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Inter-ray variation in metatarsal strength properties in humans and African apes: Implications for inferring bipedal biomechanics in the Olduvai Hominid 8 foot

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ABSTRACT

When measured as a ratio of mean midshaft diameter to bone length, the OH 8 fossil hominin foot exhibits a metatarsal (Mt) robusticity pattern of $1 > 5 > 3 > 4 > 2$, which differs from the widely perceived “common” modern human pattern ($1 > 5 > 4 > 3 > 2$); African apes generally exhibit a third pattern ($1 > 2 > 3 > 4 > 5$). Largely because of the relative ranking of Mt2 and Mt5, OH 8 metatarsals structurally resemble the pattern exhibited by bipedal humans more than the pattern of quadrupedal and climbing African apes. Considering only these three phenotypes, however, discounts the potentially important functional implications of variation in modern human (and African ape) metatarsal robusticity patterns, suggesting that they are not useful for interpreting the specific biomechanics of a bipedal gait in fossils (i.e., whether it was modern human-like or not). Using computed tomography scans to quantify metatarsal midshaft cross-sectional geometry in a large sample of *Homo* ($n=130$), *Gorilla* ($n=44$) and *Pan* ($n=80$), we documented greater variation in metatarsal robusticity patterns than previously recognized in all three groups. While apes consistently show a $1 > 2 > 3 > 4 > 5$ pattern in our larger sample, there does not appear to be a similarly precise single “common” human pattern. Rather, human metatarsals converge towards a $1 > 4/5 > 2/3$ pattern, where metatarsals 4 and 5, and metatarsals 2 and 3, often “flip” positions relative to each other depending on the variable examined. After reassessing what a “common” human pattern could be based on a larger sample, the previously described OH 8 pattern of $1 > 5 > 3 > 4 > 2$ is only observed in some humans (<6%) and almost never in apes (<0.5%). Although this suggests an overall greater similarity to (some) humans than to any ape in loading of the foot, the relatively rare frequency of these humans in our sample underscores potential differences in loading experienced by the medial and lateral columns of the OH 8 foot compared to modern humans.

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1. Introduction

Among the many significant postcranial elements attributed to early *Homo* is the near complete left foot from Olduvai Gorge: Olduvai Hominid 8 (OH 8). The foot was found in the FLK NN Level 3

and consists of all seven tarsals and five metatarsals in exceptional preservation (Fig. 1). Since its description by Day and Napier (1964), this fossil foot has received a great deal of interest from paleoanthropologists and has been at the center of many animated discussions. For example, researchers have debated whether it should be referred to as *Homo habilis* (Leakey et al., 1964; Susman and Stern, 1982; Susman, 2008) or *Paranthropus* (*Australopithecus*) *boisei* (Wood, 1974; Lewis, 1980; Gebo and Schwartz, 2006).

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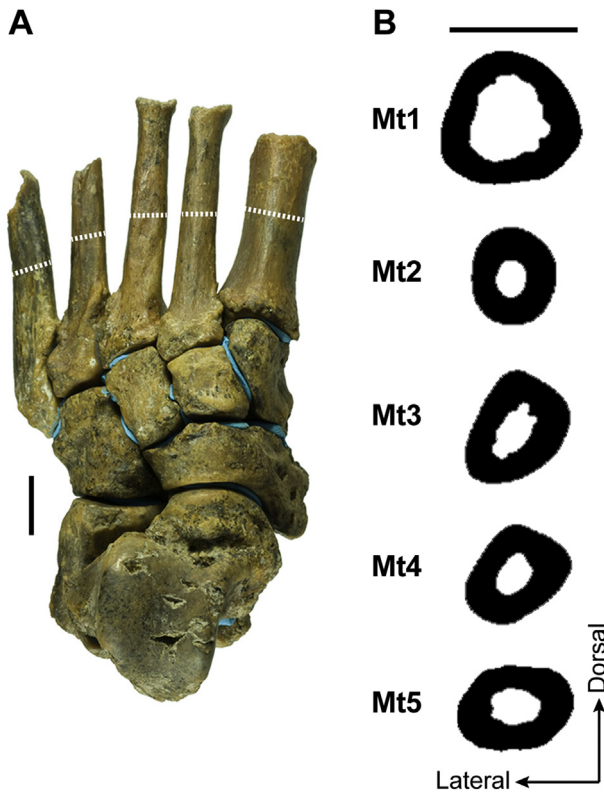


Figure 1. (A) Photograph of the articulated OH 8 foot in dorsal view (from [Susman et al., 2011](#)). The white dotted lines approximate the location of metatarsal midshafts where cross sections were extracted for analysis. (B) Midshaft cross sections obtained from CT scans for metatarsals (Mt) 1–5. Scale bars = 1 cm.

Researchers have also questioned its ontogenetic age with some favoring the hypothesis that the foot belongs to an adult ([Day and Napier, 1964](#); [Day, 1976](#); [DeSilva et al., 2010](#)) and others noting that OH 8 is a sub-adult near the age when metatarsal epiphyses begin to fuse ([Leakey, 1961](#); [Susman and Stern, 1982](#); [Susman, 2008](#); [Susman et al., 2011](#)). Additionally, studies of its talus alone (e.g., [Lisowski, 1967](#); [Day and Wood, 1968](#); [Lewis, 1980](#); [Gebo and Schwartz, 2006](#)), or when all the bones of the foot were examined collectively (e.g., [Day and Napier, 1964](#); [Susman and Stern, 1982](#); [Kidd et al., 1996](#)), have resulted in conflicting functional interpretations regarding its biomechanics. With regard to these functional interpretations, the consensus remains that the OH 8 foot belonged to a terrestrial and habitually bipedal hominin ([Day and Napier, 1964](#); [Harcourt-Smith and Aiello, 2004](#)). However, opinions have differed on whether the foot was biomechanically identical to modern humans, or if it was somewhat intermediate between modern humans and earlier australopiths ([Day and Napier, 1964](#); [Day and Wood, 1968](#); [Archibald et al., 1972](#); [Wood, 1974](#); [Lewis, 1980](#); [Oxnard and Lisowski, 1980](#); [Susman and Stern, 1982](#); [Kidd et al., 1996](#); [Harcourt-Smith et al., 2015](#)).

One of the key features originally identified by [Day and Napier \(1964\)](#) to argue that the OH 8 foot may not have been functionally identical to modern humans, and thus did not have a modern human-like bipedal gait and foot kinematics, was what they called its metatarsal (Mt) “robusticity formula”. Robusticity is a measure thought to reflect habitual stresses in long bones, and in particular, loads experienced over an animal’s lifetime (see [Pearson, 2000](#) and references therein). Examining robusticity across the metatarsals as a formula is a means to assess how rays differ from each other in terms of their absolute rigidity or strength in relation to an aspect of size (i.e., inter-ray differences). For example, a formula (or pattern) of $1 > 2 > 3$ indicates that the size adjusted strength property of

Mt1 is greater than Mt2, which in turn is greater than Mt3. Human metatarsals experience a variety of mechanical forces during locomotion, especially during the second half of support phase from midstance to toe-off ([Griffin and Richmond, 2005](#) and references therein). For the hallux metatarsal (Mt1), as well as the second, third and fourth metatarsals (Mt2–4), most of these forces likely induce bending in the sagittal plane, and for the fifth (Mt5) these forces also cause bending in the transverse plane (e.g., [Ferris et al., 1995](#); [Donahue and Sharkey, 1999](#); [Arndt et al., 2002](#); [Griffin and Richmond, 2005](#)). Apes and other non-human primates also experience a variety of loading conditions on their metatarsals that likely differ from humans in magnitude and direction since the former have a foot that is better adapted for hallux grasping and utilizing a variety of arboreal behaviors (e.g., [Preuschoft, 1970](#); [Verecke et al., 2003, 2005](#); [Wunderlich and Ischinger, 2017](#)). Because every metatarsal likely experiences unequal loads in magnitude, orientation and frequency during the step cycle (e.g., [Donahue and Sharkey, 1999](#); [Griffin and Richmond, 2005](#); [Wunderlich and Ischinger, 2017](#)), and because these patterns differ between humans and non-humans, metatarsal robusticity patterns can differ substantially across and within taxa ([Archibald et al., 1972](#); [Riesenfeld, 1974](#)).

In general, it is thought that the human Mt1 is especially robust (i.e., structurally reinforced) relative to the other metatarsals because of the larger share of weight supported by it during the second half of stance phase and into toe-off ([Verecke et al., 2003](#); [Marchi, 2005, 2010](#); [Griffin and Richmond, 2005](#); [Pontzer et al., 2010](#); [Jashashvili et al., 2015](#)). Similarly, the Mt1 of apes tends to be more robust than the lateral metatarsals (Mt2–5) because it is used in hallux grasping during arboreal locomotion (e.g., [Conroy and Rose, 1983](#); [Marchi, 2005](#); [Patel et al., 2018](#)), and in particular during bouts of vertical climbing ([Wunderlich and Ischinger, 2017](#)). In humans, the Mt5 is usually more robust than Mt2–4 because the transverse and medial longitudinal arches distribute loads that are proportionally larger on the lateral side of the foot during the middle part of the bipedal step cycle (e.g., [Aiello and Dean, 1990](#); [Griffin and Richmond, 2005](#); [Marchi, 2005](#); [Dowdeswell et al., 2017](#)). Because plantar pressure in apes is higher during vertical climbing compared to when walking quadrupedally on the ground, especially on the medial side of the foot, it has been hypothesized that this may be one reason why the great ape Mt2 and Mt3 are relatively more robust than the great ape Mt4 and Mt5 ([Wunderlich and Ischinger, 2017](#)).

[Day and Napier \(1964\)](#) used a proxy of robusticity for metatarsals that was defined by calculating a ratio of mean midshaft diameter to bone length - referred to by them as a robusticity index - and identified a relative ranking in OH 8 of $1 > 5 > 3 > 4 > 2$. They also reported that the most common pattern observed in their modern human sample was $1 > 5 > 4 > 3 > 2$. Because they observed $1 > 2 > 3 > 4 > 5$ to be the common pattern in their small gorilla sample, and because in OH 8 its Mt5 was more robust than its Mt2, Mt3, or Mt4, they characterized OH 8 as more like humans than apes, and thus suggested that it reflected a biomechanically bipedal foot. But, because the relative position of Mt4 and Mt3 were reversed in OH 8 compared to their common modern human pattern, these authors also concluded that OH 8 might have had a biomechanically different (i.e., “primitive”) bipedal foot, corroborating other aspects of foot morphology (e.g., unusual ape-like talus; [Day and Wood, 1968](#)). It is worth noting, however, that [Day and Napier \(1964: 969\)](#) offered the caveat that the OH 8 robusticity pattern could “simply be an individual variation” from the most common human pattern.

The notion of individual variation in metatarsal robusticity formulae, and by extension intraspecific variation, was subsequently raised by [Archibald and colleagues \(1972\)](#). They questioned

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