Trabecular architecture in the StW 352 fossil hominin calcaneus.

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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. *Homo 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.

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 australopith 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 australopiths from South Africa (*A. africanus* and *A. sediba*) were less well-adapted to terrestrial bipedalism than earlier australopiths from East Africa (*A. afarensis*). Thus, resolving the conflicting observations of the extent of human-like qualities in 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'Aout 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 et al., 2010; Thompson et al., 2013) 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 and colleagues (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., 2010). 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 loads (Meyer, 1867; Wolff, 1892; Odgaard et al., 1997; Pontzer et al., 2006; Barak et al., 2011). Experimental and modeling data suggest that there are correlations between external loading, trabecular fabric properties, and trabecular elastic properties (e.g., Young's modulus and shear modulus; Hodgkinson and Currey, 1990; Turner et al., 1990; Goldstein et al., 1991; Odgaard et al., 1997; Kabel et al., 1999; Ulrich et al., 1999).

Caution is warranted since not all characterizations of trabecular architecture deep to joint surfaces show the predicted functional signals (e.g., Ryan and Walker, 2010). However, these signals appear to be relatively more robust when considering multiple trabecular properties in a multivariate approach (Ryan and Shaw, 2012). Also, previous studies of trabecular bone morphology in the foot have presented conflicting results with respect to predicted muscle and joint loading patterns, with some finding significant bipedal locomotor correlates (calcaneus: Maga et al., 2006; talus: Su et al., 2013, Su and Carlson, in review; metatarsal heads: Griffin et al., 2010), but other analyses (calcaneus: Kuo et al, 2013; talus: DeSilva and Devlin, 2012) failing to differentiate between groups.

During walking gaits, humans have a relatively rigid lateral midfoot with minimal inter-bone movements during the push-off phase of stance. During load acceptance in the early part of stance phase, subtalar and transverse tarsal joints (talonavicular and CCJ) are in a loose-packed position (MacConnail and Basmajian, 1969; Sarrafian, 1993; Sammarco, 2004). At this time the posterior articular facets of the talus and calcaneus are misaligned. The transverse tarsal joints, on the other hand, are aligned (i.e., their axes are parallel in the coronal plane), allowing for greater dorsiflexion/plantarflexion movement in the sagittal plane. As the ankle dorsiflexes and

body weight passes over the foot, the subtalar joint inverts, bringing the talocalcaneal joint (TCJ) to a "close-packed" position (Sammarco, 2004). However, the transverse tarsal joints simultaneously become misaligned (i.e., their axes are no longer parallel), preventing dorsiflexion/plantarflexion movement in the sagittal plane. Concurrent exorotation of the calcaneus causes the calcaneus to swing laterally, close-packing the CCJ (Sarrafian, 1993). Thus, in humans, both the TCJ and CCJ are close-packed from midstance until the end of stance phase, transforming the foot into a rigid lever in preparation for push-off (Sammarco, 2004). Finite element analyses (FEA) of the calcaneus predict that, at heel strike and in preparation for push-off, summed force across the TCJ is elevated (3.1 times body weight at impact and 5.4 times body weight at 70% of stance phase; Giddings et al., 2000). Maximum force at both the TCJ and CCJ (4.2 times body weight) is predicted at 70% of stance phase in human walking, when both joints are close-packed and the foot propels the center of mass forward (Giddings et al., 2000). Close-packing of the TCJ is not thought to occur during push-off in non-human primates and is, therefore, considered unique to humans (Elftman and Manter, 1935a; Close et al., 1967; Lewis, 1980; Langdon et al., 1991).

Close-packing of joints is thought to be associated with the need to accommodate high compressive forces. Since joint surfaces are maximally congruent during close-packing, compressive forces are theoretically distributed over a large surface area, thereby minimizing the peak compressive force per unit area at any particular location. Thus, the loading environment of trabecular bone associated with a close-packed joint should be one of habitual load orientation (i.e., limited movement at the joint resulting in more uniform strut orientations) and relatively lower compressive forces at any given location (i.e., experienced by any individual strut) compared to a joint that is not close-packed. Trabecular strut shape, measured as the elongation

index, provides some support for this idea in that it has been shown to differ between loading environments characterized by relatively high force (i.e., low elongation index, disc-like struts) versus relatively low force (i.e., high elongation index, rod-like struts; Ding et al., 2002).

In the current study, we test the hypothesis that habitual joint forces (i.e., loading regimes) acting on the distal calcaneus during push-off are preserved in trabecular architecture deep to the cuboid facet in *H. sapiens*, *P. troglodytes*, *G. gorilla*, and *P. ursinus*. We limited our ape sample to African apes as they are the closest living relatives to humans and are more terrestrial than orangutans or hylobatids, which are generally more specialized for suspensory locomotor behaviors (i.e., their foot is used differently to interact with more compliant substrates and superstrates). Additionally, we included *Papio* in our sample since they are amongst the most terrestrial non-hominoid primates, are relatively large in body size, and because the morphology and function of the CCJ has been documented in this group (DeSilva, 2010; Nowak et al., 2010). We then use these modern comparative data to interpret trabecular structure and calcaneal loading in StW 352. We predict that the dorsal aspect of the cuboid facet in *P. troglodytes*, *G. gorilla*, *G. beringei*, and *P. ursinus* will show evidence of higher compressive joint loads (e.g., greater bone volume fraction [BV/TV] and more disc-like struts in underlying trabecular bone) relative to the plantar aspect of the facet. In contrast, we predict that BV/TV, elongation index, and strut orientation (e.g., degree of anisotropy) across dorsal and plantar regions deep to the *H. sapiens* cuboid facet will not differ appreciably. Finally, we predict that StW 352, unlike *H. sapiens*, will exhibit some degree of dorsal versus plantar differentiation in CCJ trabecular architecture if this individual was not as well-adapted to terrestrial bipedalism as *H. sapiens*, as has been recently suggested (Prang, 2015).

Because StW 352 preserves its posterior talar articular facet, its functional morphology also can be evaluated. However, since we are unaware of specific *in vivo* studies of TCJ arthrokinematics in nonhuman primates, or studies of subchondral bone apparent density patterns in the TCJ, we avoid specific regional predictions of trabecular bone structure (e.g., dorsal versus plantar BV/TV), instead favoring those reflecting theoretical loading conditions during overall TCJ close-packing. Because the TCJ is thought to achieve a close-packed position only in *H. sapiens*, we predict that compared to *P. troglodytes*, *G. gorilla*, *G. beringei*, and *P. ursinus*, humans will have a higher degree of anisotropy (i.e., more highly-oriented trabecular struts due to less variable movement in this joint), higher elongation index (i.e., more rod-like trabeculae), and that the trabeculae will be more oriented along the anteroposterior (A-P) plane (i.e., in line with the predicted joint reaction forces; Fig. 2). Once again, we predict that StW 352 will be unlike humans or apes, but rather will exhibit a pattern that is intermediate between the two.

Materials and methods

Human calcanei were obtained from the Norris Farms collection (#36 cemetery), housed at Pennsylvania State University ($n = 5$), and the Raymond A. Dart Collection of Human Skeletons, housed at the University of the Witwatersrand, Johannesburg, South Africa ($n = 10$ Zulu individuals). Materials from the Norris Farms Oneota culture are on loan from the Illinois State Museum and date to 1300 AD (Milner and Smith, 1990). Wild caught, non-pathological adult (as determined by the dental age defined in Shea [1981]) chimpanzee (*P. troglodytes*; $n = 18$) and gorilla ($n = 10$ *G. gorilla* and $n = 6$ *G. beringei beringei*) calcanei were sampled from the American Museum of Natural History (New York, NY) and the National Museum of Natural

History (Washington, DC). Gorilla species were separated in all analyses since recent studies of foot bones have found significant ecomorphological differences in mountain and lowland species (Tocheri et al., 2011; Dunn et al., 2014). Baboon calcanei (*P. ursinus*; $n = 11$) were obtained from adult individuals (determined by long bone epiphyseal fusion) in the Raymond A. Dart Collection of comparative skeletal material, housed at the University of Witwatersrand. For all species, males and females were pooled and samples also included a small number of individuals of unknown sex.

Homo sapiens calcanei from the Norris Farms collection were CT scanned on the HD-600 high-resolution industrial X-ray CT scanner at the Center for Quantitative Imaging, Pennsylvania State University. Additional *H. sapiens* and all *P. ursinus* calcanei, as well as StW 352, were scanned at the Microfocus X-ray CT Facility of the Palaeosciences Centre at the University of the Witwatersrand. The StW 352 calcaneus was scanned at 90 kV and 135 μ A, using 5600 projections with two frame averaging. A portion of the *P. troglodytes*, *G. gorilla*, and *G. beringei* sample was scanned at the High Resolution X-ray CT Facility at the University of Texas-Austin. The remaining African ape sample was scanned at the University of Southern California's Molecular Imaging Center using a SCANCO Medical μ CT 50 specimen scanner, a GE Pheonix Nanotom M scanner, or a Nikon XT H 225 scanner. All extant bones were CT scanned at the highest possible spatial resolution available for their size (26 to 56 μ m). Image data were obtained from StW 352 using 29.6 μ m voxel resolution. A customized segmentation technique was performed in Avizo Fire 8.1 software to remove internal matrix from the StW 352 specimen. Material contrast between fossilized bone comprising struts and the matrix filling intervening trabecular spaces allowed adequate separation of the two materials in StW 352 (Fig. 3).

All image stacks were converted from 16-bit TIFF (or DICOM) images to 8-bit TIFF images in ImageJ software (Rasband, 1997–2014), thereby reducing gray levels from 65,536 to 256 without affecting spatial resolution. Using Quant3D software (Ketcham and Ryan, 2004), trabeculae were sampled within three spherical volumes of interest (VOI) in each calcaneus (Fig. 3): one VOI was positioned deep to the posterior talar articular facet at the TCJ and two VOIs were positioned deep to the cuboid articular facet at the CCJ (i.e., dorsal and plantar CCJ VOIs). Spherical VOIs were chosen over cubic VOIs in order to avoid corner edge effects (Ketcham and Ryan, 2004). Each VOI was scaled to joint size for each specimen. Joint size was measured on three-dimensionally reconstructed image stacks in Avizo 9.0 software (FEI, Hillsboro, OR, USA). For the TCJ, VOI diameter was calculated as one-half the height of the talar articular facet. For the CCJ, each VOI was calculated as one-third the height of the cuboid facet. Small VOIs may not satisfy the continuum assumption (Hoffler et al., 2000) and, therefore, all VOIs were visually inspected to ensure that they contained at least five trabecular struts (Harrigan et al., 1984). Diameters of VOIs ranged in size from 3.28 mm to 16.15 mm (Table 1).

An effort was made to place VOIs in biomechanically homologous locations (Fajardo and Mueller, 2001; Maga et al., 2006; Lazenby et al., 2011; Kivell et al., 2011; Su et al., 2013; Su and Carlson, in review) despite challenges created by shape differences across taxa. Although defining the transition between trabecular struts and overlying cortical bone or densely-packed subchondral bone can be difficult, each VOI was conservatively placed as close to the perimeter of the bone as possible while still ensuring that the three-dimensional VOI contained only trabecular struts. Due to the thick subchondral bone at the TCJ in *P. ursinus* (Fig. 3), we could not confidently identify an appropriately-sized VOI containing only trabecular struts deep to the facet. As such, we excluded *P. ursinus* from the TCJ analyses.

Since image data from calcanei were not always acquired with the bones in anatomical (or at least a single consistent) position, anatomical axes were manually re-defined for each bone prior to analysis. A separate threshold was applied to each VOI using an iterative segmentation algorithm (Ridler and Calvard, 1978; Trussel, 1979). The star volume distribution (SVD) method was used to calculate trabecular fabric properties of each VOI. The SVD method measures trabecular fabric anisotropy by calculating the distance between trabecular struts in various dimensions throughout a stack of 8-bit TIFF images. Briefly, a set of points are randomly selected from within a VOI. Cones are drawn from each point and stopped when they encounter trabecular struts, resulting in a numerical quantification of anisotropy in the form of a 3 X 3 orientation matrix. Primary, secondary, and tertiary trabecular orientations and magnitudes are represented by the eigenvectors (direction) and eigenvalues (magnitude) of the matrix (Odgaard, 1997; Ketcham and Ryan, 2004). These eigenvectors and eigenvalues are used to determine trabecular fabric properties. Primary and tertiary eigenvalues are used to calculate the degree of anisotropy (DA) within a VOI (i.e., $DA = 1 - [\text{tertiary}/\text{primary eigenvalue}]$) on a scale from 0—1 where a DA equal to 0 represents a perfectly isotropic structure and a DA of 1 represents a perfectly anisotropic structure. Elongation index (E) is defined as $1 - (\text{secondary}/\text{primary eigenvalue})$. When DA is near 1, a high E value represents rod-shaped trabecular struts, while a low E value represents more disc-shaped struts. Bone volume fraction (BV/TV) is calculated as the ratio of bone voxels (BV) to total voxels (TV) in a given VOI, where a high BV/TV ratio indicates densely-packed trabecular struts. Trabecular thickness (Tb.Th) is measured as the mean minimum measured length through a random point within bone (Ketcham and Ryan, 2004). Trabecular number (Tb.N) was estimated, using the mean intercept length (MIL) method in

Quant3D, as the number of intersections between a grid of lines and the bone, and then normalized by total grid-line length.

Papio ursinus calcanei (originally scanned at 26 μm) were used to assess resolution dependency in this sample because it was most important to ensure that resolution was sufficiently high in the smallest bones. A VOI was extracted from each calcaneus and then down-sampled to one higher (20) and four lower (30, 40, 50, and 60 μm) spatial resolutions using the Resample module with a Lanczos filter in Avizo 7.1, ultimately encompassing the full range of resolutions used in this study (Ryan and Shaw, 2012). A least squares linear regression was run for Tb.Th, which can be resolution-dependent (Ryan and Shaw, 2012). Trabecular thickness was not significantly correlated with voxel size ($p > 0.05$) in this sample of calcanei and, thus, raw Tb.Th values were used in all analyses.

To visually assess differences across all taxa, boxplots and stereoplots were generated. Boxplots visually compare standard properties. Stereoplots with 95% confidence ellipses visually compare trabecular orientation. To test for statistically significant group differences in these properties, Kruskal-Wallis tests were run for each trabecular fabric property, followed by pairwise Mann-Whitney U tests. To further test for statistically significant differences between dorsal and plantar VOIs within a taxon, Wilcoxon tests were used. All statistical analyses were conducted in PAST (Hammer et al., 2001), with statistical significance determined by an $\alpha \leq 0.05$.

To further investigate whether trabecular bone properties deep to each joint surface (TCJ, dorsal CCJ, plantar CCJ, and combined dorsal and plantar CCJs) can discriminate between taxonomic groups, four variables were subjected to discriminant function analyses: Tb.Th, Tb.N, DA, and E. Each extant group (*H. sapiens*, *P. troglodytes*, *G. gorilla*, *G. beringei*, and *P.*

ursinus) was assigned to its own group a priori, while Stw 352 was not assigned a priori to any group, nor to its own group (i.e., *A. africanus*). The classification results (i.e., percent correct classifications or posterior probabilities) were evaluated to compare actual group membership to predicted group membership (e.g., Patel, 2005; Ryan and Shaw, 2012; Scherf et al., 2015).

Because the original discriminant function analyses may exaggerate estimates of classification, cross-validation tests were performed to assess the performance of the discriminant functions in measuring percent correct classifications. During cross-validation, each case or specimen in the analysis is classified by the discriminant functions derived from all cases excluding itself (i.e., the leave-one-out test was employed). The percent correct classification results of the original discriminant function analyses were then compared to the cross-validation results. If differences were great, this would suggest that trabecular properties used in the analyses are weak discriminators for taxonomic identification. Separation of groups was also evaluated by the analysis of structure coefficients (i.e., the pooled within-group correlation between the predictor variable and the discriminant score). Discriminant function analyses were performed with SPSS v. 16.0 software.

Results

Calcaneocuboid joint

Dorsal VOI: Extant sample *H. sapiens* exhibited the lowest mean BV/TV in this region (Fig. 4, Table 2), significantly lower than those of *P. troglodytes* ($p < 0.001$) and *G. gorilla* ($p < 0.05$). Mean trabecular thickness was highest in *G. gorilla* and lowest in *P. ursinus* (Fig. 4, Table 2),

differing significantly across extant taxa ($H = 15.55$, $p = 0.003$). *Gorilla gorilla* exhibited significantly higher Tb.Th than *H. sapiens* ($p = 0.005$), *P. troglodytes* ($p = 0.033$), and *P. ursinus* ($p < 0.001$), while *G. beringei* exhibited significantly higher Tb.Th than *P. ursinus* ($p = 0.007$; Table 3). Mean Tb.N was highest in *P. troglodytes* and lowest in *G. gorilla* (Fig. 4, Table 2), differing significantly across extant taxa ($H = 9.55$, $p = 0.049$).

Mean DA in the dorsal CCJ VOI was highest in *H. sapiens* and lowest in *Pan* (Table 2), differing significantly across extant taxa ($H = 37.24$, $p < 0.001$; Fig. 4, Table 3). *H. sapiens* had significantly higher DA than all other taxa ($p < 0.001$). In addition, DA in *P. troglodytes* was significantly lower than in *G. gorilla* ($p = 0.022$) and *P. ursinus* ($p = 0.005$). *Homo sapiens* had not only the highest DA values, but also the highest E values, significantly higher than all other taxa ($p < 0.001$; Table 3) and, thus, the most anisotropic and rod-like trabecular struts in the dorsal region of the CCJ. Primary trabecular orientation was generally in the A-P direction in all extant taxa, with the exception of a single *H. sapiens* and two *P. troglodytes* outliers (Fig. 5). *Gorilla beringei* displayed the most variability of extant groups, and emphasized mediolateral variability in primary orientation, while *P. troglodytes* and *H. sapiens* to a lesser extent varied along the dorsoplantar axis more than other taxa.

The multivariate discriminant function analysis produced four discriminant functions with Functions 1 and 2 accounting for 57.8% and 41.1% of trabecular variance, respectively (Table 4). Function 1 was most highly correlated with E and DA, while Function 2 was most highly correlated with Tb.N and Tb.Th (Table 5). Of the 60 individuals in this study, only 55% of the cross-validated grouped cases were correctly classified (Table 6). Approximately 93% of *H. sapiens* were classified correctly, while only 67% of *P. troglodytes*, 70% of *G. gorilla*, and

36% of *P. ursinus* were classified correctly (Table 6). Individuals within the small sample of *G. beringei* were most often misclassified as *G. gorilla* (50%; Table 6).

Dorsal VOI: StW 352 Bone volume fraction of StW 352 was closest to the *H. sapiens* mean, falling within the lower ends of *H. sapiens*, *G. gorilla*, *G. beringei*, and *P. ursinus* ranges, but below the *P. troglodytes* range (Fig. 4, Table 2). In Tb.Th, StW 352 exceeded all extant group means except *G. gorilla* and *G. beringei* (Fig. 4, Table 2). Trabecular thickness of StW 352 was within the lower end of the *G. gorilla* and *G. beringei* range, within the upper end of the *H. sapiens* and *P. troglodytes* ranges, and above the *P. ursinus* range (Fig. 4, Table 2). In Tb.N, StW 352 was considerably lower than each extant group mean, but was still within the lower end of the *P. troglodytes* and *G. gorilla* ranges (Fig. 4, Table 2). Most similar to the pattern observed in *G. gorilla*, StW 352 exhibited relatively few but thick trabecular struts in the dorsal region of the CCJ. In DA, StW 352 was most similar to *G. beringei*. StW 352 fell at the upper end of the *P. troglodytes* DA range, at the lower end of the *G. gorilla*, *G. beringei*, and *P. ursinus* DA ranges, and well below the *H. sapiens* DA range (Fig. 4, Table 2). Overall trabecular shape in StW 352 was relatively rod-like (relatively high E), being most similar to *P. ursinus* (Fig. 4, Table 2). StW 352 fell within the upper end of *P. troglodytes*, *G. gorilla*, and *G. beringei* E ranges, but below the *H. sapiens* E range (Table 2). *Homo sapiens* and *P. ursinus* patterns, which pair high DA and E, provide the best extant comparisons for the relatively anisotropic and rod-like struts in StW 352. Primary trabecular orientation of StW 352 was also A-P, similar to all extant taxa, but fell specifically only within the *G. beringei* 95% confidence interval (Fig. 5). For the dorsal CCJ VOI, the discriminant function analysis predicted StW 352 to be most similar to *P. ursinus* (0.469; Table 6).

Plantar VOI: Extant sample *Homo sapiens* exhibited the lowest mean BV/TV of all groups, while *G. gorilla* exhibited the highest (Fig. 4, Table 2). Significant differences across extant taxa were observed ($H = 32.69, p < 0.001$), particularly in the case of *H. sapiens* that had a significantly lower mean than *P. troglodytes* ($p < 0.001$), *G. gorilla* ($p < 0.001$), *G. beringei* ($p = 0.004$), and *P. ursinus* ($p < 0.001$; Table 3). In addition, the *P. ursinus* mean was significantly lower than that of *P. troglodytes* ($p = 0.016$) and *G. gorilla* ($p = 0.047$; Table 3). *Gorilla gorilla* exhibited the highest Tb.Th, while *H. sapiens* and *P. ursinus* exhibited the lowest (Fig. 4, Table 2). Trabecular thickness differed significantly across extant taxa ($H = 19.27, p < 0.001$), where *G. gorilla* had significantly higher Tb.Th than *H. sapiens* ($p = 0.001$), *P. troglodytes* ($p = 0.009$), and *P. ursinus* ($p < 0.001$; Table 3). This is the same pattern as observed in the dorsal CCJ VOI. Mean Tb.N was highest in *P. troglodytes* and lowest in *H. sapiens* (Fig. 4, Table 2), differing significantly across extant taxa ($H = 28.35, p < 0.001$; Table 3). *Homo sapiens* mean Tb.N was significantly lower than in *P. troglodytes* ($p < 0.001$), *G. gorilla* ($p = 0.002$), *G. beringei* ($p = 0.011$), and *P. ursinus* ($p < 0.001$), while *P. ursinus* mean Tb.N was significantly higher than in *G. beringei* ($p = 0.012$; Table 3). Low BV/TV values in the plantar region of the *H. sapiens* CCJ appear to reflect relatively few and moderately thin trabecular struts, while *G. gorilla*, on the opposite end of the spectrum, had relatively few, but thick trabecular struts deep to the plantar region of the CCJ.

In the plantar CCJ VOI, DA was highest in *H. sapiens* and lowest in *G. beringei* (Fig. 4, Table 2), differing significantly across extant taxa ($H = 23.85, p < 0.001$; Table 3). *Homo sapiens* drove the difference, being significantly higher than all other extant taxa: *P. troglodytes* ($p < 0.001$), *G. gorilla* ($p < 0.001$), *G. beringei* ($p = 0.002$), and *P. ursinus* ($p = 0.001$; Table 3).

Primary trabecular orientation was in the A-P plane in all extant taxa, except for a few outliers that exhibited a relatively dorsally-oriented primary trabecular orientation (Fig. 5).

Discriminant function analysis produced four discriminant functions with Function 1 accounting for 75.9% of trabecular variance, and Functions 2 and 3 accounting for 15.3% and 7.8%, respectively (Table 4). Function 1 was most highly correlated with Tb.N and DA (Table 5). Function 2 was most highly correlated with Tb.Th and Tb.N (Table 5). Functions 3 and 4 were most highly correlated with E and DA (Table 5). Of the 60 individuals in this study, 55% of the cross-validated grouped cases were correctly classified (Table 6). While only 64% of *P. ursinus*, 61% of *P. troglodytes*, and 60% of *G. gorilla* were classified correctly, 80% of the *H. sapiens* sample was correctly classified (Table 6). Once again, individuals within the small sample of *G. beringei* were most often misclassified as *G. gorilla* (50%; Table 6).

Plantar VOI: StW 352 BV/TV exceeded all extant group means, but was closest to the *G. gorilla* mean (Fig. 4, Table 2). For StW 352, BV/TV fell at the upper end of the *P. troglodytes*, *G. gorilla*, and *G. beringei* ranges, and above the upper end of the *H. sapiens* and *P. ursinus* ranges (Fig. 4, Table 2). Trabecular thickness in StW 352 also exceeded all extant group means, but again was closest to the *G. gorilla* mean (Fig. 4, Table 2). For StW 352, Tb.Th fell within the upper end of the *H. sapiens*, *P. troglodytes*, *G. gorilla*, and *G. beringei* ranges, and above the upper end of the *P. ursinus* range (Fig. 4, Table 2). In StW 352, Tb.N was lower than all extant group means except *H. sapiens* and *G. beringei* (Fig. 4, Table 2), but was still within the range for all extant groups (Fig. 4, Table 2). Similar to the dorsal region of the CCJ, and again most like the pattern in *G. gorilla*, StW 352 had relatively fewer, thicker trabecular struts deep to the plantar region of the CCJ. In StW 352, DA was uniquely low compared to extant group means,

falling below the ranges of all extant groups. Additionally, elongation index in StW 352 fell below extant group means (Fig. 4, Table 2), suggesting that trabecular struts in the plantar region of the StW 352 CCJ were relatively more isotropic and disc-like than in extant groups. *Gorilla beringei* exhibited the most similar pattern to StW 352 amongst the extant groups in exhibiting the lowest mean DA and E (Table 2). Primary trabecular orientation of StW 352 was also relatively A-P, but fell outside the 95% confidence intervals of any extant group (Fig. 5). In the DFA for the plantar CCJ VOI, StW 352 had a predicted probability of being most similar to *G. beringei* (0.494) and *G. gorilla* (0.444; Table 6).

Combined VOIs In directly comparing dorsal and plantar CCJ VOIs, E ($p < 0.001$), BV/TV ($p < 0.001$), Tb.Th ($p = 0.008$), and Tb.N ($p < 0.001$) were all significantly higher in *H. sapiens* in the dorsal CCJ VOI (Table 7). In *P. troglodytes*, Tb.Th ($p = 0.049$) was significantly higher in the dorsal than the plantar CCJ VOI, while Tb.N ($p = 0.025$) was significantly lower (Table 7). In *G. gorilla*, only DA was significantly higher ($p = 0.041$) in the dorsal than the plantar CCJ VOI (Table 7). In *P. ursinus*, DA ($p = 0.037$) and E ($p = 0.041$) were significantly higher in the dorsal than the plantar CCJ VOI (Table 7). In contrast to these groups, there were no significant differences between BV/TV, Tb.Th, Tb.N, DA, or E in the dorsal and plantar CCJ VOIs of *G. beringei* (Table 7). In StW 352, BV/TV, Tb.Th, and Tb.N were lower in the dorsal VOI than the plantar VOI, while DA and E were higher in the dorsal VOI. The overall pattern of dorsal versus plantar VOI differences in StW 352 did not match a taxon-specific pattern amongst the extant groups.

When combining results from dorsal and plantar CCJ VOIs, the discriminant function analysis produced four discriminant functions with Function 1 accounting for 64.1% of

trabecular variance, and Functions 2 and 3 accounting for 25.7% and 8.8%, respectively (Table 4). Function 1 was most highly correlated with E and DA in the dorsal CCJ, and Tb.N and DA in the plantar CCJ. Function 2 was most highly correlated with Tb.N and Tb.Th in both the dorsal and plantar CCJ. Function 3 was most highly correlated with E and DA in both the dorsal and plantar CCJ (Table 5). Of the 60 individuals in this study, 56.7% of the cross-validated grouped cases were correctly classified, which was slightly higher than for either the dorsal or plantar CCJ VOI alone (Table 6). As in the separate dorsal and plantar VOI analyses, *H. sapiens* always had the best classification rates (93%). Compared to separate dorsal and plantar VOI analyses, *P. ursinus* (82%), *P. troglodytes* (72%), and *G. gorilla* (70%) were more often classified correctly in the combined CCJ analysis. *Gorilla beringei* was again often misclassified as *G. gorilla* (67%; Table 6). For the combined CCJ analysis, StW 352 had a predicted probability of being most similar to *P. ursinus* (0.552; Table 6).

Talocalcaneal joint

TCJ VOI: Extant sample *Homo sapiens* exhibited the lowest mean BV/TV, while *P. troglodytes* exhibited the highest (Fig. 4, Table 8). Group differences were significant ($H = 18.34$, $p < 0.001$), with *H. sapiens* being significantly lower than all other taxa: *P. troglodytes* ($p < 0.001$), *G. gorilla* ($p = 0.015$), and *G. beringei* ($p = 0.035$; Table 3). Despite these differences in BV/TV, trabecular Tb.Th ($H = 6.03$, $p = 0.108$) did not differ significantly amongst extant groups (Table 3). Tb.N differed significantly across extant groups ($H = 9.23$, $p = 0.026$), being significantly lower in *G. gorilla* than *P. troglodytes* ($p = 0.010$; Tables 3 and 8).

Homo sapiens exhibited the highest mean DA, while *G. beringei* exhibited the lowest mean DA (Fig. 4, Table 8). Degree of anisotropy differed significantly across extant groups ($H = 25.67, p < 0.001$; Table 3), which appears to be driven by *H. sapiens* differing significantly from *P. troglodytes* ($p < 0.001$), *G. gorilla* ($p = 0.005$), and *G. beringei* ($p = 0.002$; Table 3). *Gorilla gorilla* had significantly higher DA than *P. troglodytes* ($p = 0.016$) and *G. beringei* ($p = 0.039$). *H. sapiens* exhibited the highest mean elongation index, while *P. troglodytes* exhibited the lowest (Table 8). Elongation index differed significantly across taxa ($H = 18.64, p < 0.001$), with *H. sapiens* having significantly higher E than *P. troglodytes* ($p < 0.001$) and *G. beringei* ($p = 0.006$), and *G. gorilla* having significantly higher E than *P. troglodytes* ($p = 0.006$) and *G. beringei* ($p = 0.026$). Primary trabecular orientation in all groups was A-P with the exception of single *H. sapiens* and *P. troglodytes* outliers in the dorsoplantar plane (Fig. 5).

Discriminant function analysis produced three discriminant functions (Table 4). Function 1 accounted for 79.8% of trabecular variance, Function 2 accounted for 13.4%, and Function 3 accounted for 6.9% (Table 4). Function 1 was most highly correlated with DA and E, while Function 2 was mostly highly correlated with Tb.N and Tb.Th (Table 6). Of the 49 individuals used to assess TCJ trabecular fabric properties, 57.1% of the cross-validated grouped cases were correctly classified (Table 7). Eighty percent of *H. sapiens* were classified correctly, while only 61% of *P. troglodytes* and 50% of *G. gorilla* were classified correctly (Table 7). *Gorilla gorilla* were most often misclassified as *H. sapiens* (30%), while *G. beringei* were most often misclassified as *P. troglodytes* (50%).

TCJ VOI: StW 352 While BV/TV of StW 352 was closest to the *P. troglodytes*, *G. gorilla*, and *G. beringei* means, it was still just above the middle of the *H. sapiens* range (Fig. 4, Table 8). In

StW 352, Tb.Th was higher than each extant group mean and fell only within the upper end of the *P. troglodytes* and *G. gorilla* range (Fig. 4, Table 8). In StW 352, Tb.N was lower than each extant group mean, falling within the lower end of the *H. sapiens*, *P. troglodytes*, and *G. gorilla* ranges, but below the *G. beringei* range (Fig. 4, Table 8). Thus, StW 352 has a relatively high BV/TV in this VOI because of particularly thick trabecular struts, though they are few in number. This pattern is closest to the *G. gorilla* pattern, which pairs the highest mean Tb.Th with the lowest mean Tb.N amongst extant groups. In StW 352, DA was intermediate between *H. sapiens* and non-human group means, falling just below the middle of the *H. sapiens* range, at the upper ends of the *P. troglodytes* and *G. gorilla* ranges, and above the upper end of the *G. beringei* range (Fig. 4, Table 8). In StW 352, E was higher than each extant group mean, falling within the upper ends of *H. sapiens*, *P. troglodytes*, and *G. gorilla* ranges, but above the *G. beringei* range (Table 8). Thus, relative to the extant groups, StW 352 had relatively anisotropic and rod-like trabecular struts. Primary trabecular orientation of StW 352 was A-P, as in extant groups, and fell within the 95% confidence intervals of *P. troglodytes* and *G. gorilla*, but outside the 95% confidence intervals of *H. sapiens* and *G. beringei* (Fig. 5). In the discriminant function analysis for the TCJ VOI, StW 352 had a predicted probability of being most similar to *G. gorilla* (0.727; Table 7).

Discussion

We tested the hypothesis that habitual joint forces acting on the calcaneus during the push-off phase of the gait cycle are preserved in trabecular architecture deep to the TCJ and CCJ, and that the morphology will be consistent with the predicted loading of each joint in each

species. For the TCJ, we specifically hypothesized that, compared to *P. troglodytes*, *G. gorilla*, *G. beringei*, and *P. ursinus*, *H. sapiens* would have the most anisotropic and rod-like trabecular struts oriented in line with the predicted principal loads (i.e., in the A-P plane). More anisotropic struts in *H. sapiens* would appear to indicate less variable and more evenly distributed compressive loading during close-packing of the TCJ in preparation for a powerful push-off. In *P. troglodytes*, *G. gorilla*, and *P. ursinus*, which are thought to lack close-packing of the TCJ, we predicted more multidirectional loading of the subchondral surface. We find support for these hypotheses, with *H. sapiens* having the most anisotropic and rod-like trabecular struts at the TCJ, followed by *G. gorilla* (Table 9).

During push-off in *H. sapiens* and during the initial stages of the midtarsal break in *P. troglodytes*, *G. gorilla*, and *Papio*, the CCJ is thought to experience compressive forces through close-packing of this joint. In *H. sapiens*, both the dorsal and plantar aspects may experience equal loading with overall relatively low peak compressive forces (Nowak et al., 2010). However, in *P. troglodytes*, *G. gorilla*, *G. beringei*, and *P. ursinus*, only the dorsal aspect of the CCJ was predicted to show trabecular evidence of relatively high peak compressive loading (Nowak et al., 2010). Results for this joint provide only partial support for these predictions. Results for *P. troglodytes* provide support in having significantly higher Tb.Th and Tb.N in the dorsal compared to the plantar region of the CCJ. Contrary to predictions, however, *H. sapiens* also exhibited significantly higher Tb.Th, Tb.N, and BV/TV in the dorsal compared to the plantar region of the CCJ. If differentials in these properties between dorsal and plantar VOIs are in fact skeletal correlates of a midtarsal break, these unexpected results could indicate that the degree of midtarsal break variability exhibited in the *H. sapiens* CCJ is under-appreciated, as recent experimental work has suggested (Bates et al., 2013; DeSilva et al., 2015). It is worth

noting, however, that the relatively high DA and E in dorsal and plantar regions of the *H. sapiens* CCJ are consistent with predictions of less variable, lower magnitude forces in a close-packed CCJ joint. Taking this mixed support into account, it is clear that loading patterns inferred from CCJ trabecular properties observed here differ from the loading patterns inferred from CCJ subchondral bone apparent density patterns of *H. sapiens*, *P. troglodytes*, and *P. ursinus* documented by Nowak et al. (2010).

The cause (or causes) of discrepant signals in the CCJ is unclear. One possibility is that subchondral and trabecular properties may not necessarily represent the same or even complementary biomechanical signals. For example, correlations of trabecular bone architecture and subchondral bone radiodensity patterns have been shown to be weak at the tibiotalar joint (distal tibia and talar trochlea) in humans, great apes, and baboons (Su, 2011). Su (2011) suggested that each bone type responds to a specific form of loading: subchondral bone responds to loading of the complementary joint surface, while trabecular bone responds to forces traveling through the bone in question. Zeininger et al. (2011) also reported that subchondral bone in metacarpal heads may be more sensitive to external loading and show evidence of more recent modeling than deeper trabecular struts. Thus, a lack of correspondence at the CCJ between subchondral (Nowak et al., 2010) and trabecular bone properties (this study) is not necessarily contradictory, or even surprising. Future investigation of this issue at the CCJ should be extended to include future analyses of subchondral and trabecular bone at the complementary joint surface of the cuboid.

Despite the discrepant functional signals observed in trabecular properties deep to the CCJ, it is worth noting that pairs of trabecular properties tended to regularly group together in explaining discriminant functions. Often, Tb.Th and Tb.N were paired and explained trends in

BV/TV amongst sample groups. Also, E and DA were frequently paired in explaining organizational trends in trabecular strut shape and orientation. Thus, our results support the findings of other studies (e.g., Ryan and Shaw, 2012; Barak et al., 2013; Scherf et al., 2015) in documenting the importance of considering suites of trabecular properties in VOIs rather than isolated properties. These pairings may be adaptive strategies for addressing functional requirements and future studies using experimental approaches are needed to explore their interdependency.

In each VOI examined here, *H. sapiens* usually had significantly lower BV/TV than other extant groups (Table 3). These results are consistent with a recent study reporting systemically lower BV/TV in the human postcranial skeleton compared to non-human primates and pre-Holocene hominins (Chirchir et al., 2015). But a non-significant difference between *H. sapiens* and *G. beringei*, or between *H. sapiens* and *P. ursinus* in the dorsal CCJ VOI, is also consistent with the suggestion by Ryan and Shaw (2015) that human BV/TV may not always be systemically reduced in certain human populations (i.e., variability in modern human populations exists, possibility related to activity differences). Group differences in BV/TV are a function of two additional variables contributing to this metric: Tb.Th and Tb. N. *Gorilla gorilla* tends to achieve high BV/TV through having thicker, sparser struts. *P. troglodytes* and *P. ursinus* tend to achieve high BV/TV through having thinner, more numerous struts. These results, at least amongst extant taxa, may represent a body mass trend. Similar patterns of Tb.Th and Tb. N have been reported for primate humeral and femoral heads (Ryan and Shaw, 2013), and in non-primate mammals (Barak et al., 2013) in which larger individuals have an overall higher BV/TV comprised of few but thick struts, while smaller individuals have an overall lower BV/TV with more but thin struts. As noted above, *H. sapiens* has a consistently high DA throughout the

calcaneus. Low BV/TV coupled with a high DA (i.e., relatively few, highly-oriented trabecular struts) has also been observed in the human femur (Ryan and Shaw, 2015) and metatarsal heads (Griffin et al., 2010). In human metatarsal heads, it has been suggested to be a functional strategy for mitigating compressive forces (i.e., at the metatarsophalangeal joint; Griffin et al., 2010), and results presented here also support this hypothesized functional strategy.

The pattern of trabecular properties in the StW 352 calcaneus is not consistent with any one extant group studied here. At the TCJ, StW 352 is most similar to *G. gorilla* in strut structure (fewer, thicker struts), but it resembles *H. sapiens* and *G. gorilla* in strut shape (rod-like) and strut orientation (relatively anisotropic; Table 9). This might suggest relatively less mobility in the TCJ of StW 352 (and by extension *A. africanus*) than in *P. troglodytes*. This is supported by the multivariate discriminant function analysis in which StW 352 TCJ trabeculae group with *G. gorilla* and *H. sapiens*, suggesting relatively less variable loading, possible close-packing of the TCJ (human-like), and a rigid foot during the stance phase of walking. Results presented here are consistent with those for the histomorphometrics of the StW 358 and StW 389 distal tibia trabeculae, in that *A. africanus* gait was inferred to be closest to humans but not entirely human-like in these specimens (Barak et al., 2013). In a recent comparative study of the shape and orientation of the posterior talar articular facet, Prang (2016) reported that StW 352 was more similar to apes than humans and that this may be indicative of a more mobile TCJ in *A. africanus*. More details about the arthrokinematics of the TCJ in humans and non-human primates, particularly gorillas, using a method such as cineradiography are needed to make better predictions of habitual load-bearing, including possible regional differences in fossil hominins. Future studies examining shod versus unshod walking and walking on mountainous (i.e.,

uneven) versus flat terrain would provide further insight into the range of variability present in human pedal arthokinematics.

At the CCJ, StW 352 also falls between humans and African apes, aligning with *G. beringei*, *G. gorilla*, or with *H. sapiens* when trabecular properties of dorsal and plantar VOIs are considered separately (Table 9). At the CCJ, StW 352 is most similar to *G. gorilla* in strut structure (fewer, thicker struts), but resembles *P. troglodytes* or *G. gorilla* in strut orientation (relatively isotropic). In strut shape, StW 352 shows a similar pattern to that of *H. sapiens* and *P. ursinus*, in which struts are more rod-like in the dorsal VOI compared to the plantar VOI (Fig. 4). When considered together in a multivariate discriminant function analysis, trabeculae in the StW 352 dorsal CCJ VOI group with *P. ursinus* or *H. sapiens*, while trabeculae in the plantar CCJ VOI group with *G. beringei* or *G. gorilla*. Functionally, these results suggest overall postures and loading regimes that are not completely human-like or ape-like.

Recent analysis of the StW 352 calcaneal tuber external dimensions concluded that this fossil fell within the ape range, and particularly close to *P. troglodytes* (Prang, 2015). In the present study, StW 352 calcaneal trabeculae were observed to be not very *Pan*-like. Trabecular similarities between StW 352, *H. sapiens*, *G. gorilla*, *G. beringei*, and *P. ursinus* (to the exclusion of *P. troglodytes*) document a clear indication of the relative importance of selection for terrestriality in the taxon represented by StW 352. Accordingly, anatomical structure based on internal trabecular architecture differs from external calcaneal anatomy documented by Prang (2015; i.e., calcaneal tuber robusticity). In considering this apparent discrepancy, it must be noted that the external assessment for an incomplete calcaneal tuber (Prang, 2015) may provide a different signal than if the entire tuber was present. As emphasized above, cineradiographic analyses of the *Gorilla* CCJ during midfoot break are needed to understand if/how *Pan* and

Gorilla differ in this respect. With such data available, reinterpretation of the loading patterns of StW 352 would be greatly facilitated.

Conclusion

Given the lack of detailed data on *G. gorilla* or *G. beringei* CCJ kinematics, our trabecular results neither support nor refute the presence of calcaneocuboid joint flexion or a midtarsal break in StW 352. But at present, the CCJ of StW 352 morphologically appears to share *Homo*-like, *Gorilla*-like, and *Papio*-like features, all of which habitually use terrestrial substrates. Trabecular results for the TCJ suggest that StW 352 may have had a *Homo*-like, close-packed morphology in this joint. These findings suggest that the StW 352 calcaneus experienced more variable load orientations than *H. sapiens* calcanei, but usually less variable load orientations than *P. troglodytes* calcanei, the most arboreal taxon of our comparative sample. This conclusion suggests that *A. africanus* was capable of a large range of foot movements across its locomotor repertoire and this range differed from those exhibited by either humans or African apes.

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Figure legends

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.

Figure 2. Predicted joint reaction forces. In the human (left), the talocalcaneal joint (TCJ) and calcaneocuboid joint (CCJ; dorsal and plantar aspects) experience compressive force (black arrows) during the push-off phase of stance. In *P. troglodytes* (right), *G. gorilla*, and *P. ursinus*, the dorsal aspect of the CCJ presumably experiences compressive force (black arrow) during midfoot flexion.

Figure 3. Volume of interest (VOI) locations. Sagittal cross sections through microCT scans of (a) *P. ursinus*, (b) *P. troglodytes*, (c) StW 352, (d) *G. gorilla*, and (e) *H. sapiens* calcanei. White circles indicate VOI locations. For illustrative purposes, cubic representations of trabecular structure are provided for each VOI. Actual quantification of trabecular properties was performed on spherical VOIs.

Figure 4. Box plots of trabecular fabric properties for each volume of interest. Boxes envelop the inter-quartile range (50% of values) of the sample distribution, and whiskers encompass the range excluding outliers, which are represented with open circles and stars. The horizontal line

within each box illustrates the median of the distribution. *H.s.* = *Homo sapiens*, *P.t.* = *Pan troglodytes*, *G.g.* = *Gorilla gorilla*, *G.b.* = *Gorilla beringei*, and *P.u.* = *Papio ursinus*.

Figure 5. Stereoplots of primary trabecular orientation, where top = dorsal CCJ, middle = plantar CCJ, and bottom = TCJ. In order to interpret this information, individuals falling toward the top and bottom poles have a primary trabecular orientation in the dorsoplantar plane. Individuals located to the left and right have a mediolateral primary trabecular orientation. The anteroposterior (A-P) plane runs through the middle of the sphere such that individuals located toward the center of the plot have an A-P primary trabecular orientation. Ellipses indicate the 95% confidence intervals for groups.

Table 1. Sample sizes and diameters of volumes of interest.^a

TCJ					CCJ ^b		
Taxon	<i>n</i>	Mean (mm)	Range	sd	Mean (mm)	Range	sd
StW 352	1	10.96	-	-	4.54	-	-
<i>H. sapiens</i>	15	12.29	9.34–15.00	1.91	7.59	6.12–9.25	0.93
<i>P. troglodytes</i>	18	10.32	7.67–12.19	1.35	5.86	4.77–6.80	0.64
<i>G. gorilla</i>	10	13.03	9.80–16.15	2.28	7.52	5.88–9.45	1.25
<i>G. beringei</i>	6	12.57	9.62–14.68	2.14	7.38	5.87–8.27	1.01
<i>P. ursinus</i>	11	-	-	-	3.82	3.28–4.26	0.30

^a TCJ = talocalcaneal joint, CCJ = calaneocuboid joint

^b Equivalently-sized dorsal and plantar volumes of interest were used in a given specimen.

Table 2. Calcaneocuboid joint (CCJ) trabecular fabric properties.^a

	Taxon	DA	E	BV/TV	Tb.Th	Tb.N
Dorsal CCJ	StW 352	0.78	0.71	0.26	0.21	1.07
	<i>H. sapiens</i>	0.92	0.87	0.29	0.19	1.34
		(0.02)	(0.04)	(0.04)	(0.03)	(0.16)
		0.88–0.94	0.78–0.92	0.23–0.36	0.14–0.23	1.12–1.77
	<i>P. troglodytes</i>	0.73	0.48	0.35	0.19	1.48
		(0.09)	(0.20)	(0.05)	(0.04)	(0.28)
		0.57–0.84	0.15–0.77	0.29–0.45	0.15–0.26	0.97–1.92
	<i>G. gorilla</i>	0.81	0.50	0.37	0.24	1.25
		(0.07)	(0.17)	(0.08)	(0.06)	(0.23)
		0.69–0.92	0.26–0.78	0.25–0.53	0.19–0.39	0.95–1.58
	<i>G. beringei</i>	0.78	0.45	0.34	0.22	1.25
		(0.09)	(0.19)	(0.08)	(0.03)	(0.11)
		0.64–0.87	0.25–0.74	0.22–0.47	0.18–0.28	1.12–1.45
	<i>P. ursinus</i>	0.82	0.68	0.33	0.18	1.46
		(0.05)	(0.11)	(0.07)	(0.02)	(0.21)
		0.74–0.89	0.47–0.82	0.21–0.43	0.16–0.20	1.08–1.71
Plantar CCJ	StW 352	0.39	0.13	0.41	0.25	1.33

<i>H. sapiens</i>	0.88	0.54	0.18	0.16	0.95
	(0.06)	(0.19)	(0.06)	(0.03)	(0.25)
	0.75–0.96	0.10–0.82	0.11–0.32	0.13–0.25	0.66–1.52
<i>P. troglodytes</i>	0.77	0.44	0.34	0.18	1.56
	(0.08)	(0.15)	(0.05)	(0.04)	(0.30)
	0.62–0.89	0.13–0.66	0.25–0.43	0.13–0.27	1.14–1.96
<i>G. gorilla</i>	0.74	0.48	0.36	0.22	1.34
	(0.07)	(0.17)	(0.07)	(0.03)	(0.20)
	0.60–0.86	0.25–0.73	0.25–0.45	0.18–0.28	0.91–1.60
<i>G. beringei</i>	0.72	0.41	0.31	0.21	1.28
	(0.07)	(0.14)	(0.08)	(0.05)	(0.15)
	0.63–0.81	0.22–0.54	0.22–0.41	0.15–0.30	1.08–1.47
<i>P. ursinus</i>	0.75	0.55	0.30	0.16	1.47
	(0.10)	(0.15)	(0.03)	(0.02)	(0.08)
	0.56–0.90	0.30–0.81	0.26–0.34	0.13–0.19	1.30–1.60

^a DA = degree of anisotropy, E = elongation index, BV/TV = bone volume fraction, Tb.Th = trabecular thickness, Tb.N = trabecular number. Cells report means, one standard deviation in parentheses below, and ranges at the bottom.

Table 3: Kruskal-Wallis and pairwise Mann-Whitney U results for individual variables in calcaneocuboid (CCJ) and talocalcaneal (TCJ) volumes of interest.^a

		DA	E	BV/TV	Tb.Th	Tb.N
Dorsal						
CCJ	Kruskal-Wallis	H = 37.24, <i>p</i> < 0.001	H = 38.34, <i>p</i> < 0.001	H = 10.13, <i>p</i> = 0.038	H = 15.55, <i>p</i> = 0.003	H = 9.55, <i>p</i> = 0.049
	<i>H. sapiens</i> vs. <i>P. troglodytes</i>	< 0.001	< 0.001	0.001	0.899	0.164
	<i>H. sapiens</i> vs. <i>G. gorilla</i>	< 0.001	< 0.001	0.025	0.005	0.437
	<i>H. sapiens</i> vs. <i>G. beringei</i>	< 0.001	< 0.001	0.172	0.054	0.213
	<i>H. sapiens</i> vs. <i>P. ursinus</i>	< 0.001	< 0.001	0.194	0.235	0.108
	<i>P. troglodytes</i> vs. <i>G. gorilla</i>	0.022	0.829	0.665	0.033	0.039
	<i>P. troglodytes</i> vs. <i>G. beringei</i>	0.229	0.789	0.763	0.169	0.039
	<i>P. troglodytes</i> vs. <i>P. ursinus</i>	0.005	0.010	0.194	0.305	0.621
	<i>G. gorilla</i> vs. <i>P. ursinus</i>	0.671	0.018	0.340	< 0.001	0.038
	<i>G. beringei</i> vs. <i>P. ursinus</i>	0.512	0.014	0.999	0.007	0.068
	<i>G. gorilla</i> vs. <i>G. beringei</i>	0.413	0.550	0.414	0.622	0.957
Plantar						
CCJ	Kruskal-Wallis	H = 23.85, <i>p</i> < 0.001	H = 6.023, <i>p</i> = 0.197	H = 32.69, <i>p</i> < 0.001	H = 19.27, <i>p</i> < 0.001	H = 28.35, <i>p</i> < 0.001
	<i>H. sapiens</i> vs. <i>P. troglodytes</i>	< 0.001	-	< 0.001	0.077	< 0.001
	<i>H. sapiens</i> vs. <i>G. gorilla</i>	< 0.001	-	< 0.001	0.001	0.002

	<i>H. sapiens</i> vs. <i>G. beringei</i>	0.002	-	0.004	0.037	0.011
	<i>H. sapiens</i> vs. <i>P. ursinus</i>	0.001	-	< 0.001	0.526	< 0.001
	<i>P. troglodytes</i> vs. <i>G. gorilla</i>	0.157	-	0.682	0.009	0.103
	<i>P. troglodytes</i> vs. <i>G. beringei</i>	0.230	-	0.439	0.330	0.062
	<i>P. troglodytes</i> vs. <i>P. ursinus</i>	0.528	-	0.016	0.247	0.514
	<i>G. gorilla</i> vs. <i>P. ursinus</i>	0.340	-	0.047	< 0.001	0.181
	<i>G. beringei</i> vs. <i>P. ursinus</i>	0.615	-	0.449	0.076	0.012
	<i>G. gorilla</i> vs. <i>G. beringei</i>	0.664	-	0.383	0.586	0.385
TCJ	Kruskal-Wallis	H = 25.67, <i>p</i> < 0.001	H = 18.64, <i>p</i> < 0.001	H = 18.34, <i>p</i> < 0.001	H = 6.03, <i>p</i> = 0.108	H = 9.23, <i>p</i> = 0.026
	<i>H. sapiens</i> vs. <i>P. troglodytes</i>	< 0.001	< 0.001	< 0.001	-	0.058
	<i>H. sapiens</i> vs. <i>G. gorilla</i>	0.005	0.999	0.015	-	0.222
	<i>H. sapiens</i> vs. <i>G. beringei</i>	0.002	0.006	0.035	-	0.846
	<i>P. troglodytes</i> vs. <i>G. gorilla</i>	0.016	0.006	0.049	-	0.010
	<i>P. troglodytes</i> vs. <i>G. beringei</i>	0.841	0.665	0.192	-	0.172
	<i>G. gorilla</i> vs. <i>G. beringei</i>	0.039	0.026	0.703	-	0.064

^a DA = degree of anisotropy, E = elongation index, BV/TV = bone volume fraction, Tb.Th = trabecular thickness, Tb.N = trabecular number. Values in bold indicate statistically significant results.

Table 4. Outcome of discriminant function analyses.

VOI^a	Function	Eigenvalue	% of Variance	Cumulative %	Canonical correlation
Dorsal CCJ	1	1.558	57.8	57.8	0.780
	2	1.107	41.1	98.9	0.725
	3	0.025	0.9	99.9	0.158
	4	0.003	0.1	100.0	0.056
Plantar CCJ	1	1.949	75.9	75.9	0.813
	2	0.394	15.3	91.3	0.531
	3	0.200	7.8	99.1	0.408
	4	0.024	0.9	100.0	0.154
Combined CCJ	1	3.010	64.1	64.1	0.866
	2	1.204	25.7	89.8	0.739
	3	0.411	8.8	98.6	0.540
	4	0.068	1.4	100.0	0.252
TCJ	1	1.315	79.8	79.8	0.754
	2	0.220	13.4	93.1	0.425
	3	0.113	6.9	100.0	0.319

^a CCJ = calcaneocuboid joint, TCJ = talocalcaneal joint.

Table 5. Structure coefficients of discriminant function analyses.^{a,b}

Dorsal CCJ	Variable	Function 1	Function 2	Function 3	Function 4
	E	0.892	-0.251	0.353	-0.127
	DA	0.845	0.174	0.060	0.503
	Tb.N	-0.114	-0.408	0.447	0.788
	Tb.Th	-0.164	0.530	0.548	-0.626
Plantar CCJ	Variable	Function 1	Function 2	Function 3	Function 4
	Tb.N	0.709	-0.609	0.263	0.238
	Tb.Th	0.313	0.880	-0.137	0.331
	E	-0.156	-0.195	-0.359	0.899
	DA	-0.519	-0.119	0.576	0.620
Combined CCJ	Variable	Function 1	Function 2	Function 3	Function 4
	Dorsal E	-0.636	-0.115	-0.406	0.409
	Dorsal DA	-0.571	0.286	-0.381	0.326
	Plantar Tb.N	0.559	-0.383	-0.196	0.355
	Dorsal Tb.Th	0.140	0.471	0.270	0.280
	Plantar Tb.Th	0.266	0.468	0.240	0.142
	Dorsal Tb.N	0.058	-0.404	-0.048	0.238
	Plantar E	-0.135	-0.020	-0.308	0.442
	Plantar DA	-0.415	-0.135	0.361	0.429
TCJ	Variable	Function 1	Function 2	Function 3	
	DA	-0.827	0.502	0.225	
	E	-0.619	-0.152	0.419	

Tb.N	0.410	0.754	0.136
Tb.Th	0.201	-0.573	0.525

^a Pooled within-group correlations between discriminating variables and standardized canonical discriminant functions.

^b CCJ = calcaneocuboid joint, TCJ = talocalcaneal joint.

Table 6. Classification results of discriminant function analyses.^{a,b}

VOI ^b	Original grouped cases correctly classified (Cross-validated grouped cases correctly classified)	Original group classification	Predicted group membership (actual/total)				
Dorsal CCJ	63.3% (55.0%)		<i>H. sapiens</i>	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>G. beringei</i>	<i>P. ursinus</i>
		Stw352 ^a	0.307				0.469
		<i>H. sapiens</i>	14/15	0/15	0/15	0/15	1/15
		<i>P. troglodytes</i>	0/18	12/18	1/18	1/18	4/18
		<i>G. gorilla</i>	1/10	2/10	7/10	0/10	0/10
		<i>G. beringei</i>	1/6	1/6	3/6	1/6	0/6
		<i>P. ursinus</i>	3/11	4/11	0/11	0/11	4/11
Plantar CCJ	60.0% (55.0%)		<i>H. sapiens</i>	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>G. beringei</i>	<i>P. ursinus</i>
		Stw352 ^a			0.444	0.494	
		<i>H. sapiens</i>	12/15	0/15	1/15	0/15	2/15
		<i>P. troglodytes</i>	1/18	11/18	2/18	1/18	3/18
		<i>G. gorilla</i>	0/10	2/10	6/10	0/10	2/10
		<i>G. beringei</i>	0/6	2/6	3/6	0/6	1/6
		<i>P. ursinus</i>	1/11	3/11	0/11	0/11	7/11
Combined CCJ	73.3% (56.7%)		<i>H. sapiens</i>	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>G. beringei</i>	<i>P. ursinus</i>

		Stw352 ^a			0.352	0.552	
		<i>H. sapiens</i>	14/15	0/15	0/15	0/15	1/15
		<i>P. troglodytes</i>	2/18	13/18	2/18	0/18	1/18
		<i>G. gorilla</i>	0/10	2/10	7/10	0/10	1/10
		<i>G. beringei</i>	0/6	1/6	4/6	1/6	0/6
		<i>P. ursinus</i>	0/11	2/11	0/11	0/11	9/11
TCJ	61.2% (57.1%)	<i>H. sapiens</i>	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>G. beringei</i>		
		Stw352 ^a	0.152		0.727		
		<i>H. sapiens</i>	12/15	2/15	0/15	1/15	
		<i>P. troglodytes</i>	2/18	11/18	3/18	2/18	
		<i>G. gorilla</i>	3/10	1/10	5/10	1/10	
		<i>G. beringei</i>	1/6	3/6	0/6	2/6	

^a First (in bold) and second highest classification probability values for Stw 352. Others not reported.

^b CCJ = calcaneocuboid joint, TCJ = talocalcaneal joint.

Table 7. Wilcoxon results for dorsal vs. plantar calcaneocuboid joint (CCJ) volumes of interest.^a

	Dorsal vs. plantar CCJ				
	DA	E	BV/TV	Tb.Th	Tb.N
<i>H. sapiens</i>	0.051	< 0.001	< 0.001	0.008	< 0.001
<i>P. troglodytes</i>	0.257	0.723	0.909	0.049	0.025
<i>G. gorilla</i>	0.041	0.953	0.645	0.201	0.074
<i>G. beringei</i>	0.075	0.600	0.685	0.346	0.346
<i>P. ursinus</i>	0.037	0.041	0.155	0.196	0.999

^a DA = degree of anisotropy, E = elongation index, BV/TV = bone volume fraction, Tb.Th = trabecular thickness, Tb.N = trabecular number. Values in bold indicate statistically significant results.

Table 8. Talocalcaneal joint (TCJ) volume of interest trabecular fabric properties.^{a,b}

	Taxon	DA	E	BV/TV	Tb.Th	Tb.N
TCJ	StW 352	0.85	0.68	0.43	0.36	1.14
	<i>H. sapiens</i>	0.91	0.66	0.35	0.25	1.28
		(0.06)	(0.11)	(0.06)	(0.04)	(0.14)
		0.72–0.97	0.41–0.81	0.27–0.50	0.18–0.33	1.02–1.57
	<i>P. troglodytes</i>	0.74	0.49	0.45	0.28	1.46
		(0.09)	(0.13)	(0.05)	(0.05)	(0.25)
		0.52–0.89	0.20–0.68	0.35–0.51	0.21–0.39	1.10–1.89
	<i>G. gorilla</i>	0.83	0.65	0.41	0.29	1.19
		(0.07)	(0.14)	(0.05)	(0.04)	(0.17)
		0.70–0.90	0.41–0.86	0.37–0.50	0.24–0.37	1.04–1.39
	<i>G. beringei</i>	0.72	0.49	0.41	0.27	1.30
		(0.10)	(0.09)	(0.06)	(0.03)	(0.08)
		0.58–0.83	0.33–0.55	0.33–0.50	0.24–0.31	1.23–1.45

^a DA = degree of anisotropy, E = elongation index, BV/TV = bone volume fraction, Tb.Th = trabecular thickness, Tb.N = trabecular number. Cells report means, one standard deviation in parentheses below, and ranges at the bottom.

Table 9. Results summary for trabecular fabric comparisons.^{a,b,c}

	DA	E	BV/TV	Tb.Th	Tb.N
Dorsal CCJ	H > B > Gg > Gb > <u>StW352</u> > P	H > <u>StW352</u> > B > Gg > P > Gb	Gg > P > Gb > B > H > <u>StW352</u>	Gg > Gb > <u>StW352</u> > P > H > B	P > B > H > Gg > Gb > <u>StW352</u>
Plantar CCJ	H > P > B > Gg > Gb > <u>StW352</u>	B > H > Gg > P > Gb > <u>StW352</u>	<u>StW352</u> > Gg > P > Gb > B > H	<u>StW352</u> > Gg > Gb > P > B ≈ H	P > B > Gg > <u>StW352</u> > Gb > H
TCJ	H > <u>StW352</u> > Gg > P > Gb	<u>StW352</u> > H > Gg > Gb ≈ P	P > <u>StW352</u> > Gb > Gg > H	<u>StW352</u> > Gg > P > Gb > H	P > Gb > H > Gg > <u>StW352</u>

^a DA = degree of anisotropy, E = elongation index, BV/TV = bone volume fraction, Tb.Th = trabecular thickness, Tb.N = trabecular number.

^b CCJ = calcaneocuboid joint, TCJ = talocalcaneal joint.

^c H = *H. sapiens*, P = *P. troglodytes*, Gg = *G. gorilla*, Gb = *G. beringei*, B = *P. ursinus*.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5