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Comparative analysis of trabecular bone structure and orientation in South African hominin tali

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A B S T R A C T

Tali of several hominin taxa are preserved in the fossil record and studies of the external morphology of these often show a mosaic of human-like and ape-like features. This has contributed to a growing recognition of variability characterizing locomotor kinematics of *Australopithecus*. In contrast, locomotor kinematics of another Plio-Pleistocene hominin, *Paranthropus*, are substantially less well-documented, in part, because of the paucity of postcranial fossils securely attributed to the genus. Since the talus transmits locomotor-based loads through the ankle and its internal structure is hypothesized to reflect accommodation to such loads, it is a cornerstone structure for reconstructing locomotor kinematics. Here we quantify and characterize trabecular bone morphology within tali attributed to *Australopithecus africanus* (StW 102, StW 363, StW 486) and *Paranthropus robustus* (TM 1517), making quantitative comparisons to modern humans, extant non-human apes, baboons, and a hominin talus attributed to *Paranthropus boisei* (KNM-ER 1464). Using high-resolution images of fossil tali (25 μm voxels), nine trabecular bone subregions of interest beneath the articular surface of the talar trochlea were segmented to quantify localized patterns in distribution and primary strut orientation. It was found that trabecular strut orientation and shape, in some cases, can discriminate amongst species characterized by different locomotor foot kinematics. Discriminant function analyses using standard trabecular bone structural properties align TM 1517 with *Pan* and *Gorilla*, while other hominin tali structurally most resemble those of baboons. In primary strut orientation, *Paranthropus* tali (KNM-ER 1464 and TM 1517) resemble the human condition in the anterior-medial subregion, where strut orientation appears positioned to distribute compressive loads medially and distally toward the talar head. In *A. africanus* tali (particularly StW 486), primary strut orientation in this region resembles that of apes. These results suggest that *Paranthropus* may have had a human-like medial weight shift during the last half of stance phase but *Australopithecus* did not.

1. Introduction

The talus, as a cornerstone bone in the foot, is an integral structure for reconstructing locomotor kinematics of hominins, and fortunately it is often preserved in the fossil record because of its compact, stout nature. Studies of the external structure of early hominin tali typically indicate a mixture of human-like and ape-like features (Wood, 1973, 1974; Kidd et al., 1996; Harcourt-Smith and Aiello, 2004; Kidd and Oxnard, 2005; Gebo and Schwartz, 2006; Jungers et al., 2009; Zipfel et al., 2011; Prang, 2016). Resemblances to a human configuration of the tibiotalar joint (e.g., a relatively more vertical tibia, neutral ankle, and less range of motion) are usually interpreted as indicating more stereotyped ankle loading associated with terrestrial bipedal gait (Latimer et al., 1987; DeSilva, 2009). Resemblances to an ape configuration of the tibiotalar joint (e.g., a relatively more dorsiflexed posture and greater overall range of motion), on the other hand, are usually interpreted as indicating more variable ankle loading associated with arboreal locomotor behaviors, such as vertical climbing (Stern and Susman, 1983; DeSilva, 2009).

Studies of talar internal structure (DeSilva and Devlin, 2012; Su et al., 2013) are comparatively rarer than studies of talar external structure, despite the critical insights such approaches offer for

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inferring ankle loading patterns from a bone that is frequently represented in the fossil record. Wolff's Law posits that trabecular struts tend to optimize according to loading beneath joints by aligning along lines of principal stress through a long bone (Wolff, 1986; Ruff et al., 2006). The capacity of trabecular bone to adjust and realign itself throughout life, according to its customary mechanical environment, is supported by comparative (Fajardo and Müller, 2001; MacLatchy and Müller, 2002; Ryan and Ketcham, 2002; Ryan and Shaw, 2012) and controlled experimental studies (Pontzer et al., 2006; Barak et al., 2011). Despite pervasive negative allometry in trabecular scaling with body mass (Barak et al., 2013a; Ryan and Shaw, 2013), trabecular bone in different regions of the limbs does not appear to respond to loading in similar fashions during a given locomotor behavior (Carlson et al., 2008; Wallace et al., 2012). This suggests that the trabecular bone immediately beneath a joint surface can be locally responsive to joint or load-specific factors. On the other hand, others (Fajardo et al., 2007; Shaw and Ryan, 2011; Hébert et al., 2012) have noted the overall complexity in trabecular responses, suggesting that inferred loading environments in joints may not be decipherable in a straightforward fashion, unless specific suites of properties are examined (Ryan and Shaw, 2012). For example, humans (bipeds) exhibit femoral head trabecular structure characterized by thin, sparse, plate-like struts that are relatively anisotropic, while chimpanzees (quadrupedal climbers) exhibit femoral head trabecular structure characterized by thick, numerous struts that are relatively isotropic (Ryan and Shaw, 2012).

Within the ankle joint of extant hominoids, some studies have noted that trabecular bone appears to distinguish taxa in ways that reflect predicted loading patterns inferred from observed differences and similarities in locomotor kinematics. For example, humans differ from other hominoids (e.g., chimpanzees and gorillas) in several trabecular properties of the talus and distal tibia (Su, 2011; Barak et al., 2013b; Su et al., 2013). Barak et al. (2013b) observed trabecular strut alignment in chimpanzee distal tibiae that corroborates their greater habitual ankle dorsiflexion relative to humans. Noting similarities in the trabecular structure and orientation of distal tibiae from humans and *Australopithecus africanus*, Barak et al. (2013b) suggested that *A. africanus* may have loaded their ankles in more plantarflexed postures than chimpanzees, but also in more diverse and intensive ways than humans. Su et al. (2013) noted unique trabecular alignment beneath the talar trochlea of humans, particularly its anteromedial region, corroborating a greater medial weight shift through the talar neck and head compared to other extant hominoids. Su et al. (2013) also observed dissimilarities between talar trabecular structure in humans and a hominin talus (KNM-ER 1464) attributed to *Paranthropus boisei* (Grausz et al., 1988; Feibel and Brown, 1989). In contrast to these studies, while DeSilva and Devlin (2012) observed some intraspecific and interspecific differences, the lack of predicted differences in regional comparisons of trabecular structure in human, extant ape and several hominin tali from South Africa (i.e., SKX 42695, StW 88, StW 102, StW 363, StW 347, StW 486, and TM 1517) led them to suggest that the talus may not be an ideal bone for studying axial loading. DeSilva and Devlin (2012) concluded that architecture and anisotropy in trabecular bone of the talar body does not vary amongst extant hominoids in ways that one would predict from models of loading, despite a substantial number of studies documenting differences in foot use between humans and other apes (Lundberg et al., 1989a,b; Rome, 1996; D'Août et al., 2002; Sockol et al., 2007; DeSilva, 2009; Raichlen et al., 2009). Ultimately, DeSilva and Devlin (2012) endorsed caution when using trabecular properties for interpreting loading patterns in the hominin ankle due to the presence of deeply conserved regional architecture in extant hominoids. The lack of predicted differences in trabecular structure of tali reported by DeSilva and Devlin (2012) may have been partially due to the use of insufficient spatial resolutions, relatively small samples, and/or their use of relatively large volumes of interest (e.g., quadrants of the entire talar body), unlike other studies that have emphasized high resolution image data, larger samples, and/or more strategic volumes of interest (VOIs) that may have greater functional resolution (Lazenby et al., 2011; Barak et al., 2013b; Su et al., 2013). Whether correspondence in hominin (e.g., *A. africanus*) distal tibiae and tali reflects a functional/biological signal or sampling procedures would clearly benefit from additional investigation.

The first goal of the present study is to evaluate predicted structural differences and similarities within extant hominoids. We base these predictions on kinematics reported for terrestrial walking gaits (Elftman and Manter, 1935; Morton, 1935; Sockol et al., 2007), as it is the dominant form of locomotion in chimpanzees (Hunt, 1992) and humans. Humans bear more weight on their calcaneus during heel strike than do African apes, as demonstrated by plantar pressure measurements (Elftman and Manter, 1935; Wunderlich, 1999; Vereecke et al., 2003) and the presence of an enlarged calcaneal tuberosity (Latimer and Lovejoy, 1989). Also, the ground reaction force at heel strike typically passes slightly posterior to the talocrural joint as a human foot is forced into plantarflexion. Based on these differences, we predict that trabecular properties beneath the posterior portion of the talar trochlea would be more reinforced in humans than in other apes. Moreover, based on the path of the center of pressure over the course of stance phase (Hutton and Dhanendran, 1979; Giacomozzi et al., 2000), although variable, the human talar trochlea would be expected to be more laterally reinforced in the middle regions and more medially reinforced in the anterior regions (Fig. 1). African apes, on the other hand, appear to have a more lateral center of pressure over the duration of stance during terrestrial quadrupedal locomotion (Elftman and Manter, 1935; Vereecke et al., 2003; Crompton et al., 2012) and would be expected to have a talar trochlea that was more reinforced anteriorly than posteriorly, and laterally than medially (Fig. 1). Orangutans would be expected to have more homogenous properties across the talus due to their variable arboreal quadrumanous ankle joint positions (Thorpe and Crompton, 2006). Baboons maintain a plantarflexed ankle throughout stance phase of terrestrial locomotion (Berillon et al., 2010) and so, as in humans, it would be expected that trabecular properties of the baboon talar trochlea are reinforced more posteriorly than anteriorly.

The second goal of this study is to provide the first systematic internal characterization of hominin talar trabecular structure using high resolution computed tomography (CT). These data will allow assessment of structural differences between trabecular architecture in tali assigned to *Australopithecus* (*africanus*) and *Paranthropus* in order to compare ankle loading patterns in these hominins, and possibly to infer additional information about their comparative gait kinematics. Broad generic differences between the locomotor kinematics of *Australopithecus* and *Paranthropus* are not well-established because of the paucity of solidly attributable postcranial fossils to *Paranthropus* (Constantino and Wood, 2007; Wood and Constantino, 2007; Domínguez-Rodrigo et al., 2013; Carlson and Edland, 2016). Su et al. (2013) compared an East African fossil talus, KNM-ER 1464, attributed to *P. boisei*, to extant hominoids finding a mosaic of similarities in trabecular orientation and structure. Based on external morphology, for example, a grooved trochlea and curvature of the medial trochlear rim, similarities have been proposed between the *Paranthropus robustus* talus (TM-1517) and tali (e.g., KNM-ER 1464) from East African robust australopithecines (*P. boisei*) (Gebo and Schwartz, 2006). Gebo and Schwartz (2006) suggest that talar features of