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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*). Instead, 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.

1. 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 et al., 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).

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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, 2015) make previous suggestions than 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.

2. 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 (*H. 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.,