A quantification of calcaneal lateral plantar process position with implications for bipedal locomotion in *Australopithecus*

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ABSTRACT

The evolution of bipedalism in the hominin lineage has shaped the posterior human calcaneus into a large, robust structure considered to be adaptive for dissipating peak compressive forces and energy during heel-strike. A unique anatomy thought to contribute to the human calcaneus and its function is the lateral plantar process (LPP). While it has long been known that humans possess a plantarly positioned LPP and apes possess a more dorsally positioned homologous structure, the relative position of the LPP and intraspecific variation of this structure have never been quantified. Here, we present a method for quantifying relative LPP position and find that, while variable, humans have a significantly more plantar position of the LPP than that found in the apes. Among extinct hominins, while the position of the LPP in *Australopithecus afarensis* falls within the human distribution, the LPP is more dorsally positioned in *Australopithecus sediba* and barely within the modern human range of variation. Results from a resampling procedure suggest that these differences can reflect either individual variation of a foot structure/function largely shared among *Australopithecus* species, or functionally distinct morphologies that reflect locomotor diversity in Plio-Pleistocene hominins. An implication of the latter possibility is that calcaneal changes adaptive for heel-striking bipedalism may have evolved independently in two different hominin lineages.

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1. Introduction

Scholars have identified many anatomical and morphological differences between the human calcaneus and that of our ape relatives (Weidenreich, 1923, 1940; Morton, 1935; Latimer and Lovejoy, 1989; Gebo, 1992; Gebo and Schwartz, 2006; Zipfel et al., 2011; Prang, 2015a). One such difference is the positioning of the processus lateralis, or lateral plantar process (LPP). In humans, the LPP occupies a plantar position, in which the medial and lateral plantar processes are often in roughly the same transverse plane, although the medial process is typically more plantar (Kirby et al., 1988). Both structures are thought to increase the surface area of the heel in contact with the ground during bipedal gait and increase the volume of the calcaneal tuber. A larger area of heel contact would lower peak compressive forces at heel strike, while volume increase may be an adaptation for energy absorption at, and immediately after, heel strike (Latimer and Lovejoy, 1989; Swanson et al., 2016). The heel of apes is quite different (Weidenreich, 1923; Latimer and Lovejoy, 1989; Gebo, 1992; Prang, 2015a). A region homologous to the LPP in humans can be palpated in the ape calcaneus and is in a relatively more dorsal position (Latimer and Lovejoy, 1989). Plantarly, the heel tapers to a narrow point, with only the medial plantar process occupying the plantar position. The medial plantar process is often beaked, a morphology suggested to occur with an enlarged superficial head of the flexor digitorum brevis, which is thought to be associated with pedal grasping (Sarmiento, 1983).

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Latimer and Lovejoy (1989) first described these anatomical differences as developmental shifts in the positioning of the apophyseal flange for the LPP. According to Latimer and Lovejoy (1989), these shifts result in different relative positions of three anatomical structures along the lateral side of the calcaneus: the peroneal trochlea (PT), retrotrochlear eminence (RE), and the LPP (Fig. 1). In humans, the PT comprises a variably defined trochlear process anteriorly adjacent to the RE, which serve as an insertion for the retinaculum of the peroneal tendons (Kelikian, 2011). A bony rugosity extends posteriorly to the LPP, which we here include as a part of the RE following the terminology of Latimer and Lovejoy (1989). In the apes, a human-like trochlear process is not seen, and a prominent, often knob-like, bony process is formed at the location of the peroneal tendon retinaculum insertion. Previous researchers have referred to this structure in apes as either the peroneal trochlea (e.g., Latimer and Lovejoy, 1989) or the peroneal tubercle (e.g., Gebo, 1992; Gebo and Schwartz, 2006), which we term the PT. In apes, the RE is a rugosity extending posteriorly from the PT along the long axis of the calcaneal body. It terminates in a dorsally positioned flange of bone homologous to the LPP. In humans, however, the RE is typically more diagonally oriented because the LPP is positioned plantarly. Even in infant calcanei, the apophyseal flanges for the LPP are already positioned dorsally in apes, and more plantarly in humans (Latimer and Lovejoy, 1989).

Latimer and Lovejoy (1989) hypothesized that the positioning of the calcaneal LPP represented an important skeletal adaptation for bipedalism, with important implications for the hominin fossil record. Based on three adult calcanei from Hadar, Ethiopia (A.L. 333-8,

-37, -55), Latimer and Lovejoy (1989) concluded that *Australopithecus afarensis* had evolved the human-like positioning of the LPP by at least 3.2 Ma. Despite the human-like position of the LPP, it has also been noted that the *A. afarensis* LPP is relatively small (Latimer et al., 1982; Stern and Susman, 1983; Susman et al., 1984). Weidenreich (1923, 1940) and others (Lewis, 1983; Susman et al., 1984) have suggested that the LPP and PT may share a developmental connection resulting in a large PT and small LPP in the apes, but a small PT and large LPP in humans. This hypothesis is relevant to understanding the functional anatomy of *A. afarensis*, since this hominin possessed a large PT and a small LPP (like an ape), but a human-like positioning of the LPP. Latimer and Lovejoy (1989) countered that the PT and LPP are not developmentally linked and that their relative sizes are independent. This hypothesis was recently tested in a large sample of humans and no such inverse relationship was found between the PT and the LPP (Gill et al., 2014). Instead, it appears that LPP size in humans is correlated with overall body size (Gill et al., 2014). *Australopithecus afarensis* may therefore have had a relatively small LPP, because most individuals were relatively small-bodied (~25—64 kg) compared to modern humans (Grabowski et al., 2015). Although it retained a large and primitive PT, the proximal tuber of *A. afarensis* with a low position of the LPP appears quite human-like, implying adaptations for human-like heel striking bipedalism by 3.2 Ma.

Given this early (~3.2 Ma) evolution of a human-like position of the LPP, it was surprising to discover an apparently more ape-like anatomy of the proximal tuber in the calcaneus of *Australopithecus sediba* (Zipfel et al., 2011; Prang, 2015a), a hominin
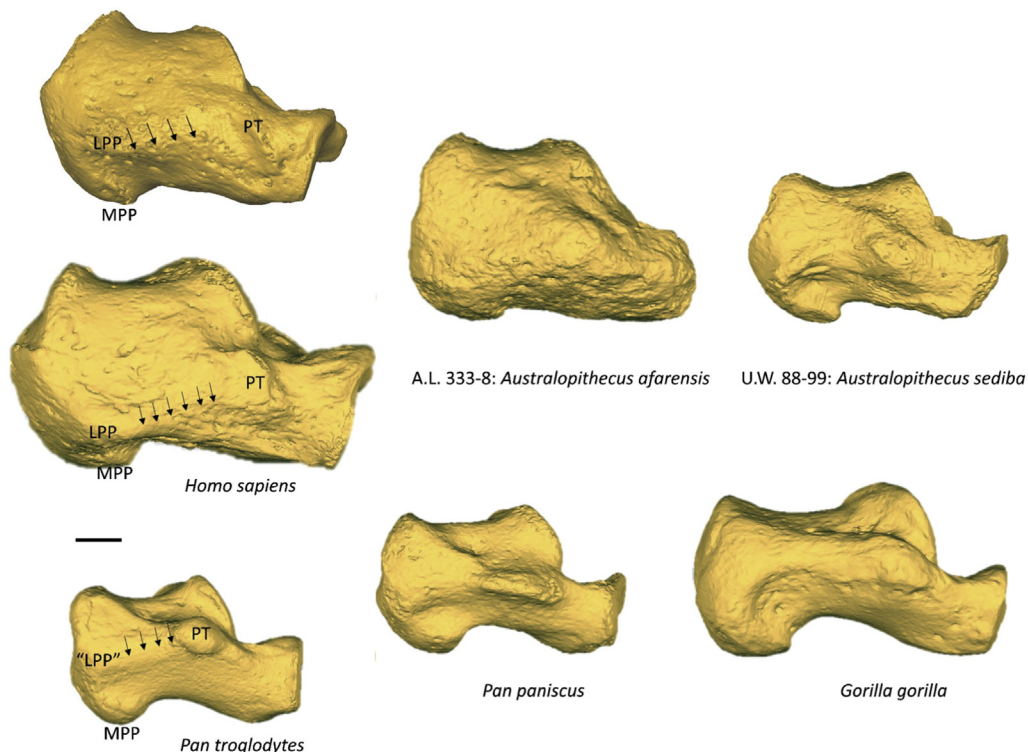

Figure 1. Calcanei in lateral view illustrating the anatomies of importance in this study. In the two human calcanei (top and middle left), notice that a ridge of bone termed the retrotrochlear eminence (delineated with arrows) connects the peroneal trochlea (PT) to the lateral plantar process (LPP). Note the flat vertical lateral surface of the tuber, the prominent PT process, and the weak posteroinferior extension of the retrotrochlear eminence. Medial and plantar to the LPP is the medial plantar process (MPP). Note the variation in LPP position. The calcaneus of *Australopithecus afarensis* (A.L. 333-8) possesses a plantarly positioned LPP and downward deflecting retrotrochlear eminence. The latter, together with the LPP, delineate the plantar surface of the posterior calcaneus. The chimpanzee (bottom left) also possesses a ridge of bone (retrotrochlear eminence, delineated with arrows) connecting the PT to a bony protuberance homologous to the LPP. However, these structures are more dorsally positioned and the LPP and MPP are separated by a strong plantolaterally oriented surface or concavity (especially in gorillas). Though there are important differences as well, the general anatomy of the posterior calcaneal tuber is similar in the chimpanzee, bonobo, and gorilla. *Australopithecus sediba* (U.W. 88-99) appears to have a more dorsally positioned LPP and the concavity inferior to the LPP is reminiscent of that found in the apes. However, superior to the LPP is a flat vertical lateral surface as found in the Hadar calcaneus. Scale bar is 10 mm.

species currently known from deposits over a million years younger than *A. afarensis* (Pickering et al., 2011). Compared to known examples of *A. afarensis*, the calcaneus of the adult female MH2 (U.W. 88-99) possesses a dorsally positioned LPP connected to a large PT via a more horizontally oriented RE. Plantarly, the medial plantar process is beak-shaped, as is often the case in modern apes and less frequently in humans. Prang (2015a) found that the size-standardized cross-sectional area of the proximal tuber of U.W. 88-99 is within the ape range and well outside the human distribution, whereas the most complete calcaneus of *A. afarensis* (A.L. 333-8) is human-like in this metric—a finding consistent with Latimer and Lovejoy (1989).

However, there are still questions regarding the functional significance of the LPP. Kirby et al. (1988) found that weight is centered over the medial plantar process in standing humans ($n = 100$), and that the LPP serves only a minor weight-bearing role. They suggested that the LPP may help mitigate peak compressive forces during initial heel-contact, when the foot is most inverted (Kirby et al., 1988). Whether this is accurate or not remains unknown, and is worthy of future study. Rather than the LPP solely serving to increase the plantar surface area, Latimer and Lovejoy (1989) hypothesized that the plantar occurrence of this structure was a part of a general restructuring of the posterior calcaneus including an increase of tuber volume. The latter is the more functionally relevant attribute related with energy dissipation (Latimer and Lovejoy, 1989). Therefore, further considerations of the slender but long U.W. 88-99 calcaneus of *A. sediba* are necessary, because energy absorption capacity directly relates to the volume of cancellous bone available for deformation (Latimer and Lovejoy, 1989; Currey, 2002). Relative to body mass, tuber volume of U.W. 88-99 may differ less from the A.L. 333-8 condition (Zipfel et al., 2011:Table S7; Prang, 2015a:Table 3). Compared with apes, this suggests a greater energy dissipation capacity of the *A. sediba* calcaneus despite its slenderness. This is consistent with *A. sediba* being a bipedal hominin, although perhaps possessing a kinematically different form of bipedalism from that of *A. afarensis* (DeSilva et al., 2013). A calcaneal apophysis of MH1 (U.W. 88-113) is also mediolaterally narrow and preserves a dorsally positioned apophyseal flange, indicating that MH2 is not aberrant in calcaneal morphology (Zipfel et al., 2011).

Although differences between the calcanei of *A. sediba* and *A. afarensis* have been identified (Zipfel et al., 2011; Prang, 2015a, b; 2016a, b), such as LPP position (Zipfel et al., 2011; Fig. 1), assessments of this particular anatomy remain qualitative. Therefore, quantitative comparisons that take into account extant hominoid variation are needed. In this study, we quantify the dorsoplantar position of the LPP in great apes, and in different populations of humans, including those that were habitually shod and presumably unshod to varying degrees. Using this comparative sample, we then test the hypothesis that there is no difference in LPP position between *A. sediba* and *A. afarensis*.

2. Materials and methods

2.1. Specimen selection

Extant non-pathological adult ape dry-bone calcanei were studied at the following institutions (Table 1): the Harvard Museum of Comparative Zoology, Cambridge, MA, USA; the American Museum of Natural History, New York, NY, USA; and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. Calcanei of *Homo sapiens* were studied at: Harvard University's Peabody Museum of Archaeology and Ethnology (Mérida, Maya period from Yucatan, Mexico); the R.A. Dart Collection, University of the Witwatersrand, Johannesburg, South Africa

Table 1
Extant ape calcanei measured in this study ($n = 67$).

Species	Male	Female	Sex unknown	Total sample size
Gorilla beringei beringei	5	2	–	7
Gorilla gorilla gorilla	14	11	2	27
Pan paniscus	2	2	–	4
Pan troglodytes	15	6	3	24
Pongo pygmaeus	1	1	3	5

(Zulu)—ethics waiver number W-CJ-140604-1; and the Florisbad Quaternary Research Station, National Museum, Bloemfontein, South Africa (presumably unshod, prepastoral South Africans). Microcomputed tomography (μCT) scan images were taken of prehistoric Japanese Jomon (sampled materials predominantly from 3000 to 4000 BP), presumably unshod or minimally shod hunter-gatherer-fishers, and modern Japanese *H. sapiens* calcanei at the University Museum, The University of Tokyo, Japan (Table 2). Original calcanei of *A. afarensis* and *A. sediba* were studied at the Authority for Research and Conservation of Cultural Heritage (Addis Ababa, Ethiopia) and the Evolutionary Studies Institute (Johannesburg, South Africa), respectively, although the measurements used in this study were collected on high-quality research casts as described below.

2.2. Anatomical measurements

It is difficult to standardize calcaneal orientation. An isolated calcaneus placed in an inverted set may give the appearance of having a plantarly positioned LPP whereas an everted calcaneus would yield a more dorsal LPP. In order to objectively quantify LPP position, all dry-bone calcanei were articulated with their associated tali and oriented such that, in frontal view, the superior margin of the talar trochlea was parallel to the transverse plane. The bones were articulated with museum putty with the subtalar joint placed in maximum congruence, and then anchored in sand and photographed in posterior view (analogous to Fig. 2). The Jomon and modern Japanese bones were μCT scanned in articulated positions, and posterior view surface renders were obtained.

The original *A. sediba* fossils U.W. 88-98 (talus) and U.W. 88-99 (calcaneus) remain physically cemented together in a slightly shifted position from proper anatomical position. These fossils were μCT scanned using a Nikon Metrology XTH 225/320 LC dual source industrial CT system at the Palaeosciences Centre Micro-focus X-ray CT facility at the University of the Witwatersrand, Johannesburg, South Africa. The scan parameters and segmentation procedure are described elsewhere (DeSilva et al., in press). 3D renderings of the talus and calcaneus from Malapa were articulated in the same manner as the extant specimens. The Malapa specimens went through the additional steps of segmentation of the μCT scans and 3D rendering. The initially available 3D renderings (based on medical CT scan data of lower resolution; Berger et al., 2010; Zipfel et al., 2011) showed some interarticular incongruence, introducing the potential for error. This resulted in both a preliminary assessment of a particularly high LPP position (Boyle et al., 2015) and inter-trial discrepancies stemming from apparent

Table 2
Calcanei of *Homo sapiens* measured in this study ($n = 154$).

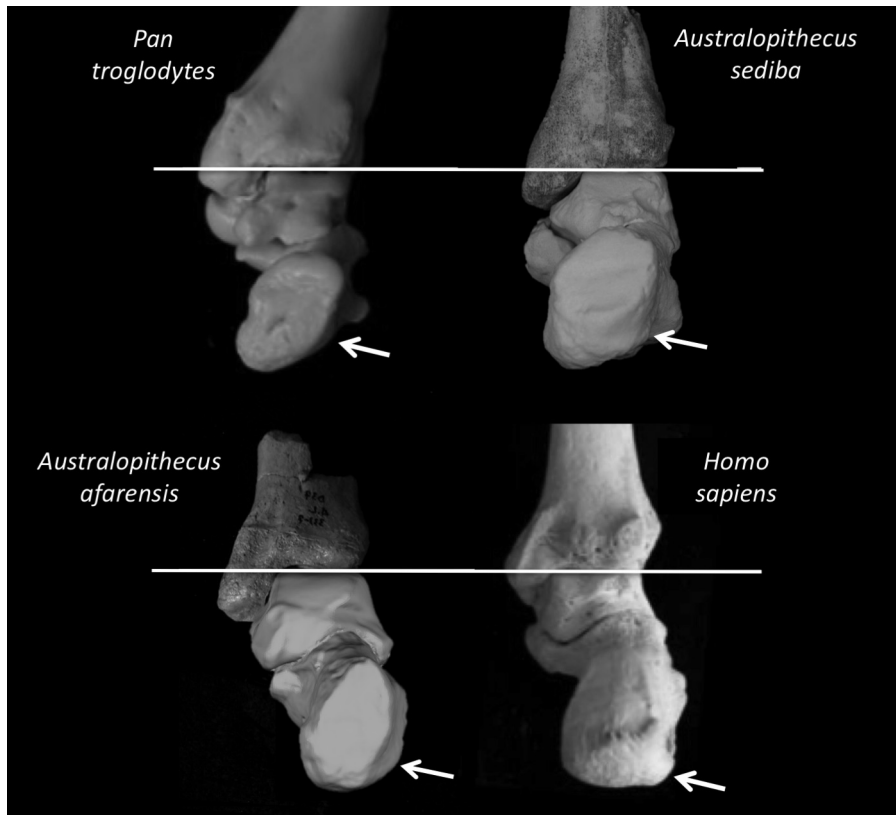| Population	Male	Female	Sex unknown	Total sample size
Jomon, Prehistoric Japanese	–	–	23	23
Modern Japanese	10	12	–	22
Mérida	24	24	2	50
Prepastoral South African	–	–	22	22
Zulu	20	17	–	37

Figure 2. Posterior views of articulated calcanei, tali, and tibiae for a chimpanzee (top left), *A. sediba* (top right), *A. afarensis* (bottom left), and a human (bottom right). Note that while the tibia, talus, and calcaneus are from the same individual in the chimpanzee, *A. sediba*, and modern humans, *A. afarensis* is a composite of individuals of similar size (A.L. 333-7 tibia, image reversed; A.L. 333-147 talus with mirrored A.L. 333-55 calcaneus). White arrows indicate LPP positions and white lines denote the transverse plane of the ankle joint. Note the plantar position of the LPP in the human and in *A. afarensis* and the more dorsal position of the LPP in the chimpanzee and *A. sediba*. All specimens scaled so that the mediolateral width of the talar trochlea is approximately the same.

limitations of the digital segmentation. In this study, we therefore used the newly acquired set of higher resolution μCT scans. We also took the additionally step to examine inter-observer replicability of articulating the digitally derived surfaces. This was done by having the six authors each independently follow the protocol described above to measure the position of the LPP. The average of these six measurements and the range are provided in the results section.

Linear measurements (mm) were taken on the photograph of each specimen using ImageJ Version 1.46r (Rasband, 1997), or equivalent metrics were taken on surface rendered images generated from the μCT scans. Dorsoplantar calcaneal height was measured as the projected distance between the dorsal tip of the proximal calcaneal tuber and the plantar most part of the bone (typically the base of the medial plantar process). The midpoint of the LPP was identified as the most laterally protruding point on the lateral aspect of the tuber and demarcated with a horizontal line. The height of the LPP was obtained by measuring the distance from this line to the plantar base of the calcaneus, which was usually level with the medial plantar process. In the event the height of the midpoint of the LPP would be below the plantar base of the calcaneus, and therefore lower than the medial plantar process, a negative value of the LPP measurement would be observed. A ratio between dorsoplantar calcaneal height and height of the midpoint of the LPP was calculated as the relative height of the LPP, with high values indicating a dorsally positioned LPP, and ratios closer to 0.0 indicating a more plantar LPP position (Fig. 3A). All ratios are rounded to one decimal place.

We found that interobserver differences in evaluating *A. sediba* LPP position largely stem from slight differences in how each

investigator articulated the talus and calcaneus. The calcaneus in a more everted or inverted position would result in a higher or lower LPP position, respectively. Therefore, we conducted an additional simulation test to see 1) if the range of articulations were comparable in congruency regardless of slight differences in articulation, or 2) if congruency tended to change according to degree of calcaneal eversion/inversion. For this purpose, one of the authors (G.S.) made additional sets of articulated talus and calcaneus with museum putty, at relatively inverted and everted calcaneal positions. These articulated sets were μCT scanned, and the digital models were used in examining actual interarticular congruence between the talocalcaneal facets. This was done quantitatively by using the 'mesh deviation' tool of the software Geomagic XOS 2014 (3D Systems, Rock Hill, South Carolina). This tool calculates the minimum distance from each point (polygon node) of a designated surface of the target model (e.g., the talocalcaneal facet of the talus) to the corresponding surface of the reference model (e.g., the talocalcaneal facet of the calcaneus). Further details of this numerical method are outlined in Figure 4.

Fossil calcanei from Hadar, A.L. 333-8 and A.L. 333-55, were considered sufficiently well-preserved to apply the above method of characterizing the lateral plantar process position. These two fossils have been considered to represent different individuals (Latimer and Lovejoy, 1989), and were entered separately in our statistical analysis. However, the Hadar calcanei may be from a single individual (antimeres), the possibility of which we discuss below; A.L. 333-8 (right side) has a slightly eroded LPP and A.L. 333-55 (left side) has a considerably abraded peroneal trochlear region. In either case, these calcanei each lack an associated talus. We
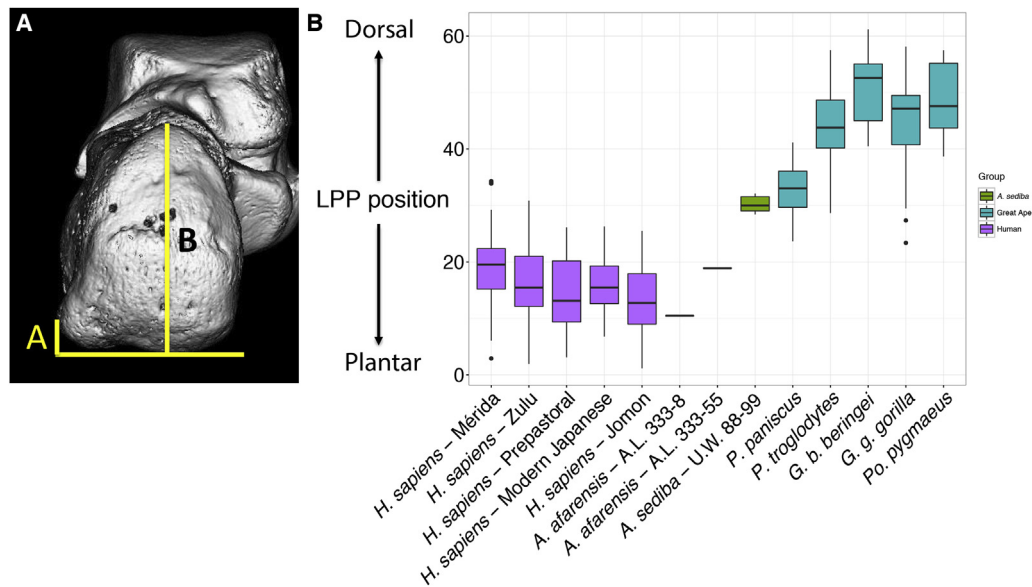
Figure 3. A) Calcaneal calcaneal measurement taken to quantify the position of the lateral plantar process (LPP). All calcanei were articulated with their associated tali, and measurements were taken with the talar trochlea kept parallel to the transverse plane. LPP position is quantified as a ratio between height of the midpoint (or apex) of the LPP ('A') and height of the tuber ('B'). B) Boxplots showing the dorsoplantar positions of the lateral plantar process in humans, apes, and australopiths. Boxes span the interquartile ranges, with the horizontal center lines indicating median values. Whiskers indicate sample range, excluding outliers (dots). While there exists considerable variation in LPP position across populations and taxa, there is minimal overlap between apes and humans. Note that the two calcanei from *A. afarensis* fall within the range of distribution of modern humans and are entirely outside the range of distribution in modern apes. Note as well that the calcaneus from *A. sediba* has an LPP that is within the range of distribution found in modern apes, and at the margins of the range found in modern humans.
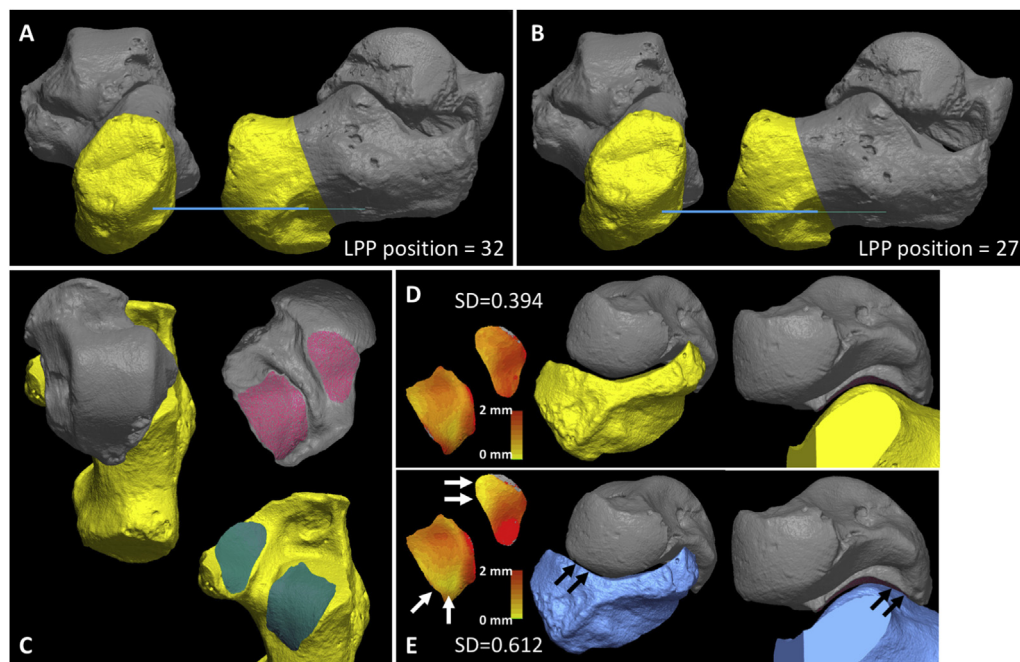

Figure 4. Alternative articulations of the *A. sediba* talus and calcaneus, and a quantitative evaluation of interarticular congruency. Five alternative articulations were investigated, two of which are shown here, the calcaneus in most everted (A and E) and inverted (B and D) positions. In panels A and B, the posterior tuber is shown in yellow, and a horizontal line runs through mid-LPP position. Congruency of the subtalar articulation was numerically evaluated using the Geomagic XOS 2014 software 'mesh deviation' tool. Interarticular distances are calculated as minimum distances from each polygon node of the target shell (talus) to the reference shell (calcaneus). Panel C shows the masked areas of the anterior and posterior calcaneal facets that were used in deriving the intermesh distances and how they correspond to the calcaneus in position. The numbers of measured points on the talus were 20667 and 20474, respectively, in the panels D and E trials. The numbers of points differed between trials because distances at the articular margins were not calculated (gray areas in the color maps). The mesh deviation tool calculates the average and standard deviation (SD) of the interarticular distances, and visualizes this in graded color from 0 mm (green) to 2 mm (red). To make things comparable among articulated sets, the following procedure was followed. Keeping the talus fixed, we translated the calcaneal shell (i.e., without rotating it) so that each articulation had (near-) identical average interarticular distances of 1.0 mm for the posterior talar facet. We then searched for the calcaneal position (without rotation) that retains the average inter-articular distance of 1.0 mm, and at the same time gives the lowest SD between the subtalar articular surfaces. This was done by iterative translations in three directions at increments of 0.1 mm. A higher SD shows that the interarticular distances between the two bones vary more, that is, the opposing articular surfaces are less congruent. Panels D and E show that congruency is better in the relatively inverted position (B and D), and that in the everted position (A and E) the articular surfaces start to be impacted (pushed against each other) anteriorly and posteriorly. This is seen both in the oblique views of the articulated talus and calcaneus (arrows indicate impacted areas) and in the color graded interarticular distance maps. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

therefore used A.L. 333-147, a right *A. afarensis* talus of comparable size and geological age as A.L. 333-8 and A.L. 333-55 (Ward et al., 2012), with the understanding that these bones probably do not derive from the same individual. However, A.L. 333-147 and its mirrored 3D print articulate reasonably well with A.L. 333-8 and A.L. 333-55, respectively. The A.L. 333-37 calcaneus was not included in this study, as it does not preserve enough of the talar facets to articulate a talus and use the methods described here. Qualitatively, however, A.L. 333-37 is similar to, though smaller than, the other calcanei.

2.3. Statistical analysis

We used a one-way analysis of variance (ANOVA) in RStudio v0.99.485 (RStudio Team, 2015) with Tukey's post-hoc correction to identify significant group differences in LPP position among the human populations. Differences among the ape species were determined with a Kruskal-Wallis test with a post-hoc Dunn test for multiple comparisons. The difference between the human average and the ape average was determined with a Welch's t-test. To test the probability of sampling three calcanei with such LPP variation as that found in fossil *Australopithecus* spp., we employed a resampling with replacement approach in Excel (Resampling Stats, 2013). LPP position measurements were taken on 154 human calcanei (Table 2). However, the hominin fossil record consists of only three well-preserved calcanei (two from Hadar, and one from Malapa). To statistically model this, and to use modern human variation to assess how different the Hadar calcanei are from the Malapa calcaneus, we first averaged the LPP values measured from two randomly selected (with replacement) human calcanei. Next, out of the same human calcaneus sample, we randomly sampled a single human calcaneus and calculated the absolute value of the difference in LPP position in this single calcaneus from the average of the two initially sampled. This value is the difference in LPP position when, out of 154 human calcanei, just three are sampled and compared (average of two against the third). This exercise was then repeated with replacement 5000 times to create a distribution of expected LPP differences if only three calcanei are sampled. The actual difference between the Hadar LPP average position and the Malapa LPP position was then compared to this resampled distribution of humans, and the process was repeated using data from chimpanzees and from gorillas. The same resampling approach was repeated on the entirety of the ape dataset to test whether the calcaneal differences found in *A. afarensis* and *A. sediba* could be sampled from a mixed assemblage of calcanei from different ape species. Finally, the resampling procedure was used on the entire dataset such that two human calcanei were randomly selected and compared with one randomly selected ape calcaneus. The differences between the LPP positions were calculated and repeated with replacement 5000 times. It is important to recognize that this statistical procedure only examined LPP position and did not include additional information about calcaneal morphology, nor did it include information about geological age, geographical position, or taxonomic status.

3. Results

Results from the quantification of LPP position are summarized in Table 3 and illustrated in Figure 3B. Modern humans exhibit considerable variation in LPP position (range = 1.1–34.3). We did not obtain any negative measurements, meaning that the mid-LPP is always more dorsal than the medial plantar process, consistent with the findings of Kirby et al. (1988). Most of the sampled populations have, on average, statistically indistinguishable LPP positions. Only the Mérida population differs in having a more dorsally positioned LPP than Jomon ($p = 0.003$) and from prepastoral South African populations ($p = 0.021$). The average human LPP position (16.3 ± 6.6) is significantly ($p < 0.0001$) more plantarly positioned than the average great ape LPP (44.5 ± 8.4). Great apes (range = 23.4–61.2) demonstrate slightly more variation in LPP position than humans. On average, ape calcanei possess a statistically similar dorsally positioned LPP, with the exception of *Pan paniscus*, which differs from *Pan troglodytes* ($p = 0.017$), from *Gorilla beringei beringei* ($p = 0.001$), from *Gorilla gorilla gorilla* ($p = 0.009$), and from *Pongo pygmaeus* ($p = 0.007$). This finding warrants further investigation with a larger sample of *P. paniscus*.

The *A. afarensis* calcanei are human-like in LPP position, comparable to the human population means. The A.L. 333-55 calcaneus, with an intact LPP region, has a LPP position of 18.9. In A.L. 333-8, LPP position was estimated to be 10.5, although the exact position of the LPP is difficult to discern and its value could have been slightly higher.

The average of independent measurements taken by each of the authors of LPP position in *A. sediba* is 30.2 with a range of 28.1–32.1. Our metric evaluation of actual congruence between the opposing articular surfaces of the two bones showed that congruency declines as the calcaneus is articulated in more everted positions (at LPP positions over 30); that is, the anterior portion of the anterior talar facet and the posterior-most posterior talar facet get increasingly impacted (Fig. 4). The interobserver average of *A. sediba* (30.2) is at the upper end of the human range. It is also within the low end of the ape range and close to the mean of four *Pan paniscus* specimens. The absolute difference in LPP positioning between the average of the two measured Hadar calcanei and the Malapa calcaneus is 15.5.

Table 3
Descriptive statistics of the calcaneal lateral plantar process (LPP) position for all human populations and ape species included in this study, as well as for two australopith species.

Population/Species	*n*	Mean LPP position	Standard deviation	Range[a]
G. b. beringei	7	50.6	7.4	40.5–61.2
G. g. gorilla	27	44.5	8.4	23.4–58.1
P. paniscus	4	32.7	7.2	23.6–41.2
P. troglodytes	24	43.9	7.2	28.7–57.5
Po. pygmaeus	5	48.5	7.8	38.7–57.5
H. sapiens (Jomon, Prehistoric Japanese)	23	13.2	6.7	1.1–25.5
H. sapiens (modern Japanese)	22	15.7	4.9	6.8–26.3
H. sapiens (Mérida)	50	19.1	6.3	2.9–34.3
H. sapiens (prepastoral South African)	22	14.1	6.5	3.1–26.1
H. sapiens (Zulu)	37	16.4	6.6	1.9–30.9
A. afarensis (Hadar)	2	14.7	5.9	10.5–18.9
A. sediba (Malapa)	1	30.2	1.8	28.1–32.1

[a] Range for *A. sediba* indicates the range of six independent measurements made by the coauthors.

Resampling with replacement from a large collection of human calcanei from diverse populations yielded an average difference between randomly selected calcanei of 6.4 ± 4.9. In a resampled collection of 5000 human calcanei, it was unlikely ($p = 0.056$) but statistically possible for samples to exceed the difference between the Hadar and Malapa calcanei (Fig. 5A). The probabilities of sampling such differences were higher within the more variable chimpanzee ($p = 0.075$; Fig. 5B) and lowland gorilla ($p = 0.129$; Fig. 5C) samples. We also calculated the same probability ($p = 0.129$) of sampling the LPP differences between the Hadar and Malapa calcanei in the combined collection of all ape calcanei (Fig. 5D). The probability of sampling two human calcanei and one randomly sampled ape calcaneus with the LPP positional differences as large or larger than found between the fossils from Hadar and Malapa is high ($p = 0.899$; Fig. 5E).

4. Discussion

4.1. LPP position in modern humans and great apes

Humans are variable in lateral plantar process position, although the mean LPP position in the human calcaneus is significantly more plantar than that of apes. It should be noted that, in humans, our metric of LPP position is influenced by both position and size of the LPP. This is because we measured LPP position at the center of its outer surface, and therefore the recorded LPP position will be displaced more inferiorly in the calcanei with more inferolaterally protuberant LPPs. In modern humans, considerable variation is seen in LPP size, from a localized, slight prominence to a more massive protuberance. If LPP position were to be measured at a position corresponding to its original apophyseal surface, its value may differ either minimally or substantially (average LPP position difference was 6.4 in 10 modern Japanese examples). Thus, the human-ape differences in measured LPP position are based on both dorsoplantar LPP position and extent of inferolateral LPP projection. This is of significance because all known calcanei of A. afarensis and A. sediba exhibit minimal or little projection of the LPP, and hence will tend to exhibit higher LPP values than in modern humans when LPP position is equivalent. This observation likely explains why the small-bodied human population from Mérida, Mexico possesses the highest LPP values among the humans included in this study.

The 'LPP' position in great apes is also variable, as the species studied here present an extensive range of dorsal positions. In fact, the range of variation in G. g. gorilla exceeds that demonstrated in humans. It should be noted that when calcanei are oriented by the method used in the present study (trochlear surface of the articulated talus horizontal), ape calcanei usually have tubers that are considerably inverted, whereas the calcanei of modern humans, A. afarensis and A. sediba exhibit vertical to only weakly inverted tubers. Since an inverted calcaneus results in a lower LPP position, strong inversion may yield some of the lower LPP positions
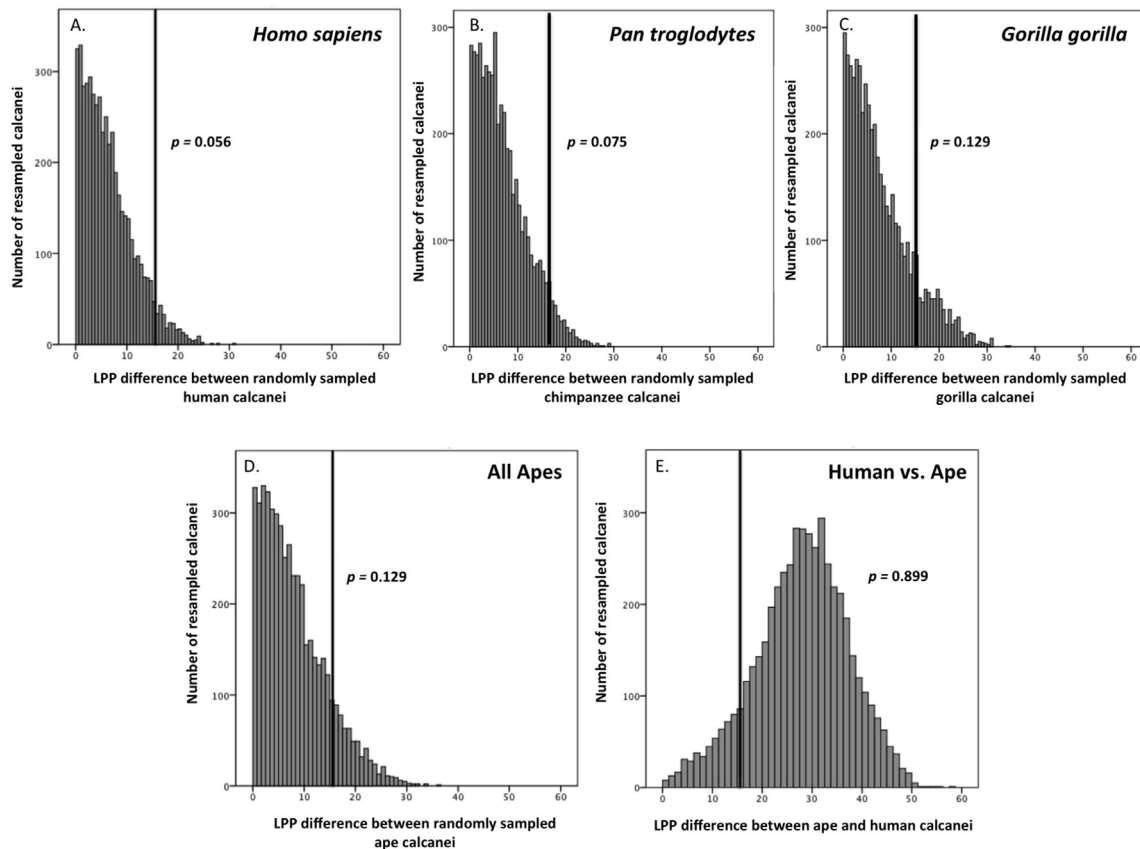

Figure 5. Results of the resampling procedures. In all graphs, the absolute difference in LPP position between the resampled calcanei is on the x-axis and the number of resampled calcanei (out of 5000) which possess that magnitude of LPP position difference are plotted along the y-axis. The solid black vertical line in all three graphs is the quantified difference (15.5) in LPP position between the Hadar (average) and Malapa calcanei. A–C) The probability of sampling calcanei with such different LPP positions from a human collection is statistically unlikely (A; $p = 0.056$), but is slightly higher in a chimpanzee sample (B; $p = 0.075$) and a gorilla sample (C; $p = 0.129$). D) The probability of sampling calcanei with such different LPP positions as Hadar (average) and Malapa from a combined species sample of apes is similarly high ($p = 0.129$). E) The LPP position difference between the Hadar (average) and Malapa calcanei falls well within the distribution of calcanei LPP differences between one sample extracted from humans and the other from apes ($p = 0.899$).

recorded in the apes. Although there are no significant differences between *P. troglodytes* and *G. g. gorilla*, *P. paniscus* was found to possess calcanei with significantly more plantar LPPs than all other ape species, although we tentatively attribute this result as a consequence of the small sample size (*n* = 4). While interspecific variation is expected, exactly how LPP position contributes to locomotor differences among ape taxa is again not clear. Differences in LPP position could have functional consequences when loading the foot during both bipedal and quadrupedal locomotion, but these gait differences will also be influenced by anatomy in other regions of the foot and the rest of the skeleton. Due to the gracility of the LPP homologue in apes, this feature probably does not contribute to dissipating forces or absorbing energy. The medial plantar process, which comprises a large part of the calcaneal tuber in apes and has more extensive contact with substrates, is likely more functionally relevant during terrestrial locomotion and climbing.

While we acknowledge considerable intraspecific variation in calcaneal geometry in humans and the apes examined in this study, our findings also support the observation that fundamental differences in calcaneal structure exist between humans and the great apes (Figs. 1 and 2). Although this has been known for some time (Weidenreich, 1923; Morton, 1935) and qualitatively described in the context of foot evolution (Latimer and Lovejoy, 1989), this is the first study to quantify the relative position of the LPP in humans and apes. There is a notable difference in LPP position between humans and apes, with minimal overlap between the extremes of the two groups (Fig. 3B). In humans, the low LPP position is a part of a calcaneal structure that includes a superoinferiorly tall calcaneal body and a variably developed RE connected (or juxtaposed) to a typically well-developed LPP. This structural package is associated with an increase of the volume of the calcaneus, considered essential in dissipating load and absorbing energy during heel-striking bipedalism (Latimer and Lovejoy, 1989; Swanson et al., 2016). As part of this morphological package, two distinct calcaneal surfaces are delineated or separated by the RE and LPP. An extensive planar surface occurs above the RE/LPP, forming the lateral face of the posterior calcaneus, while a plantar (or infero-lateral) surface is delineated below the RE/LPP (Fig. 1). In humans, in addition to LPP position, the size and inferolateral prominence of the LPP contribute to both calcaneal volume increase and further plantar disposition of the plantar surface. The abductor digiti minimi and the short digital flexors (quadratus plantae and flexor digitorum brevis) originate on this surface. The plantar disposition of the intrinsic foot muscles enables them to contribute to arch support and in controlling forefoot placements as suggested from known muscle recruiting patterns (Reeser et al., 1983; Kelley et al., 2012; McKeon et al., 2015).

4.2. Implications of LPP position in Australopithecus

The results of the resampling procedure (Fig. 5) can be evaluated with the above considerations as background. If the quantification of LPP position presented here reasonably represents variation in *A. afarensis*, then it is possible, albeit statistically unlikely, that calcanei exhibiting LPP positional differences as large as seen between *A. afarensis* and *A. sediba* would be sampled from a functionally restricted single species distribution. While *A. afarensis* is more human-like in its LPP positioning, *A. sediba* falls within the lower range of values in *Pan* and on the fringe of the upper range of modern humans (Fig. 3B). However, given the minimally developed LPP in *A. sediba*, LPP position itself may be better considered to lie within the upper range of human variation. It is the combination of LPP position and minimal extent that makes the *A. sediba* calcaneus an outlier when compared with that of humans.

There are three ways to interpret these findings. First, the Malapa and Hadar calcanei may simply be sampling the normal, functionally irrelevant range of variation found in australopith LPP position in the Plio-Pleistocene. Our resampling results indicate that, on statistical grounds (*p* = 0.056), it is possible to sample such distinct LPP positions from a sample of modern humans or single species of apes (*p* = 0.075 with chimpanzees and *p* = 0.129 with lowland gorillas). One could conclude, therefore, that the difference in LPP position between the Malapa and Hadar calcanei simply reflects individual variation in related species with similar foot structures. Moreover, if A.L. 333-8 and A.L. 333-55 are antimeres of the same individual (Fig. 6), this would alter the resampling statistics and make it even more likely to sample such calcanei from a single population of human calcanei (*p* = 0.11). The calcaneus of *A. sediba* does exhibit shared structural similarities with that of *A. afarensis*, such as a tall lateral calcaneal surface dominated by a centrally located PT and a RE that extends posteriorly to the LPP, which together separate the posterior calcaneus into two distinct faces (Fig. 1). A well-developed flat triangular surface occurs superior to the RE/LPP and forms the vertical lateral surface of the middle to posterior tuber (Latimer and Lovejoy, 1989). This surface is relatively confined in the *A. sediba* calcaneus because of its more superior LPP position. The difference between the Malapa and Hadar calcanei in this feature parallels the difference seen between human individuals with higher and lower LPP positions (Fig. 1). A second planar or concave (in *A. sediba*) surface occurs inferior to the RE/LPP, and faces more plantar than the lateral tuber surface. The occurrence of these two separate faces is shared by human calcanei, although, in humans, the lateral surface is typically more extensive due to a reduced PT and an inferolaterally projecting LPP. This pattern, shared by human and the australopith calcanei, can be interpreted as a consequence of a superoinferior expansion of the calcaneal body accompanied by plantar migration of the LPP anlagen during development (Latimer and Lovejoy, 1989). Therefore, despite the higher LPP position of the Malapa calcaneus, two of us (G.S. and T.S.) regard it to exhibit functionally relevant resemblance to the Hadar calcaneus rather than to those of apes; hence it is considered plausible that *A. afarensis* and *A. sediba* calcanei shared a common structural bauplan committed to heel-striking bipedalism, especially given the many other anatomies observed in *A. sediba* (e.g., orthogonal tibial plafond, bicondylar angle, stout ilia, lordotic lumbar region) consistent with human-like upright walking (Berger et al., 2010; Kibii et al., 2011; Zipfel et al., 2011; DeSilva et al., 2013; Williams et al., 2013). While the other authors (E.B., E.M., B.Z., J.D.) regard this interpretation of the data as possible, and testable with the recovery of additional fossil material, these authors consider the two alternative explanations presented below as more probable.

The second way to interpret these findings is that these morphological differences in the Malapa and Hadar calcanei reflect plasticity in the heel of individuals in australopith populations that face different ecological challenges. Under this interpretation, the general australopith pedal skeleton remains conserved, but population (or species)-level variation reflect developmental adaptations to substrate differences and diverse locomotor strategies in *A. afarensis* and *A. sediba*. In other words, while the Hadar australopiths were primarily terrestrial and walked with heel-striking bipedalism, the Malapa australopiths—facing different ecological challenges—may have climbed more frequently and have walked with a different kinematic strategy, leading to the development of a differently shaped calcaneal tuber. Evidence for this includes the U.W. 88-113 juvenile *A. sediba* calcaneal apophysis, and its nearly identical proximal anatomy as that found in U.W. 88-99 (Fig. 7). Unfortunately, we cannot repeat the methods used in this study on U.W. 88-113, as there is no talus and the calcaneal body is not
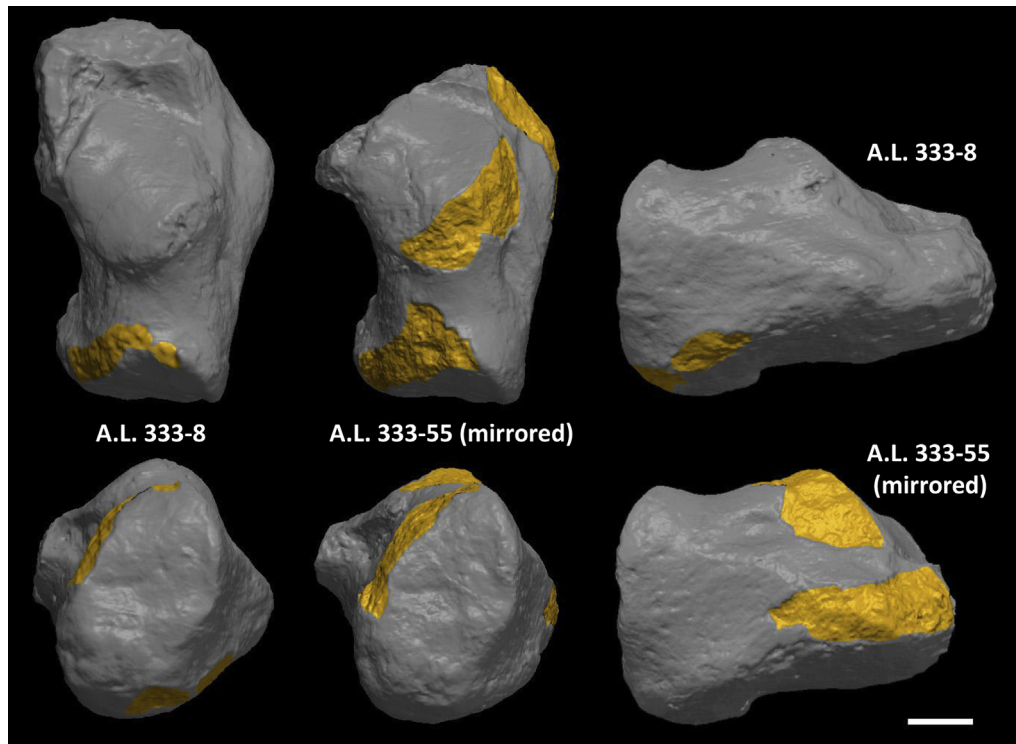
Figure 6. A comparison of *A. afarensis* calcanei, A.L. 333-8 (right calcaneus) and A.L. 333-55 (mirrored left calcaneus) in superior (top left and middle), posterior (bottom left and middle), and lateral (right top and bottom) views. Areas with substantial damage are masked in deep-yellow. Note that a large portion of the A.L. 333-55 peroneal tubercle is missing. Note also that, in A.L. 333-8, the most protuberant part of the LPP appears missing. When these and other obvious damage is taken into account, the two bones are seen to exhibit near-identical overall structure and morphology. Although the length of the tuber (shorter in A.L. 333-8 by ~1 mm) and estimated LPP position (slightly lower in A.L. 333-8) differ between the two calcanei, the idiosyncratic fine details of surface morphology of the two calcanei show close similarities. Such a situation corresponds to bilateral differences often seen in human calcanei, suggesting that these calcanei may be antimeres of the same individual. Scale bar is 10 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
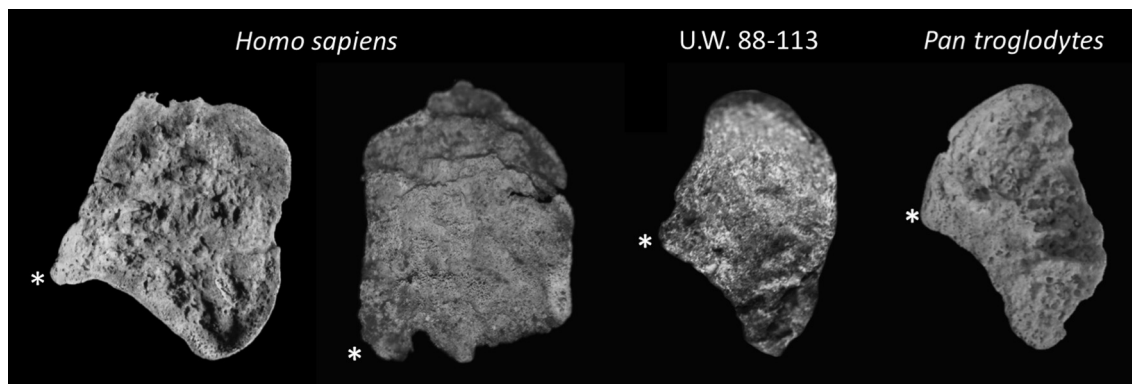
Figure 7. Juvenile calcaneal apophyses in two humans (far left), *Australopithecus sediba* (U.W. 88-113), and a chimpanzee (far right). In juveniles, the position of the LPP is determinable from a flange of bone on the calcaneal apophysis, or on the calcaneal bone by a spur in the proximal epiphyseal surface or as a separate epiphyseal center (which may persist throughout growth). The flange is labeled with an asterisk in each image. The left two specimens illustrate the range of variation in plantar position of the apophyseal flange commonly seen in humans. To the right, the flange is more dorsally positioned in a chimpanzee. The calcaneal apophysis of the juvenile *A. sediba* MH1 (U.W. 88-113) is strikingly mediolaterally narrow as in chimpanzees and located dorsally as is found in apes. It is probable, therefore, that the dorsally positioned LPP in the adult calcaneus from *A. sediba* (U.W. 88-99) is not an aberrant morphology. In this image, the calcaneal apophyses have been scaled to the same dorsoplantar height.

preserved. However, if we assume the same LPP value in U.W. 88-113 and repeat the resampling procedure, the probability of the Malapa ($n = 2$) and Hadar ($n = 2$) calcanei being sampled from a single population of humans drops considerably ($p = 0.018$). The point in conducting this exercise is to illustrate how challenging it is to work with small sample sizes and to illustrate how the inclusion of additional fossils will allow us to test these alternative hypotheses. However, it needs to be emphasized that this paper examines just one feature of a single bone in the postcranial

skeletons of *A. afarensis* and *A. sediba*. The position of the lateral plantar process is but one of many anatomical differences between *A. afarensis* and *A. sediba* that imply differing locomotor adaptations between these taxa. Compared with *A. sediba*, *A. afarensis* has a more robust, human-like tuber well-suited for terrestrial bipedalism (Latimer and Lovejoy, 1989; Zipfel et al., 2011; Prang, 2015a). While the lateral metatarsals of *A. afarensis* are consistent with a stiff foot during push-off (Ward et al., 2012), the known midfoot of *A. sediba* was more mobile (DeSilva et al., 2013). These

differences suggest for *A. sediba* a greater reliance on arboreal locomotion in tandem with a potentially unique form of bipedal kinematics during terrestrial travel (Zipfel et al., 2011; DeSilva et al., 2013). Some consider that adaptations for arboreality in *A. sediba*, compared with the more terrestrial *A. afarensis* (Drapeau et al., 2005; Haile-Selassie et al., 2010), can also be seen in differences in the adult shoulder (Churchill et al., 2013) and the forearm (Rein et al., 2017).

A third hypothesis is that Hadar and Malapa represent two distinct calcaneal morphs and are evidence for not only locomotor diversity in australopiths (as scenario 2 posited above), but potentially for the independent evolution of habitual heel-striking bipedalism in two different lineages of early hominins. While the calcaneal morphology of the earliest hominins remains unknown, it is reasonable to assume that it was modern ape-like in possessing a dorsally positioned LPP and in being gracile relative to the modern human condition. Although there are bipedal adaptations in the Malapa calcaneus, it exhibits a more primitive, dorsal position of the LPP, and has a gracile tuber (Zipfel et al., 2011; Prang, 2015a). If recent phylogenetic analyses based on craniodental anatomy are correct (Dembo et al., 2015, 2016) and *A. sediba* is more closely related to *Homo* than *A. afarensis* is (but see Kimbel and Rak, 2017), then the plantar shift of the LPP from a presumably ape-like ancestral condition would have happened at least twice: once in the *A. afarensis* lineage, and again in the lineage leading to modern humans via *A. sediba*. Homoplasy has been invoked by others (McHenry and Berger, 1998; Green et al., 2007; Zipfel et al., 2011; Prang, 2015a,b, 2016a) to explain the patterning of postcranial anatomies, including those found in the foot, between the eastern African and South African australopiths. Testing this evolutionary scenario will benefit from further discovery of fossil assemblages that preserve associated craniodental and pedal remains and on cladistic analyses that incorporate both craniodental and postcranial data. In this context, it is important to note that the recently described Middle Pleistocene species *Homo naledi* (Berger et al., 2015; Dirks et al., 2017) is closely aligned in craniodental morphology with *A. sediba* according to Dembo et al. (2016), but possesses a human-like, plantar positioning of the LPP (Harcourt-Smith et al., 2015), raising the possibility of proximal calcanei homoplasy in *A. afarensis* and *Homo*. Unfortunately, erosion to the tuber of *H. naledi* (U.W. 88-1322) prevents quantification of the anatomy as presented in this study.

4.3. Limitations

As mentioned above, LPP position as quantified in the present study is influenced by both dorsoplantar position and inferolateral projection. The measurements we take in this study do not inherently capture the variation in projection of the LPP, nor do they measure how much the LPP anlagen cumulatively contributed to adult posterior calcaneal volume. As variation in LPP position and size likely influences substrate contact patterns and force transmission through the heel, quantifying these aspects should be the subjects of future research.

5. Conclusions

After quantifying the dorsoplantar position of the LPP in a large sample of human and great ape calcanei, it is clear that, although this feature is variable, humans have lateral plantar processes that are more plantarly positioned while the homologous structure in apes occupies a more dorsal position. More research is needed to explore the functional implications of LPP position variation on locomotion in both humans and great apes. Within a species, given the large degree of individual variation that we found, LPP position

itself may not strongly influence gait kinematics, though interspecific differences in LPP position likely do.

Our evaluation of LPP position in fossil hominins revealed differences in the known calcanei of *A. afarensis* and *A. sediba*. Based on our resampling approach, it is possible, but statistically unlikely ($p = 0.056$), that the Hadar and Malapa calcanei represent different ends of a largely overlapping range of variation in LPP position. By this hypothesis, both calcanei would represent morphological variation of a foot adapted to a human-like heel striking bipedalism. Alternatively, the calcanei of the two species may represent distinct morphofunctional structures sampled from different LPP position distributions, one human-like and the other ape-like. This latter hypothesis suggests that gait mechanics may have been different in *A. afarensis* and *A. sediba* (DeSilva et al., 2013). In this latter case, whether the two calcaneal morphs are regional variants of a common australopith pedal structure, or evolved independently, remain an open question. Fossil hominin calcanei that preserve the proximal tuber are rare (i.e., there are only three adult australopith calcanei that preserve this anatomy). The discovery of additional calcanei from the Plio-Pleistocene will help to further refine our understanding of calcaneal variation, and allow us to further test the three interpretive scenarios presented in this paper.

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