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Calcaneal robusticity in Plio-Pleistocene hominins: Implications for locomotor diversity and phylogeny

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ABSTRACT

A key pedal adaptation to bipedality is a relatively large, weight-bearing calcaneus. The earliest evidence for a human-like, robust calcaneus is at 3.2 Ma in *Australopithecus afarensis* (A.L. 333-8, A.L. 333-55, A.L. 333-37) from Hadar, Ethiopia. *Australopithecus sediba* at 1.98 Ma from Malapa, South Africa displays a unique combination of primitive australopith features and more derived *Homo*-like features, but surprisingly is characterized by a gracile, chimpanzee-like calcaneus. The differences in calcaneal morphology suggest that these taxa differed in the frequency of arboreality and in the manner of foot function during terrestrial bipedal locomotion. This study examines calcaneal morphology in extant hominids (i.e., great apes and humans; $N = 95$) and fossil hominins ($N = 5$) to better understand the evolutionary development of calcaneal robusticity in early hominins. In particular, this study focuses on two additional fossil hominin calcanei that have not figured prominently in previous discussions of calcaneal robusticity: StW 352 and Omo 33-74-896. A measure of calcaneal robusticity was quantified as the ratio of calcaneal tuber cross-sectional area to calcaneal tuber length, which significantly differs between humans and non-humans using a sequential Bonferroni alpha adjustment for multiple comparisons. Additional multivariate analyses using Mosimann shape variables show that StW 352 and Omo 33-74-896 are more similar to *Au. sediba* in calcaneal tuber morphology than to *Au. afarensis*, suggesting that the latter taxon is better adapted for terrestrial bipedalism than at least some later species of *Australopithecus*. This finding implies the possibility of several complex evolutionary scenarios involving either multiple reversals in postcranial morphology in *Australopithecus* or the independent acquisition of adaptations to terrestrial bipedalism in *Au. afarensis* and *Homo*.

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Introduction

Among primates, humans are characterized by a unique locomotor behavior in which we are anatomically obligated to walk upright on two legs (Harcourt-Smith and Aiello, 2004). There are examples of other bipedal vertebrates with semi-upright postures (e.g., kangaroos and birds) and non-human primates that occasionally walk bipedally (Du Brul, 1962), but all show locomotion and posture fundamentally different from human bipedalism (Weidenreich, 1923). The evolution of human bipedalism required a reorganization of the entire hominine body plan, especially the vertebral column, pelvis, lower limb, and foot. The human foot, in particular, has been adapted to terrestrial bipedalism with a permanently adducted hallux (Morton, 1922; Weidenreich, 1923; Latimer and Lovejoy, 1990) for effective propulsion and an energy-saving longitudinal arch (Ker et al., 1987). Humans, great apes, and ursids are unique among all mammals in the use of plantigrade foot postures (Gebo, 1992). Thus, one of the other major pedal adaptations to bipedality is a large, weight-bearing calcaneus with an enlarged heel process (Weidenreich, 1923; Morton, 1924; Latimer and Lovejoy, 1989; Gebo, 1992; Gebo and Schwartz, 2006).

Among mammals, humans uniquely combine two-legged terrestrial locomotion with repetitive plantigrade heel strike (Latimer and Lovejoy, 1989; Gebo, 1992), thus concentrating longitudinal loading on weight bearing joints over two limbs instead of four. Several studies (Simon and Radin, 1972; Radin et al., 1973) have shown that the greatest risk to non-renewable synovial joint cartilage is repetitive longitudinal loading, which radiates throughout the entire skeleton (Voloshin and Wosk, 1982). As such, humans have evolved exceptionally large weight-bearing joints in the hindlimb (Jungers, 1988) and a robust calcaneus to absorb the ground reaction forces generated by heel strike. The earliest potential evidence for a prominent heel strike comes from the 3.7 Ma

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(mega-annum) fossilized footprints of *Australopithecus afarensis* at Laetoli, Tanzania (Leakey and Hay, 1979; White, 1980; Raichlen et al., 2010). Pedal fossils from Afar Locality 333 at Hadar, Ethiopia (Latimer et al., 1982; Latimer and Lovejoy, 1989) show that *Australopithecus afarensis* was characterized by a robust calcaneus with a human-like plantarly positioned lateral plantar process by at least 3.2 Ma.

The morphological variation in hominin pedal fossils has prompted several researchers to suggest that early hominin lineages were diverse in their locomotor behavior (Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004; Lovejoy et al., 2009; Zipfel et al., 2011; Haile-Selassie et al., 2012; DeSilva et al., 2013). Understanding of the hominin calcaneus and its implications for interpreting locomotor diversity and early hominin paleobiology has been hampered by a relative lack of fossil calcanei. The recently discovered nearly complete calcaneus of *Australopithecus sediba* (Berger et al., 2010; Zipfel et al., 2011) differs markedly from that of *Au. afarensis* in having a more primitive morphology with a gracile tuber, dorsally positioned lateral plantar process, and a curved posterior talar facet. The differences in calcaneal morphology suggest that these taxa differed in the frequency of arboreality and in the manner of foot function during terrestrial bipedal locomotion (Zipfel et al., 2011; DeSilva et al., 2013). However, two additional hominin calcanei, StW 352 and Omo 33-74-896, that have not figured prominently in discussions of calcaneal evolution have the potential to contribute an important new perspective to our understanding of early hominin locomotor diversity.

StW 352 is a partial calcaneus from Member 4, Sterkfontein (2.0–2.6 Ma; Pickering and Kramers, 2010), South Africa (Deloison, 2004; Zipfel et al., 2011) that has previously been described as 'robust' (Deloison, 2004). It preserves the mid-portion of the calcaneal tuber and the posterior talar facet. The most posterior portion of the tuber is broken just proximal to the coronal plane in which the medial plantar process would lie. The shape and curvature of the anterior and posterior talar facets is similar to U.W. 88-99, the calcaneus belonging to the MH2 (Malapa Hominin 2) individual of *Australopithecus sediba* (Prang, 2014). The lateral surface of the sustentaculum tali is mostly preserved proximodistally, but the distal and medial surface is missing. Likewise, the calcaneocuboid joint of StW 352 is not completely preserved, precluding an adequate assessment of its morphology. The calcaneus is characterized by a very large and laterally protruding peroneal trochlea, which divides the tendons of fibularis longus and fibularis brevis, and may indicate the importance of the peroneal musculature in foot eversion. The taxonomic affinity of this specimen is problematic because there is a possibility that more than one hominin taxon is represented at Sterkfontein, Member 4 (Calcagno et al., 1997; Lockwood and Tobias, 2002; Clarke, 2013), but no consensus has been reached (Ahern, 1998; Grine et al., 2013). Additionally, there is no indication that *Australopithecus sediba* occurs outside of Malapa. At present, when considering the lack of consensus about how many taxa are represented at Sterkfontein, Member 4, the null hypothesis for the taxonomic affinity of StW 352 should be that it belongs to *Australopithecus africanus* until more fossils show otherwise.

Omo 33-74-896 is a 2.36 Ma partial calcaneus from the Omo Shungura Formation (Member E, Tuff F), Ethiopia (Deloison, 1986; Feibel et al., 1989; Gebo and Schwartz, 2006). It is mostly complete except for the most plantar and lateral corner of the tuber. The medial tuber, including the dorso-medial portion of the attachment site for the tendon of the triceps surae, is preserved. The taxonomic affinity of this specimen is completely unknown, although Gebo and Schwartz (2006) argue that it belongs to early *Homo* based on their qualitative observations of its anatomy, but it is equally likely that it could represent *Paranthropus* or an unknown taxon. Unfortunately, very little is known about the postcranium of *Paranthropus* (Grausz et al., 1988; Dominguez-Rodrígo et al., 2013), including the calcaneus. The calcaneus of OH 8, which could represent *Homo habilis* or *Paranthropus boisei*, is very fragmentary (Day and Napier, 1964), precluding any type of morphological assessment of its tuber and there are no published calcanei associated with early African *Homo erectus* or *Homo rudolfensis*. *Australopithecus garhi* (Asfaw et al., 1999) is a potential taxon to which the Omo 33-74-896 calcaneus could belong. However, *Au. garhi* is known only from the Middle Awash at 2.5 Ma (Asfaw et al., 1999). Thus, the taxonomic placement of the Omo 33-74-896 calcaneus is problematic and unknown, though it could represent a late species of *Australopithecus, Paranthropus*, or early *Homo* given that 'large' and 'small' hominin teeth have been found in Members E and F of the Omo Shungura Formation (Howell, 1969; Howell and Coppens, 1973, 1974; Coppens, 1975; Howell and Coppens, 1976; Suwa et al., 1996; Gebo and Schwartz, 2006). Although there is taxonomic uncertainty regarding both Omo 33-74-896 and StW 352, it is very unlikely that they represent either *Au. afarensis* or *Au. sediba*, respectively.

Both StW 352 (Zipfel et al., 2011) and Omo 33-74-896 (Gebo and Schwartz, 2006) have been described as being similar to the A.L. 333 calcanei in tuber expansion and robusticity. However, the degree to which they are similar has not been assessed quantitatively. Whether these calcanei are more similar to the robust calcanei from Hadar or the more gracile calcaneus from Malapa has implications for understanding the evolution of bipedalism and locomotor diversity in Plio-Pleistocene hominins as well as for interpreting hypotheses concerning the phylogenetic relationships of early hominins (White et al., 1983; McHenry and Berger, 1998; Berger, 2002; Zipfel et al., 2011). This study seeks to better understand the variation in calcaneal robusticity among humans, great apes and early hominins to test the hypothesis that *Australopithecus sediba* is primitive among early hominins in calcaneal robusticity (Zipfel et al., 2011) and that *Au. afarensis* is more derived in the direction of *Homo*.

Materials and methods

The non-human comparative sample comprises adult, wild-caught individuals in the collections of the American Museum of Natural History (AMNH), the Cleveland Museum of Natural History (CMNH), the Academy of Natural Sciences (ANSP), the Center for the Study of Human Origins at New York University (CSHO), and Stony Brook University (SBU). The modern human sample ($N = 34$) is mostly composed of individuals of European and African-American descent but also includes three individuals from the Andaman Islands and one Mbuti 'pygmy' individual (Table 1). The fossil sample includes casts of U.W. 88-99, StW 352, Omo 33-74-896, A.L. 333-8, and A.L. 333-55, which are listed in Table 2, along with locality, stratigraphic information, and estimated dates. The fossil specimens have previously been described elsewhere (Latimer et al., 1982; Deloison, 1985, 1986; Latimer and Lovejoy, 1989; Deloison, 2004; Gebo and Schwartz, 2006; Zipfel et al., 2011).

Table 1
Extant sample used for this study.[a]

	AMNH	CMNH	ANSP	SBU	CSHO	Total
Homo sapiens	4	11	0	18	1	34
Pan troglodytes	23	0	0	0	2	25
Gorilla gorilla	15	10	0	0	0	25
Pongo pygmaeus	5	2	4	0	0	11

[a] AMNH = American Museum of Natural History; CMNH = Cleveland Museum of Natural History; ANSP = Academy of Natural Sciences Philadelphia; SBU = Stony Brook University; CSHO = Center for the Study of Human Origins.