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# 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.



## 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 | *Australopithecus africanus*? | StW 89 | 2.0–2.6 | This study |
| 2 | Hominin indet. | BRT-VP-2/73b | 3.4 | Haile-Selassie et al., 2012 |
| 3 | *Ardipithecus ramidus* | 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 | *Australopithecus afarensis* | A.L. 333-160 | 3.2 | Ward et al., 2011 |
| 4 | Early *Homo* | D2669 | 1.78 | Pontzer et al., 2010 |
| 5 | *Australopithecus africanus* | 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).


**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.

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