



## Trabecular architecture in the StW 352 fossil hominin calcaneus



Angel Zeininger<sup>a,\*</sup>, Biren A. Patel<sup>b,c</sup>, Bernhard Zipfel<sup>c,d</sup>, Kristian J. Carlson<sup>b,c,d,e</sup>

<sup>a</sup> Department of Evolutionary Anthropology, Duke University, Box 90383, Durham, NC 27708, USA

<sup>b</sup> Department of Cell and Neurobiology, Keck School of Medicine, University of Southern California, Los Angeles, CA 90033, USA

<sup>c</sup> Evolutionary Studies Institute, University of the Witwatersrand, WITS 2050, Johannesburg, South Africa

<sup>d</sup> School of Geosciences, University of the Witwatersrand, WITS 2050, Johannesburg, South Africa

<sup>e</sup> Department of Anthropology, Indiana University, Bloomington, IN 47405, USA

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### ABSTRACT

*Australopithecus africanus* has been interpreted as having a rigid lateral foot. One mechanism contributing to a rigid foot during push-off in humans is a calcaneocuboid joint (CCJ) with limited dorsiflexion and a “close-packed” talocalcaneal joint (TCJ). In contrast, apes likely have a greater CCJ range of motion and lack a close-packed TCJ. Differences in tarsal arthrokinematics may result in different joint loading environments. In *Homo sapiens*, we tested the hypothesis that dorsal and plantar CCJ and the TCJ show evidence of predictable habitual loading. In *Pan troglodytes*, *Gorilla gorilla*, *Gorilla beringei*, and *Papio ursinus*, we tested the hypothesis that only the dorsal CCJ shows evidence of predictable loading. Specifically, we predicted similarity in trabecular properties across the dorsal and plantar CCJ in *H. sapiens*, but dissimilarity in non-humans. Additionally, we investigated trabecular properties of an *A. africanus* calcaneus (StW 352) to evaluate joint loading patterns in this hominin and ultimately address the evolution of these properties in *H. sapiens*. Contrary to predictions, the *H. sapiens* dorsal CCJ has a significantly higher elongation index, bone volume fraction, trabecular thickness, and trabecular number than the plantar CCJ, while trabecular properties in non-humans do not always differ as predicted between regions. *H. sapiens* exhibits trabecular morphology indicative of less variable TCJ loading than other groups, having the most anisotropic and rod-like struts oriented in line with predicted principal loads. Multivariate analysis shows that the StW 352 dorsal CCJ matches *P. ursinus* best, while the plantar CCJ matches *G. beringei* best and the TCJ matches that of *G. gorilla* best. Overall patterns suggest that the StW 352 calcaneus experienced more variable loading than *H. sapiens*, but less variable loading than *P. troglodytes*, *G. gorilla*, *G. beringei*, and *P. ursinus*, consistent with a large range of foot movements, probably reflecting locomotor kinematics that are unlike those of living humans or apes.

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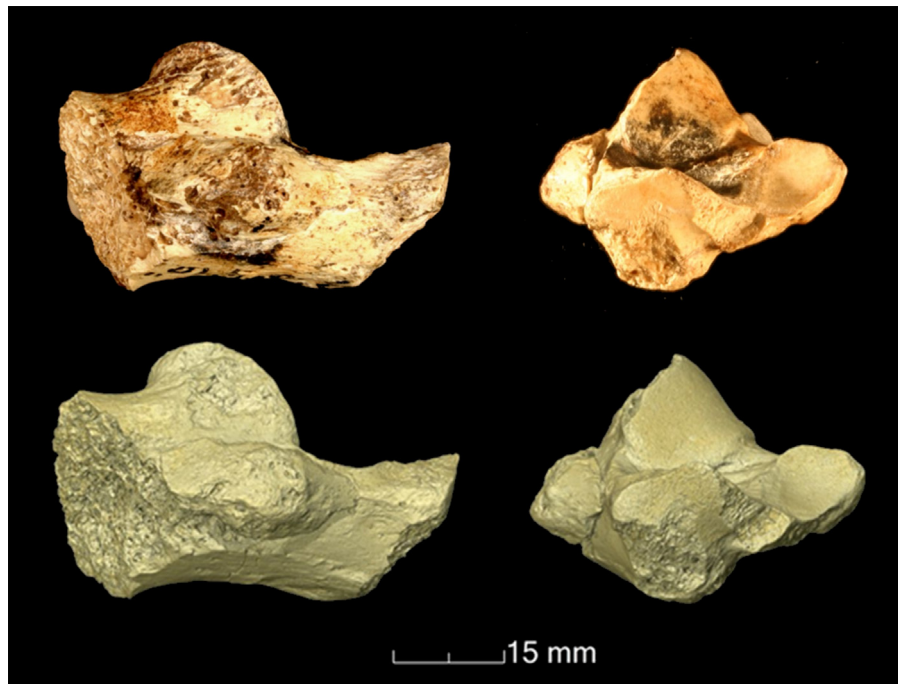
### 1. Introduction

The partial right calcaneus, StW 352, from Member 4 of Sterkfontein, South Africa, is missing only the posterior portion of its calcaneal tuber (Fig. 1). Despite being incomplete, it still represents one of the better-preserved calcaneal specimens in the hominin fossil record. Although the presence of at least two australopithecine species in Member 4 has been suggested (Clarke, 2013), this specimen is most commonly attributed to *Australopithecus africanus* (Deloison, 2003; Prang, 2015). Deloison (2003) originally described StW 352 as having an enlarged peroneal process and a human-like robust tuber, longitudinal axis, and cuboid facet inclination angle.

Based in part on the latter constellation of characters, she suggested that *A. africanus* (as represented by StW 352) likely had an elevated calcaneocuboid joint resulting from a human-like plantar arch, and thus inferred a human-like foot function (Deloison, 2003, 2004). In a more recent study, however, Prang (2015) concluded that the remaining part of the calcaneal tuber of StW 352 is relatively gracile and more chimpanzee-like than previously thought. Moreover, Prang (2015) observed that the cross-sectional area of the remaining part of the calcaneal tuber of StW 352 was more similar to that of *Australopithecus sediba* from Malapa (Zipfel et al., 2011) and less robust than *Australopithecus afarensis* calcanei from Hadar (Latimer and Lovejoy, 1989). He suggested that this demonstrated evidence that later australopithecines from South Africa (*A. africanus* and *A. sediba*) were less well-adapted to terrestrial bipedalism than earlier australopithecines from East Africa (*A. afarensis*). Thus, resolving the conflicting observations of the extent of human-like qualities in

\* Corresponding author.

E-mail address: [angel.zeininger@duke.edu](mailto:angel.zeininger@duke.edu) (A. Zeininger).



**Figure 1.** Photographs of the StW 352 partial right calcaneus (top) and images of a rendering (bottom) generated from high resolution CT scans. Left = lateral view, right = anterior view.

StW 352 may have significant implications for interpreting the evolution of bipedalism within the hominin clade. To further evaluate hominin calcaneal morphology, and hopefully shed light on the functional basis for these opposing views, the aim of this study is to investigate an additional aspect of the StW 352 calcaneus, its trabecular structure, and interpret it within a comparative context using a sample of humans (*Homo sapiens*), African apes (*Pan troglodytes*, *Gorilla gorilla*, and *Gorilla beringei*), and baboons (*Papio ursinus*).

Calcaneal morphology beyond absolute and relative measures of tuber robusticity can be informative when reconstructing hominin foot function. For example, analyzing functional morphology of the StW 352 distal cuboid articular facet (i.e., the articulation with the cuboid at the calcaneocuboid joint [CCJ]) may indicate whether this individual had a relatively more stable (i.e., rigid) or a more mobile midfoot, the latter condition being considered more characteristic of apes and monkeys, and the former condition being considered more characteristic of modern humans (Elftman and Manter, 1935a; Morton, 1935; Bojsen-Møller, 1979; Susman, 1983). In contrast to humans, both apes and monkeys dorsiflex their midfoot following flat foot and during the push-off phase of bipedal or quadrupedal locomotion. Although the CCJ has traditionally been viewed as the site of dorsiflexion in the midfoot (Elftman and Manter, 1935a; Susman, 1983), more recent work (D'Août et al., 2002; Vereecke et al., 2003; DeSilva, 2010; Bates et al., 2013; Thompson et al., 2014; DeSilva et al., 2015) suggests that initial dorsiflexion occurs at the CCJ, followed by additional dorsiflexion at the talonavicular joint and more substantial dorsiflexion at the tarsometatarsal joint between the cuboid and fourth and fifth metatarsals.

Non-human primates can lift the heel independently of the rest of the foot, known as the 'midtarsal break,' because of movement capability in several joints (Elftman and Manter, 1935b). Dorsiflexion of the foot involves a number of joints, one of which, the CCJ, makes an important contribution to this midtarsal break. Kinematic and cineradiographic data (e.g., DeSilva, 2010; Thompson et al., 2014)

demonstrate that greater amounts of midtarsal break occur in the CCJ of *P. troglodytes*, *G. gorilla*, and *Papio* compared to *H. sapiens*. Based on lateral view video footage of captive apes performing slow quadrupedal walking gaits on flat, concrete surfaces, DeSilva (2010) measured a mean CCJ dorsiflexion angle of 16.1° in *P. troglodytes* and 14.1° degrees in *G. gorilla*. Thompson et al. (2014) correspondingly reported mean dorsiflexion of 14° at the CCJ using cineradiography during passive foot movements in anesthetized *P. troglodytes*. By comparison, approximately 2.3° of dorsiflexion in the *H. sapiens* CCJ has been reported (Ouzounian and Shereff, 1989). Subchondral bone radiodensity data are also consistent with results from kinematic and cineradiography studies: *P. troglodytes* and *P. ursinus* exhibit relatively more expansive areas of high radiodensity (a proxy for higher compressive strength) in the dorsal region of the cuboid facet compared to its plantar region, in contrast to *H. sapiens*, in which there are no significant differences in areas of relatively high radiodensity between the dorsal and plantar regions (Nowak et al., 2010).

While subchondral bone apparent density patterns have proven useful in documenting the loading history of joints in extant animals (Carlson and Patel, 2006; Patel and Carlson, 2007, 2008; Polk et al., 2008; Nowak et al., 2010; Su, 2011; Carlson et al., 2013), there are obstacles in applying this approach to fossils. Namely, local variation in diagenetic processes can differentially affect mineralization of a joint region. Thus, there is no guarantee after mineral exchange during fossilization that density gradients in a fossil reflect those that were present in vivo (Patel and Carlson, 2007; Polk et al., 2008). Evaluating the trabecular bone deep to the subchondral region of a joint surface of a fossil offers a useful alternative for linking calcaneal joint anatomy with joint movement and loading history (e.g., Su, 2011; Zeininger et al., 2011). Trabecular bone, a network of tiny struts (i.e., individual trabeculae) positioned deep to the cortical shell, is found throughout the skeleton, including within a significant proportion of tarsals (Currey, 1984). Bone modeling over the lifetime of an individual has been shown, in some cases, to align trabeculae with the direction of principal

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