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

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Text: 26 pages (plus references)

Tables: 7

Figures: 10 (plus 2 pages captions)

Abstract

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 μ m 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

1 apes. These results suggest that *Paranthropus* may have had a human-like medial weight shift
2 during the last half of stance phase but *Australopithecus* did not.

3

4 **Keywords:** *Australopithecus*, *Paranthropus*, Sterkfontein, foot, locomotor, functional
5 morphology

1 **Introduction**

2 The talus, as a cornerstone bone in the foot, is an integral structure for reconstructing
3 locomotor kinematics of hominins, and fortunately it is often preserved in the fossil record
4 because of its compact, stout nature. Studies of the external structure of early hominin tali
5 typically indicate a mixture of human-like and ape-like features (Wood, 1973; 1974; Kidd et al.,
6 1996; Harcourt-Smith and Aiello, 2004; Kidd and Oxnard, 2005; Gebo and Schwartz, 2006;
7 Jungers et al., 2009; Zipfel et al., 2011; Prang, 2016). Resemblances to a human configuration of
8 the tibiotalar joint (e.g., a relatively more vertical tibia, neutral ankle, and less range of motion)
9 are usually interpreted as indicating more stereotyped ankle loading associated with terrestrial
10 bipedal gait (Latimer et al., 1987; DeSilva, 2009). Resemblances to an ape configuration of the
11 tibiotalar joint (e.g., a relatively more dorsiflexed posture and greater overall range of motion),
12 on the other hand, are usually interpreted as indicating more variable ankle loading associated
13 with arboreal locomotor behaviors, such as vertical climbing (Stern and Susman, 1983; DeSilva,
14 2009).

15 Studies of talar internal structure (DeSilva and Devlin, 2012; Su et al., 2013) are
16 comparatively rarer than studies of talar external structure, despite the critical insights such
17 approaches offer for inferring ankle loading patterns from a bone that is frequently represented in
18 the fossil record. Wolff's Law posits that trabecular struts tend to optimize according to loading
19 beneath joints by aligning along lines of principal stress through a long bone (Wolff, 1986; Ruff
20 et al., 2006). The capacity of trabecular bone to adjust and realign itself throughout life,
21 according to its customary mechanical environment, is supported by comparative (Fajardo and
22 Müller, 2001; MacLatchy and Müller, 2002; Ryan and Ketcham, 2002; Ryan and Shaw, 2012)
23 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 and colleagues (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 and colleagues (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 and colleagues (2013) noted unique trabecular alignment beneath the talar trochlea of humans, particularly its

1 anteromedial region, corroborating a greater medial weight shift through the talar neck and head
2 compared to other extant hominoids. Su and colleagues (2013) also observed dissimilarities
3 between talar trabecular structure in humans and a hominin talus (KNM-ER 1464) attributed to
4 *Paranthropus boisei* (Grausz et al., 1988; Feibel and Brown, 1989). In contrast to these studies,
5 while DeSilva and Devlin (2012) observed some intraspecific and interspecific differences, the
6 lack of predicted differences in regional comparisons of trabecular structure in human, extant ape
7 and several hominin tali from South Africa (i.e., SKX 42695, StW 88, StW 102, StW 363, StW
8 347, StW 486, and TM 1517) led them to suggest that the talus may not be an ideal bone for
9 studying axial loading. DeSilva and Devlin (2012) concluded that architecture and anisotropy in
10 trabecular bone of the talar body does not vary amongst extant hominoids in ways that one would
11 predict from models of loading, despite a substantial number of studies documenting differences
12 in foot use between humans and other apes (Lundberg et al., 1989a,b; Rome, 1996; D'Août et al.,
13 2002; Sockol et al., 2007; DeSilva, 2009; Raichlen et al. 2009;). Ultimately, DeSilva and
14 Devlin (2012) endorsed caution when using trabecular properties for interpreting loading
15 patterns in the hominin ankle due to the presence of deeply conserved regional architecture in
16 extant hominoids. The lack of predicted differences in trabecular structure of tali reported by
17 DeSilva and Devlin (2012) may have been partially due to the use of insufficient spatial
18 resolutions, relatively small samples, and/or their use of relatively large volumes of interest (e.g.,
19 quadrants of the entire talar body), unlike other studies that have emphasized high resolution
20 image data, larger samples, and/or more strategic volumes of interest (VOIs) that may have
21 greater functional resolution (Lazenby et al., 2011; Barak et al. 2013b; Su et al. 2013). Whether
22 correspondence in hominin (e.g., *A. africanus*) distal tibiae and tali reflects a functional/
23 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 and Raichlen, 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 (Figure 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 (Figure 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.

1 The second goal of this study is to provide the first systematic internal characterization of
2 hominin talar trabecular structure using high resolution computed tomography (CT). These data
3 will allow assessment of structural differences between trabecular architecture in tali assigned to
4 *Australopithecus (africanus)* and *Paranthropus* in order to compare ankle loading patterns in
5 these hominins, and possibly to infer additional information about their comparative gait
6 kinematics. Broad generic differences between the locomotor kinematics of *Australopithecus*
7 and *Paranthropus* are not well-established because of the paucity of solidly attributable
8 postcranial fossils to *Paranthropus* (Constantino and Wood, 2007; Wood and Constantino, 2007;
9 Domínguez-Rodrigo et al., 2013; Carlson and Edlund, 2016). Su and colleagues (2013)
10 compared an East African fossil talus, KNM-ER 1464, attributed to *P. boisei*, to extant
11 hominoids finding a mosaic of similarities in trabecular orientation and structure. Based on
12 external morphology, for example, a grooved trochlea and curvature of the medial trochlear rim,
13 similarities have been proposed between the *Paranthropus robustus* talus (TM-1517) and tali
14 (e.g., KNM-ER 1464) from East African robust australopithecines (*P. boisei*) (Gebo and
15 Schwartz, 2006). Gebo and Schwartz (2006) suggest that talar features of *Paranthropus*,
16 amongst other traits, would have contributed to a less efficient bipedal gait compared to that of
17 modern humans. However, they also note that TM 1517 has a much larger talar head than
18 KNM-ER 1464, making taxonomic allocations “problematic” in this case.

19 Current reconstructions of *A. africanus* locomotor behavior suggest an important arboreal
20 component (Berger and Tobias, 1996; McHenry and Berger, 1998; but see Zipfel and Berger,
21 2009), while the extent of arboreality attributed to *Paranthropus* is generally considered to be
22 lower (Susman and Brain, 1988, but see Domínguez-Rodrigo et al., 2013). This would suggest
23 greater ankle mobility in the former, perhaps indicating more similarity in talar structure between

A. africanus and chimpanzee than between *Paranthropus* and chimpanzee. In this study, we test two specific predictions about trabecular structure in hominin tali. First, we predict that hominin (i.e., *A. africanus* and *Paranthropus*) tali differ from extant hominoid tali in trabecular structure and orientation because the hominins are bipeds. Also, based on the findings of DeSilva and Devlin (2012), trabecular properties of *A. africanus* should not be distinct from those of modern humans; however, based on the more recent study by Su and colleagues (2013), who used smaller and more functionally strategic volumes of interest (VOIs), we would expect to observe differences from modern humans. Second, we predict that *Australopithecus (africanus)* and *Paranthropus* tali differ from those of extant hominoid groups in different ways, indicating differences in ankle kinematics that can distinguish the two hominin genera. Similar structural divergence in these hominin taxa from extant hominoid patterns could indicate overall similarity in their ankle joint kinematics, while substantial differences in structural divergence between the hominin genera relative to extant hominoids could indicate dissimilar bipedal gait kinematics. In the case of the latter, we would expect that *Paranthropus* may more resemble the human configuration than would *Australopithecus (africanus)*, given the aforementioned studies documenting the importance of arboreality in the activity profile of *A. africanus* (Susman and Brain, 1988; Berger and Tobias, 1996; McHenry and Berger, 1998).

Materials and methods

Sample

The comparative sample used in this study consisted of tali from adult humans (*Homo sapiens*; $n = 18$), chimpanzees (*Pan troglodytes*; $n = 20$), gorillas (*Gorilla gorilla*; $n = 15$),

1 orangutans (*Pongo pygmaeus*; $n=13$), and baboons (*Papio cynocephalus*; $n=18$) from collections
2 at the Cleveland Museum of Natural History, the American Museum of Natural History, the
3 Smithsonian National Museum of Natural History, and the University of Texas - Austin. Human
4 tali are from 20th century Americans (Hamann-Todd Collection, Cleveland Museum of Natural
5 History). The non-human tali are primarily from wild-shot specimens, except the baboons,
6 which were wild-caught but subsequently kept captive (Coelho and Bramblett, 1981). Adult
7 females of each hominoid species were exclusively selected for the study in an effort to
8 minimize the potential effects of body size on both locomotor behavior and bone morphology.
9 Baboons were included in the study as a non-hominoid outgroup, and also as a representative of
10 large-bodied terrestrial digitigrade quadrupeds. Again, to minimize potential effects of body size
11 across the sample, male rather than female baboons were selected. Any potential sex-based
12 effects on talar trabecular bone structure (e.g., hormone differences or joint loading differences)
13 are likely minimal in comparison to interspecific variation based on results of a recent study of
14 calcaneal trabecular bone structure using pooled-sex baboons (Zeininger et al., 2016). All
15 comparative specimens lacked signs of any skeletal pathology or traumatic injury to the limbs.
16 Extant primate tali were scanned using an eXplore Locus SP scanner (General Electric
17 Healthcare, London, ON, Canada) at a resolution of 45 μm (see Su et al., 2013 for additional
18 details).

19 Hominin fossil tali attributed to *Australopithecus* include: StW 102, StW 363 and StW
20 486 from Sterkfontein (University of the Witwatersrand); those attributed to *Paranthropus*
21 include: TM 1517 (Ditsong Museum of Natural History) and KNM-ER 1464 (Kenya National
22 Museum) (Figure 2). Specimens StW 102 and StW 486 have been initially described as
23 originating from Sterkfontein Member 5, while StW 363 has been initially described as

1 originating from Member 4/5 (Deloison, 2003). Deloison (2003), in describing early hominin
2 foot bones from South Africa, interpreted the anatomical features of all three tali as being
3 consistent with those of *Australopithecus*. There is, however, no other evidence of
4 *Australopithecus* in Member 5 at Sterkfontein (Kuman and Clarke, 2000; Clarke, 2013).
5 Complexity of the stratigraphy of the Sterkfontein cave system and its associated infills is
6 becoming increasingly apparent (Kuman and Clarke, 2000; Clarke, 2006; Stratford, 2012, 2013).
7 While the boundary between Members 4 and 5 had been difficult to pinpoint, which made it
8 difficult to assign these tali to specific Members and/or taxa in their original descriptions (i.e.,
9 Deloison, 2003), revision of the stratigraphy at Sterkfontein indicates that Member 4
10 australopithecine breccias (2.8-2.6 Ma) extend into what was previously thought to be Member 5
11 (Kuman and Clarke, 2000). Thus, the three Sterkfontein tali analyzed in the present study (StW
12 102, StW 363, and StW 486) are now considered to be unambiguously from Member 4, and thus
13 they are reasonably attributable to *Australopithecus*.

14 At present, *A. africanus* is one of two hominins recognized in Member 4 deposits
15 (Kuman and Clarke, 2000; Pickering and Kramers, 2010), with *Australopithecus prometheus*
16 now being recognized in both Members 2 and 4 (Clarke, 2013). While for the purposes of the
17 present study we follow the attribution of StW 102, StW 363, and StW 486 to *A. africanus* (e.g.,
18 see DeSilva and Devlin, 2012), we acknowledge that eventual comparative studies with tali of
19 the StW 573 skeleton, and/or other material attributed to *A. prometheus*, may require revision of
20 these taxonomic assessments. The talus, TM 1517, from Kromdraai is regarded by most as
21 belonging to *P. robustus* (Susman et al., 2001), while the talus, KNM-ER 1464, from Koobi Fora
22 is presumed to be *P. boisei* (Grausz et al., 1988; Gebo and Schwartz, 2006; Wood and
23 Constantino, 2007). While taxonomic diversity exists during the time sampled by these two

fossils, and recognizing that attributions of postcranial specimens to *Paranthropus* are tenuous because few are associated with diagnostic craniodental material (e.g., OH 8), we follow these authors in using the aforementioned taxonomic attributions for the tali.

Trabecular bone analysis

High resolution image data from South African fossil tali (25 μ m voxels) were acquired in the Microfocus X-ray CT Facility of the Palaeosciences Centre at the University of the Witwatersrand (www.wits.ac.za/microct). Relevant acquisition parameters included: 65 – 95kV, 110 – 220 μ A, and either 0.5 or 1.0 frames per second. For each of these acquisitions, 5200 projections were obtained, where each projection was the average of two frames, and 1.8 mm of aluminum was used to ‘pre-filter’ low energy X-rays (i.e., the metal filter was positioned between the source and the fossil in order to selectively remove X-rays at the low end of the energy spectrum).

After obtaining volume data for a specimen, but before extracting trabecular volumes of interest (VOIs), a rendering corresponding to a volume, whether a fossil or an extant specimen, was digitally-oriented in a standardized horizontal plane using VGStudio Max 2.2 (Volume Graphics GmbH, Heidelberg, Germany) and the supratolar plane of the ankle joint (Latimer et al., 1987). The standardized position is such that in lateral or medial view the base of the neck and the most posterior point of the trochlear surface fall in the same horizontal plane. In addition, in both coronal and transverse planes, the superiormost points on the medial and lateral trochlear rims fall within a parallel, second horizontal plane. Once a rendering was situated in this standard position, its corresponding volume data were resliced and saved as 16-bit TIF files.

Each 16-bit TIF stack was imported into Amira software (Visage Imaging, San Diego, CA, USA) where each complete specimen was segmented into nine roughly cubic subregions (Figure 1). For a couple of fossils (e.g., StW 486 and TM 1517), only eight subregions were used because there were missing regions in their trochlea. To extract the subregions, the trochlear surface was divided into a 3x3 grid using its maximum linear mediolateral (ML) dimension and the arc between its posteriormost and anteriormost points, and subsequently dividing each of these into equal thirds. Trabecular bone in each region immediately deep to the trochlear cortical shell was isolated and saved as a separate volume. A Gaussian filter ($\sigma=1$) was applied to reduce noise in image data.

Material within a VOI was binarized into bone and non-bone. Image data of extant specimens were binarized using an adaptive, iterative threshold technique (Ryan and Ketcham, 2002). Segmentation of the fossils required separation and removal of matrix infill, which occasionally presented a challenge due to the brightness of the matrix often being at or above the level of bone gray scale values (i.e., poor material contrast) such that a single threshold value would not easily segment bone from matrix. Thus, a hysteresis algorithm (Canny, 1986) was implemented, which assigns intermediate-value voxels to bone based on their connectivity to voxels that are indisputably bone. After binarizing segmented volumes, they were imported into Quant3D software (Ryan and Ketcham, 2002) for quantitative analysis of trabecular structure. A VOI was defined in the binarized volume as the largest centered sphere to fit completely within each extracted (cube) region of trabecular bone.

Trabecular structure of each VOI was quantified in Quant3D using the star volume distribution (SVD) algorithm following methods described in Su et al. (2013). Relative bone volume (BV/TV), also known as “bone volume fraction,” is the dimensionless ratio of the

1 number of bone voxels present in the VOI to the total number of voxels in the VOI (Goulet et al.
 2 1994). Trabecular strut thickness (Tb.Th) is the average minimum measured length (mm)
 3 through a random point within the bone (Ketcham and Ryan, 2004). Trabecular number (Tb.N)
 4 is the estimated number of trabecular struts in the VOI, based on the number of intersections
 5 between a superimposed grid of lines and bone voxels (Hildebrand and Ruegsegger, 1997). The
 6 distribution of bone was defined using a fabric tensor, three eigenvectors and three
 7 corresponding eigenvalues. The eigenvectors represent the orientation in three-dimensional space
 8 of the primary, secondary, and tertiary material axes. The corresponding eigenvalues (τ_1 , τ_2 , τ_3)
 9 represent the relative magnitudes of each of the three material axes, defined such that $\tau_1 + \tau_2 + \tau_3$
 10 $= 1$ and $\tau_1 > \tau_2 > \tau_3$. The degree of anisotropy (DA) was calculated as $1 - (\tau_3/\tau_1)$, such that the
 11 values are bounded between 0 (perfect isotropy; i.e., a solid sphere of bone) and 1 (perfect
 12 anisotropy; i.e., bony struts aligned in a single plane) (Harrigan and Mann, 1984; Doube et al.,
 13 2010). Although we acknowledge that another conventional way to report DA is (τ_1/τ_3) , with a
 14 lower boundary value of 1 and no upper boundary (Fajardo and Müller, 2001; Ryan and
 15 Ketcham, 2002), we chose the convention bounded between 0-1 for ease of statistical analysis.
 16 Trabecular elongation index (E) distinguishes between rod-shaped and plate-shaped trabeculae
 17 by indicating the extent of preferred orientation of trabeculae in the major plane. If DA is close
 18 to 1, concurrent E values closer to 0 denote more plate-shaped trabecular struts, while E values
 19 closer to 1 denote more rod-shaped struts. If DA is close to 0, E values are less meaningful.
 20 Triangular diagrams were used to visualize these relationships (Benn, 1994; Graham and
 21 Midgley, 2000). Values of DA close to 0 can describe either a volume with numerous thin
 22 trabeculae that are randomly-oriented, or a volume that is completely filled with bone, both
 23 morphologies being the end result of a lack of dominant orientation. Importantly, DA is a

measure of the level of uniformity in strut direction, but it does not given information on direction relative to anatomical planes.

Statistical methods

For each structural variable, an analysis of variance with Tukey post-hoc tests was used to statistically assess predicted differences between subregions within each specific taxon (i.e., intraspecific patterns) and differences among taxa across each specific subregion (i.e., interspecific patterns). Subsequently, a stepwise discriminant function analysis was conducted to test the ability of the structural bone variables to differentiate among the five extant taxa. SPSS v.12.0 (SPSS, Chicago, IL) was used for all statistical calculations with significance determined by $p < 0.05$.

Results

Structural patterns in BV/TV, Tb.Th, Tb.N

Australopithecus tali (StW 102, StW 363, and StW 486) and *Paranthropus* tali (KNM-ER 1464 and TM 1517) exhibit variability in trabecular bone structure that is generally on the order of the variability expressed by more comprehensively-sampled extant species, including the most variable group – orangutans (Tables 1-5). Thus, the amount of variability expressed in the fossil specimens pooled into their respective genera generally suggests that the observed intragroup variability of each reflects plausible levels of intraspecific variability. *Australopithecus* and *Paranthropus* usually, but not always, cluster together relative to extant groups in comparisons of properties.

1 Among extant taxa, humans consistently exhibit the lowest BV/TV in each subregion,
2 while baboons consistently exhibit the highest BV/TV in each subregion (Table 1 and Figure 3).
3 The kinematic-based prediction that chimpanzees and gorillas would have greater BV/TV in the
4 lateral versus medial regions was met, driven primarily by the anterior-lateral and central-lateral
5 regions ($p < 0.001$, Supplementary Online Material [SOM] Table S1.B-C). The prediction that
6 humans would have greater BV/TV in the anterior-medial and central-lateral regions also was
7 partially met ($p < 0.001$, Table 1, Figure 3), as both regions along with the central-medial tended
8 to exhibit significantly greater BV/TV than other regions (SOM Table S1.E). Both fossil genera
9 tend to exhibit similar BV/TV levels as chimpanzees, gorillas, and orangutans, particularly in
10 anterior-lateral and central-lateral subregions (Table 1 and Figure 3). Interestingly,
11 *Australopithecus* follows the same pattern as observed in chimpanzees, gorillas, and orangutans
12 in having significantly greater BV/TV than humans in all three lateral subregions (Table 1).
13 *Paranthropus* also tends to have greater BV/TV than humans in the lateral subregions, but only
14 significantly so in the central-lateral subregion (Table 1).

15 Amongst extant taxa, humans consistently exhibit the lowest Tb.Th in each subregion,
16 while baboons consistently exhibit the highest Tb.Th in each subregion (Table 2 and Figure 4).
17 As predicted by kinematics, humans had the highest Tb.Th in the anterior-medial region,
18 although the difference from other regions often was not statistically significant (SOM Table
19 S2.E). *Australopithecus* and *Paranthropus* tend to exhibit higher Tb.Th than other groups,
20 including baboons, particularly in the three anterior and three coronally-central subregions
21 (Table 2 and Figure 4). Differences in posterior subregions were less distinct, except in the
22 posterior-lateral subregion where the fossil groups had relatively higher Tb.Th than the extant
23 groups (Table 2 and Figure 4). Chimpanzees, gorillas, and *Australopithecus* have higher Tb.Th

1 in the anterior subregions compared to other subregions, while the trend is less apparent in
2 humans, baboons and *Paranthropus* (Table 2, Figure 4, SOM Table S2).

3 Fewer significant group differences in Tb.N were observed, with the most notable trend
4 being the generally distinct (low) values in baboons (Table 3 and Figure 5). Unsurprisingly,
5 most of the significant pairwise differences between extant groups incorporate baboons.
6 Chimpanzees and gorillas have greater Tb.N in lateral versus medial regions, but these
7 differences less consistently reach the level of statistical significance compared to the differences
8 between anterior versus coronally-central or posterior regions (Table 3, Figure 5, SOM Table
9 S3.B-C). Although not significantly different from extant taxa, except for a few instances where
10 Tb.N is significantly lower than in humans (e.g., the central-lateral subregion), tali from both
11 hominin genera tend to have low Tb.N relative to other hominoids, particularly in the coronally-
12 central subregions (Table 3 and Figure 5). Most groups, including *Australopithecus*, have non-
13 significantly lower Tb.N in the anterior-central and anterior-medial subregions compared to the
14 anterior-lateral subregion, and in the central-central and central-medial subregion compared to
15 the central-lateral subregions, while the trend is less apparent in baboons and *Paranthropus*
16 (Table 3, Figure 5, and SOM Table S3).

18 *Structural patterns in Tb.DA and Tb.E*

19 Humans exhibit greater DA across the nine subregions, while orangutans and baboons
20 tend to exhibit the lowest DA across the subregions (Table 4 and Figure 6). Chimpanzees and
21 gorillas tend to exhibit intermediate DA in anterior and posterior subregions, and orangutan- and
22 baboon-like low DA in coronally-central subregions (Table 4 and Figure 6). Few of the
23 intraspecific regional differences in DA are statistically significant, except within humans and

1 baboons where the former tend to exhibit significantly more anisotropic struts in lateral and
2 sagittally-central subregions and the latter tend to exhibit significantly more anisotropic struts in
3 medial subregions (Table 4, Figure 6, SOM Table S4). In a majority of the nine trabecular
4 subregions, DA in *Australopithecus* (except StW 363) and *Paranthropus* resembles the overall
5 higher DA observed in humans more than the lower DA observed in other extant anthropoids, or
6 is at least intermediate between the two (Table 4 and Figure 6). Specifically, DA observed in
7 *Australopithecus* tends to resemble that of humans in central-medial and posterior-lateral
8 subregions more than does that of *Paranthropus*, which tends to resemble that of humans in
9 anterior-lateral and central-lateral subregions (Table 4 and Figure 6). Neither hominin group is
10 particularly human-like in anterior-central, anterior-medial, and central-central subregions (Table
11 4 and Figure 6).

12 All taxa tend to have relatively more plate-like trabeculae except for humans (Table 5,
13 Figures 7-8). Human trabeculae particularly stand out as significantly more rod-like in lateral
14 subregions, while other anthropoids (except orangutans) tend to exhibit significantly more rod-
15 like trabeculae in central-central and posterior-central subregions compared to other subregions
16 (Table 5, Figures 7-8, SOM Table S5). *Australopithecus tali* and the *P. boisei* talus (KNM-ER
17 1464) have elongated, rod-like trabeculae in lateral subregions, approaching the highly
18 elongated, rod-like trabeculae observed in humans, while other extant anthropoids tend to have
19 more plate-like trabeculae in lateral subregions (Table 5, Figures 7-8). Interestingly, in the
20 anterior-medial and central-lateral regions, TM 1517 exhibits particularly low elongation indices
21 (i.e., plate-like trabecular shapes) resembling anthropoid indices more than the indices of the
22 other *Paranthropus* specimen (KNM-ER 1464) in the study (Figure 8). This is responsible for

creating the particularly large spread in the *Paranthropus* boxplot of Tb.E for these subregions (Figure 7).

Discriminant function analysis

Assessing wholesale structural properties of subregions using a discriminant function analysis reveals that the first discriminant function (DF1) accounts for at least 72% of the variance among extant groups, usually separating baboons at one extreme from humans at the other (Table 6 and Figure 9). Across the nine subregions, and particularly within lateral subregions, DF1 typically reflects high BV/TV, low Tb.N, and low DA in baboons versus low BV/TV, high Tb.N, and high DA in humans (Table 6 and Figure 9). Projecting *Australopithecus* and *Paranthropus* fossils into the discriminant space indicates that in anterior regions and the central-lateral subregion they cluster with chimpanzees, gorillas, and orangutans in being intermediate to humans and baboons in DF1, while in the remaining coronally-central and posterior regions they tend to project within the human cluster (Figure 9).

The second discriminant function (DF2) accounts for between 12% and 23.1% of the variance among extant groups (Table 6 and Figure 9). DF2 typically reflects relatively high DA and E, clustering humans and baboons at the positive extreme and separating them from orangutans at the negative extreme (Table 6 and Figure 9), for instance in the central-lateral and all three posterior subregions. In anterior subregions, the fossils tend to group with chimpanzees, gorillas, and orangutans, while in the coronally-central and posterior subregions the fossils tend to group with humans and baboons more than with the other extant groups.

Predicted group classification of specimens is presented in Table 7. Summarily considering all regions, no fossil talus consistently resembles any one particular extant group to the exclusion of all other groups in terms of structural properties. Fossil tali, however, do vary in relative consistency of these resemblances, or lack thereof: StW 102 and KNM-ER 1464 resemble baboons in five of nine subregions (including throughout coronally-central subregions); StW 486 resembles baboons in five of seven subregions; StW 363 resembles baboons and chimpanzees each in three of nine subregions; and TM 1517 resembles chimpanzees and gorillas each in three of eight subregions. The fossils were most often classified with baboons in the coronally-central regions, driven by their shared high BV/TV and low DA.

Primary orientation of trabeculae

Primary orientation of trabeculae is distinct among groups in only a few subregions, predominantly those that are depicted as enlarged circles in Figure 10. In the anterior-central and anterior-medial subregions *Paranthropus*, relative to *Australopithecus*, tends to emulate the human pattern where primary strut orientations are directed towards the talar neck and head. Among the fossils, StW 486 least resembles human primary strut orientation in these two subregions, instead most resembling primary strut orientations exhibited by chimpanzees and gorillas.

In posterior subregions, *Australopithecus* and *Paranthropus* have primary strut orientations that resemble those of humans in some cases (e.g., the posterior-lateral region). In the posterior-lateral subregion, primary orientation of human trabecular struts is directed postero-inferiorly towards the posterior calcaneal facet. Interestingly, in other posterior subregions (e.g.,

posterior-central), primary strut orientation in some fossils (e.g., TM 1517 and StW 363) is more anteriorly-directed, differing substantially from orientations exhibited in humans. Other fossils (e.g., KNM-ER 1464 and StW 486) are less anteriorly-directed, thus approaching the relatively more posteriorly-directed orientation observed in humans.

Discussion

Consistent with some of our predictions, this study observed that hominin talar trabecular structure and orientation differed significantly in several ways from the pattern of trabecular structure and orientation in extant hominoid tali (Tables 1-5). Specifically, hominin tali are more ape-like in bone volume fraction (BV/TV) and trabecular thickness, but often more human-like in anisotropy and to a lesser extent elongation, particularly along the lateral and posterior subregions of the talar trochlea. In subregions besides the lateral and posterior, trabecular structure tended to vary among the fossils, possibly supporting a varied loading regime associated with individual hominin activity. Overall, these results are contra DeSilva and Devlin (2012), who did not find predicted significant regional differences between anthropoids and hominins, likely due to the use of poorer spatial resolutions, smaller sample sizes and/or larger volumes of interest (i.e., sampling of the entire talar body).

Only partial support was found for the second prediction that *Australopithecus* and *Paranthropus* differ from each other in trabecular properties of the talar body. Trabecular structural properties beneath the trochlea did not always clearly distinguish *Australopithecus* from *Paranthropus*, whether comparing *Australopithecus* tali to those from the East African species, *P. boisei*, or to those from the South African species, *P. robustus*. In certain

1 characteristics, however, *Paranthropus* does appear to be more consistently human-like (e.g.,
2 primary strut orientation in anterior-medial and central-medial subregions; DA in anterior-lateral
3 and central-lateral subregions). This may indicate that in certain respects, such as weight transfer
4 from the lateral hindfoot to the medial midfoot during the last half of stance phase, *Paranthropus*
5 may have exhibited comparatively more human-like foot kinematics during bipedal locomotion
6 than *Australopithecus*.

7 Although uniquely distinguishing features of trabecular structure were not systematically
8 observed throughout the talus of either hominin genus, specific similarities between tali of fossil
9 hominins and some of the extant hominoids are noteworthy. In this manner, the observed
10 patterns of significant differences between extant properties contribute to an improved
11 understanding of functional morphology of the hominin tibiotalar joint. Importantly, this study
12 found that considering suites of traits, as suggested by Ryan and Shaw (2012), is more
13 informative to a functional understanding of the tibiotalar joint than is considering specific traits
14 in isolation.

15 First, *Australopithecus* and *Paranthropus* tali in the study exhibited increased DA and
16 elongation laterally and posteriorly, which are features shared with tali from both humans and
17 baboons. Greater strut elongation and anisotropy typically occur with decreased bone volume,
18 effectively lessening overall bone mass, but still retaining compressive strength in the face of a
19 predictable load environment (Goulet et al., 1994; Nafei et al., 2000a, b; Tanck et al., 2001; Ryan
20 and Krovitz, 2006). Thus, we interpret this similarity as an indicator of hominin foot postures
21 associated with terrestrial locomotor activities rather than arboreal locomotor activities (i.e., use
22 of comparatively more horizontal and less complex substrate surfaces).

1 Second, humans exhibit comparatively greater reductions in bone volume fraction
2 throughout the lateral region of the trochlea. This indicates relative unloading of the lateral
3 region of the human ankle joint throughout stance, possibly as a correlate of a vertically-
4 positioned tibia accompanied by a non-weight-bearing fibula (Marchi, 2007). Human tali in the
5 sample effectively reduce bone volume fraction by reducing strut thickness rather than strut
6 number (Figures 4-5). In contrast, other apes effectively increase bone volume fraction by
7 increasing strut thickness rather than strut number, except for baboons which compensate for
8 their reduced number of struts by exhibiting even greater strut thickness (Figures 4-5). Others
9 have suggested that in humeral and femoral sites, larger-bodied primates (e.g., gorillas) tend to
10 pair thinner and more numerous struts in comparison to smaller-bodied primates (Ryan and
11 Shaw, 2013), but our talar sample across a relatively narrower body size range does not
12 necessarily support such a trend, nor have we analyzed the same humeral and femoral sites in our
13 sample. Partitioning the functional versus phylogenetic signal behind these combinations of traits
14 would benefit from additional research. *Australopithecus* and *Paranthropus* tali examined in the
15 present study are intermediate between humans and other anthropoids in bone volume fraction of
16 the lateral region, indicating a degree of lateral loading in these hominin tali that appears to be
17 intermediate in magnitude to the loading experienced by anthropoid and human tali.

18 Third, quantification of primary strut orientation further refines tibiotalar joint loading
19 regimes depicted by bone volume fraction. Barak et al. (2013b) quantified strut orientation in the
20 *A. africanus* distal tibia, suggesting the taxon was more human-like during stance phase in its
21 vertical tibia posture and ankle dorsiflexion than chimpanzee-like. Our analysis of primary strut
22 orientation beneath the hominin trochlea, particularly in anterior-central and anterior-medial
23 subregions, adds further insight to the findings of Barak et al. (2013b) in that we observed less

1 consistent load direction towards the talar head (i.e., less human-like) in *Australopithecus* than in
2 *Paranthropus*. Rather, primary strut orientations of most of the *Australopithecus* tali examined in
3 this study resemble primary strut orientations of ape tali in both of these subregions. Trends in
4 DA in anterior-lateral and central-lateral also support this finding. We interpret this as suggestive
5 evidence for the absence of a medial weight transfer from the hindfoot to the midfoot during the
6 last half of stance phase of *Australopithecus* bipedal locomotion (i.e., ape-like loading of the
7 lateral regions), but a comparatively more human-like habitual medial weight transfer to the
8 midfoot during the last half of stance phase in *Paranthropus*. Alternatively, elevated
9 compressive forces in the lateral subregions of the joint may stem from the peroneal muscles, in
10 line with studies that indicate enlarged peroneal musculature in *Australopithecus* either to
11 maintain an inverted foot for climbing (Stern and Susman, 1983), or for propulsion during
12 terrestrial bipedalism (Latimer and Lovejoy, 1989).

13 Our results agree with the findings of others who demonstrate that hominin structural
14 properties (i.e., bone volume fraction, trabecular thickness) from other regions of the skeleton are
15 similar in magnitudes to ape structural properties (Chirchir et al., 2015), but regional
16 distributions (i.e., anisotropy and elongation) and primary strut orientations can reflect more
17 human-like patterns (Barak et al., 2013b). Thus, considering results of the present study taken as
18 a whole, trabecular structure within *Australopithecus* and *Paranthropus* tali suggests a mosaic of
19 human-like and ape-like similarities. Our results also support external morphological studies of
20 hominin ankle and foot elements in that, although bipedal, these individuals loaded their foot and
21 ankle in a manner unlike modern humans (Susman and Brain, 1988; Susman and de Ruiter,
22 2004; Gebo and Schwartz, 2006; Zipfel and Kidd, 2006; Prang, 2016). We interpret this in turn
23 to reflect that non-human-like and non-ape-like foot kinematics characterize *Australopithecus*

1 and *Paranthropus* stance phases of bipedal locomotion, although the latter appears to exhibit
2 more of a human-like habitual medial weight shift than the former. In this regard, the present
3 study also supports an emerging consensus that emphasizes the importance of variability
4 characterizing hominin bipedal kinematics (Robinson, 1972; Harcourt-Smith and Aiello, 2004;
5 Zipfel et al., 2011; DeSilva et al., 2013).

6 That clear, consistent separation of *Australopithecus* tali from Sterkfontein Member 4
7 into two morphs was not found in the present study is relevant to the suggestion that two
8 australopith morphs may exist in Sterkfontein Member 4 (Clarke, 2013). In part based on
9 differences in proximal extension of the dorsal facet from the hallucal metatarsal head, Clarke
10 (2013) has suggested the possibility of two *Australopithecus* species in Sterkfontein Member 4,
11 namely one that possessed a human-like toe-off mechanism and one that did not. With a limited
12 ability to dorsiflex at the lateral tarsometatarsal joint during gait (DeSilva, 2010), it would be
13 reasonable to propose that one morph should exhibit a decreased range of motion at the ankle
14 joint (Hall and Nester, 2004). However, in the present study, which includes three
15 *Australopithecus* tali from Sterkfontein Member 4 (StW 102, StW 363, StW 486), we found no
16 clear evidence for a difference in range of motion based on our quantitative analysis of internal
17 structure (i.e., trabecular structure and orientation). It bears mentioning that additional hominin
18 tali from Sterkfontein have been recovered (e.g., StW 88, StW 347), but were not included in this
19 analysis of internal structure for reasons of incompleteness or poor material contrast in image
20 data (Figure 2). Thus, while the present study did not discern two morphs in Sterkfontein
21 Member 4, analyses of internal structure in additional tali, or similar analyses of other skeletal
22 elements from Member 4 may be able to do so. Alternatively, as in modern humans, there may
23 be a wide continuum of individual variability in mid- and forefoot joint mobility (DeSilva et al.,

2015) that would preclude the identification of two morphs based strictly on internal foot and ankle structure.

Comparisons of trabecular structure of two hominin tali in the present study that are currently attributed to *Paranthropus* are relevant to prior comparisons of their external morphology. Gebo and Schwartz (2006) note that KNM-ER 1464 and TM 1517 share external features such as moderate curvature of the medial trochlear rim, but ultimately they suggest that their overall talar morphology is not especially similar due to the large talar head of TM 1517. This could be viewed as consistent with the idea that *Paranthropus* was not a monophyletic group (Constantino and Wood, 2007; Patterson et al., 2014; Carlson and Edland, 2016). In the present study, however, trabecular structure does not consistently distinguish between KNM-ER 1464 and TM 1517. While predicted groups for KNM-ER 1464 VOIs tend to match predicted groups for StW 102 and StW 486 VOIs more than do those for TM 1517 VOIs, internal morphology does not argue for one *Paranthropus* talus appearing any more derived (i.e., human-like) than the other. Thus, general similarity in talar internal structure of KNM-ER 1464 and TM 1517 could be viewed as consistent with the idea that *Paranthropus* was a monophyletic group. More fossils securely attributed to *Paranthropus* (e.g., associated with diagnostic craniodental material) are required in order to definitively assess this possibility.

Analysis of hominin footprint trackways has provided crucial indirect evidence in reconstructing hominin gait kinematics (Leakey and Hay, 1979; Bennett et al., 2009; Dingwall et al., 2013; Hatala et al., 2016). General similarities in trabecular structure of *Australopithecus* and *Paranthropus* tali relative to extant anthropoids suggest that tibiotalar joint mechanics in both genera are broadly similar. Thus, to the extent that footprint trackways reflect the mechanics of the tibiotalar joint, differentiating between those of the two hominins may require

1 consideration of subtle mechanical differences. One potential means of distinguishing between
2 *Australopithecus* and *Paranthropus* trackways may come from the apparently more human-like
3 mechanism of the latter in medially transferring body weight from the hindfoot to the midfoot.
4 Potentially greater internal structural similarity in anterior regions of the *Paranthropus* and
5 human talar trochlea, to the relative exclusion of the *Australopithecus (africanus)* talus, suggests
6 that mid- to latestance kinematic events may be fruitful when attempting to discriminate one
7 hominin from the other in attributing footprint makers.

8 As in other studies of external (Gebo and Schwartz, 2006) and internal morphology
9 (DeSilva and Devlin, 2012), we found that fossil tali did not systematically and cleanly separate
10 along either taxonomic or geographic boundaries. When using current taxonomic attributions to
11 *Australopithecus* and *Paranthropus*, and as outlined above, the fossil tali exhibited variability in
12 trabecular bone structure similar to the variability observed in extant species. This may imply
13 that the hominin tali in each group are attributed correct species designations, and have similar
14 levels of intraspecific variability as extant species. If tali ultimately are derived from hominin
15 species different from those to which they are currently attributed, however, this may imply that
16 individuals in the conflated groups exhibited similar locomotor mechanics with regards to the
17 tibiotalar joint, or alternatively that trabecular structure as quantified in this study is not useful
18 for discriminating among these hominin taxa. Assessment of trabecular structure in additional
19 fossils, including specimens from both hominin genera sampled in this study and further
20 quantitative comparisons with the present extant sample, will aid in discerning which of these
21 possibilities may be more likely.

22 An unfortunate limitation to this study was the presence of missing VOIs in two fossils,
23 namely StW 486 and TM 1517 (Figure 2). For example, the posterior-lateral subregion was

capable of discriminating among extant hominins, with elongated trabecular struts distinguishing humans from more arboreal hominoids (i.e., chimpanzees, gorillas, and orangutans) (Figure 9). The three *Australopithecus* fossils and KNM-ER 1464 clearly fell with humans in this regard (Figures 6 - 8). When considering all properties in this subregion, the three *Australopithecus* fossils and KNM-ER 1464 again cluster with the terrestrial group of humans and baboons (Figure 9). Additionally, in the posterior-lateral region, the three *Australopithecus* specimens cluster closely near humans in primary strut orientation, while KNM-ER 1464 clusters with baboons (Figure 10). It is thus unfortunate that trabecular properties of TM 1517 could not be assessed in this region. It is anticipated that future analyses of other fossil specimens will assist in assessing the discriminatory power of this particular subregion.

In studies of internal structure of fossils, one must be mindful of another potential limitation. Specifically, matrix incursion inside fossils can result in over (or under-)estimating volume of trabecular struts. StW 363 and StW 486 had defects in their anterior-central and central-central subregions that allowed matrix to infiltrate. In the case of image data acquired in the present study, reasonable material contrast between bone and matrix in fossils was achieved for all specimens in the analyses (Figure 2). Nonetheless, in order to be conservative, a matrix segmentation algorithm was applied systematically across specimens, increasing confidence in the validity of relative comparisons. Thus, while we are confident in our quantitative measurements of strut characteristics, it is still prudent to acknowledge that the high Tb.Th in fossil tali could be, in part, an artifact of this preservation and segmentation process. In light of this possibility, it is worth noting that StW 102 did not have matrix incursion, and was not found to differ significantly from other fossils (including StW 363 and StW 486) in measures of BV/TV or Tb.Th. Moreover, analysis of trabecular structure in three-dimensions, as was

performed in the present study, can help ameliorate any potential errors associated with inaccurate matrix segmentation, particularly in comparison to two-dimensional analyses, for which there is a much greater potential of choosing a non-representative slice afflicted by localized areas of poor contrast.

Conclusion

This study has demonstrated that trabecular bone structure and orientation in the talus may help in inferring joint posture in fossil hominins. Although fossil tali attributed to *Australopithecus* and *Paranthropus* were not systematically identifiable to particular extant taxa, as groups these hominins displayed hallmark characteristics of terrestrial locomotion – high anisotropy in the lateral talus. Several hominin tali, including both *Paranthropus* fossils, also shared distinctive human-like primary strut orientations beneath the anteromedial trochlea that may indicate medial weight transfer to the talar head during the last half of stance phase. The intermediate bone volume fraction characterizing hominin tali in the present study indicates greater loading than modern humans along the lateral talus, which may be related to a more variable leg posture, including a more frequent varus position, similar that in to extant apes. Trabecular structure in tali from both hominin genera suggests ankle arthrokinematics that are neither distinctly human-like nor distinctly ape-like. Moreover, the observed structural variability in hominin talus trabecular bone underscores the important variability that appears to characterize hominin bipedal kinematics.

Acknowledgements

1 The Centre of Excellence –Palaeosciences (CoE-Pal) at the University of the Witwatersrand and
2 the National Research Foundation (South Africa) and Department of Science and Technology
3 (South Africa) provided funding to KC for this research. We also acknowledge the financial
4 support of the University of the Witwatersrand and the National Research Foundation (South
5 Africa) and Department of Science and Technology (South Africa) that made the scanning and
6 image analysis facilities possible. We are grateful to the Fossil Access Committee of the
7 University of the Witwatersrand for granting access to fossil specimens studied in this work (all
8 except KNM-ER 1464). We are especially grateful to the curator, B. Zipfel, for his assistance
9 with fossil access and for also generously providing insightful comments and discussion on an
10 earlier version of this manuscript. We thank A. Zeininger and J. DeSilva also for helpful
11 discussions on this project. We thank the Microfocus X-ray Computed Tomography (CT)
12 Facility of the Palaeosciences Centre at the University of the Witwatersrand
13 (www.wits.ac.za/microCT) and the Virtual Imaging in Palaeontology (VIP) laboratory for
14 providing access to their scanning and image analysis facilities. For use of the KNM-ER 1464
15 data, we are grateful to I. Wallace, M. Nakatsukasa, and E. Mbua at the National Museums of
16 Kenya. For access to the comparative specimens, we thank L. Jellema (CNMH), E. Westwig
17 (AMNH), L. Gordon at the Smithsonian (NMNH), and J. Kappelman curator of the Bramblett
18 Baboon Collection at the University of Texas.

Figure captions

Figure 1. The nine volumes of interest sampled in the present study in relationship to the articular surface of the trochlea (see also Su et al., 2013: Figure 3). A. Coronal slice through the posterior regions, B. Transverse slice through volumes of interest, C. Parasagittal slice through lateral regions. Based on differences in gait kinematics, it is predicted that humans will show relatively greater structural bone strength in the posterior, central-lateral, and anterior-medial subregions (H), while chimpanzees and gorillas will show relatively greater structural bone strength anteriorly and laterally (P/G).

Figure 2. Renderings of fossils in superior view, with accompanying coronal and parasagittal gray scale slices. The parasagittal slice is positioned through the lateral rim of each talar trochlea. Note the excellent material contrast present in fossil specimens (except for StW 88) that permitted segmenting trabecular struts from intervening matrix, including within StW 486 and TM 1517. The latter two specimens were deemed “too heavily mineralized to yield any useable information” by a previous study of their internal talar structure (DeSilva and Devlin, 2012, p. 543) that also included StW 88 in the sample, but which we excluded from the present analysis because of poor contrast between struts and intervening matrix.

Figure 3. Boxplot indicating bone volume fraction (BV/TV) by subregion across groups. Horizontal lines inside boxes indicate median values, boxes indicate 25th and 75th percentiles, and whiskers indicate minimum and maximum values, except for open circles that denote outliers (defined as between 1.5 and 3 box lengths from the median). Note the hominin tali resemble extant hominoids, particularly in anterior-lateral (A-L) and central-lateral (C-L) regions.

Figure 4. Boxplot indicating trabecular thickness (Tb.Th) by subregion across groups. Horizontal lines inside boxes indicate median values, boxes indicate 25th and 75th percentiles, and whiskers indicate minimum and maximum values, except for open circles that denote outliers (defined as between 1.5 and 3 box lengths from the median). Note the hominin tali have greater Tb.Th than other groups. *Australopithecus* resembles chimpanzees and gorillas in having greater Tb.Th in anterior regions.

Figure 5. Boxplot indicating trabecular number (Tb.N) by subregion across groups. Horizontal lines inside boxes indicate median values, boxes indicate 25th and 75th percentiles, and whiskers indicate minimum and maximum values, except for open circles that denote outliers (defined as between 1.5 and 3 box lengths from the median). Note the hominin tali tend to have low Tb.N relative to extant hominoids, although the differences were not statistically significant.

Figure 6. Boxplot indicating degree of trabecular strut anisotropy (Tb.DA) by subregion across groups. Horizontal lines inside boxes indicate median values, boxes indicate 25th and 75th percentiles, and whiskers indicate minimum and maximum values, except for open circles that denote outliers (defined as between 1.5 and 3 box lengths from the median). Note the hominin tali have elevated DA laterally and posteriorly, resembling humans and baboons. In particular, *Paranthropus* is human-like in the anterior-lateral (A-L) and central-lateral (C-L) regions.

Figure 7. Boxplot indicating degree of trabecular strut elongation (Tb.E) by subregion across groups. Horizontal lines inside boxes indicate median values, boxes indicate 25th and 75th percentiles, and whiskers indicate minimum and maximum values, except for open circles that denote outliers (defined as between 1.5 and 3 box lengths from the median). Note the

1 *Australopithecus* and KNM-ER 1464 tali resemble the highly elongated, rod-shaped trabeculae
2 in humans in the lateral regions.

3 **Figure 8.** Triangular diagram indicating the combined degree of trabecular strut anisotropy
4 (Tb.DA) and trabecular strut elongation (Tb.E) by subregion across groups. Columns represent
5 lateral, sagittally-central, and medial subregions from left to right, respectively; rows represent
6 anterior, coronally-central, and posterior subregions from top to bottom, respectively.

7 **Figure 9.** Plots of Discriminant Function 1 versus Discriminant Function 2 for individuals in
8 groups summarizing scalar values by subregions. Columns represent lateral, sagittally-central,
9 and medial subregions from left to right, respectively; rows represent anterior, coronally-central,
10 and posterior subregions from top to bottom, respectively.

11 **Figure 10.** Stereoplots in each region indicate superior-to-inferior trajectory of the primary
12 eigenvector of trabecular orientation. Columns represent lateral, sagittally-central, and medial
13 subregions from left to right, respectively; rows represent anterior, coronally-central, and
14 posterior subregions from top to bottom, respectively. 95% confidence regions are drawn for
15 each extant species. The regions that distinguished among extant species are enlarged.

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Tables 1-5: Mean and standard deviation of structural variables by region, along with results of analysis of variance. Symbols indicate posthoc pairwise comparisons between groups, *Pongo* ($\square$), *Pan* (λ), *Gorilla* (Υ), *Papio* ($\diamond$), *Homo* ($\circ$), *Australopithecus*, and *Paranthropus*. Superscripts indicate level of significance of pairwise differences, 3: $p < 0.001$, 2: $p < 0.01$, and 1: $p < 0.05$.

Table 1: Bone volume fraction (BV/TV).

	<i>Pongo</i> ($\square$)	<i>Pan</i> (λ)	<i>Gorilla</i> (Υ)	<i>Papio</i> ($\diamond$)	<i>Homo</i> ($\circ$)	<i>Australopithecus</i>	<i>Paranthropus</i>	ANOVA	
Region	$n = 13$	$n = 20$	$n = 14$	$n = 18$	$n = 17$	$n = 3$	$n = 2$	F	P
A-L	0.58 (0.08) $\diamond^3 \circ^3$	0.58 (0.06) $\diamond^3 \circ^3$	0.55 (0.05) $\diamond^3 \circ^3$	0.74 (0.08) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.39 (0.04) $\square^3 \lambda^3 \Upsilon^3 \diamond^3$	0.56 (0.03) $\diamond^3 \circ^3$	0.48 (0.07) $\diamond^3$	49.26	<0.001
A-C	0.41 (0.09) $\diamond^1$	0.44 (0.06) $\circ^3$	0.43 (0.06) $\circ^2$	0.49 (0.08) $\square^1 \circ^3$	0.35 (0.04) $\lambda^3 \Upsilon^2 \diamond^3$	0.51 (0.07) $\circ^2$	0.51 (0.01) $\circ^1$	8.52	<0.001
A-M	0.43 (0.11) $\diamond^3$	0.47 (0.06) $\diamond^3$	0.47 (0.07) $\diamond^3$	0.63 (0.09) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.40 (0.05) $\diamond^3$	0.57 (0.10) $\circ^2$	0.56 (0.04)	16.26	<0.001
C-L	0.49 (0.05) $\diamond^3 \circ^3$	0.54 (0.05) $\diamond^3 \circ^3$	0.51 (0.05) $\diamond^3 \circ^3$	0.62 (0.06) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.41 (0.03) $\square^3 \lambda^3 \Upsilon^3 \diamond^3$	0.54 (0.01) $\circ^3$	0.54 (0.03) $\circ^3$	30.74	<0.001
C-C	0.36 (0.06) $\diamond^3$	0.41 (0.04) $\diamond^3$	0.41 (0.05) $\diamond^3$	0.47 (0.07) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.36 (0.04) $\diamond^3$	0.45 (0.05)	0.46 (0.04)	8.81	<0.001
C-M	0.44 (0.07) $\diamond^3$	0.46 (0.04) $\diamond^3$	0.44 (0.04) $\diamond^3$	0.66 (0.10) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.40 (0.06) $\diamond^3$	0.43 (0.18) $\diamond^3$	0.51 (0.04)	26.98	<0.001
P-L	0.44 (0.03) $\diamond^3 \circ^3$	0.47 (0.06) $\Upsilon^1 \diamond^3 \circ^3$	0.41 (0.04) $\diamond^3 \circ^2$	0.60 (0.07) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.34 (0.03) $\square^3 \lambda^3 \Upsilon^2 \diamond^3$	0.55 (0.04) $\Upsilon^1 \circ^3$	0.51 (0.00)	44.63	<0.001
P-C	0.38 (0.06) $\lambda^1 \diamond^3$	0.45 (0.03) $\Upsilon^2 \diamond^3 \circ^3$	0.36 (0.04) $\lambda^2 \diamond^3$	0.64 (0.08) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.34 (0.05) $\lambda^3 \diamond^3$	0.44 (0.03) $\diamond^3$	0.37 (0.05) $\diamond^3$	62.95	<0.001
P-M	0.45 (0.08) $\diamond^3 \circ^2$	0.49 (0.06) $\diamond^3 \circ^3$	0.41 (0.05) $\diamond^3$	0.70 (0.10) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.36 (0.04) $\square^2 \lambda^3 \diamond^3$	0.38 (0.04) $\diamond^3$	0.42 (0.06) $\diamond^3$	42.56	<0.001
ANOVA	F=20.90, $p < 0.001$	F=20.02, $p < 0.001$	F=18.35, $p < 0.001$	F=2.44, $p < 0.065$	F=10.80, $p < 0.001$				

Table 2: Average trabecular thickness (Tb.Th) within each subregion, in units of mm.

	<i>Pongo</i> ($\square$)	<i>Pan</i> (λ)	<i>Gorilla</i> (Υ)	<i>Papio</i> ($\diamond$)	<i>Homo</i> ($\circ$)	<i>Australopithecus</i>	<i>Paranthropus</i>	ANOVA	
Region	$n = 13$	$n = 20$	$n = 14$	$n = 18$	$n = 17$	$n = 3$	$n = 2$	F	P
A-L	0.23 (0.04) $\diamond^3$	0.25 (0.04) $\circ^3$	0.26 (0.04) $\circ^3$	0.28 (0.04) $\square^3 \circ^3$	0.20 (0.03) $\lambda^3 \Upsilon^3 \diamond^3$	0.32 (0.06) $\square^3 \circ^3$	0.26 (0.07)	10.88	<0.001
A-C	0.21 (0.06)	0.25 (0.03) $\circ^1$	0.25 (0.05) $\circ^1$	0.25 (0.04) $\circ^2$	0.20 (0.03) $\lambda^1 \Upsilon^1 \diamond^2$	0.36 (0.03) $\square^3 \lambda^3 \Upsilon^2 \diamond^2 \circ^3$	0.32 (0.01) $\square^1 \circ^2$	9.28	<0.001
A-M	0.21 (0.05) $\Upsilon^2 \diamond^3$	0.26 (0.04)	0.27 (0.06) $\square^2 \circ^2$	0.30 (0.05) $\square^3 \circ^3$	0.21 (0.03) $\Upsilon^3 \diamond^3$	0.35 (0.08) $\square^3 \lambda^1 \circ^3$	0.36 (0.06) $\square^2 \circ^2$	11.44	<0.001
C-L	0.21 (0.03) $\diamond^3$	0.24 (0.03) $\diamond^2 \circ^2$	0.24 (0.04) $\diamond^1 \circ^2$	0.29 (0.04) $\square^3 \lambda^2 \Upsilon^1 \circ^3$	0.19 (0.02) $\lambda^2 \Upsilon^2 \diamond^3$	0.31 (0.04) $\square^3 \circ^3$	0.33 (0.07) $\square^3 \lambda^1 \Upsilon^1 \circ^3$	16.28	<0.001
C-C	0.19 (0.04) $\diamond^3$	0.20 (0.02) $\diamond^1$	0.22 (0.02)	0.23 (0.04) $\square^3 \lambda^1 \circ^2$	0.19 (0.03) $\diamond^2$	0.30 (0.04) $\square^3 \lambda^3 \Upsilon^2 \diamond^1 \circ^3$	0.30 (0.02) $\square^3 \lambda^2 \Upsilon^1 \circ^3$	12.25	<0.001
C-M	0.21 (0.04) $\diamond^3$	0.22 (0.03) $\diamond^3$	0.23 (0.03) $\diamond^3$	0.28 (0.04) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.20 (0.03) $\diamond^3$	0.29 (0.15) $\circ^1$	0.32 (0.04) $\square^2 \lambda^2 \Upsilon^1 \circ^3$	12.83	<0.001
P-L	0.19 (0.03) $\diamond^3$	0.20 (0.03) $\diamond^3$	0.20 (0.02) $\diamond^2$	0.24 (0.03) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.18 (0.02) $\diamond^3$	0.26 (0.04) $\circ^2$	0.29 (0.00)	10.82	<0.001
P-C	0.19 (0.04) $\diamond^3$	0.19 (0.02) $\diamond^3$	0.19 (0.02) $\diamond^3$	0.28 (0.04) $\square^3 \lambda^3 \Upsilon^3 \circ^3$	0.18 (0.03) $\diamond^3$	0.25 (0.04) $\circ^1$	0.21 (0.04) $\diamond^1$	20.02	<0.001
P-M	0.20 (0.04) $\diamond^1$	0.20 (0.02) $\diamond^2$	0.20 (0.02) $\diamond^2$	0.23 (0.02) $\square^1 \lambda^2 \Upsilon^2 \circ^3$	0.18 (0.02) $\diamond^3$	0.21 (0.07)	0.23 (0.04)	7.57	<0.001
ANOVA	F=7.85, $p < 0.001$	F=14.89, $p < 0.001$	F=10.31, $p < 0.001$	F=1.71, $p = 0.176$	F=1.29, $p = 0.256$				

Table 3: Average number of trabeculae per mm (Tb.N) within each subregion, in units of mm^{-1} .

	<i>Pongo</i> ($\square$)	<i>Pan</i> ($\wedge$)	<i>Gorilla</i> (Υ)	<i>Papio</i> ($\diamond$)	<i>Homo</i> ($\circ$)	<i>Australopithecus</i>	<i>Paranthropus</i>	ANOVA	
Region	$n = 13$	$n = 20$	$n = 14$	$n = 18$	$n = 17$	$n = 3$	$n = 2$	F	P
A-L	1.87 (0.40) $\diamond^3$	1.76 (0.26) $\diamond^3$	1.74 (0.27) $\diamond^3$	1.20 (0.22) $\square^3\wedge^3\Upsilon^3\circ^3$	1.88 (0.32) $\diamond^3$	1.41 (0.23)	1.62 (0.24)	10.95	<0.001
A-C	1.49 (0.25)	1.46 (0.24)	1.48 (0.24)	1.44 (0.23)	1.57 (0.32)	1.21 (0.14)	1.49 (0.27)	1.00	0.428
A-M	1.55 (0.22) $\diamond^1$	1.47 (0.22) $\circ^2$	1.45 (0.22) $\circ^2$	1.27 (0.17) $\square^1\circ^3$	1.74 (0.25) $\wedge^2\Upsilon^2\diamond^3$	1.28 (0.29) $\circ^1$	1.38 (0.15)	7.67	<0.001
C-L	1.94 (0.27) $\diamond^3$	1.79 (0.22) $\diamond^2$	1.81 (0.29) $\diamond^1$	1.48 (0.21) $\square^3\wedge^2\Upsilon^1\circ^3$	2.00 (0.32) $\diamond^3$	1.49 (0.19) $\circ^1$	1.39 (0.20) $\circ^1$	8.26	<0.001
C-C	1.69 (0.23)	1.77 (0.18)	1.67 (0.22)	1.52 (0.24) $\circ^1$	1.82 (0.40) $\diamond^1$	1.41 (0.18)	1.40 (0.01)	3.20	0.007
C-M	1.83 (0.22) $\diamond^3$	1.78 (0.18) $\diamond^3$	1.67 (0.18) $\diamond^1$	1.39 (0.19) $\square^3\wedge^3\Upsilon^1\circ^3$	1.89 (0.37) $\diamond^3$	1.39 (0.47)	1.43 (0.20)	8.46	<0.001
P-L	1.93 (0.24)	1.96 (0.21)	1.79 (0.22)	1.73 (0.20)	1.80 (0.32)	1.75 (0.30)	1.37 (0.00)	2.54	0.027
P-C	1.61 (0.27) $\wedge^1$	1.93 (0.20) $\square^1\diamond^3$	1.71 (0.23)	1.45 (0.22) $\wedge^3\circ^2$	1.80 (0.41) $\diamond^2$	1.61 (0.37)	1.59 (0.08)	5.47	<0.001
P-M	1.80 (0.25) $\diamond^1$	1.91 (0.23) $\diamond^2$	1.78 (0.28) $\diamond^2$	1.27 (0.23) $\square^1\wedge^2\Upsilon^2\circ^3$	1.86 (0.28) $\diamond^3$	1.77 (0.59)	1.61 (0.15)	12.11	<0.001
ANOVA	F=9.96, $p<0.001$	F=13.93, $p<0.001$	F=3.95, $p<0.001$	F=0.99, $p=0.482$	F=5.08, $p<0.001$				

Table 4: Degree of anisotropy (DA) within each subregion. Values are bounded between 0 (perfect isotropy) and 1 (perfect anisotropy).

	<i>Pongo</i> ($\square$)	<i>Pan</i> ($\wedge$)	<i>Gorilla</i> (Υ)	<i>Papio</i> ($\diamond$)	<i>Homo</i> ($\circ$)	<i>Australopithecus</i>	<i>Paranthropus</i>	ANOVA	
Region	$n = 13$	$n = 20$	$n = 14$	$n = 18$	$n = 17$	$n = 3$	$n = 2$	F	P
A-L	0.44 (0.14) $\circ^3$	0.64 (0.08) $\diamond^3\circ^3$	0.70 (0.08) $\diamond^2\circ^3$	0.47 (0.09) $\wedge^3\Upsilon^3\circ^3$	0.88 (0.04) $\square^3\wedge^3\Upsilon^3\diamond^3$	0.67 (0.11) $\square^3\diamond^2\circ^2$	0.75 (0.12) $\square^3\diamond^3$	40.37	<0.001
A-C	0.56 (0.16) $\circ^3$	0.68 (0.09) $\diamond^3\circ^3$	0.62 (0.10) $\diamond^2\circ^3$	0.47 (0.08) $\wedge^3\Upsilon^2\circ^3$	0.91 (0.04) $\square^3\wedge^3\Upsilon^3\diamond^3$	0.50 (0.26) $\circ^3$	0.64 (0.06) $\circ^2$	30.10	<0.001
A-M	0.54 (0.14) $\circ^1$	0.52 (0.13) $\circ^2$	0.54 (0.11) $\circ^1$	0.56 (0.11)	0.67 (0.08) $\square^1\wedge^2\Upsilon^1$	0.53 (0.11)	0.40 (0.11) $\circ^1$	3.83	0.002
C-L	0.48 (0.13) $\wedge^2\Upsilon^2\circ^3$	0.67 (0.10) $\square^2\circ^3$	0.66 (0.13) $\square^2\circ^3$	0.55 (0.10) $\circ^3$	0.87 (0.04) $\square^3\wedge^3\Upsilon^3\diamond^3$	0.72 (0.02) $\square^2$	0.85 (0.06) $\square^3\diamond^2$	23.58	<0.001
C-C	0.57 (0.18) $\circ^3$	0.58 (0.10) $\circ^3$	0.69 (0.08) $\circ^2$	0.58 (0.11) $\circ^3$	0.86 (0.07) $\square^3\wedge^3\Upsilon^2\diamond^3$	0.63 (0.22)	0.64 (0.04)	11.41	<0.001
C-M	0.49 (0.12) $\wedge^3\Upsilon^3\diamond^3\circ^3$	0.66 (0.10) $\square^3\circ^3$	0.66 (0.09) $\square^3\circ^2$	0.70 (0.11) $\square^3\circ^1$	0.82 (0.08) $\square^3\wedge^3\Upsilon^2\diamond^1$	0.80 (0.04) $\square^2$	0.68 (0.06)	13.77	<0.001
P-L	0.53 (0.16) $\diamond^1\circ^3$	0.54 (0.15) $\diamond^2\circ^3$	0.57 (0.11) $\diamond^2\circ^3$	0.41 (0.11) $\square^1\wedge^2\Upsilon^3\circ^3$	0.80 (0.05) $\square^3\wedge^3\Upsilon^3\diamond^3$	0.68 (0.10) $\diamond^1$	0.58 (0.00)	17.05	<0.001
P-C	0.49 (0.16) $\Upsilon^3\circ^3$	0.58 (0.11) $\diamond^2\circ^3$	0.71 (0.07) $\square^3\diamond^3\circ^1$	0.42 (0.12) $\wedge^2\Upsilon^3\circ^3$	0.85 (0.10) $\square^3\wedge^3\Upsilon^1\diamond^3$	0.68 (0.26) $\diamond^1$	0.79 (0.12) $\square^1\diamond^2$	24.65	<0.001
P-M	0.37 (0.11) $\wedge^3\Upsilon^3\diamond^3\circ^3$	0.61 (0.13) $\square^3$	0.63 (0.12) $\square^3$	0.64 (0.09) $\square^3$	0.71 (0.13) $\square^3$	0.67 (0.11) $\square^1$	0.80 (0.13) $\square^3$	13.35	<0.001
ANOVA	F=16.91, $p<0.001$	F=3.75, $p<0.001$	F=3.42, $p=0.001$	F=0.77, $p=0.638$	F=2.49, $p=0.016$				

Table 5: Elongation index of trabeculae (Tb.E) within each subregion. If DA (Table 4) is close to 1, concurrent E values closer to 0 denote more plate-shaped trabecular struts, while E values closer to 1 denote more rod-shaped struts.

	<i>Pongo</i> (□)	<i>Pan</i> (λ)	<i>Gorilla</i> (Υ)	<i>Papio</i> (◇)	<i>Homo</i> (○)	<i>Australopithecus</i>	<i>Paranthropus</i>	ANOVA	
Region	<i>n</i> = 13	<i>n</i> = 20	<i>n</i> = 14	<i>n</i> = 18	<i>n</i> = 17	<i>n</i> = 3	<i>n</i> = 2	F	P
A-L	0.24 (0.13) ○ ³	0.24 (0.13) ○ ³	0.28 (0.11) ○ ³	0.22 (0.10) ○ ³	0.62 (0.13) □ ³ λ ³ Υ ³ ◇ ³	0.46 (0.06) ◇ ¹	0.44 (0.10)	23.01	<0.001
A-C	0.29 (0.16)	0.27 (0.12)	0.24 (0.13)	0.27 (0.12)	0.38 (0.11)	0.24 (0.11)	0.30 (0.02)	2.16	0.056
A-M	0.33 (0.13) ○ ¹	0.23 (0.14) ○ ³	0.23 (0.10) ○ ³	0.21 (0.14) ○ ³	0.50 (0.11) □ ¹ λ ³ Υ ³ ◇ ³	0.31 (0.10)	0.18 (0.23) ○ ¹	10.95	<0.001
C-L	0.28 (0.15) ○ ³	0.28 (0.14) ○ ³	0.30 (0.12) ○ ³	0.34 (0.12) ○ ³	0.59 (0.12) □ ³ λ ³ Υ ³ ◇ ³	0.61 (0.01) □ ² λ ² Υ ² ◇ ¹	0.27 (0.23) ○ ¹	13.29	<0.001
C-C	0.29 (0.17)	0.38 (0.14)	0.43 (0.12)	0.39 (0.12)	0.38 (0.12)	0.28 (0.15)	0.26 (0.00)	1.74	0.122
C-M	0.15 (0.06) λ ² Υ ³ ○ ³	0.30 (0.11) □ ²	0.38 (0.10) □ ³ ◇ ³	0.21 (0.10) Υ ³ ○ ²	0.35 (0.13) □ ³ ◇ ²	0.31 (0.13)	0.20 (0.01)	8.41	<0.001
P-L	0.29 (0.12) ○ ³	0.26 (0.09) ○ ³	0.33 (0.11) ○ ³	0.25 (0.10) ○ ³	0.66 (0.07) □ ³ λ ³ Υ ³ ◇ ³	0.52 (0.01) □ ¹ λ ² ◇ ²	0.35 (0.00)	35.69	<0.001
P-C	0.26 (0.13) λ ¹ Υ ¹ ○ ¹	0.39 (0.11) □ ¹ ◇ ²	0.40 (0.07) □ ¹ ◇ ²	0.25 (0.14) λ ² Υ ² ○ ²	0.41 (0.11) □ ¹ ◇ ²	0.24 (0.07)	0.28 (0.23)	5.77	<0.001
P-M	0.17 (0.09) λ ¹ Υ ¹	0.33 (0.14) □ ¹	0.32 (0.12) □ ¹	0.29 (0.15)	0.27 (0.09)	0.34 (0.16)	0.17 (0.08)	2.79	0.016
ANOVA	F=4.72, <i>p</i> <0.001	F=4.12, <i>p</i> <0.001	F=5.56, <i>p</i> <0.001	F=4.88, <i>p</i> =0.004	F=2.68, <i>p</i> =0.010				

Table 6: Summary of discriminant function analysis.

								Structure Matrix				Functions at Centroids				
Region	Func	Wilks' Lambda	p value	Eigen value	% of Variance	Cumul %	Canonical Corr	BV/TV	Tb.N	DA	E	Homo	Pan	Gorilla	Pongo	Papio
A-L	1	0.05	0.00	5.13	76.31	76.31	0.91	0.89	-0.29	-0.73	-0.53	-3.72	0.33	-0.36	1.06	2.86
	2	0.33	0.00	1.19	17.75	94.06	0.74	0.41	-0.61	0.44	0.22	0.51	-0.31	0.14	-2.09	1.30
	3	0.71	0.00	0.40	5.89	99.95	0.53	0.01	0.19	0.49	-0.70	-0.50	0.64	0.78	-0.64	-0.47
	4	1.00	0.64	0.00	0.05	100.00	0.06	0.21	0.71	0.20	0.43	0.01	0.07	-0.09	-0.02	0.00
A-C	1	0.20	0.00	2.55	86.50	86.50	0.85	-0.41	0.09	0.97	0.19	2.70	0.12	-0.36	-0.88	-1.86
	2	0.71	0.00	0.35	11.95	98.45	0.51	0.71	-0.18	0.07	-0.32	-0.23	0.65	0.27	-1.13	0.07
	3	0.96	0.53	0.05	1.55	100.00	0.21	0.40	0.07	0.12	0.87	0.15	-0.10	-0.25	-0.17	0.31
	4	1.00	1.00	0.00	0.00	100.00	0.00	0.42	0.98	-0.19	-0.31	0.00	0.00	0.00	0.00	0.00
A-M	1	0.20	0.00	2.20	80.23	80.23	0.83	0.81	-0.49	-0.17	-0.52	-1.89	0.12	0.28	-1.09	2.31
	2	0.64	0.00	0.51	18.77	99.00	0.58	0.41	0.20	0.65	0.75	0.94	-0.61	-0.60	-0.51	0.69
	3	0.97	0.75	0.02	0.85	99.85	0.15	-0.20	0.19	0.63	-0.30	0.07	0.06	0.16	-0.30	-0.07
	4	1.00	0.58	0.00	0.15	100.00	0.06	0.37	0.82	-0.39	-0.28	0.00	0.09	-0.10	-0.03	0.00
C-L	1	0.09	0.00	3.31	72.09	72.09	0.88	0.87	-0.37	-0.58	-0.36	-2.88	0.37	0.00	-0.13	2.53
	2	0.39	0.00	1.02	22.22	94.31	0.71	0.20	-0.29	0.72	0.52	0.86	-0.04	-0.28	-1.98	0.91
	3	0.79	0.00	0.25	5.51	99.82	0.45	-0.25	-0.02	-0.38	0.76	0.29	-0.58	-0.52	0.54	0.45
	4	0.99	0.45	0.01	0.18	100.00	0.09	0.37	0.88	-0.04	0.12	0.01	0.11	-0.16	0.02	-0.01
C-C	1	0.18	0.00	2.09	74.60	74.60	0.82	-0.57	0.24	0.48	-0.09	2.17	-0.40	-0.37	0.81	-1.97
	2	0.57	0.00	0.65	23.09	97.69	0.63	0.36	-0.03	0.74	0.27	0.85	-0.46	0.28	-1.45	0.55
	3	0.94	0.34	0.04	1.60	99.29	0.21	0.53	0.94	-0.28	0.38	-0.01	0.32	0.00	-0.26	-0.17
	4	0.98	0.24	0.02	0.71	100.00	0.14	-0.52	-0.23	0.37	0.88	-0.06	-0.06	0.28	-0.01	-0.11
C-M	1	0.07	0.00	4.22	74.20	74.20	0.90	0.75	-0.36	0.16	-0.11	-1.01	-0.48	-0.60	-2.16	3.72
	2	0.35	0.00	1.12	19.73	93.93	0.73	-0.36	0.14	0.86	0.68	1.50	-0.02	0.32	-1.86	-0.36
	3	0.74	0.00	0.33	5.89	99.82	0.50	0.12	0.41	0.29	-0.59	0.59	-0.08	-1.08	0.38	0.16
	4	0.99	0.40	0.01	0.18	100.00	0.10	0.55	0.83	-0.39	0.42	-0.05	0.17	-0.08	-0.07	-0.03
P-L	1	0.07	0.00	4.60	75.14	75.14	0.91	0.87	-0.04	-0.53	-0.64	-3.23	0.54	-0.45	-0.18	3.12
	2	0.37	0.00	1.37	22.33	97.48	0.76	0.29	-0.27	0.14	0.70	1.25	-1.15	-0.67	-0.93	1.41
	3	0.86	0.03	0.14	2.26	99.74	0.35	0.40	0.72	0.34	0.26	0.14	0.39	-0.70	0.04	-0.02
	4	0.98	0.29	0.02	0.26	100.00	0.13	-0.01	-0.63	0.77	0.18	0.02	0.11	0.07	-0.26	-0.01
P-C	1	0.05	0.00	6.70	83.38	83.38	0.93	0.86	-0.16	-0.47	-0.19	-2.59	0.10	-1.45	-1.08	4.55

	2	0.38	0.00	1.04	12.97	96.35	0.71	0.20	0.08	0.79	0.29	1.33	-0.22	-0.07	-1.89	0.41
	3	0.77	0.00	0.25	3.10	99.45	0.45	0.13	0.95	-0.24	0.53	-0.20	0.84	-0.24	-0.41	-0.27
	4	0.96	0.08	0.04	0.55	100.00	0.21	-0.46	-0.25	0.30	0.77	-0.18	-0.01	0.40	-0.19	-0.02
P-M	1	0.07	0.00	4.63	78.16	78.16	0.91	0.86	-0.40	-0.01	0.03	-2.21	-0.16	-0.95	-0.79	3.83
	2	0.39	0.00	1.03	17.44	95.60	0.71	-0.03	-0.15	1.00	0.26	1.20	-0.10	0.06	-2.02	0.39
	3	0.78	0.00	0.19	3.26	98.86	0.40	0.26	0.84	0.08	0.58	-0.30	0.73	-0.10	-0.35	-0.21
	4	0.94	0.03	0.07	1.14	100.00	0.25	0.43	0.32	0.02	-0.77	0.21	0.08	-0.52	0.15	0.04

Table 7: Predicted group membership (percentage) by the discriminant function analysis. The highest percentage within each column is highlighted in bold.

Region		<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>	<i>Papio</i>	StW 102	StW 363	StW 486	TM 1517	KNM-ER 1464
A-L	<i>Homo</i>	94	5	14	0	0	6	1	4	96	2
	<i>Pan</i>	0	26	36	8	6	15	35	24	0	31
	<i>Gorilla</i>	6	47	43	8	0	78	32	69	4	66
	<i>Pongo</i>	0	16	7	75	13	0	31	0	0	1
	<i>Papio</i>	0	5	0	8	81	1	1	3	0	0
A-C	<i>Homo</i>	100	5	7	17	0	2	0	0	0	1
	<i>Pan</i>	0	53	29	17	6	61	0	19	35	59
	<i>Gorilla</i>	0	16	7	0	13	32	1	20	34	32
	<i>Pongo</i>	0	16	43	42	6	2	1	1	3	2
	<i>Papio</i>	0	11	14	25	75	2	98	60	28	6
A-M	<i>Homo</i>	63	11	0	33	0	0	4	0	0	0
	<i>Pan</i>	0	16	36	42	0	0	30	8	48	11
	<i>Gorilla</i>	0	32	21	0	19	1	26	7	42	12
	<i>Pongo</i>	38	26	29	25	0	0	39	2	5	2
	<i>Papio</i>	0	16	14	0	81	99	1	83	5	74
C-L	<i>Homo</i>	100	5	14	8	0	0	1	1	0	0
	<i>Pan</i>	0	42	50	8	6	4	23	19	48	23
	<i>Gorilla</i>	0	32	0	8	0	2	14	10	52	11
	<i>Pongo</i>	0	16	29	75	0	0	1	0	0	0
	<i>Papio</i>	0	5	7	0	94	95	61	69	0	66
C-C	<i>Homo</i>	94	0	14	25	0	0	0	0	0	0
	<i>Pan</i>	0	42	29	17	6	1	43	11	15	3
	<i>Gorilla</i>	6	42	21	8	25	5	12	43	32	6
	<i>Pongo</i>	0	16	14	50	6	0	5	1	1	0
	<i>Papio</i>	0	0	21	0	63	95	40	45	52	91
C-M	<i>Homo</i>	69	16	14	0	6	0	56	-	3	0
	<i>Pan</i>	6	42	14	17	0	0	12	-	61	6
	<i>Gorilla</i>	6	32	57	0	0	0	31	-	31	3
	<i>Pongo</i>	19	11	14	83	0	0	2	-	4	0
	<i>Papio</i>	0	0	0	0	94	100	0	-	0	90

P-L	<i>Homo</i>	100	0	7	8	0	14	2	0	-	0
	<i>Pan</i>	0	42	7	17	6	2	13	0	-	3
	<i>Gorilla</i>	0	11	50	25	6	39	9	0	-	7
	<i>Pongo</i>	0	37	36	50	0	4	17	0	-	2
	<i>Papio</i>	0	11	0	0	88	41	58	100	-	88
P-C	<i>Homo</i>	88	0	7	0	0	55	0	92	6	98
	<i>Pan</i>	0	84	29	8	6	5	72	0	5	0
	<i>Gorilla</i>	6	5	57	25	0	39	2	8	72	2
	<i>Pongo</i>	6	11	7	67	0	1	26	0	17	0
	<i>Papio</i>	0	0	0	0	94	0	0	0	0	0
P-M	<i>Homo</i>	75	11	21	0	0	40	22	-	85	72
	<i>Pan</i>	0	37	29	8	13	7	19	-	2	8
	<i>Gorilla</i>	25	32	36	8	0	53	55	-	13	20
	<i>Pongo</i>	0	16	14	83	6	1	4	-	1	0
	<i>Papio</i>	0	5	0	0	81	0	0	-	0	0

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10