Reevaluating the functional implications of *Australopithecus afarensis* navicular morphology

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Abstract

The longitudinal arch is a unique characteristic of the human foot, yet the timing and pattern of its evolution remain controversial, in part due to the disagreement among researchers over which skeletal traits are the best indicators of its presence or absence. The small size of the human navicular tuberosity has previously been linked to the presence of a longitudinal arch, implying that the large tuberosity of early hominins such as *Australopithecus afarensis* reflects a flat foot. However, this hypothesis is at odds with other evidence of pedal form and function, such as metatarsal, tarsal, and footprint morphology, which show that a longitudinal arch was probably present in *A. afarensis*. This study reevaluates the morphometric affinities of the *A. afarensis* naviculars among other Plio-Pleistocene fossil hominins and anthropoid primates ($N = 170$). Multivariate cluster analyses show that all fossil hominin naviculars, including those attributed to *A. afarensis*, are most similar to modern humans. A measure of navicular tuberosity size quantified as the ratio of the tuberosity volume to the surface area of the talar facet shows that *Ateles* has the largest navicular tuberosity among the anthropoid sample and that there is no difference between highly arboreal and terrestrial taxa in this metric (e.g., *Hylobates* and *Gorilla beringei*). A relatively large navicular tuberosity may reflect the development of leg musculature associated with ankle plantarflexion. The functional inferences derived from the morphology of the *A. afarensis* naviculars are consistent with the morphology of the Laetoli footprints.

KEYWORDS: foot morphology; navicular; longitudinal arch

Introduction

The human foot is uniquely characterized by an energy saving, spring-like longitudinal arch that reflects an adaptation to terrestrial walking and running (Ker et al., 1987; Bramble and Lieberman, 2004; DeSilva and Throckmorton, 2010; Ward, 2011; Prang, 2015b; Stearne et al., 2016). The presence of a longitudinal arch is reflected in the geometric relationships among the bones of the human foot and ankle (DeSilva and Throckmorton, 2010; Ward et al., 2011; Prang, 2015b), including the declination of the talar head relative to the plane of the talocrural joint (Day and Wood, 1968; Peeters et al., 2013) and the declination of the calcaneocuboid joint relative to its proximodistal axis (Aiello and Dean, 1990; Prang, 2015b). Humans also possess soft tissue specializations associated with the longitudinal arch, such as a well-developed plantar aponeurosis, calcaneonavicular ligament, and long plantar ligament (Gomberg, 1981, 1985), which all contribute to midtarsal stabilization via the ‘windlass mechanism’ (Hicks, 1954; reviewed by Griffin et al., 2015). Other primates lack these hard and soft tissue specializations and instead have much more mobile feet that are probably adapted for varying degrees of arboreal and terrestrial locomotion (e.g., DeSilva, 2010). For example, great apes lack the dorsoplantarly expanded and flattened metatarsal bases characteristic of humans, which provide bony stabilization of the lateral tarsometatarsal joints during the midstance phase of the gait cycle (DeSilva, 2010). They additionally lack the proximomedial positioning of the cuboid beak and the laterally rotated talar head, which help to stabilize the transverse tarsal joint in the latter part of stance phase. The ape foot lacks these features of the tarsometatarsal, calcaneocuboid, and talonavicular joints resulting in midtarsal mobility during midstance, a kinematic pattern that has been termed the ‘midtarsal break’ (Elftman and Manter, 1935; Vereecke et al., 2003;

DeSilva, 2010; Thompson et al., 2014). It must be noted that modern humans with an arched foot can still display some midfoot mobility (Lundgren et al., 2008; Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015) and fossil hominins with a flat foot can have a rigid midfoot (Prang, 2015b).

Understanding the evolution of the hominin longitudinal arch and its morphological correlates is necessary because they reflect a predominantly terrestrial adaptation (DeSilva, 2010; Ward et al., 2011; Prang, 2015b) and the ability to save energy during running via longitudinal arch compression and elastic recoil (Ker et al., 1987; Bramble and Lieberman, 2004; Stearne et al., 2016). The discovery of postcranial fossils attributed to the Plio-Pleistocene hominin taxon *Australopithecus afarensis* (Johanson et al., 1982; Latimer et al., 1982) started a crucial debate regarding the roles of arboreality and terrestriality in the locomotor repertoire of early hominins (e.g., Stern and Susman, 1983; Susman et al., 1984) and their evolutionary importance (sensu Latimer, 1991; reviewed by Stern, 2000 and Ward, 2002). Two of the key sources of evidence for locomotor function and adaptation in *A. afarensis* are the fossilized footprints at Laetoli, Tanzania, dated to 3.7 Ma (mega annum) (Leakey and Hay, 1979) and the 3.3 Ma fossil foot bones from the A.L. 333 site at Hadar, Ethiopia (Latimer et al., 1982). The Laetoli footprints provide nearly direct evidence of foot function in an early hominin taxon, displaying a longitudinal arch and a relatively adducted hallux compared to chimpanzees (Leakey and Hay, 1979; Day and Wickens, 1980; White, 1980; White and Suwa, 1987; Bennett et al., 2009; Raichlen et al., 2010; Crompton et al., 2012; Bennett et al., 2016). The discovery of a complete fourth metatarsal (A.L. 333-160) provided support for the hypothesis that *A. afarensis* had both longitudinal and transverse arches (Ward et al., 2011; but see Drapeau and Harmon, 2013 and Mitchell et al., 2012 for alternative views), and a recent analysis of rearfoot angular relationships

also found support for this hypothesis (Prang, 2015b). Thus, there are several lines of evidence based on foot morphology suggestive of a longitudinal arch in *A. afarensis*, which are congruent with the structural and functional inferences derived from the Laetoli footprints (Day and Wickens, 1980; White, 1980; White and Suwa, 1987; Bennett et al., 2009; Raichlen et al., 2010; Crompton et al., 2012; Bennett et al., 2016).

In contrast, some researchers have challenged the hypothesis that *A. afarensis* had a longitudinal arch based on some ape-like aspects of the A.L. 333 tarsals, such as a low sustentaculum tali on the A.L. 333-8 calcaneus (Harcourt-Smith et al., 2015) and a prominent tuberosity on the naviculars (A.L. 333-36, -47) from Hadar (Sarmiento and Marcus, 2000; Harcourt-Smith, 2002, 2005; Harcourt-Smith and Aiello, 2004; see also Berillon, 2003). The large navicular tuberosity was suggested to indicate that the medial column of the foot was weight bearing in a terrestrial context and that a longitudinal arch could not have been present in *A. afarensis* (Sarmiento and Marcus, 2000; Harcourt-Smith, 2002, 2005; Harcourt-Smith and Aiello, 2004). The association of a large navicular tuberosity with terrestrial weight-bearing is predominantly based on the observation that African apes lack a longitudinal arch and combine a large tuberosity with moderate terrestriality compared to orangutans, which have comparatively smaller tuberosities and spend almost all of their time in trees. Under this hypothesis, a large weight-bearing tuberosity represents a hominine synapomorphy associated with a terrestrially weight-bearing midfoot (Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004), and hominins with these primitive retentions such as *Homo floresiensis* (Jungers et al., 2009) and *A. afarensis* would have flat feet.

The potential disparity between the functional inferences derived from the morphology of the A.L. 333 foot fossils and the Laetoli footprints raises the possibility that the prints were made

by a hominin other than *A. afarensis* (Tuttle, 1981, 1985; Tuttle et al., 1990, 1991; Harcourt-Smith, 2002, 2005; Harcourt-Smith and Aiello, 2004). The recent discoveries of the BRT-VP-2/73 partial foot with a divergent, ape-like hallux from Burtele, Ethiopia (Haile-Selassie et al., 2012), and craniodental fossils of *Australopithecus deyiremeda* (Haile-Selassie et al., 2015), show that there was functional and taxonomic diversity in the Pliocene of eastern Africa c. 3.4 Ma. If the ape-like aspects of the A.L. 333 naviculars are incompatible with the presence of a longitudinal arch, then they could belong to a species other than *A. afarensis*. Since significant hallucal abduction (e.g., as seen in extant African apes) is functionally incompatible with the ‘windlass mechanism’ associated with the longitudinal arch (Hicks, 1954; Griffin et al., 2015), and thus necessarily reflective of a flat foot, a candidate taxon for the A.L. 333 naviculars could be the one to which the BRT-VP-2/73 foot belongs. In other words, the recent fossil discoveries in eastern Africa c. 3.4 Ma (Haile-Selassie et al., 2012; Haile-Selassie et al., 2015) make previous suggestions that a hominin other than *A. afarensis* made the Laetoli footprints less improbable. However, if navicular morphology does not provide information relevant for inferring the presence or absence of a longitudinal arch, there would be no reason to reject the null hypothesis that *A. afarensis* made the footprints at Laetoli or that the A.L. 333 naviculars belong to *A. afarensis*.

The purpose of this study is to reevaluate the morphometric affinities of the *A. afarensis* naviculars (A.L. 333-36, -47). First, I test the hypothesis that the relative size of the navicular tuberosity is positively correlated with midfoot weight bearing. If this hypothesis is true, then more terrestrial species should have relatively larger navicular tuberosities compared to more arboreal ones, especially those that engage in more forelimb dominated suspension, and thus less direct and habitual hindlimb weight bearing (e.g., *Pongo*, *Hylobates*, *Ateles*). I test these

predictions by comparing the relative volume of the navicular tuberosity across a sample of anthropoid primates that differ in frequency and manner of arboreality. If this hypothesis is supported, the large navicular tuberosity of *A. afarensis* would indicate that this species had a weight-bearing medial midfoot reflective of an absent longitudinal arch (Harcourt-Smith, 2002, 2005; Harcourt-Smith and Aiello, 2004). Second, since the navicular tuberosity is only one component of navicular shape, I test the hypothesis that the overall shape of the *A. afarensis* naviculars is morphometrically most similar to those of African apes (Sarmiento and Marcus, 2000; Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004). I evaluate this hypothesis using three-dimensional (3D) coordinate data derived from landmarks in a sample of anthropoid primates. The results of this study have implications for understanding the evolution of the longitudinal arch in the hominin clade, especially in *A. afarensis*, and will help shed further light on the makers of the Laetoli footprints and the taxonomic attribution of the A.L. 333 tarsals.

Materials and methods

The extant sample of naviculars ($N = 166$) derives from the following collections: American Museum of Natural History (AMNH), Academy of Natural Sciences Philadelphia (ANSP), Center for the Study of Human Origins (CSHO) at New York University, Cleveland Museum of Natural History (CMNH), United States National Museum (USNM), and SUNY Stony Brook. The fossil hominin sample includes A.L. 333-36, A.L. 333-47 (*A. afarensis*), LB 1 (*Homo floresiensis*), and OH 8 (*Homo habilis/Paranthropus boisei?*), and derives from research-quality casts housed at the CMNH, CSHO, and elsewhere (Table 1).

Most naviculars were scanned with a NextEngine desktop laser scanner in two orientations with a minimum of 10 rotations per orientation. Each resultant triangular mesh was imported into Geomagic Studio software for merging different orientations and cleaning of imperfections to create a complete 3D model of each bone. A subset of the modern human and gorilla models were produced using computed tomography, which are directly comparable to those produced by desktop laser scanners (Tocheri et al., 2011). The volume of the navicular tuberosity was quantified by passing an approximately transverse plane through the most medioplantar points of the talar and medial cuneiform articular surfaces (defined by Type II landmarks; Figure 1) and calculating the volume of the 3D model plantar to the plane using Geomagic Studio software. The surface area of the talar facet was used as a size proxy, given that it is a significantly weight bearing articular surface, and was quantified by segmenting the articular surface from the surrounding non-articular surface following the methods outlined in Tocheri (2007) and Tocheri et al. (2011). Since ratios are bounded by zero on the low end of their distributions and unbounded on the high end of their distributions, they cannot be normally distributed (Smith, 1999). However, logging ratios solves this problem since ratios less than one become negative and ratios greater than one become positive, and therefore become unbounded at both ends of their distribution (Smith, 1999). As such, a relative tuberosity metric was calculated as $(\ln(\text{navicular tuberosity volume}/\text{talar facet surface area}^{1.5}))$.

Landmark-based geometric morphometric techniques were employed to quantify and statistically compare navicular shape among extant anthropoids. Landmark Editor software (Wiley et al., 2005) was used to digitize a total of 25 landmarks and semilandmarks on each surface model (Fig. 1). These landmarks were carefully chosen to maintain homology across a diverse sample of anthropoid primates that differ substantially in navicular shape. Most taxa in

this study have never been included in previous studies of navicular morphology (e.g., Sarmiento and Marcus, 2000; Harcourt-Smith, 2002) and they do not preserve distinct margins for the intermediate-medial cuneiform articulation as African apes and modern humans do. Furthermore, the articular margin of the talar facet lacks anatomical areas where homologous landmarks can be placed. As such, semilandmarks were necessarily used to quantify these areas. The landmark data were subjected to a generalized Procrustes analysis (GPA), which translates and rotates each set of landmark coordinates and scales them to unit centroid size (Gower, 1975; Rohlf and Slice, 1990) in order to generate shape variables for further analysis. All semilandmarks were slid along their tangent directions using the bending energy criterion (Bookstein, 1997; Gunz et al., 2005) to ensure homology across all specimens. The resulting Procrustes residuals were projected into a linear tangent space and subjected to principal components analysis (PCA) to ordinate and visualize the variation in navicular shape in extant anthropoids and fossil hominins. All shape changes were visualized by warping a 3D reference model of the navicular along principal component axes. A molecular consensus phylogeny for the extant taxa sampled for this study was downloaded from the 10k trees site (Arnold et al., 2010) and fossil taxa were added using the program Mesquite based on a recent Bayesian analysis of hominin phylogeny (Dembo et al., 2015). This tree was used in conjunction with the 3D multivariate data to construct phylomorphospace plots of navicular shape evolution throughout the anthropoid clade. Squared change parsimony (Maddison, 1991) was used to reconstruct hypothetical ancestral states of navicular shape for the internal nodes of the anthropoid phylogeny.

Univariate pairwise comparisons with a Tukey's post-hoc alpha adjustment were conducted in order to assess the quantitative differences in the relative size of the navicular tuberosity among extant anthropoids. Regression was used to characterize the scaling

relationships between the volume of the navicular tuberosity, body mass, and the surface area of the talar facet of the navicular across all taxa, using both reduced major axis (RMA) and ordinary least-squares (OLS) methods. Body mass data for all extant taxa were taken from the literature (Smith and Jungers, 1997). All statistical analyses were conducted using the ‘geomorph’ package (Adams and Otárola-Castillo, 2013) in R (R Core Team, 2012), and PAST (Hammer et al., 2001; Hammer and Harper, 2006).

Results

Metric comparisons of talar facet surface area, navicular tuberosity volume, and the relative volume of the navicular tuberosity show that *Ateles* has the largest navicular tuberosity relative to talar facet surface area, whereas *Pongo* has the smallest (Table 2). *Hylobates* cannot be distinguished from *Pan*, *Gorilla gorilla*, or *Gorilla beringei* in the relative size of the tuberosity (Table 3), and *Homo* is distinct from all other taxa in relative tuberosity volume (Fig. 2). All of the fossil hominins sampled here have relative tuberosity volumes, outside the range of variation of *Homo* (Table 2, Fig. 2), although OH 8 is very near the high end. The volume of the navicular tuberosity was regressed onto the surface area of the talar facet using RMA and OLS regression in order to gain an additional perspective on the relationship between these two variables, which is significant ($p = < 0.0001$; $r^2 = 0.80$; Fig. 3). *Homo* and *Pongo* are clearly distinct from the rest of the extant sample in falling below both the RMA and OLS regression lines, demonstrating that they have relatively small tuberosities, whereas *Ateles* is far above. As expected, all the fossil hominins sampled fall above the regression lines, though OH 8 is nearly on the line itself. An isometric scaling relationship should result in a slope of 1.5 since a volume

is regressed on an area, and the OLS slope may represent a slightly negative allometric relationship (slope = 1.4, 95% CI = 1.33, 1.48), whereas the 95% CI for the RMA slope (1.57) includes isometry (1.49, 1.64). Additionally, average navicular tuberosity volume was regressed on average body mass for extant taxa (Smith and Jungers, 1997) and the results are very similar to the previous analysis ($p = 0.003$; $r^2 = 0.74$; Fig. 4). An isometric scaling relationship cannot be rejected since the 95% confidence intervals for both RMA and OLS regressions include isometry (i.e., a slope of 1.0 for a volume regressed on a volume). The hypothesis that the relative size of the navicular tuberosity reflects the degree of terrestriality in a species' locomotor repertoire does not receive support.

Generalizations about navicular morphology in extant anthropoids and fossil hominins cannot be made on the basis of navicular tuberosity comparisons alone (i.e., without reference to overall navicular shape), since it would ignore the rest of the bone. An ordination of the multivariate data on total navicular shape is presented as a PCA in order to assess the morphometric affinities of the *A. afarensis* naviculars (Fig. 5). The *A. afarensis* naviculars fall intermediately between *Homo* and African apes, near *Pongo*, when viewing the first two principal components. It is tempting to say that they are morphometrically most similar to *Pongo*, but these two axes only account for 55% of the total sample variance. Accordingly, PC3 separates all taxa from *Pongo* and *Ateles*, and all hominins, including *A. afarensis*, group with *Homo*, *Pan*, and *Gorilla*. Although the relative size of the *A. afarensis* navicular tuberosity falls within the ranges of variation for *Pan* and *Gorilla*, the overall 3D shape of the navicular is not best described as African ape-like, since it does not cluster with these taxa (see below).

The first principal component (PC) separates great apes (hominids) from all other anthropoid taxa and primarily represents the anteroposterior length and mediolateral width of the

navicular (Fig. 6). The anthropoid taxa at the low end of PC1 have anteroposteriorly elongate naviculars and taxa at the high end have anteroposteriorly compressed naviculars. The *A. afarensis* naviculars (A.L. 333-36, -47) fall at the low end of the range of variation for the *Homo* distribution, and within the lower range of variation for *Pongo*, whereas LB1 and OH 8 fall within the *Homo* distribution. The second PC separates *Homo* from all other taxa and primarily represents the dorsoplantar depth, the transverse plane orientation of the cuneiform facets, and the mediolateral width of the navicular (Fig. 6). Compared to other taxa, humans have a mediolaterally expanded, dorsoplantarly shallow navicular, with more distally (rather than medially) oriented cuneiform facets. *Pan*, *G. gorilla*, *G. beringei*, and *Hylobates* are all similar to one another, whereas *Pongo*, *Macaca*, and *Cebus* are all intermediate between the apes and modern humans. In this regard, all fossil hominins except for OH 8 are intermediate between non-*Pongo* hominoids and *Homo*. OH 8 falls within the range of variation of the *Homo* sample. *Australopithecus afarensis* naviculars differ substantially from *Homo* only along the second PC, and in no PC does *A. afarensis* group with African apes to the exclusion of *Homo*.

The third PC separates *Pongo* and *Ateles* from all other taxa at the low and high ends of the axis, respectively (Fig. 7). The shape changes associated with this axis are the plantar expansion of the navicular tuberosity and the long axis of the talar facet relative to the dorsoplantar articulation for the cuboid. Taxa at the higher end of PC3 have a more medially projecting navicular relative to its cuboid articulation, whereas taxa at the lower end of PC3 have a more mediolaterally compressed navicular. There is no clear pattern to the separation of taxa along the fourth PC and, importantly, although *G. beringei* and *G. gorilla* differ substantially on this axis, total navicular shape does not differ between these two taxa, despite their differences in frequency of terrestriality. *Hylobates*, *Homo*, and *G. beringei* fall at the lower end, whereas

Ateles falls at the high end of PC4. The shape changes associated with this axis are primarily related to the proximodistal expansion of the navicular tuberosity and the shape of the talar facet. Taxa at the low end of this axis have more mediolaterally expanded talonavicular joints, whereas taxa at the higher end have more mediolaterally compressed talonavicular joints. The fossil hominins fall within the ranges of variation for all taxa except for *Ateles*. The average Procrustes distances between all taxa (Table 4) were used to construct an unweighted pair group with arithmetic mean (UPGMA) phenogram, which shows that all fossil hominins, including *A. afarensis*, are most similar to *Homo* despite their differences in the relative size of the navicular tuberosity (Table 5, Fig. 8). This study, therefore, does not find support for the hypothesis that the *A. afarensis* naviculars are predominantly African ape-like (Sarmiento and Marcus, 2000; Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004).

Finally, the anthropoid phylogeny was superimposed on the average navicular shapes for each taxon and ancestral states for each internal node were reconstructed using squared changed parsimony in 3D shape space (i.e., for the first three PCs; Fig. 9). The first three PCs were used to maximize the observed shape variation. The distance between each taxon mean and the reconstructed ancestral state is proportional to the magnitude of evolutionary change, whereas the angles between sister taxa indicate direction from the reconstructed ancestral morphology. The combined 3D phylomorphospace plot shows three distinct clusters: hominins (including modern humans), great apes, and non-hominid anthropoids (Fig. 9), which closely mirrors the cluster analysis (Fig. 8). Importantly, these analyses demonstrate that the navicular morphology of *A. afarensis* is distinct from African apes and had already been modified in a more *Homo*-like direction from the reconstructed morphology of the *Pan-Homo* last common ancestor.

Discussion

This study quantified the 3D shape of the navicular and the relative size of its tuberosity in a sample of anthropoid primates in order to evaluate the hypothesis that the navicular morphology of *A. afarensis* reflects a flat, weight-bearing medial midfoot. *Australopithecus afarensis* has a navicular that combines some African ape-like characteristics, such as a large plantarly-projecting tuberosity and a prominent navicular-cuboid articulation, with some traits derived in the direction of modern humans, such as talar and cuneiform facet angular relationships and increased anteroposterior thickness. The fact that great apes occupy a distinct morphospace, combined with their hypothetical ape-like ancestral states, suggests that an anteroposteriorly short navicular is homologous for the clade and that humans are derived in their navicular elongation, which contrasts with some previous suggestions of extensive homoplasy in hominoids (Lovejoy et al., 2009). Furthermore, these results also contrast with some previous studies on hominin naviculars, which argued for a predominantly African ape-like form for *A. afarensis* (Sarmiento and Marcus, 2000; Harcourt-Smith, 2002), a result that may be explained by the use of sliding semilandmarks to quantify morphology. This approach represents the most rigorous way of maintaining landmark homology across the morphologically diverse clade sampled here (see Gunz et al., 2005).

The present study demonstrates no clear relationship between the relative size of the navicular tuberosity and frequency of arboreality. For example, *Hylobates* spends nearly one hundred percent of its locomotor budget in the trees (Fleagle, 1980) and lacks postcranial specializations for terrestrial locomotion, yet it cannot be distinguished from *G. beringei*, the most terrestrially adapted African ape (Doran and McNeilage, 1998; Tocheri et al., 2011; Dunn

et al., 2014). Therefore, the relative size of the navicular tuberosity is probably a poor indicator of midfoot weight bearing, and thus is not informative for making inferences about the presence or absence of a longitudinal arch in fossil hominins. Nonetheless, the multivariate and univariate results presented here have implications for understanding foot function in *A. afarensis*.

One of the implicit components of prior hypotheses about the relationship between navicular tuberosity size and midfoot weight bearing (Sarmiento and Marcus, 2000; Harcourt-Smith, 2002) is that the presence of a large tuberosity in African apes is a derived trait related to terrestriality. In other words, if orangutans are predominantly adapted to arboreal locomotion and if African apes and humans share a greater degree of terrestriality, perhaps a large navicular tuberosity evolved at the base of the hominine clade in association with terrestriality. The fact that chimpanzees and gorillas are both characterized by knuckle-walking hand postures and adaptations for heel-strike plantigrady present the possibility that the hominine last common ancestor also possessed these traits in some form (Gebo, 1992; Richmond and Strait, 2000; but see Lovejoy et al., 2009; Kivell and Schmitt, 2009). Orangutans were presumed to have retained the ancestral condition of small navicular tuberosity size associated with a predominantly arboreal adaptation (Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004). However, it becomes clear that both orangutans and modern humans are probably derived among hominoids in navicular shape (Fig. 9) and in their reduction of the navicular tuberosity (Gomberg, 1981), especially when consideration is given to additional anthropoid taxa (e.g., *Hylobates*, *Ateles*). Thus, the link between large navicular tuberosity size and midfoot weight-bearing reflects a mischaracterization of character polarity due to incomplete taxonomic sampling.

Limited data on the size of lower limb muscles (Gomberg, 1981; Wickiewicz, et al., 1983; Thorpe et al., 1999; Payne et al., 2006; Zihlman et al., 2011) suggest that, compared to

gorillas and chimpanzees, humans and orangutans have both reduced the tibialis posterior muscle relative to other lower limb musculature, which supports the hypothesis that the relative size of the tuberosity (i.e., the most prominent attachment site for this muscle) reflects myological differences among taxa. Under this hypothesis, the large navicular tuberosity of *A. afarensis* and other fossil hominins such as *H. floresiensis* (Jungers et al., 2009) would reflect the presence of enlarged musculature associated with plantarflexion and inversion. Additional evidence for strong leg musculature in hominins derives from the enlarged peroneal trochlea of Plio-Pleistocene fossil hominin calcanei (Stern and Susman, 1983; Susman et al., 1984; Latimer and Lovejoy, 1989; Gebo and Schwartz, 2006; Zipfel et al., 2011; Gill et al., 2014; Prang, 2015a) and the large tuberosity on the plantar surface of hominin lateral cuneiforms (e.g., A.L. 333-78; OH 8) associated with the peroneal musculature. It is unknown whether the inferred plantarflexion via the peroneal musculature was functionally involved in the propulsion associated with bipedalism in the absence of a well-developed Achilles tendon (Latimer and Lovejoy, 1989), the propulsion associated with vertical climbing (Stern and Susman, 1983), or some combination of both (Gill et al., 2014).

In modern humans, the tibialis posterior is an important active contributor to medial longitudinal arch support (Kitaoka et al. 1997). Modern humans with a weak tibialis posterior have a lower longitudinal arch, increased midfoot plantar pressure, increased medial weight transfer, and increased rearfoot eversion (Neville et al., 2015). The fossilized footprints at Laetoli, Tanzania display modern human-like characteristics, such as a relatively adducted hallux compared to chimpanzees, a deep impression associated with heel-strike, and a medial longitudinal arch (Leakey and Hay, 1979; Day and Wickens, 1980; White, 1980; White and Suwa, 1987; Bennett et al., 2009; Raichlen et al., 2010; Crompton et al., 2012; Bennett et al.,

2016). However, more recent quantitative studies suggest the Laetoli footprints show less medial weight transfer than would be found in modern humans (Bennett et al., 2009; Crompton et al., 2012; Bennett et al., 2016; see also DeSilva and Gill, 2013; DeSilva et al., 2015) and a longitudinal arch that was probably not as well developed as the modern human arch (Bennett et al., 2009, 2016). The reduction in medial weight transfer observed in the Laetoli footprints could therefore reflect an enlarged tibialis posterior muscle, as it would in modern humans (Neville et al., 2015) and as evidenced by the large navicular tuberosity of *A. afarensis*. Therefore, in contrast to some previous suggestions (Tuttle, 1981, 1985; Tuttle et al., 1990, 1991; Harcourt-Smith, 2002, 2005; Harcourt-Smith and Aiello, 2004), the morphology of the Laetoli footprints is consistent with the functional inferences derived from the morphology of the *A. afarensis* foot fossils from Hadar. There is no indication that variation in the relative size of the navicular tuberosity reflects increased medial midfoot weight bearing and, therefore, no justification for rejecting the null hypothesis that the Laetoli footprints were made by *A. afarensis*.

Although all known evidence from foot fossils and footprint morphology suggests that *A. afarensis* possessed an arched foot, caution is warranted in falsely dichotomizing the comparatively more rigid, arched human foot with the more mobile, flat ape foot, because it does not allow for “intermediate” or other forms as might be expected in the evolving hominin foot. Although recent quantitative studies on the morphology of the Laetoli footprints support the hypothesis that *A. afarensis* possessed a longitudinally arched foot, they also suggest that it was not as well developed as it is in modern humans (Bennett et al., 2009; Bennett et al., 2012). Our understanding of the fossil hominin longitudinal arch is complicated by the fact that there is no living analog for extinct taxa such as *A. afarensis*. Importantly, some aspects of navicular morphology may support the suggestion that the *A. afarensis* longitudinal arch was not

functionally equivalent to that of modern humans. Great apes have a prominent navicular-cuboid articulation, lacking in an estimated 80% of modern humans (Gomberg, 1981, 1985). Navicular-cuboid articulations, therefore, occur at a relatively low frequency in modern humans compared to great apes and are somewhat irregular in morphology when they occur (Gomberg, 1981, 1985). Instead, the modern human navicular and cuboid are connected by an interosseous ligament, which has previously been interpreted as preventing navicular-cuboid frontal plane rotation and the collapse of the transverse arch under load (Gomberg, 1985). However, one could also reasonably argue that the prominent navicular-cuboid articulation of great apes reduces navicular-cuboid frontal plane mobility since the joint surfaces are dorsoplantarly flattened and strongly congruent, and that the human condition allows for more mediolateral autonomy. For example, the modern human transverse tarsal joint must simultaneously achieve lateral rigidity via the locking mechanism of the calcaneocuboid joint (Bojsen-Moller, 1979), but also allow for the compression and recoil of the medial longitudinal arch (Ker et al., 1987; Stearne et al., 2016), which could be made possible by the modification of a bony navicular-cuboid articulation to a ligamentous one, not seen in *A. afarensis* and other fossil hominins (Fig. 10; Gomberg and Latimer, 1984). Experimental in vivo data on modern humans seems to support this hypothesis, given that the range of motion at the talonavicular joint is greater than the range of motion at the calcaneocuboid joint during gait (Lundgren et al., 2008). Lundgren et al. (2008: 99) also report that the considerable mobility between the navicular and cuboid “...contradicts concepts in which these bones act as a rigid unit”. More work needs to be done on these detailed aspects of inter-tarsal mobility in modern humans and apes to resolve these issues, but it has the potential to help understand the functional morphology of the *A. afarensis* longitudinal arch better.

Interpreting the evolutionary significance of ancestral traits (e.g., large navicular tuberosity size) is difficult because they could be the result of “phylogenetic inertia” or active maintenance by stabilizing selection, which has led to many disagreements among researchers regarding the role of arboreality for *A. afarensis* (Stern, 2000; Ward, 2002). All available evidence on the feet of *A. afarensis* suggests that terrestriality was adaptively significant due to the presence of many derived traits related to midtarsal stability, propulsion, and heel-strike (Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990; DeSilva, 2009, 2010; Ward et al., 2011; Crompton et al., 2012; Prang, 2015a, b), which other hominins, such as *A. sediba* and *A. africanus*, lack (Zipfel et al., 2011; DeSilva, et al., 2013; Prang, 2015a, b, 2016). The presence of a longitudinal arch does not preclude a total locomotor repertoire that includes some degree of arboreality in *A. afarensis* (shown most recently by data on developmental changes in scapular morphology in juvenile apes related to climbing; Green and Alemseged, 2012; Young et al., 2015), African ape-like phalangeal morphology (Stern and Susman, 1983), and advanced climbing capabilities in some modern humans (Venkataraman et al., 2012). Although data on foot morphology (Latimer et al., 1987; Latimer and Lovejoy, 1989; DeSilva, 2009; Ward et al., 2011; Zipfel et al., 2011; Crompton et al., 2012; DeSilva et al., 2013; Prang, 2015a, b, 2016), limb size proportions (Green et al., 2007), and hindlimb joint size (McHenry and Berger, 1998; Dobson, 2005) suggest that *A. afarensis* was the most terrestrial *Australopithecus* currently known, the potential for a locomotor repertoire including some amount of arboreality is not easily discounted.

Conclusions

This study reevaluated the morphometric affinities of *A. afarensis* naviculars and tested the hypotheses that the relative size of the navicular tuberosity is positively correlated with midfoot weight bearing and that the *A. afarensis* naviculars are most similar in shape to those of African apes. Variation in the relative size of the navicular tuberosity is not a correlate of terrestriality, and therefore cannot be used to make inferences about the presence or absence of a longitudinal arch. Instead, the relative size of the navicular tuberosity more likely reflects variation in the soft tissue elements that directly interact with the medial midfoot (e.g., the tibialis posterior muscle), though additional work is needed to understand the relationship between muscle size and bony morphology. If the enlarged navicular tuberosity of *A. afarensis* is associated with a powerful tibialis posterior muscle, it may have resulted in reduced medial weight transfer, as it does in modern humans and as suggested by more shallow depths at the medial forefoot of the Laetoli footprints. Accordingly, the functional inferences derived from the A.L. 333 naviculars are consistent with the morphology of the Laetoli footprints. The 3D shape of the *A. afarensis* navicular is not predominantly African ape-like as previously suggested and instead shows modifications from a hypothetical African ape-like ancestral morphology in the direction of modern humans and other hominins, which does not support previous hypotheses regarding the evolution of the navicular (Lovejoy et al., 2009). In contrast to some prior suggestions (Tuttle, 1981, 1985; Tuttle et al., 1990, 1991; Harcourt-Smith, 2002, 2005; Harcourt-Smith and Aiello, 2004), the evidence derived from foot fossils (Latimer et al., 1987; Latimer and Lovejoy, 1989; Ward et al., 2011; Prang, 2015b) and footprint morphology (Leakey and Hay, 1979; Day and Wickens, 1980; White, 1980; White and Suwa, 1987; Bennett et al., 2009; Raichlen et al., 2010; Crompton et al., 2012; Bennett et al., 2016) supports the hypothesis that *A. afarensis* possessed a longitudinal arch. Although several recent studies suggest the longitudinal arch of *A. afarensis*

was low compared to modern humans (Bennett et al. 2009, 2016), the extent of their functional similarity or difference is presently unknown.

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Figure legends

Figure 1. Landmarks and semi-landmarks used to quantify navicular shape. Fixed landmarks are white and sliding semi-landmarks are black. 1 = most dorsolateral corner of talar facet, 2 = most plantarolateral corner of talar facet, 3 = most medioplantar point on talar facet, 4 = most dorsolateral corner of lateral cuneiform facet, 5 = most dorsomedial corner of lateral cuneiform facet, 6 = most plantarolateral corner of lateral cuneiform facet, 7 = most medioplantar corner of lateral cuneiform facet, 8 = deepest point of lateral cuneiform facet, 9 = most plantar point of medial cuneiform facet. Semi-landmarks were spaced evenly between fixed landmarks and slid to minimize bending energy.

Figure 2. Boxplots of the relative size of the navicular tuberosity. Bars represent the mean, box represents the bootstrapped 95% confidence interval, whiskers represent $\pm$ one standard error of the mean, and the circles represent individual data points. 3D models below represent the minimum (*Pongo*) and maximum (*Ateles*) values for navicular tuberosity size, and the dashed line represents the articular margin of the cuneiform facets. Note the large size of the tuberosity in *Ateles* (denoted by the asterisk) and the atrophied tuberosity of *Pongo*. *Homo floresiensis* (LB1) and *A. afarensis* (A.L. 333-36, -47) fall outside of the range of the modern human sample, whereas OH 8 falls at the high end of the distribution.

Figure 3. Log-log plot of navicular tuberosity volume against the surface area of the talar facet ($r^2 = 0.80$; $p = 0.0001$). Dashed line = OLS slope (1.40, CI = 1.33, 1.49), solid line = RMA slope (1.57, CI = 1.49, 1.64), blue squares = *G. beringei*, green squares = *G. gorilla*, purple triangles = *P. troglodytes*, black pluses = *H. sapiens*, orange diamonds = *Pongo pygmaeus*, red circles = *Hylobates* spp., black crosses = *Macaca* spp., inverted light purple triangles = *Ateles* spp., inverted light blue triangles = *Cebus apella*. Note the placement of *Ateles* far above and *Pongo* far below the regression lines. The fossil hominins all fall above the regression lines, except for OH 8, which falls directly on the regression lines.

Figure 4. Log-log plot of average navicular tuberosity volume against average body mass ($r^2 = 0.74$; $p = 0.003$). Dashed line = OLS slope (1.00, CI = 0.75, 1.47), solid line = RMA slope (1.17, CI = 0.81, 1.44), blue square = *G. beringei*, green square = *G. gorilla*, purple triangle = *P. troglodytes*, black plus = *H. sapiens*, orange diamond = *Pongo pygmaeus*, red circle = *Hylobates* spp., black cross = *Macaca* spp., inverted light purple triangle = *Ateles* spp., inverted light blue triangle = *Cebus apella*. Note the similarity between this plot and the regression using the talar facet surface area.

Figure 5. Principal Components Analysis (PCA) on 3D shape variables generated with a generalized Procrustes analysis (GPA). Blue squares = *G. beringei*, green squares = *G. gorilla*, purple triangles = *P. troglodytes*, black pluses = *H. sapiens*, orange diamonds = *Pongo pygmaeus*, red circles = *Hylobates* spp., black crosses = *Macaca* spp., inverted light purple triangles = *Ateles* spp., inverted light blue triangles = *Cebus paella*, gray circle = 95% confidence ellipse for the modern human sample. Note the placement of all hominins, except OH 8, between African apes and humans, as well as the placement of *Ateles* nearest to hominoids along PC2 and PC3.

Figure 6. Boxplots of the first two principal components and their associated shape changes. Bars represent the mean, box represents the bootstrapped 95% confidence interval, whiskers represent +/- one standard error of the mean, and the circles represent individual data points. 3D navicular scans are warped to the minimum (MIN) and maximum (MAX) values relative to the average shape (AVG) to demonstrate shape changes along these axes. PC1 is primarily related to the anteroposterior and mediolateral dimensions of the navicular and separates great apes from all other anthropoids. PC2 is primarily related to the dorsoplantar dimension of the navicular and separates humans from all other taxa. Note the intermediate placement of *A. afarensis* (A.L. 333-36, -47) and *H. floresiensis* (LB1) between African apes and humans along the second axis.

Figure 7. Boxplots of the third and fourth principal components and their associated shape changes. Bars represent the mean, box represents the bootstrapped 95% confidence interval, whiskers represent +/- one standard error of the mean, and the circles represent individual data points. 3D navicular scans are warped to the minimum (MIN) and maximum (MAX) values relative to the average shape (AVG) to demonstrate shape changes along these axes. PC3 is primarily related to the frontal plane orientation of the navicular relative to the dorsoplantar long axis of the lateral articular margin of the lateral cuneiform facet. PC3 separates *Pongo* from all other taxa. Variation in PC4 is primarily related to the plantar expansion of the navicular tuberosity. PC4 separates *Ateles* from all other taxa and represents its dramatically expanded tuberosity. Note the intermediate placement of *A. afarensis* (A.L. 333-36, -47) and *H. floresiensis* (LB1) between African apes and humans along the second axis.

Figure 8. UPGMA phenogram based on Procrustes distances between extant anthropoids and fossil hominins. Note the placement of the fossil hominins and modern humans within their own group distinct from African apes.

Figure 9. Phylomorphospace plots of navicular shape in anthropoid primates. (A) Principal Components 1 and 2; (B) Principal Components 1 and 3; (C) Principal Components 1, 2, and 3. White circles represent ancestral states of internal nodes reconstructed using squared change parsimony. Note the placement of the fossil hominins near modern humans, great apes distinct from all other taxa, and non-hominid anthropoids within a third group. In the combined 3D plot (C), *Pongo* is distinct from *Gorilla* and *Pan* in this combination of axes in a way that is difficult to observe in a 2D plot.

Figure 10. The bony navicular-cuboid articulation in fossil hominins. All naviculars are scaled to dorsoplantar height and aligned by the dorsoplantar long axis of the cuneiform facets. Note the cuboid facet on the *Pan troglodytes* navicular (highlighted in red) and the ligamentous region in *Homo sapiens*. The A.L. 333 and OH 8 naviculars possess this articular surface, whereas the LB1 navicular does not. Instead, LB1 has a proximodistally compressed navicular, as previous researchers have noted.

Table 1. Fossil hominin naviculars examined for this study.

Acc. No.	Taxon	Locality/Site	Date	References
A.L. 333-36	<i>Australopithecus afarensis</i>	Afar Locality 333, Hadar Formation, Ethiopia	3.2 Ma	Johanson et al. (1982), Latimer et al. (1982)
A.L. 333-47	<i>Australopithecus afarensis</i>	Afar Locality 333, Hadar Formation, Ethiopia	3.2 Ma	Johanson et al. (1982), Latimer et al. (1982)
LB 1	<i>Homo floresiensis</i>	Liang Bua	18 ka	Jungers et al. (2009)
OH 8	<i>Homo habilis/Paranthropus boisei?</i>	Olduvai Gorge, Tanzania	1.8 Ma	Leakey et al. (1964), Day and Wood (1968)

Table 2. Navicular metric comparisons in extant and fossil taxa^a.

Taxon		TFSA	NTVOL	RELVOL
<i>Homo sapiens</i>	$\bar{X}$	455	952	-1.09
<i>N</i> = 28	σ	72	284	0.11
<i>Pan troglodytes</i>	$\bar{X}$	337	1094	-0.765
<i>N</i> = 30	σ	10	346	0.09
<i>Gorilla gorilla</i>	$\bar{X}$	610	2982	-0.732
<i>N</i> = 21	σ	98	1210	0.12
<i>Gorilla beringei</i>	$\bar{X}$	600	3223	-0.671
<i>N</i> = 11	σ	135	1193	0.09
<i>Pongo pygmaeus</i>	$\bar{X}$	263	124	-1.55
<i>N</i> = 16	σ	65	48	0.16
<i>Hylobates</i> spp.	$\bar{X}$	64	93	-0.77
<i>N</i> = 22	σ	11	36	0.13
<i>Macaca</i> spp.	$\bar{X}$	82	103	-0.88
<i>N</i> = 18	σ	18	42	0.12
<i>Ateles</i> spp.	$\bar{X}$	88	339	-0.40
<i>N</i> = 10	σ	17	103	0.08
<i>Cebus apella</i>	$\bar{X}$	35	33	-0.81
<i>N</i> = 10	σ	5	7	0.08
AL 333-36		395	1667	-0.67
AL 333-47		370	1414	-0.70
LB 1		241	591	-0.85
OH 8		249	554	-0.80

^aTFSA = Talar facet surface area (mm²), NTVOL = Navicular tuberosity volume (mm³), RELVOL = Relative volume of navicular tuberosity ($\ln(\text{NTVOL}/\text{TFSA}^{1.5})$). $\bar{X}$ = mean, σ = standard deviation.

Table 3. Pairwise comparisons of relative tuberosity volume^a.

	<i>Homo</i>	<i>Pan</i>	<i>G. gorilla</i>	<i>G. beringei</i>	<i>Pongo</i>	<i>Hylobates</i>	<i>Macaca</i>	<i>Ateles</i>	<i>Cebus</i>
<i>Homo</i>	-	-	-	-	-	-	-	-	-
<i>Pan</i>	<0.001	-	-	-	-	-	-	-	-
<i>G. gorilla</i>	<0.001	0.997	-	-	-	-	-	-	-
<i>G. beringei</i>	<0.001	0.335	0.857	-	-	-	-	-	-
<i>Pongo</i>	<0.001	<0.001	<0.001	<0.001	-	-	-	-	-
<i>Hylobates</i>	<0.001	1.000	0.980	0.207	<0.001	-	-	-	-
<i>Macaca</i>	0.023	0.079	0.005	<0.001	<0.001	0.147	-	-	-
<i>Ateles</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-	-
<i>Cebus</i>	<0.001	0.957	0.534	0.013	<0.001	0.989	0.718	<0.001	-

^aBold values indicate statistical significance at the $p = 0.05$ level using Tukey's pairwise comparisons

Table 4. Pairwise comparisons of Procrustes distances between taxa^{a, b}.

	<i>Homo</i>	<i>Pan</i>	<i>G. gorilla</i>	<i>G. beringei</i>	<i>Pongo</i>	<i>Hylobates</i>	<i>Macaca</i>	<i>Ateles</i>	<i>Cebus</i>
<i>Homo</i>	-	0.206	0.207	0.227	0.222	0.264	0.185	0.261	0.254
<i>Pan</i>	0.001	-	0.056	0.102	0.200	0.201	0.200	0.242	0.277
<i>G. gorilla</i>	0.001	0.209	-	0.080	0.191	0.173	0.184	0.220	0.258
<i>G. beringei</i>	0.001	0.009	0.145	-	0.222	0.169	0.198	0.229	0.263
<i>Pongo</i>	0.001	0.001	0.001	0.001	-	0.235	0.192	0.295	0.252
<i>Hylobates</i>	0.001	0.001	0.001	0.001	0.001	-	0.134	0.168	0.169
<i>Macaca</i>	0.001	0.001	0.001	0.001	0.001	0.001	-	0.161	0.117
<i>Ateles</i>	0.001	0.001	0.001	0.001	0.001	0.001	0.001	-	0.179
<i>Cebus</i>	0.001	0.001	0.001	0.001	0.001	0.001	0.011	0.001	-

^a Procrustes distances above diagonal, *p*-values below the diagonal^b Bold values indicate statistical significance at the *p* = 0.05 level using standard t-test

Table 5. Average Procrustes distance between each fossil and extant taxon^a.

Taxon/fossil	AL 333-36	AL 333-47	LB1	OH 8
<i>Homo</i>	0.173	0.198	0.178	0.119
<i>Pan</i>	0.176	0.179	0.165	0.220
<i>G. gorilla</i>	0.161	0.169	0.164	0.218
<i>G. beringei</i>	0.162	0.173	0.181	0.236
<i>Pongo</i>	0.249	0.223	0.231	0.247
<i>Hylobates</i>	0.162	0.189	0.226	0.248
<i>Macaca</i>	0.160	0.177	0.210	0.188
<i>Ateles</i>	0.180	0.200	0.236	0.235
<i>Cebus</i>	0.215	0.226	0.282	0.253
AL 333-36	-	0.127	0.182	0.153
AL 333-47	-	-	0.184	0.163
LB1	-	-	-	0.172
OH 8	-	-	-	-

^aProcrustes distances between fossils are not averages since each pair represents two individuals

Figure 1

Figure 2

*

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Homo sapiens

Pan troglodytes

A.L. 333-36

Australopithecus afarensis

A.L. 333-47

LB1

H. floresiensis

OH8

H. habilis?