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Metatarsal torsion in monkeys, apes, humans and australopiths

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ABSTRACT

This paper presents an analysis of metatarsal torsion in apes, cercopithecoids and humans, compares australopiths with these species, and discusses their inferred foot morphology and function relative to prehensility, arboreality and the presence or absence of a longitudinal arch. Our results show that locomotor modes are reflected in metatarsal torsion values. Apes, which climb vertically with their foot inverted, have hallucal metatarsal heads that are turned toward the other toes and lateral toes that are inverted. Cercopithecoids, which tend to orient their feet in an axis more parallel to the line of motion, present signs of prehensility by having inverted 2nd metatarsals that oppose the hallux, while their two lateral-most metatarsals are strongly everted. Humans, with their rigid feet and longitudinal arches, have all toes that present their plantar surface toward the ground, resulting in hallucal and 2nd metatarsals that are relatively untwisted and the others that are strongly everted. Humans are different from all taxa only for the 2nd and 3rd metatarsal. It is hypothesized that the untwisted 2nd metatarsal reflects the lack of digit opposability of the medial foot and the strongly everted 3rd metatarsal reflects the longitudinal arch. *Australopithecus afarensis* was characterized by an everted lateral foot, the prerequisite for the development, but not necessarily an indicator, of a longitudinal arch. In *Australopithecus africanus*, torsion of fragmentary and complete 1st, 2nd, 3rd and 5th metatarsals suggest that the species did not have a foot with monkey- or ape-like prehensile capabilities and did not have a human-like longitudinal arch. In the Swartkrans remains, torsion is consistent with an unprehensile foot. The morphology of the fossils indicates that there was strong selection to orient the plantar surface of the toes facing the ground at the expense of a grasping foot and inversion ability.

Introduction

The foot is particularly interesting to study since it is the anatomical region that is in direct contact with the substrate during locomotion. Its study has been predominant in the debate about the locomotor adaptation of australopiths, with researchers alternatively arguing for a bipedality that was basically human-like (e.g., Latimer and Lovejoy, 1989, 1990a,b) or one that retained important ape-like characteristics (e.g., Stern and Susman, 1983; Duncan et al., 1994). These interpretations were based on complete or fragmented bones such as the calcaneus, talus, navicular, cuneiforms, cuboid, metatarsals, and phalanges. Although the focus has often been on prehensile capacities of the hallux, presence or not of a longitudinal arch, and degrees of dorsoplantar flexion of the different joints, little consensus has been reached on any of these issues. Metatarsal heads experience high plantar pressure during locomotion in primates (Wunderlich, 1999), and thus the study of metatarsal orientation is interesting because it reflects the positioning of the toes and their direction of flexion and extension, which is important for determining how the foot is being used during locomotion. Recently, torsion of the 4th metatarsal was used as an argument that the *Australopithecus afarensis* foot had a longitudinal arch (Ward et al., 2011). The reasoning is based, in part, on the assumption that the head is positioned to allow flexion of the toe in a parasagittal plane, and the base, instead of having its plantodorsal axis also perpendicular to the ground, is rotated and raised as part of the transverse arch of the foot (Pontzer et al., 2010). Both Pontzer et al. (2010) and Ward et al. (2011) equate the presence of a transverse arch with that of a longitudinal arch. However, humans are not unique in having a transverse arch since it is observed in monkeys and in extant and fossil apes (Weidenreich, 1923; Morton, 1935; Elftman and Manter, 1935a,b; Aiello and Dean, 1990; Rose, 1994; Sarmiento, 1994) and the evidence linking lateral metatarsal eversion with a longitudinal arch is very

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limited (Pontzer et al., 2010; Ward et al., 2011). This study presents the result of an analysis of the degree of metatarsal torsion in extant humans, apes, and monkeys and how it relates to locomotion in these species, and determines whether metatarsal torsion can predict prehensility and the presence or absence of a longitudinal arch. In light of these results, we measured metatarsal torsion in specimens from Hadar, Sterkfontein and Swartkrans to determine how their metatarsal morphology compares with extant primates and how it informs us about their locomotion and foot architecture.

Background

The human foot is derived relative to that of apes and monkeys to facilitate bipedality in which the foot acts as a stable, propulsive lever during weight transmission and extreme dorsiflexion, with integration of the 1st digit in the lever (Morton, 1922, 1924; Elftman and Manter, 1935a,b; Oxnard and Lisowski, 1980; Lewis, 1980, 1989). The salient features of such a foot include an adducted hallux, a longitudinal arch, reduced ray lengths, increased length of some tarsals, and features of the calcaneus and talus that allow for correct positioning of the foot relative to an upright leg (Morton, 1935; Elftman and Manter, 1935a,b; Stern and Susman, 1983; Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990a,b; Aiello and Dean, 1990). The lateral four metatarsals in humans differ from those of apes in a number of ways. Human metatarsal heads are deeper dorsoplantarly compared with ape metatarsal heads (Latimer and Lovejoy, 1990a). In contrast to the expanded plantar surface of the heads in apes, humans have expanded dorsal surfaces (Stern and Susman, 1983; Susman et al., 1984; Latimer and Lovejoy, 1990a; Zipfel et al., 2009). Relative to the long axis of the metatarsal shaft, human heads are dorsally tilted, while those of African apes are more plantarly tilted (Latimer and Lovejoy, 1990a; but see Duncan et al., 1994, for a different opinion). One apparent byproduct of the dorsal tilt of the articular surface is the presence of a shallow groove or sulcus oriented transversely and that marks the junction of the diaphysis and head (Stern and Susman, 1983; Latimer and Lovejoy, 1990a; Lovejoy et al., 2009; Zipfel et al., 2009). These traits reflect the enhanced dorsiflexion capability of the human toes (Susman, 1983; Griffin and Richmond, 2009; Griffin et al., 2010). According to Latimer and Lovejoy (1990a), the range of excursion in dorsiflexion is 74° on average in humans compared with 57° in chimpanzees and 45° in gorillas, when measured on bony specimens. The human hallucal metatarsal is characterized by a large, mediolaterally wide head, particularly dorsally, with an articular surface that extends dorsally (Susman et al., 1984), while that of apes is more globular and does not present a dorsal widening and flattening. In humans, the metatarsal bases are modified to limit movement with the tarsals and keep the foot rigid (DeSilva, 2010; Ward et al., 2011). The articular facets with the tarsals are flat and the 2nd and 4th metatarsals are indented into the tarsal row, both presenting an articulation with the lateral cuneiform (DeSilva, 2010). In apes, these articulations tend to be concavo-convex allowing for some flexion–extension and the 4th tarsometatarsal articulation is not indented into the tarsal row as in humans (DeSilva, 2010). Indentation of the 2nd metatarsal and articulation with the lateral cuneiform, however, is a human trait shared with African apes. The human hallucal metatarsal articular surface is reniform and flat and combined with a usually flat articular surface on the medial cuneiform, a morphology that limits motion at that joint (Morton, 1922; Schultz, 1930; Elftman and Manter, 1935a; Susman, 1983; Susman et al., 1984; Latimer and Lovejoy, 1990b; Susman and de Ruiter, 2004). In other primates, the articular surface is concave on the metatarsal and convex on the medial cuneiform (Lewis, 1972), allowing for considerable movement at that joint and hallux abduction.

One of the most notable traits related to bipedality in the human foot is the presence of a longitudinal arch, particularly developed on the medial side. As a consequence, in normal posture and locomotion, the distal tarsal bones are raised from the ground medially, while laterally, the longitudinal arch is shallow and rests on the ground when loaded (Palastanga et al., 2002). The longitudinal arch of the human foot results in large ground reaction forces to be born at the heel and metatarsal heads (see for example Elftman and Manter, 1935a; Vereecke et al., 2003; Lieberman et al., 2010), while in apes, the ground reaction forces are lower (Vereecke et al., 2003) and much less standardized (Vereecke et al., 2003; Crompton et al., 2008). Since this arch has its greatest curvature on the medial side, the base of the medial metatarsals and the associated distal tarsals are raised from the ground. As a consequence, the dorsoplantar axes of the bases are approximately perpendicular to the ground (Koura, 1984) and the head of the hallucal and 2nd metatarsals present little torsion relative to the orientation of the base (Fig. 1A, B; Morton, 1922; Elftman and Manter, 1935a; Lewis, 1980, 1989; Aiello and Dean, 1990; Berillon, 1998; Drapeau and Harmon, 2008). However, at the proximal metatarsal level, the arch descends laterally and the dorsoplantar axis of the bases rotates slightly, converging plantaromedially (Fig. 1A, B). As a result, the heads of the lateral-most metatarsals are twisted about the shafts so that their plantar surface is in contact with the ground (Fig. 1A, B; Morton, 1922; Elftman and Manter, 1935a; Lewis, 1980, 1989; Susman, 1983; Aiello and Dean, 1990; Berillon, 1998; Drapeau and Harmon, 2008).

The ape foot, in contrast, does not have a longitudinal arch. However, the distal tarsal bones and metatarsal bases are organized in a transverse arch (Weidenreich, 1923; Morton, 1935; Elftman and Manter, 1935a,b; Aiello and Dean, 1990; Sarmiento, 1994; Vereecke and Van Sint Jan, 2008) without a highly raised medial side as observed in humans (Fig. 1C, D). The lateral digits have plantar surfaces that are rotated toward the hallux (Fig. 1C, D; Elftman and Manter, 1935a). As a consequence, their lateral-most metatarsals, which have bases that are inverted, present little or no torsion relative to their base, while the 2nd metatarsal, which has its base with a dorsoplantar axis that is closer to being perpendicular to the ground, presents inversion so that the plantar surface of that digit faces the hallux (Fig. 1C, D; Morton, 1922; Elftman and Manter, 1935a; Lewis, 1980, 1989; Susman, 1983; Drapeau and Harmon, 2008). Similarly, the hallucal metatarsal is strongly everted so that it opposes the other digits (Fig. 1C, D; Morton, 1922; Elftman and Manter, 1935a; Lewis, 1980, 1989; Drapeau and Harmon, 2008) in a position that facilitates prehension.

The differences between the flexible prehensile foot of apes and that of the rigid, unprehensile foot of humans are quite marked and, if the hominin foot evolved from an ape-like foot, these differences involve major evolutionary changes. Models proposed to explain the evolution of the human foot from that of a flexible, prehensile ape-like foot have been reviewed in Harcourt-Smith and Aiello (2004), but include achieving an adducted hallux through reorientation of the forefoot medially toward the 1st ray (Lewis, 1989). A different notion emphasizes that stability was achieved first through evolution in the lateral foot, such as the calcaneocuboid joint, followed by the medial column, including the creation of the longitudinal arch (Morton, 1935; Kidd et al., 1996; Kidd, 1999; Kidd and Oxnard, 2005). Harcourt-Smith and Aiello (2004) propose that, in some instances, the proximal foot, i.e., the ankle, became human-like while maintaining a more ape-like distal foot with an opposable hallux. More recently, Lovejoy et al. (2009), based on their analysis of *Ardipithecus ramidus*, hypothesized to be arboreal as well as bipedal when terrestrial, proposed that the hominin foot would have evolved from a morphology more monkey-like than African ape-like. They suggest that the last common ancestor of *Pan* and