islands. *Am. J. Phys. Anthropol.* 115, 337–348.
- Susman, R.L., Brain, T.M., 1988. New first metatarsal (SKX 5017) from Swartkrans and the gait of *Paranthropus robustus*. *Am. J. Phys. Anthropol.* 77, 7–15.
- Susman, R.L., de Ruiter, D.J., 2004. New hominin first metatarsal (SK 1813) from Swartkrans. *J. Hum. Evol.* 47, 171–181.
- Susman, R.L., Stern, J.T., Jungers, W.L., 1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* 43, 113–156.
- Ward, C.V., Kimbel, W.H., Johanson, D.C., 2011. Complete fourth metatarsal and arches in the foot of *Australopithecus afarensis*. *Science* 331, 750–753.
- Zipfel, B., 2004. Morphological variation in the metatarsal bones of selected recent and pre-pastoral humans from South Africa. Ph.D. Dissertation, University of the Witwatersrand.
- Zipfel, B., Berger, L.R., 2009. Partial hominin tibia (StW 396) from Sterkfontein, South Africa. *Paleontol. Afr.* 44, 71–75.
- Zipfel, B., DeSilva, J.M., Kidd, R.S., 2009. Earliest complete hominin fifth metatarsal – implications for the evolution of the lateral column of the foot. *Am. J. Phys. Anthropol.* 140, 532–545.
- Zipfel, B., DeSilva, J.M., Kidd, R.S., Carlson, K.J., Churchill, S.E., Berger, L.R., 2011. The foot and ankle of *Australopithecus sediba*. *Science* 333, 1417–1420.
- Zipfel, B., Kidd, R.S., Clarke, R.J., 2010. The 'second australopithecine species hypothesis' in Sterkfontein Member 4: the post-cranial evidence. In: *Proceedings of the 16th Conference of the Palaeontological Society of Southern Africa (Howick, 5–8 August, 2010)*. Interpak Books, Pietermaritzburg, pp. 124–125.