



Functional aspects of metatarsal head shape in humans, apes, and Old World monkeys



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ABSTRACT

Modern human metatarsal heads are typically described as “dorsally domed,” mediolaterally wide, and dorsally flat. Despite the apparent functional importance of these features in forefoot stability during bipedalism, the distinctiveness of this morphology has not been quantitatively evaluated within a broad comparative framework. In order to use these features to reconstruct fossil hominin locomotor behaviors with any confidence, their connection to human bipedalism should be validated through a comparative analysis of other primates with different locomotor behaviors and foot postures, including species with biomechanical demands potentially similar to those of bipedalism (e.g., terrestrial digitigrady). This study explores shape variation in the distal metatarsus among humans and other extant catarrhines using three-dimensional geometric morphometrics (3DGM). Shape differences among species in metatarsal head morphology are well captured by the first two principal components of Procrustes shape coordinates, and these two components summarize most of the variance related to “dorsal doming” and “dorsal expansion.” Multivariate statistical tests reveal significant differences among clades in overall shape, and humans are reliably distinguishable from other species by aspects of shape related to a greater degree of dorsal doming. Within quadrupeds, terrestrial species also trend toward more domed metatarsal heads, but not to the extent seen in humans. Certain aspects of distal metatarsus shape are likely related to habitual dorsiflexion of the metatarsophalangeal joints, but the total morphological pattern seen in humans is distinct. These comparative results indicate that this geometric morphometric approach is useful to characterize the complexity of metatarsal head morphology and will help clarify its relationship with function in fossil primates, including early hominins.

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1. Introduction

The evolutionary transition of the hominin foot from a primitive grasping organ into a propulsive lever adapted for obligate terrestrial bipedality—a hallmark of human evolution—is a key focus of paleoanthropological research (Morton, 1922, 1924; Elftman and

Manter, 1935; Wood-Jones, 1944; Bojsen-Møller, 1979; Lewis, 1980; Susman, 1983; Latimer et al., 1987; Richmond et al., 2001; Harcourt-Smith and Aiello, 2004; Jungers et al., 2009; Lovejoy et al., 2009; Pontzer et al., 2010). Researchers have proposed different mechanistic models for the evolutionary sequence of modifications that led to the derived human condition (e.g., Morton, 1964; Susman, 1983; Lewis, 1989; Kidd, 1999; DeSilva, 2010). However, the fragmentary fossil record and the mosaic nature of fossil hominin pedal morphologies complicates attempts to build a

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consensus model of hominin foot evolution despite the extensive literature on the topic (Stern and Susman, 1983; Latimer et al., 1987; Susman and Brain, 1988; Latimer and Lovejoy, 1990; Harcourt-Smith and Aiello, 2004; Susman and de Ruiter, 2004; Zipfel and Kidd, 2006; Jungers et al., 2009, 2015; Zipfel et al., 2009, 2011; Pontzer et al., 2010; Ward et al., 2011, 2012; DeSilva et al., 2012; Haile-Selassie et al., 2012). What remains clear, however, is that modern human feet are well adapted for obligate bipedal locomotion. In combination, several derived features (e.g., an adducted, robust hallux; a midfoot stabilized by various soft tissues) enable the human foot to act efficiently as a stiff lever during the propulsive phases of bipedal gait (Elftman and Manter, 1935; Hicks, 1954; Morton, 1964; Lewis, 1980; Gomberg, 1985; Sarrafian, 1987; Harcourt-Smith and Aiello, 2004; but see Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015). These derived features presumably evolved as a consequence of selective pressures acting on the hominin foot during its transition from a primitive grasping organ used in arboreal locomotion (Stern and Susman, 1983; Susman et al., 1984; Stern, 2000; Lovejoy et al., 2009; but see Ward, 2002) to one used during habitual terrestrial bipedalism (Susman and Stern, 1982; Spoor et al., 1994; Ruff, 2008, 2009; Pontzer et al., 2010).

The forefoot is a functionally important region that includes the metatarsophalangeal joints (MTPJs). A more dorsally projecting metatarsal (MT) head is thought to increase the dorsiflexion range of motion (ROM) at the MTPJs (Ward et al., 2011; DeSilva et al., 2012). This increased ROM serves to stabilize the forefoot and aids propulsion at the end of stance phase by tightening the plantar aponeurosis, which is a fibrous band that originates from the calcaneal tuberosity and inserts distally on the proximal phalanges (DeSilva, 2010; Griffin et al., 2015). This tightening of the plantar aponeurosis has been likened to a “windlass mechanism” (Hicks, 1954; Bojsen-Møller, 1979; Susman, 1983; Griffin and Richmond, 2010; Griffin et al., 2015) wherein it is analogous to a cable, the metatarsal head a drum, and the proximal phalangeal base a handle. During toe-off, the plantar aponeurosis becomes taut and the medial longitudinal arch of the foot is raised. This changes the conformation of the midfoot into a more rigid lever that improves propulsion and stability during bipedalism. Conversely, a more plantar oriented MT head is hypothesized to increase plantar flexion ROM for arboreal pedal grasping (Stern and Susman, 1983; Hamrick, 1996); this plantar orientation likely impedes the mechanical advantage of the windlass mechanism, resulting in reduced dorsiflexion at toe-off (Griffin et al., 2010b; Holowka et al., 2014). However, additional factors such as digit length may also reduce toe-off dorsiflexion in apes because their longer toes would be subject to greater bending stresses while dorsiflexed compared to the shorter toes of modern humans (Preuschoft, 1970; Tuttle, 1970).

In addition to MT head projection, other researchers have emphasized a flattened mediolateral expansion of the dorsal aspect of the MT head as necessary for joint stability under increased loads during modern human-like toe-off (Susman and Brain, 1988; Susman and de Ruiter, 2004; Pontzer et al., 2010). Wide and flat MT heads in humans are easily distinguished qualitatively from the narrow, rounded condition seen in *Pan* and other primates (Fig. 1). Dorsal mediolateral expansion of the MT head allows for “close-packing” of the MTPJs by tightening the collateral MTP ligaments in the dorsiflexed configuration. In the close-packed position, the contact surface of the MT head and proximal phalangeal base articular surfaces is maximized, and tightening of collateral ligaments limits joint motion in other anatomical planes when the MTPJs are dorsiflexed, thus increasing joint stability when maximum joint congruency is achieved (MacConaill and Basmajian, 1969; Stern and Susman, 1983; Susman et al., 1984; Susman and

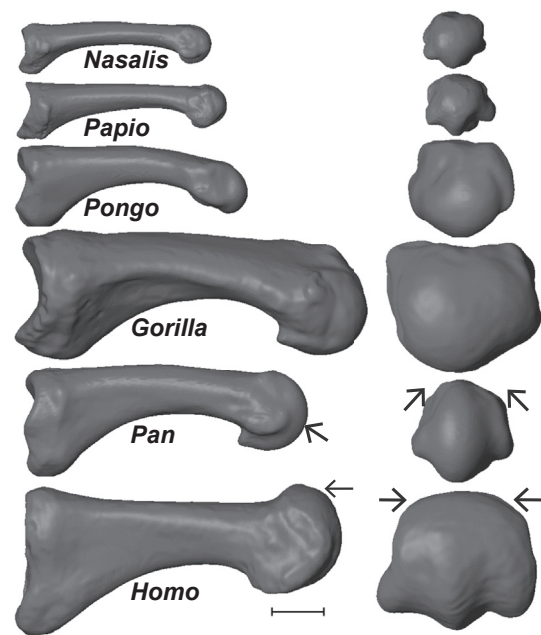


Figure 1. Comparative morphology of catarrhine right first metatarsals (MTs). Apes are characterized by highly curved MT shafts terminating in a strong plantar orientation of the MT head and narrow, rounded MT heads (arrows); monkeys and humans have straight MTs terminating in a more dorsally oriented MT head. Note that *Homo* is characterized by dorsal overlap of the distal articular surface onto the MT shaft and by wide flattening of the dorsal articular surface (arrows). Left column: lateral view. Right column: distal view. Bar: 1 cm.

Brain, 1988; Susman and de Ruiter, 2004). This same mechanism is hypothesized to close-pack the ape MTPJs in plantar flexion for increased stability during pedal grasping (Susman, 1983).

Detailed morphometric analyses have been conducted on the proximal MT articular surface (Proctor et al., 2008; Proctor, 2010a, b; 2013), and a few quantitative approaches to distal MT and proximal phalangeal functional morphology (e.g., Duncan et al., 1994; Griffin et al., 2010a; Congdon et al., 2011) have been investigated as well. MT head “dorsal doming” has been qualitatively described in fossil hominins extensively (Stern and Susman, 1983; Susman and Brain, 1988; Latimer and Lovejoy, 1990; Susman and de Ruiter, 2004; Jungers et al., 2009; Lovejoy et al., 2009; Ward et al., 2011; DeSilva et al., 2012; Haile-Selassie et al., 2012), but quantitative data on distal MT surface morphology relating to “dorsal doming” is lacking, therefore precluding morphometric comparisons of this phenomenon. The current lack of quantitative data makes it difficult to ascertain more precisely the functional importance of hypothesized bipedal specializations, especially when these complex morphologies are combined and simplified into a binary character state (e.g., domed versus not domed). Additionally, although modern humans qualitatively possess dorsally oriented and dorsally flat, wide MT heads, many fossil hominins lack one or more of these “defining bipedal features” (Susman and de Ruiter, 2004; Lordkipanidze et al., 2007; Pontzer et al., 2010; DeSilva et al., 2012).

The goal of this study is to quantify “dorsal doming” in all five MTs within an extant comparative context. Dorsal MT head orientation, mediolateral dorsal expansion of the MT head, and dorsal overlap of the MT head onto the diaphysis are often considered signature features of human bipedality. However, we hypothesize that some of these characters might reflect signals of terrestriality more generally for other taxa that stereotypically dorsiflex their forefoot joints during quadrupedal locomotion.

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