Earliest Complete Hominin Fifth Metatarsal—Implications for the Evolution of the Lateral Column of the Foot

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ABSTRACT   StW 114/115, from Sterkfontein, South Africa, is the earliest complete hominin fifth metatarsal. Comparisons of StW 114/115 to modern humans, extant apes, and partial hominin metatarsals AL 333-13, AL 333-78, SKX 33380, OH 8, and KNM-ER 803f reveal a similar morphology in all six fossils consistent with habitual bipedality. Although StW 114/115 possesses some primitive characters, the proximal articular morphology and internal torsion of the head are very human-like, suggesting a stable lateral column and the likely presence of lateral longitudinal and transverse tarsal arches. We conclude that, at least in the lateral component of the foot of the StW 114/115 individual, the biomechanical pattern is very similar to that of modern humans. This, however, may not have been the case in the medial column of the foot, as a mosaic pattern of hominin foot evolution and function has been suggested. The results of this study may support the hypothesis of an increased calcaneo-cuboid stability having been an early evolutionary event in the history of terrestrial bipedalism. Am J Phys Anthropol 000:000–000, 2009.   © 2009 Wiley-Liss, Inc.

A complete, undistorted right fifth metatarsal, StW 114/115, was recovered in August 1982 by the Sterkfontein excavation team under A.R. Hughes. The specimen was provisionally identified as belonging to *Australopithecus robustus* from Member 5. However, the stratigraphy of the Sterkfontein cave systems and associated infills are complex (Kuman and Clarke, 2000; Clarke, 2006), resulting in the boundary of Members 4 and 5 being unclear and making it difficult to assign StW 114/115 to any specific member and/or taxon.

DeLoison (2003), in describing early hominin foot bones from South Africa, interpreted the anatomical features of StW 114/115 as being consistent with those of *Australopithecus* from Member 5. There is, however, no evidence of *A. africanus* occurring in Member 5. Pickering et al. (2004), in a taphonomic reassessment of Sterkfontein fossils, listed this specimen as coming from Member 4 implying that it may belong to *A. africanus*. Hominin dental remains StW 116 and StW 120 were recovered in the same grid and depth as StW 114/115, thought to stratigraphically belong to Member 4 (Moggi-Cecchi et al., 2006). Although there is no evidence that the dental remains and the fifth metatarsal are from the same individual, it is noteworthy that the dimensions of the StW 116 lower incisors and canines exceed the range known in both early *Homo* and robust australopithecines from South African sites and can be accommodated only within the taxon *Australopithecus africanus* (Moggi-Cecchi et al., 2006). Given the proximity of StW 114/115 to these dental remains, it is reasonable to hypothesize that the metatarsal belongs to *A. africanus*, though we caution that given the complex stratigraphy of Sterkfon-

tein, there remains the possibility that StW 114/115 is from early *Homo* or from *Paranthropus robustus*. Member 5 was dated to 1.5–2.0 Ma (Kuman and Clarke, 2000), and Member 4 has been estimated to be 2.4–2.8 Ma (Vrba, 1985; Delson, 1988; McKee et al., 1995; Kuman and Clarke, 2000). Berger et al. (2002), in a revision of the *Australopithecus*-bearing deposits of Sterkfontein, interpreted Member 4 more likely to fall between 1.5 and 2.5 Ma.

Pedal elements within the fossil record are extremely rare, in particular the anterior elements consisting of the metatarsals and phalanges. Within the fossil record, there is as of yet no complete pre-human metatarsus available comprising all five bones. The most complete early hominin foot is that from East Africa, the OH 8 foot from Olduvai, of which the metatarsal heads are missing from all five bones (Leakey et al., 1964; Susman and Stern, 1982). The 3.2 Ma (Walter, 1994) Hadar fossils A.L. 333-115 consist of only the five metatarsal heads of a single foot (Latimer et al., 1982; Susman et al., 1984).

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TABLE 1. Measurement of hominin fifth metatarsals

	Measurement (mm)					
	StW 114/115	SKX 33380	OH 8	AL 333-78	AL 333-13	KNM ER 803
Length functional	54.9	–	–	42.6 (min)	–	–
Length total	60.7	–	–	54.4 (min)	–	–
Base-dorsoplantar	11.0	–	9.6	11.0	12.1	12.0
Base-mediolateral	16.5	–	12.2	15.7	18.1	20.3
Head-dorsoplantar	12.6	11.2	–	–	–	–
Head-mediolateral	8.7	8.1	–	–	–	–
Midshaft-dorsoplantar	7.4	7.3	5.8	6.4	7.3[a]	–
Midshaft-mediolateral	8.7	8.9	7.2	7.0	9.4[a]	–

[a] Measured at the point of fracture probably slightly proximal of the midshaft.

The hominoid foot consists of a lateral column (that leads to the fourth and fifth digits) and a medial column (that leads to the hallux and the second and third digits) (Aiello and Dean, 1990). The medial column of the anterior elements of the hominin foot, best represented by the first metatarsal, has received attention in a number of studies (e.g., Lewis, 1980; Susman and Brain, 1988; DeLoison, 2003; Susman and de Ruiter, 2004; Zipfel and Kidd, 2006). The lateral column of the anterior foot, however, has received less attention due to the paucity of complete fourth and fifth metatarsals in the fossil record. The StW 114/115 fifth metatarsal, therefore, being the earliest complete hominin fifth metatarsal to date, provides a unique opportunity to further investigate the lateral column of the hominin foot and its evolution.

A complete lateral metatarsal will also allow us to address the contentious question of midfoot stability in early hominins. Some have argued based on the Laetoli footprints (White, 1980; White and Suwa, 1987) and evidence for a well developed calcaneonavicular ligament (Lamy, 1986) and cubonavicular ligament (Stern and Susman, 1983; Lamy, 1986; Gebo, 1992) that *A. afarensis* may have possessed a longitudinal arch. Others, however, have argued based on the dorsally inclined facets on the tarsals and metatarsals (Sarmiento, 1991; Berillon, 2003), and a weight-bearing navicular (Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004), that the arch was absent in this taxa, and the Laetoli prints may have been made by another hominin (Tuttle, 1985; Harcourt-Smith and Hilton, 2005; Bennett et al., 2009).

South African australopithecines may have possessed at least a weakly developed arch on the medial side of the foot based on the nonweight-bearing navicular in StW 573 (Harcourt-Smith, 2002), though the degree of midfoot stability on the lateral side of the foot in South African australopithecines has not been studied. The presence or absence of a longitudinal arch in Plio-Pleistocene East African hominins continues to be a controversial topic. The morphology of the calcaneocuboid joint in OH 8 provides evidence for lateral stability and a stable lever at push-off (Lewis, 1980; Susman, 1983; Susman and Stern, 1982; Langdon et al., 1991; Kidd et al., 1996; Kidd, 1998), which has led some to argue for the presence of a well-developed longitudinal arch (Day and Napier, 1964; Susman, 1983; Lamy, 1986; Berillon, 2003). However, others have interpreted the morphology of the medial aspect of the foot as inconsistent with the presence of a well-developed longitudinal arch (Oxnard and Lisowski, 1980; Kidd et al., 1996; Kidd, 1998). Study of this complete hominin fifth metatarsal will provide additional evidence for the evolution of the lateral longi-tudinal arch and the timing and pattern of foot evolution in early hominins.

The following is a descriptive account of the StW 114/115 fossil with comparisons to other early hominin, ape, and modern human fifth metatarsals and a discussion of the functional affinities of the lateral column of the hominin foot.

MATERIALS AND METHODS

The fossil was compared to human and great ape counterparts. Morphological comparisons were made on fifth metatarsals from Victorian British humans (11 females and 16 males) in the Spitalfields Collection (British Museum of Natural History). Also included in comparisons were wild-shot great ape individuals comprising chimpanzees (20 females and 19 males) and gorillas (20 females and 19 males) from the Powell-Cotton Museum, England, and orangutans (16 females and 11 males) from the Smithsonian Institution, Washington, DC. In addition to extant apes and humans, StW 114/115 was compared to the partial fifth metatarsals SKX 33380 from Member 3 of Swartkrans, South Africa, OH 8 from Bed I, Olduvai Gorge, Tanzania, AL 333-13 and AL 333-78 from the Afar Locality, Ethiopia, and KNM ER-803f from Koobi Fora, Kenya. All the fossils studied were original specimens except for Hadar *A. afarensis* metatarsals, which were high-quality casts made available for research by the Cleveland Museum of Natural History and the Harvard Peabody Museum. The SKX 33380 distal two-thirds of a fifth metatarsal is attributed to *Paranthropus robustus* (Susman, 2004) and OH 8 proximal two-thirds of a fifth metatarsal is attributed to *Homo habilis* (Day and Napier, 1964; Leakey et al., 1964; Susman and Stern, 1982; Susman, 2008) though others consider this fossil to belong to *Paranthropus boisei* (Wood, 1974; Grausz et al., 1988; Gebo and Schwartz, 2006). AL 333-13 and AL 333-78 partial fifth metatarsals are attributed to *Australopithecus afarensis* (Latimer et al., 1982), and the KNM-ER 803f proximal fifth metatarsal is attributed to *Homo erectus* (=*ergaster*) (Day and Leakey, 1974; McHenry, 1994; Antón, 2003).

Morphometric analyses of StW 114/115 are based on the four extant species, and females and males were treated as separate groups. Eight variables were chosen so as to reflect the broad morphology of the bone and its functional attributes. The comparative fossils are excluded in the morphometric analysis because of their fragmentary nature (Table 1). Measurements obtained from the fifth metatarsal are defined in relation to the mediolateral dimension of the base, considered to be

coincident with the transverse plane and perpendicular to the sagittal plane.

Using these defined planes, the following linear variables are defined (see Fig. 1):

1. *The functional length* is measured from the extreme of the anterior articular surface to the articular margin dividing the shaft and the styloid process. This dimension captures the length of the metatarsal that articulates with the cuboid representing a substantial portion of the short lever arm of the foot.
2. *The total length* is measured from the extreme of the anterior articular surface to the most proximal extreme of the styloid process. This dimension captures the length of the metatarsal including the non-articular tuberosity to which the *M. fibularis brevis* attaches.
3. *The dorsoplantar height of the base* is the maximum height measured from the most dorsal point on the base to the most plantar point on the base at right angles to the assumed transverse plane.
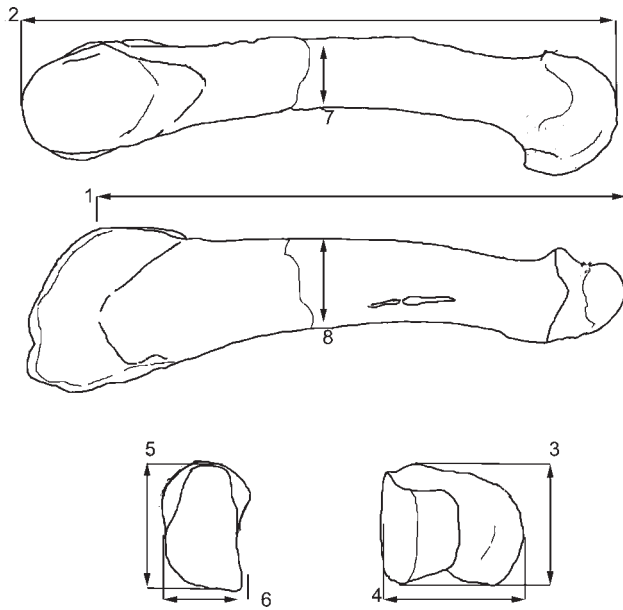
4. *The mediolateral breadth of the base* is the maximum breadth measured from the most medial point on the base to the most lateral point on the base in the assumed transverse plane.
   The dorsoplantar and mediolateral dimensions of the base capture the area that corresponds to a portion of the cuboid responsible for stability or flexion in the metatarsocuboid joint.
5. *The dorsoplantar height of the head* is the maximum height measured from the most dorsal point on the distal articular surface to the most plantar point of the distal articular surface.
6. *The mediolateral breadth of the head* is the maximum bone span measured from the most medial point on the head to the most lateral point on the head.
   The dorsoplantar and mediolateral dimensions of the head capture the area of articulation with the proximal phalanx, playing a role in stability of the joint and degree of metatarsophalangeal dorsiflexion.
7. *The dorsoplantar height of the midshaft* is measured at a point midway between the most medial point on the proximal articular surface to the most distal point of the distal articular surface at right angles to the assumed transverse plane.
8. *The mediolateral breadth of the midshaft* is measured at a point midway between the most medial point on the proximal articular surface to the most distal point of the distal articular surface in the assumed transverse plane.
   The dorsoplantar and mediolateral dimensions of the midshaft capture the relative robusticity of the bone in relation to the length.

All dimensions were obtained using standard digital sliding calipers (Tables 1 and 2). All readings were taken in millimeters and recorded to 0.01 mm.

Plots of means against their standard deviations revealed a clear positive regression; as a consequence, all data were transformed to their natural logarithms. Subsequent plots of the transformed mean and standard deviation data did not reveal any obvious correlation, and thus the transformed data were used for the multivariate analyses. The multivariate objective of the study was to establish patterns of morphological discrimination within and between the groups, initially using principal components analysis (PCA) (Blackith and Reyment, 1971; Bryant and Yarnold, 2001) and subsequently using canonical variates analysis (CVA) (Albrecht, 1980a,b, 1992; Reyment et al., 1984). Computations for both analyses were undertaken using PC $SAS^{\circledR}$ 9.1.

Fig. 1. Fifth metatarsal dimensions. Numbers indicate measurements in the text.

TABLE 2. *Means and standard deviations (in parentheses) of samples of comparative extant species fifth metatarsals and the StW 114/115 fossil*

	Measurement (mm)								
	Human		Chimpanzee		Gorilla		Orangutan		StW
	M (11)	F (16)	M (19)	F (20)	M (19)	F (20)	M (11)	F (16)	114/115
Length functional	57.46 (3.50)	55.46 (3.04)	61.24 (2.89)	58.37 (2.81)	76.23 (4.42)	64.56 (3.63)	85.13 (8.18)	74.50 (4.15)	54.94
Length total	67.86 (4.94)	63.05 (3.34)	69.22 (4.11)	66.09 (3.14)	88.14 (4.09)	73.59 (4.01)	91.56 (8.23)	79.81 (4.72)	60.66
Base-dorsoplantar	14.20 (1.63)	13.16 (1.22)	11.26 (0.71)	10.55 (1.06)	17.37 (1.69)	13.35 (1.24)	13.11 (1.97)	11.05 (1.26)	10.99
Base-mediolateral	20.44 (2.54)	18.70 (2.14)	18.36 (1.39)	16.82 (1.52)	25.82 (1.88)	19.40 (1.35)	17.22 (2.42)	13.78 (1.21)	16.54
Head-dorsoplantar	12.72 (1.50)	10.52 (1.21)	13.35 (0.89)	12.35 (0.87)	16.91 (1.92)	14.27 (0.91)	17.68 (1.54)	13.86 (0.88)	12.55
Head-mediolateral	10.65 (1.59)	9.51 (1.34)	8.61 (0.79)	8.21 (0.90)	11.25 (0.93)	9.26 (0.74)	11.42 (1.38)	9.63 (0.79)	8.68
Midshaft-dorsoplantar	6.92 (1.41)	7.18 (1.57)	6.51 (0.49)	6.34 (0.57)	9.65 (0.88)	7.59 (0.58)	7.30 (0.92)	5.94 (0.44)	7.38
Midshaft-mediolateral	9.19 (1.78)	7.11 (1.28)	6.26 (0.54)	5.67 (0.54)	7.49 (0.62)	5.89 (0.47)	7.53 (0.99)	6.38 (0.53)	8.65

In the CVA part of this study, the fossil was entered directly as part of the overall canonical structure as a sample size of unity, rather than by interpolation into a matrix of the extant species. A weighted analysis was used. While there has been debate with regard to the relative merits of weighted and unweighted analyses (e.g., Albrecht, 1980a,b, 1992), they do serve to maximize the amount of discrimination held within early variates (Albrecht, 1980b, 1992). However, an unweighted analysis of these data also revealed no qualitative difference in the patterns of discrimination between the fossil and extant group means.

The torsion angle of the StW 114/115 metatarsal head relative to the base was measured utilizing digital photographs but not entered as a variable into the multivariate analyses. Metatarsal robusticity was assessed based on an index of the length and midshaft dimensions utilizing the formula ([midshaft width + midshaft height]$^{1/2}$/ functional length $\times$ 100). Qualitative assessments of the sagittal and transverse curvatures of the shaft were made. In addition, plain film radiographs are examined for cortical thickness and pathology.

RESULTS

Descriptive morphology

A right distal fifth metatarsal bone (StW 114) was recovered from grid square W/44 depth 8′9″–9′10″ (2.6–3.0 m) and a right proximal fifth metatarsal bone (StW 115) recovered from grid square W/45 depth 7′10″–8′10″ (2.4–2.7 m). The two portions belong to the same individual; the shaft was broken just proximal to the midpoint; however, this is hardly noticeable after reassembly (see Fig. 2). The preservation of the fossil is exceptionally good with no evidence of postfossilization damage, pathology, nor any cut or bite marks. StW 114/115 is therefore unique insomuch as it is at present the only known complete hominin fifth metatarsal from the early Plio-Pleistocene.

The general morphology of the bone appears to be very human-like and of an adult as the epiphysis is completely fused. The shaft curves in the transverse plane with the concavity on the lateral side. There is a medial (internal) torsion of the head of ~10° measured as the deviation from the vertical axis of the metatarsal head relative to the vertical axis of the base. The shaft is short and stout with a distinct sagittal curvature plane producing a plantar concavity (see Fig. 2). In profile, the shaft has approximately the same dorsoplantar height from just distal to the base, to just proximal to the head giving it a parallel sided appearance (see Fig. 3). There is a dorsal shaft edge on the middle third of the dorsum and dorsal tubercle proximally, adjacent to the facet for the fourth metatarsal that could indicate the insertion of the *M. fibularis tertius* (=peroneus tertius), but is not conclusive evidence for the presence of this muscle (Eliot and Jungers, 2000).

The base is expanded and the lateral border traces a gentle curve as it passes from the proximal end to the shaft. The articular surface of the base is set at an acute angle to the shaft with the angle formed between the medial and posterior articular facets being ~120°. On the proximal articular surface, both the posterior and medial articular surfaces are slightly convex in the dorsoplantar plane. There is a cavity dorsal to the margin of the proximal articular surface for the cuboid bone close to the junction between the posterior and medial
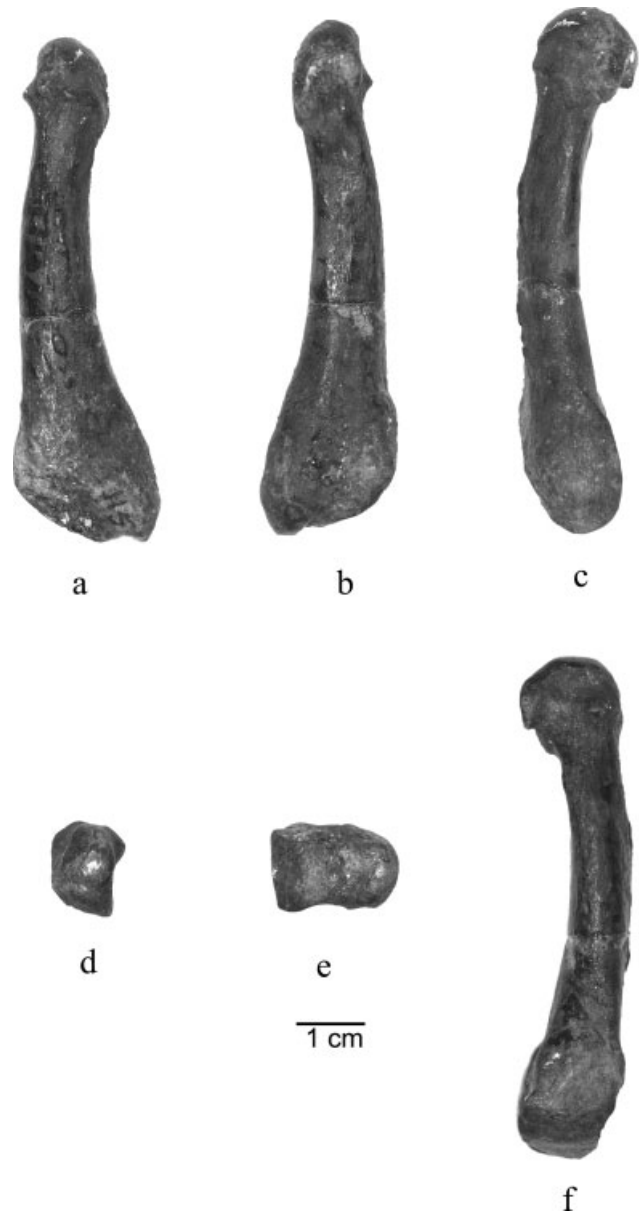

Fig. 2. StW 114/115, right fifth metatarsal from Sterkfontein: **a**) dorsal, **b**) plantar, **c**) lateral, **d**) anterior, **e**) posterior, **f**) medial.

basal articular facets. The posterior tuberosity for insertion of the tendon of the *M. fibularis brevis* (=peroneus brevis) is a prominent point facing directly posteriorly.

In profile, the distal articular surface extends well onto the dorsum of the bone and is flanked by prominent epicondyles. On the plantar aspect of the distal articular surface, the lateral plantar extension extends more posteriorly than the medial. The medial plantar extension has a small sharp lip extending posteriorly. On the dorsum, there is a shallow sulcus, or depression, between the head and the shaft. No nutrient foramina were observable on the shaft of the fossil; in humans, a single nutrient foramen is most commonly found on the medial side of the shaft (Singh, 1960; Patake and Mysorekar, 1977). A cursory observation of chimpanzee and gorilla
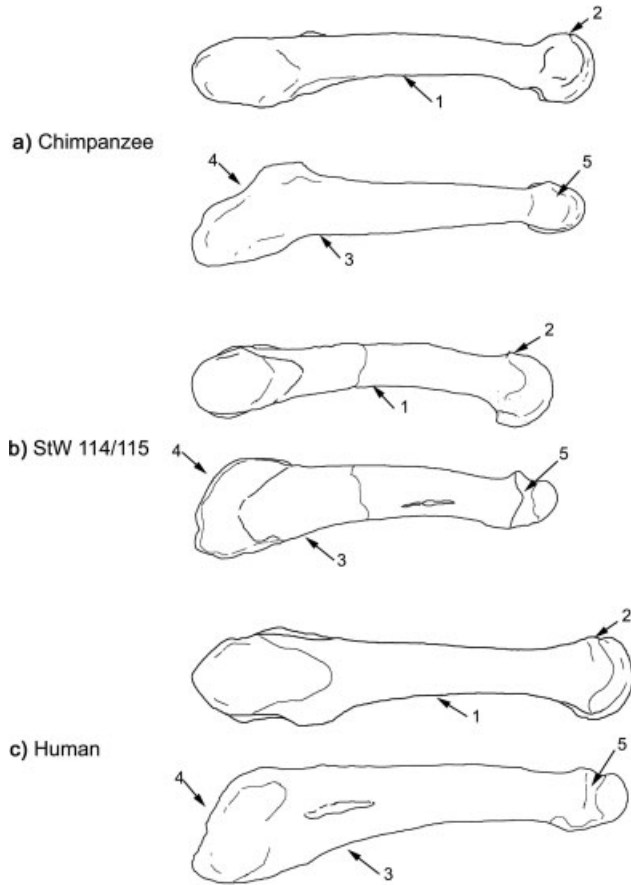
Fig. 3. Lateral and dorsal views of fifth metatarsals. In profile, a sagittal plane curvature of the shaft with a lack of expansion plantar posteriorly (1) is seen in chimpanzees (**a**) and the fossil (**b**). Humans have a straighter shaft (**c**, 1). StW 114/115 (b) and humans (c) have an extension of the phalangeal surface onto the dorsum of the bone (2). Viewed dorsally, chimpanzees (a) have a straight lateral shaft (3). The shaft of the fossil and humans curves in the transverse plane with an expanded base (b and c, 3). The posterior articular surface in chimpanzees is mediolaterally concave (a, 4), and in the fossil and humans it is convex (b and c, 4). In StW 114/115 and humans, there is a shallow sulcus behind the head (b and c, 5). This feature is absent in chimpanzees (a, 5). Features 2–5 seen in the fossil are derived, human-like traits.

Fig. 4. Dorsoplantar and mediolateral radiographs of StW 114/115 and SKX 33380. Dorsoplantar radiographs of human and chimpanzee fifth metatarsals.

fifth metatarsals, although not formally studied, suggests a similar pattern to that in humans.

The internal bony architecture of StW 114/115 reveals no signs of either disease or serious injury in the base, shaft, or head (see Fig. 4). The trabecular patterns appear normal when compared to healthy humans, chimpanzees, and gorillas. The cortex of the shaft is thinner distally and achieves its maximum thickness just proximal to the base. The cortex thickness measures 2.5 mm (55.5% of the mediolateral thickness of the shaft) at midpoint. Dorsoplantarly, the cortex measures 2 mm at midshaft (57.1% of the dorsoplantar diameter of the shaft).

Comparative anatomy

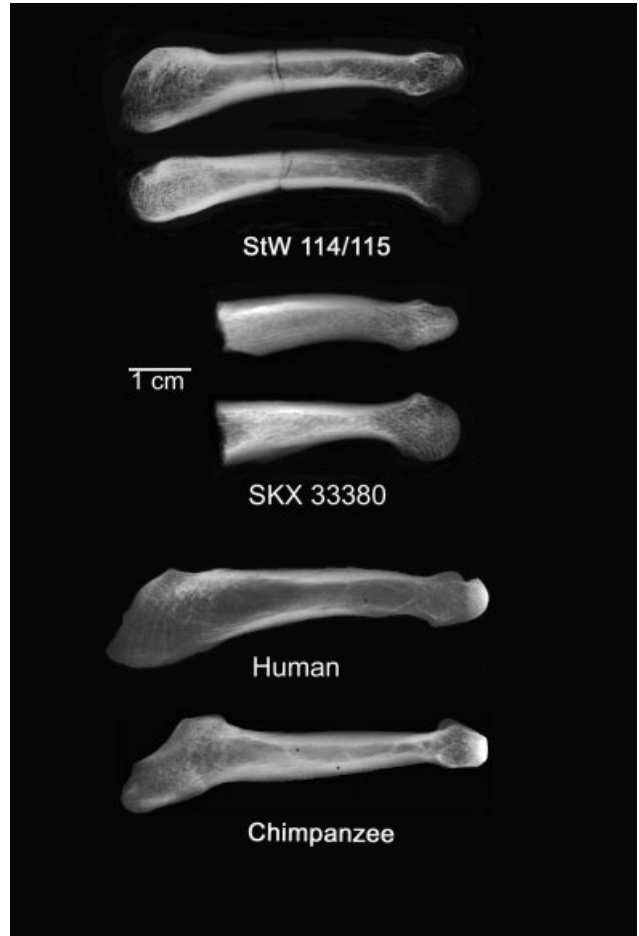StW 114/115 is similar in size and morphology to the distal shaft and head of SKX 33380, the almost complete AL 333-78, and AL 333-13. It is smaller than the proximal base of KNM-ER 803f and slightly larger than the partial proximal shaft and base of the OH 8 fifth metatarsal (Table 1). Like StW 114/115, SKX 33380 and AL 333-78 also have a pronounced curvature (concave laterally) (see Fig. 5). As in SKX 33380 (Susman, 2004), AL 333-13, and AL 333-78 (Latimer et al., 1982), StW 114/115 has a faint ridge dorsally on the shaft possibly for insertion of fibularis tertius. The East African fossils have in common with the Sterkfontein fifth metatarsal an expanded base with the lateral border tracing a gentle curve as it passes from the base to the shaft. In profile, the distal articular surface of StW 114/115 extends onto the dorsum of the bone as in modern humans. In contrast, SKX 33380 resembles more closely the condition found in apes. Dorsally, the head of StW 114/115 has a less obvious shallow sulcus compared with humans. This feature is completely absent in SKX 33308, although the head is also flanked by prominent epicondyles with a small ridge between them. Both AL 333-78 and the OH 8 fifth metatarsals appear not to have the sagittal curvature with the plantar concavity seen in StW 114/115 and in SKX 33308. The SKX 33308 distal shaft has a plantar concavity that expands more posteriorly than in StW 114/115 but may have been exaggerated as a result of taphonomic deformation. However, due to the fragmentary nature of the comparative

Fig. 5. Dorsal view of the fifth metatarsal of chimpanzee (**a**), AL 333-13 (**b**), AL 333-78 (**c**), OH 8 (**d**), StW 114/115 (**e**), KNM-ER 803f (**f**), SKX 33308 (**g**), and human (**h**). The fossils have been inverted to all represent the left side.

Fig. 6. Fifth metatarsal bivariate plot of principal components one and two of log-transformed dimensions including extant Hominoids and the StW 114/115 fossil.

fossils, with the exception of AL 333-78 and OH 8, we are not able to ascertain the presence or absence of this feature.

The Sterkfontein metatarsal StW 114/115 thus displays a combination of primitive (hominoid) and derived (hominin) characters. Ape-like features are observed in the sagittal curvature of the metatarsal shaft and the lack of an expanded plantar shaft toward the base. In both StW 114/115 and SKX 33308, the sulcus, or depression, between the head and the shaft is not as pronounced as in humans, but is present in contrast to the total lack of this feature in apes. The presence of this sulcus or depression, although not as obvious as in humans, appears to be a derived character. The head of StW 114/115 displays an axial torsion, which is medial or internal and similar to that of modern humans. In contrast, the apes have a torsion of the metatarsal that is laterally or externally rotated so that the head faces the other metatarsals (Morton, 1922; Lewis, 1980; Aiello and Dean, 1990). The basal articulations for the cuboid and fourth metatarsals are human-like. This human-like shape is evident in the acute angle of the articulation with the cuboid with respect to the shaft. This condition is seen to some extent in gorillas, but not in chimpanzees or orangutans (Aiello and Dean, 1990). The dorsoplantar shape of the proximal articular surface of StW 114/115 is similar to all of the other known hominin metatarsals in being flatter than modern African ape metatarsal facets and falling in the distribution of modern human fifth metatarsal-cuboid facet curvature (DeSilva, 2008). The ape proximal articulation with the cuboid is "elongated" in the mediolateral direction (Susman, 1983) and appears also to be more mediolaterally concave than in humans, StW 114/115, OH 8, AL 333-78, and KNM ER-803; this is therefore a distinct feature discriminating the apes from hominins. AL 333-13 has a slightly concave articulation for the cuboid in the mediolateral direction.

Radiographically, the cortical thickness (mediolateral thickness of the midshaft) of StW 114/115 (56%) is greater than that of humans (36%; $n = 10$), less than that of chimpanzees (71%; $n = 4$), and similar to the fos-
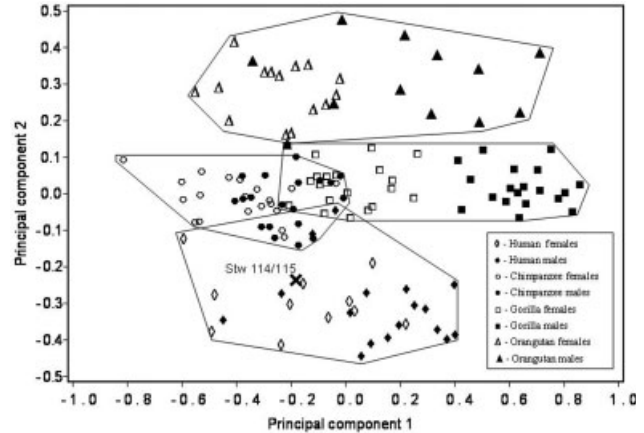
sil distal fifth metatarsal SKX 33380 (estimated at 53%), the only comparative fossil for which a radiograph could be obtained (see Fig. 4). From a radiograph of the OH 8 metatarsus figured in a recent study by Susman (2008), an estimated cortical thickness of 54% was calculated. StW 114/115 is a robust metatarsal with a robusticity index value of 13.3, well within the human (mean = 14.4; range = 11.2–17.1) and gorilla range (mean = 13.8; range = 11.2–15.4), but outside the range of the chimpanzee and orangutan samples (chimpanzee = 9.14; range = 9.2–12.6 and orangutan = 11.6; range = 8.5–12.7). Relative robusticity, however, varies between different groups of humans (Archibald et al., 1972; Zipfel, 2004) as well as in apes (Day and Napier, 1964; Archibald et al., 1972).

Multivariate analysis

PCA of the eight linear measurements reveals that the majority of the variation lies within the first two principal components, together accounting for just over 76% of the total variance. The third principal component contains just over 13% of the total variance and the fourth less than 4%. As most of the total variance is contained in the first two principal components, the subsequent components are considered to contain largely redundant information and are therefore not described. A plot of the first two components giving the positions of each individual is illustrated in Figure 6. The eigenvectors from principal component one are all of positive sign and would tend to indicate that most of the variance contained within this component is associated with size and size-related shape (Table 3) (Jolicoeur, 1963). The fossil StW 114/115 lies centrally on the first principal component within the spread of humans. On the second principal component, containing 17.86% of the total variation, the eigenvectors are both of positive and negative sign, indicating a large component of size-independent shape content. On this component, the fossil lies negatively to all the apes, centrally within the humans.

In the CVA of the fossil together with the extant species, the majority of the discrimination lies within the first two variates, together accounting for over 83% of the total discrimination. Subsequent variates contain

TABLE 3. *Eigenvalues, eigenvectors, and percentage of variance for principal components analysis of the fifth metatarsal in the hominoid species and StW 114/115*

	Prin 1	Prin 2	Prin 3
Eigenvalue	0.139	0.042	0.032
% of variance	58.71	17.86	13.45
Eigenvector			
Length functional	0.237	0.526	0.153
Length total	0.265	0.406	0.116
Base-dorsoplantar	0.460	−0.205	−0.083
Base-mediolateral	0.416	−0.415	−0.319
Head-dorsoplantar	0.338	0.440	−0.030
Head-mediolateral	0.336	0.017	0.320
Midshaft-dorsoplantar	0.405	0.001	−0.521
Midshaft-mediolateral	0.313	−0.390	0.693

TABLE 5. *Eigenvalues, percentage of discrimination, and pooled within-class standardized canonical coefficients of the fifth metatarsal in the hominoid species and StW 114/115*

	Can 1	Can 2	Can 3
Eigenvalue	11.630	3.993	2.086
% of discrimination	61.95	21.27	11.11
Coefficients			
Length functional	0.939	−0.149	0.286
Length total	−0.004	0.439	−0.338
Base-dorsoplantar	−0.475	0.153	0.571
Base-mediolateral	−0.487	0.772	−0.514
Head-dorsoplantar	0.683	0.133	−0.247
Head-mediolateral	0.108	−0.151	0.522
Midshaft-dorsoplantar	−0.398	0.179	0.056
Midshaft-mediolateral	−0.173	−0.512	0.633

TABLE 4. *Fifth metatarsal group means along canonical variates one, two, three, and four*

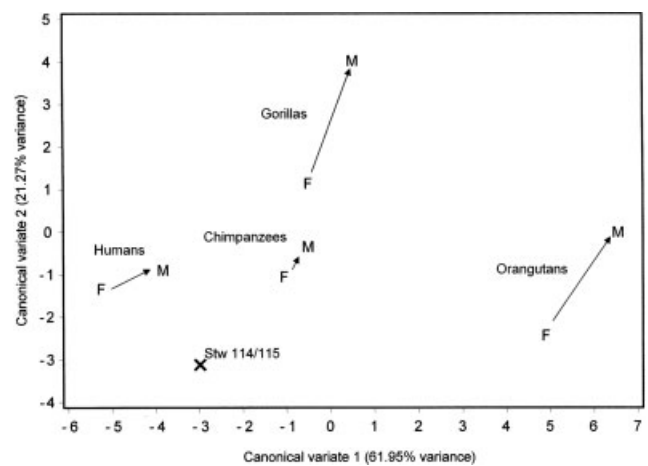| Group	Sex	Can 1	Can 2	Can 3	Can 4
% of total discrimination		61.95	21.27	11.11	3.88
StW114/115		−2.98	−3.12	1.07	2.66
Homo	F	−5.22	−1.34	1.19	−1.74
	M	−3.83	−0.90	2.21	1.09
Pan	F	−1.01	−1.05	−1.89	0.15
	M	−0.49	−0.35	−1.48	0.78
Gorilla	F	−0.48	1.13	−0.96	−0.50
	M	0.49	4.02	0.63	−0.16
Pongo	F	4.94	−2.43	0.59	−0.78
	M	6.56	0.01	1.29	0.60

Fig. 7. Fifth metatarsal bivariate plot of canonical means along canonical variates one and two (apes, humans, and fossil). Note the position of the fossil StW 114/115 on the line discriminating humans and African apes from orangutans.

considerably less variation, with the third variate accounting for 11.11% of the total discrimination and the fourth variate accounting for 3.88% of the total discrimination. The group mean scores along the first four canonical variates are given in Table 4, and the pooled within class standardized canonical coefficients are given in Table 5.

Along the first canonical variate, the group centroids are spread over ∼12 standard deviation units (SDU) with the orangutan males on the most positive extreme and the human females on the negative extreme. The fossil lies between the human males and chimpanzee females (see Fig. 7). The main dimensions contributing to this variation are the basal dorsoplantar and mediolateral dimensions and the dorsoplantar dimension of the head (Table 5).

On the second canonical variate the fossil lies between 0.5 and 1.5 SDU negatively to the human, chimpanzee, and orangutan female centroids, which together lie negatively to the gorillas (see Fig. 6). The main dimensions responsible for this variation are the mediolateral dimension of the base and the midshaft (Table 5). The fossil is thus of distinct form but has the greatest affinity for humans and chimpanzees. This is also borne out by the Mahalonobis distances (Table 6).

On the third canonical variate, the fossil lies broadly between the humans on the one hand and the apes on the other (Fig. 8). More specifically, the fossil lies closest to the human females, gorilla males, and orangutan females. The main dimensions responsible for this discrimination are the dorsoplantar and mediolateral dimensions of the base, head, and midshaft (Table 5).

DISCUSSION

Functional affinities

The principal features that distinguish human from ape fifth metatarsals are shaft robusticity, the sagittal and lateral curvatures of the metatarsal shaft, the torsion of the metatarsal head, the extension of the distal articular surface onto the dorsum of the head, and the shape of the proximal cuboid facet. Arrows in Figure 3 highlight some of the important differences in apes and humans. StW 114/115 possesses a mosaic of these features. The dorsal extension of the distal articular surface of StW 114/115, for instance, would allow for a human-like metatarsophalangeal dorsiflexion, which is essential for successful toe-off during the propulsive phase of bipedal gait (Bojsen-Møller, 1979; Bojsen-Møller and Lamoreux, 1979; Latimer and Lovejoy, 1990a). A distinctive feature of the human metatarsal shaft is that it is relatively straight in the sagittal (dorsoplantar plane) and has a concavity on the lateral side. In contrast, the ape fifth metatarsal has a curvature in the sagittal plane with the concavity on the plantar side and a straighter lateral border than in humans. The dorsoplantar curvature suggests that a primitive trait perhaps related to arboreal climbing has been retained. However, it is

TABLE 6. *Mahalonobis* D^2 *distances from the fossil to group centroids of the fifth metatarsal*

Group	Sex	D^2
StW114/115		0
Homo	F	35.89
Homo	M	23.10
Pan	F	34.09
Pan	M	34.52
Gorilla	F	51.04
Gorilla	M	81.43
Pongo	F	87.36
Pongo	M	114.08

Fig. 8. Fifth metatarsal bivariate plot of canonical means along canonical variates one and three (apes, humans, and fossil). Note the position of the fossil StW 114/115 lying on the line discriminating the apes from humans.

unclear how to interpret the sagittal curvature of the StW 114/115 metatarsal in context of many other features related to bipedality. Some have argued that the evolution of bipedality maladapts hominins for arboreality (Latimer et al., 1987; Latimer and Lovejoy, 1989; Latimer, 1991; Lovejoy, 2005a,b, 2007), whereas others have argued that the australopithecine postcranial anatomy is consistent with both terrestrial bipedality and arboreality (Stern and Susman, 1983; Susman et al., 1984, 1985). Though sagittal curvature of the metatarsal may very well be evidence for continued arboreality in *A. africanus*, we suggest that the variation of this feature across primates, and the effect of body size on sagittal curvature within humans, deserves further study before it is assumed to be functionally related to tree climbing.

Another compelling feature suggesting a bipedal gait in the StW 114/115 specimen is the internal (medial) torsion of the metatarsal head (Morton, 1922; Lewis, 1980; Aiello and Dean, 1990). In humans, the heads of the metatarsals have rotated in relation to their bases to lie squarely on the ground. In apes, the head of the first metatarsal is oriented toward the other metatarsals with the second to fourth oriented toward the first (Fig. 9a). In humans, there is very little torsion in the first metatarsal, with progressively more torsion from the second to fifth metatarsals (Fig. 9b) (Elftman and Manter, 1935a; Aiello and Dean, 1990; Largey et al., 2007). The opposite occurs in the apes where there is progressively less torsion from the second to fifth metatarsal, allowing the forefoot to lie in an inverted position (Morton, 1922; Lewis, 1980; Aiello and Dean, 1990). The human foot is unique in having both a transverse tarsal and longitudinal metatarsal arch, which results in a half dome shape with hollow surfaces facing both downward and medially. It should, however, be noted that there is no distal (metatarsal) functional transverse arch (Cavanaugh et al., 1987; Luger et al., 1999; Weishaupt et al., 2002; Kanatli et al., 2003); it is a transverse arch more proximally in the tarso-metatarsal region. Other primates have only the transverse tarsal arch, their feet being flat in the longitudinal direction (Aiello and Dean, 1990). Humans, by having the metatarsal torsion increase toward the lateral side of the foot allow for the orientation of the proximal articular surfaces to be more medially oriented from second to fifth metatarsal with the metatarsal heads in a plantigrade position and arches are formed in both the sagittal and coronal planes. It follows that this torsion of the metatarsal head in the StW 114/115 individual (10°) falls within the range of humans (10°–15°) with a mean of 12° (n = 10), strongly suggesting that this hominin had both transverse and longitudinal arches. African apes, on the other hand, have less torsion in the fifth metatarsal (4°–9°) with a mean of 7°
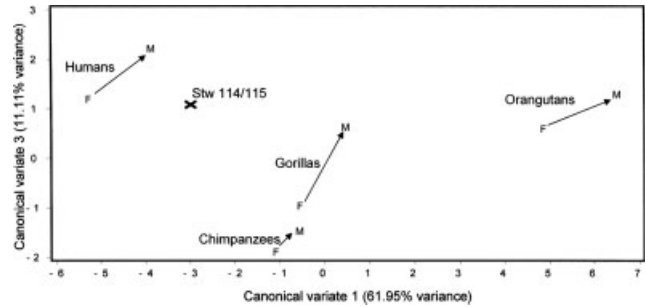
(n = 6). Lordkipanidze et al. (2007) describe a similar condition in early *Homo* from Dmanisi, interpreting the torsion of the metatarsals as being human-like and suggesting a transverse tarsal arch.

In the CVA, StW 114/115 lies on the line between the African apes and humans and orangutans in a plot of variates one and two. Figure 6 illustrates a broad geographic and functional discrimination between the Homininae of African origin and the Ponginae of Asian origin. Orangutans have longer metatarsals than any of the African apes and humans, and the length dimensions have a higher correlation on principal component two, canonical variate one for the functional length, and canonical variate two for the total length (Tables 3 and 5). This discrimination is not surprising as orangutans are functionally and phylogenetically distinct from the African apes and modern humans. The dorsoplantar head dimension on canonical variate one has a heavily weighted coefficient, indicating variation in this dimension particularly in gorillas and orangutans. On canonical variate two, the mediolateral dimensions of the base and midshaft have heavily loaded coefficients, suggesting perhaps discrimination based on dimorphism in the apes. Interestingly, a similar pattern has been noted in hominoid first metatarsals in a multivariate study of hominins SKX 5017 and SK 1813 from Swartkrans (Zipfel and Kidd, 2006).

On a plot of variate one against variate three, the fossil lies on a line discriminating the humans on the one hand and the apes on the other (see Fig. 7). As the plots of the apes and humans possibly suggest discrimination in terms of locomotion, being quadrupedal terrestrial and arboreal for the apes and habitual bipedalism for the humans, the position of the fossil suggests a unique morphology and perhaps associated function. The isolated fossil does, however, lie closest to the humans and chimpanzees, located in a unique position of the group means along the first two variates (Table 4), which is also confirmed by the Mahalonobis distances (Table 6). The heavily weighted coefficients on canonical variate three are associated with the mediolateral dimensions of the head and midshaft and both dimensions of the base. The base contributes to the overall shape-associated variation; gorillas have a styloid process that juts out laterally more than in humans. This may also indicate that on canonical variate three, with four heavily weighted coefficients, the overall morphology discriminates the humans from the apes with the fossil lying between them.
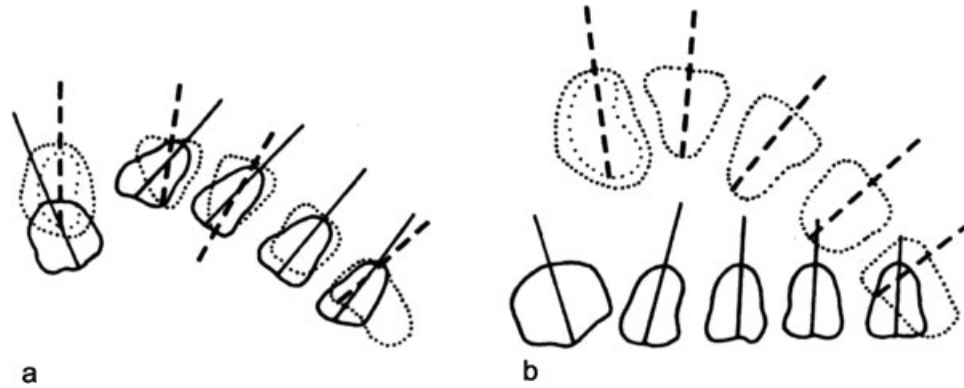
Fig. 9. Transverse sections through the metatarsals of a gorilla foot and a human foot. In the gorilla metatarsals II–V, the metatarsal heads (solid lines) are externally rotated in relation to the bases (dotted lines) with the proximal and distal ends in the same plane (**a**). In human metatarsals II–V, the heads (solid outlines) are internally rotated in relation to the bases (dotted lines) allowing for the formation of a transverse arch (**b**). After Morton (1922).

In summary, the derived (human-like) features in StW 114/115 are as follows: 1) a short robust bone, 2) an internal torsion of the head, 3) a distal articular surface extending onto the dorsum of the metatarsal head with a sulcus or depression between the head and shaft, 4) a transverse plane curvature (lateral concavity) tracing a gentle curve as it passes to the expanded base and, 5) a dorsoplantar flattened proximal articular surface. Primitive (ape-like) features in StW 114/115 are as follows: 1) a curvature in the sagittal plane (plantar concavity) of the shaft and 2) a lack of posterior expansion of the plantar shaft at the base.

Clearly, the StW 114/115 fifth metatarsal is very human-like and the available evidence suggests that the function of this element may not have been much different (if different at all) from that of modern humans. These results are consistent with others from the postcranial skeleton of *A. africanus* suggesting that this hominin was a capable, committed biped (Robinson, 1972; Lovejoy, 1974; Reed et al., 1993; Sanders, 1998; Häusler and Berger, 2001; Häusler, 2002; Kibii and Clarke, 2003; Touissaint et al., 2003). It should, however, be noted that StW 114/115 is only an isolated element of the foot and mixed affinities have been noted in hominin feet, including those of *A. africanus*, suggesting that the medial and lateral columns have not necessarily evolved in concert (e.g., Kidd et al., 1996; Harcourt-Smith and Aiello, 2004; Kidd and Oxnard, 2005).

Lateral column function and evolution of the hominin foot

Vereecke et al. (2003) in their studies on dynamic foot pressures on *Pan paniscus* reveal that during both bipedal and quadrupedal locomotion, considerable pressure exists on the lateral aspects of the foot, with flexion possibly occurring at the tarso-metatarsal joint of the fifth metatarsal. This flexion is associated with, though more distal to, the midtarsal break (flexion of the transverse tarsal joint) (Elftman and Manter, 1935b; Susman, 1983). Midfoot flexion may be an adaptation that allows climbing primates to have both the grasping forefoot required to hold onto a vertical substrate and the stable hindfoot necessary for propulsion during both climbing and terrestrial quadrupedalism (Meldrum and Wunderlich, 1998; Meldrum, 2002). A detailed comparative study has revealed that the midtarsal break is a complex motion involving flexion at both the transverse tarsal joint and the tarsometatarsal joint (DeSilva and MacLatchy, 2008; DeSilva, 2008). A skeletal correlate of midfoot mobility is the dorsoplantar convexity of the ape fourth and fifth metatarsal, functionally hypothesized to facilitate flexion at the tarsometatarsal joint (DeSilva, 2008; DeSilva, submitted). Additionally, the proximal articular mediolateral "elongation" and concavity of the ape fourth and fifth metatarsal is thought to increase the range of motion in the metatarsocuboid joint (Jungers, 1988; Lewis, 1989; Swartz, 1989; Godfrey et al., 1995; D'Août et al., 2002; Vereecke et al., 2003).

Stress on the bones of the human foot during locomotion begins with heel strike at which compression forces are directed primarily at the plantar aspect of the calcaneal tuberosity and the talo-crural joint (Manter, 1946; Scott and Winter, 1993; Chen et al., 2001). In vivo studies have shown that during walking, the medial metatarsals incur more pressure than the lateral metatarsals (Hills et al., 2001; Ledoux and Hillstrom, 2002). A plantar pressure study has shown that specifically during the push-off phase of walking, forces are highest on the medial metatarsals, with the first and second metatarsals incurring the greatest pressure, and the lateral metatarsals the least (Hayafune et al., 1999). In human bipedal feet, weight is effectively borne on the talo-crural joint, and transferred inferiorly to the calcaneus. This weight is transferred from the heel to the forefoot which then adapts from a more mobile structure, absorbing the ground reaction forces, to a rigid lever at push-off phase (Hicks, 1954). This requires considerable stability of the foot in which the calcaneocuboid joint "locks" and there is little or no motion in the metatarsocuboid or the tarsometatarsal joints (Bojsen-Møller, 1979; Lewis, 1980; Blackwood et al., 2005).

Skeletal correlates of midfoot stiffness and stability, including a mediolaterally shortened and dorsoplantarly flat proximal fifth metatarsal facet, can be found in both humans and StW 114/115. These results are consistent with an *A. africanus* fourth metatarsal from Sterkfontein, StW 485, which also displays joint morphology consistent with lateral foot stability (DeSilva, 2008). This morphology aids in the midfoot becoming a rigid lever, shifting motion to the metatarsophalangeal joint during the push-off phase of gait. A skeletal correlate of this

metatarsophalangeal motion is a dorsally extended articular surface on the distal head of human metatarsals. In contrast, the dorsal-most portion of the metatarsal head of apes appears flat in profile (Susman, 1988; Aiello and Dean, 1990; Latimer and Lovejoy, 1990a,b). Interestingly, the fossil, StW 114/115, displays a very human-like dorsally extended articular surface. Additionally, in the human lesser metatarsals, there is also a depression between the head and shaft (Aiello and Dean, 1990). This also relates to an increased capability for dorsiflexion at the metatarsophalangeal joints. This is essential to a habitual bipedal gait where the metatarsophalangeal joint acts as a fulcrum so that the posterior part of the foot can "roll" over during the toe off phase of gait. This feature is present, though not as well developed in the Sterkfontein specimen as in modern humans. Nevertheless, the extended articular surface onto the dorsum of the head would probably have allowed for the phalanx to dorsiflex enough to facilitate a bipedal gait.

Two axes of progression in the midfoot have been described by Bojsen-Møller (1979). The transverse or high gear axis across the metatarsal heads one and two and the oblique or low gear axis transects the metatarsal heads two to five. The perpendicular bisections of each axis to the heel show the longer radial arm from heel to the transverse axis and the shorter radial arm to the oblique axis (Bojsen-Møller, 1979; Bojsen-Møller and Lamoreux, 1979). The greater the radial arm length, the better the ability to develop greater thrust hence "high gear" push. Once the longer radial arm becomes engaged by weight shift to the transverse axis, it causes "closed packing" of the calcaneocuboid joint and secondary tarsal and midtarsal stability. Lateral column stability is therefore a key evolutionary development in habitual bipedalism. The proximal articular surface of the StW 114/115 fossil, which is virtually indistinguishable from that of humans, serves as compelling evidence for a stable lateral column in a hominin foot, the case of which is even stronger coupled with the internal torsion of the metatarsal head suggesting both transverse and longitudinal arches.

The relatively thick cortex of the StW 114/115 shaft may at first be suggestive of a slightly different kinematic approach to walking than that practiced by modern humans, though it is of note that Griffin and Richmond (2005) have found that the cortical thickness and bending strength of human metatarsals are not perfectly matched to loading patterns known from plantar pressure studies. Nevertheless, the relative robusticity of the metatarsals has been correlated with generalized locomotor strategies across hominoids (Marchi, 2005). In particular, Marchi (2005) noted that the robust fifth metatarsal in humans is in stark contrast to the relatively slender fifth metatarsal in the apes. Though apes have a higher plantar pressure on the lateral side of the foot during quadrupedal locomotion (Vereecke et al., 2003), the pressure is medial during climbing bouts (Wunderlich, 1999). Wunderlich (1999) also found that the relative metatarsal robusticity in the apes is more consistent with loading patterns incurred during climbing bouts than during quadrupedalism. The mid-shaft robusticity of the StW 114/115 metatarsal may therefore suggest a human-like bipedal locomotion for this individual. Additionally, a comparison of StW 114/115 to the medial metatarsals from Sterkfontein may help in forming hypotheses of climbing in the South African australopithecines.

The first evidence for the appearance of bipedal locomotion is arguably from *Sahelanthropus tchadensis* dating to c. 7 Ma (Brunet et al., 2002; Zollikofer et al., 2005; Lebatard et al., 2008), *Orrorin tugenensis* dating to ~6 Ma (Senut et al., 2001; Richmond and Jungers, 2008) and *Ardipithecus ramidus kadabba* from ~5.2 Ma (Haile-Selasie, 2001). This places taxa such as *A. africanus, H. habilis* and *P. robustus* phylogenetically closer to modern humans than to the earlier purportedly bipedal hominins (Strait and Grine, 2004). It is therefore reasonable to hypothesize that the forms of bipedalism in these later taxa may be more advanced than the earlier ones. It may therefore not be surprising that StW 114/115 is quite human-like. The human-like functional affinities of this fifth metatarsal, however, do not necessarily indicate that the remainder of the foot would have the same degree of human-like function. Furthermore, it is possible that the lateral side of the hominin foot may not have evolved in concert with the medial side of the foot. A study of the OH 8 hindfoot has provided some evidence for this hypothesis, the medial side perhaps being more pongid-like, while the lateral side is more human-like (Kidd et al., 1996).

In contrast the well-developed calcaneocuboid joint in the OH 8 foot is strongly indicative of a stable lateral column. This in turn suggests the presence of at least a degree of lateral longitudinal arching in this foot. On the other hand, the low talar head torsion may suggest an undeveloped midtarsal restraining mechanism on the medial side of the foot. Thus, the presence of the lateral components of these modifications, but the absence of equivalent medial components, may be seen as evidence as to the chronology of evolutionary events with the lateral side of the foot evolving structural stability earlier than the medial side (Kidd et al., 1996, Kidd, 1998, 1999). This hypothesis has also been supported by an analysis of the so-called "Little Foot" assemblage StW 573 (Clarke and Tobias, 1995; Kidd and Oxnard, 2005). In both these pedal assemblages, where the lateral column is suggested to be stable, the medial column may not be as well developed as in modern humans.

Even though others have also argued for the presence of mosaic locomotor affinities in Plio-Pleistocene hominins (e.g., Harcourt-Smith and Aiello, 2004), differing interpretations of these pedal fossils have conflicted with this "lateral-first, medial-second" hypothesis. Some have argued, as in the case of StW 573, that the posterior part of the foot evolved derived features first while the anterior part remained apelike (Clarke and Tobias, 1995; Tobias, 1998). Others have regarded the morphology of the OH 8 foot and the StW 573 pedal remains as more human-like and derived. Day and Napier (1964) and Leakey et al. (1964) originally suggested that the OH 8 foot reflected a fully developed bipedal adaptation of midfoot stability. Subsequent researchers have suggested that the hallux of OH 8 was adducted and nonopposable (Berillon, 1999; Harcourt-Smith and Aiello, 1999; Harcourt-Smith, 2002; McHenry and Jones, 2006). Additionally, further analysis of the StW 573 medial column suggests that the hallux was fully adducted and that the medial column of this individual was not as ape-like as originally described (Harcourt-Smith, 2002; McHenry and Jones, 2006).

Australopithecus afarensis foot bones from Hadar, Ethiopia (~3.0–3.4 Ma), have also featured prominently in hypotheses of foot evolution. These bones have been described by some to be consistent with full bipedal loco-

motion (Latimer et al., 1982; Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990a,b) and by others as having traits that suggest a mosaic of terrestrial and arboreal locomotion (Stern and Susman, 1983, 1991; Susman, 1983; Susman et al., 1984; Susman and Stern, 1991; Duncan et al., 1994; Berillon, 1999, 2003). These arguments can also be supported by evidence from the Laetoli footprints; those who argue that the footprints are strong evidence for a human-like arched foot (Leakey and Hay, 1979; White, 1980; White and Suwa, 1987; Feibel et al., 1996) and those arguing against that (Stern and Susman, 1983, 1991; Susman, 1983; Susman et al., 1985; Duncan et al., 1994; Berillon, 1999).

A. afarensis appears to have a very human-like talus (Latimer et al., 1987), though the calcaneocuboid joint may have allowed more mobility than that found in modern humans (Gomberg and Latimer, 1984; White and Suwa, 1987). The *A. afarensis* foot has also been described as having the derived human-like traits of an unopposable hallux (Latimer and Lovejoy, 1990b) and longitudinal arches (White, 1980; White and Suwa, 1987; Latimer and Lovejoy, 1989). However, others have postulated that *A. afarensis* may have had a grasping hallux based on the convex shape of the medial cuneiform (Hunt, 1994; Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 1999).

Should *A. africanus* (if represented by StW 573) and *A. afarensis* pedal assemblages be contemporaneous (disputed by Berger et al., 2002), then their mosaic morphology and associated function may be distinctly different. This has been argued by Harcourt-Smith and Aiello (2004) who suggest that while *A. afarensis* retains a divergent toe and a weight-bearing navicular, it possesses a human-like derived ankle, whereas *A. africanus* possesses a derived adducted hallux and navicular and a more primitive ankle complex. Clark and Tobias (1995) also regarded the *A. africanus* ankle, as represented by the StW 573 talus, to be human-like, although Kidd and Oxnard (2005), in contrast, found the StW 573 talus to be decidedly ape-like. In a study of the hominin talus, Gebo and Schwartz (2006) describe the talus from Omo (323-76-898) best allocated to the genus *Homo* as similar to KNM-ER-813 and to modern human tali. In contrast, the tali from Kromdraai (TM-1517; ~2 Ma), Olduvai Gorge (OH 8), and Koobi Fora (KNM-ER-1476a) show distinctive talar features suggestive of a side branch of hominin locomotor evolution, perhaps occupied by the robust australopithecines.

Hominin first metatarsals from Swartkrans (SKX 1517 and SK 1813) and Sterkfontein (StW 562 and StW 595) represent the most important component of the medial column of the anterior foot, and though quite human-like in appearance, they display more primitive features (Susman and Brain, 1988; DeLoison, 2003; Susman and de Ruiter, 2004; Zipfel and Kidd, 2006) than the lateral column as represented by the StW 114/115 fifth metatarsal. These first metatarsals undoubtedly allow for bipedal gait, evidenced by the extension of the distal articular surface onto the dorsum of the metatarsal head, allowing for increased metatarsophalangeal joint dorsiflexion. The SKX 1517 first metatarsal from Member 3 of Swartkrans is attributed to *Paranthropus robustus* and dated to 1.8 Ma. SK 1813 cannot be reliably assigned to any taxon, though it too may be *P. robustus*. The nonmetrical observations reveal that the basal morphology, shaft robusticity, and head articular surface suggest human-like foot posture and human-like dorsiflexion of the first metatarsophalangeal joint. However, the mediolateral diameters of the distal articular surface, being narrower dorsally, indicates that the modern human-like toe-off mechanism may have been absent in *Paranthropus* (Susman and Brain, 1988; Susman and de Ruiter, 2004). Both SKX 1517 and SK 1813 may well be contemporaneous or slightly younger than StW 114/115. The possibility of them belonging to the same taxon cannot be ruled out, and should this be the case, the hypothesis of a mosaic of derived features evolving first in the lateral column followed by the medial column would further be supported.

The inferred diversity of taxa and existing evidence of postcranial variation suggests that there may have been a considerable degree of locomotor diversity among early hominins (Harcourt-Smith and Aiello, 2004), although the apparent mosaic nature of the hominin skeleton is often interpreted in different ways (see Ward, 2002). We cautiously suggest from the available evidence that the lateral column of the foot as presented by the fifth metatarsal was very similar in early hominins regardless of the greater differences evident in some of the other pedal elements.

CONCLUSION

Both primitive and derived features of an anatomical structure are informative in interpreting the functional morphology of early hominin fossils (e.g., Duncan et al., 1994; Lauder, 1995; Susman and de Ruiter, 2004). We caution against concluding too much from isolated skeletal elements as they largely represent function in only that component. In addition, due to the small numbers of mostly fragmentary comparative fossils, variation of a skeletal element within a species cannot be easily assessed. We also caution against assuming that an ape-like morphology by default implies a modern ape-like behavior without fully understanding the biomechanics of particular locomotor strategies and thereby the functional anatomy of the bone. However, by carefully considering both the primitive and derived features as seen in StW 114/115, some insight into hominin lateral column foot function may be gained. We conclude based upon the morphology of the complete fifth metatarsal StW 114/115 that hominins had by this time evolved a stable lateral column complete with, at least to some extent, transverse tarsal and longitudinal arches. This implies a biomechanical pattern consistent with a form of bipedal locomotion—the exact mode, in the absence of more evidence, is as yet uncertain.

ACKNOWLEDGMENTS

and David Pilbeam and Michele Morgan of the Harvard Peabody Museum for allowing study of casts of the Hadar metatarsals. We acknowledge the staff of the Smithsonian Institution, Powell-Cotton Museum, and British Museum of Natural History for access to human and ape skeletal specimens. This manuscript was greatly improved by the thoughtful comments from Dr. Christopher Ruff, the Associate Editor, and two anonymous reviewers.

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