Skeletal development of hallucal tarsometatarsal joint curvature and angulation in extant apes and modern humans

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ABSTRACT

The medial cuneiform, namely the curvature and angulation of its distal facet with metatarsal 1, is crucial as a stabilizer in bipedal locomotion and an axis upon which the great toe medially deviates during arboreal locomotion in extant apes. Previous work has shown that facet curvature and angulation in adult dry-bone specimens can distinguish African apes from *Homo*, and can even distinguish among species of *Gorilla*. This study provides the first ontogenetic assessment of medial cuneiform curvature and angulation in juvenile (n = 68) and adult specimens (n = 102) using computed tomography in humans and extant ape specimens, including *Pongo*. Our data find that modern human juveniles initially have a convex and slightly medially oriented osseous surface of the developing medial cuneiform distal facet that flattens and becomes more distally oriented with age. The same pattern (though of a different magnitude) occurs developmentally in the chimpanzee medial cuneiform, but not in *Gorilla* or *Pongo*, whose medial cuneiform facet angulation remains unchanged ontogenetically. These data suggest that the medial cuneiform ossifies in a distinguishable pattern between *Pongo*, *Gorilla*, *Pan*, and *Homo*, which may in part be due to subtle differences in the loading environment at the hallucal tarsometatarsal joint—a finding that has important implications for interpreting fossil medial cuneiforms.

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1. Introduction

The medial cuneiform is the most medial distal tarsal bone in the foot, articulating distally with metatarsal 1 and proximally with the navicular. In modern humans, the medial cuneiform is thought to reach adult morphology by six years of age (Scheuer and Black, 2000). Its articulation with the hallux makes the medial cuneiform an essential part of the abduction and grasping mechanism during arboreal locomotion in extant apes and of the propulsive mechanism in *Homo*. The medial cuneiform further contributes to the transverse arch of the foot, along with the intermediate and lateral cuneiforms and cuboid. Moreover, the medial cuneiform serves as a medial attachment site for tibialis anterior, which is crucial for foot inversion, as well as an attachment site for peroneus longus, which everts the foot.

Scholars have long recognized that the adducted hallux is a unique characteristic of the human foot when compared to other primates (Tyson, 1699; Wood Jones, 1916; Keith, 1923; Weidenreich, 1923; Gregory, 1928; Keith, 1929; Schultz, 1930, 1934; Midlo, 1934; Morton, 1935). Schultz (1930, 1934), in particular, noted that the morphology of the medial cuneiform was critical for assessing the relative opposability of the hallux and attempted to quantify both the orientation and curvature of the facet in different species of apes and humans. However, application of these approaches to the fossil record was limited by paucity of hominin medial cuneiforms or first metatarsals (but see Day and Napier, 1964; Lewis, 1972).

Following the recovery and study of a large collection of pedal remains from Hadar, Ethiopia (Latimer et al., 1982), Latimer and Lovejoy (1990) completed the first detailed analysis of medial cuneiform morphology in *Australopithecus (Au.) afarensis*. Using sectioned casts from dry-bone adult specimens of *Pan*, *Gorilla*, and *Homo*, they found that the angular orientation of the distal facet with metatarsal 1 was most oblique in *Pan* specimens with *Homo*

having an orientation near 90°. With this measurement, they determined that the 3.2 Ma A.L. 333-28 medial cuneiform assigned to *Au. afarensis* was within the range of variation in modern humans. They further identified differences in the curvature of the distal facet of the medial cuneiform. Latimer and Lovejoy (1990) found that *Pan* had the highest degree of curvature, which they associated with the ability for hallucal abduction and opposability at the tarsometatarsal joint. The more flattened surface of the distal medial cuneiform facet in modern humans was argued to be associated with an increase in the efficiency of the propulsive bipedal push-off mechanism and a decrease in relative mobility at the joint. In the A.L. 333-28 specimen, there was heightened curvature compared to modern humans, which was interpreted as evidence that peroneus longus served as a plantarflexor in the absence of a derived triceps surae. This interpretation has been challenged and the "markedly convex" (Latimer et al., 1982) facet of the A.L. 333-28 medial cuneiform (Stern and Susman, 1983; Susman, 1983; Susman et al., 1984; Deloison, 1992; Berillon, 1999), along with anatomies of the first metatarsal (Proctor, 2010) and the Laetoli footprints (Bennett et al., 2009), have been interpreted as evidence that *Au. afarensis* may have retained some grasping ability with its big toe.

Interpretations of the StW 573 ("Little Foot") medial cuneiform have likewise varied. Originally described as possessing a moderately divergent hallux (Clarke and Tobias, 1995), others have found little evidence for grasping potential in this South African australopith (Harcourt-Smith, 2002; Harcourt-Smith and Aiello, 2004; McHenry and Jones, 2006; Lovejoy et al., 2009).

New methodology has also contributed to our understanding of medial cuneiform morphology in apes and humans. Tocheri et al. (2011) and Solhan (2011) acquired 3D (three-dimensional) models of medial cuneiforms using computed tomography and surface scanning to quantify angulation and curvature of the distal medial cuneiform facet in hominoids. In particular, Tocheri et al. (2011) examined different *Gorilla* species and subspecies to test observations of intrageneric differences in medial cuneiform morphology originally made by Schultz (1930, 1934). They determined that the more arboreal western gorilla has a more curved and medially oriented distal facet, supporting the notion that both measurements can be potentially diagnostic in differentiating degree of arboreality in extant ape populations.

These and other (e.g., Gomberg, 1981; Berillon, 1999; Harcourt-Smith, 2002; McHenry and Jones, 2006) studies established the significance of both angulation and curvature of the distal medial cuneiform facet as functionally informative morphologies in adult apes and humans. How these anatomies develop ontogenetically, however, is entirely unknown. While most ontogenetic studies in paleoanthropology have focused on the skull and/or neurocranium (e.g., Zollikofer and Ponce de León, 2013), an ontogenetic characterization of the postcranium can yield important functional insights into individual behavior (Ward, 2002) and has been used to interpret phalangeal curvature (Richmond, 1998), knuckle-walking adaptation in the apes (Kivell and Schmitt, 2009), and the hominin shoulder (Green and Alemseged, 2012), leg (Tardieu, 2010), and knee (Tardieu, 1999; Shefelbine et al., 2002; Glard et al., 2005). Here, we apply this same approach to the hominoid first tarsometatarsal joint. These data may reveal how functionally critical aspects of adult pedal skeletal morphology actually form in apes and humans and could eventually be useful for interpreting pedal material from juvenile hominins (e.g., Alemseged et al., 2006) and hominoids (e.g., Napier and Davis, 1959; Dunsworth, 2006).

In this study, we test the null hypothesis that there is no significant alteration in bony curvature or angulation of the hallucal tarsometatarsal joint from birth through adulthood in extant ape and modern human medial cuneiforms. Using high-resolution computed tomography (CT), we quantify these measures in juvenile and adult *Pongo*, *Gorilla*, *Pan*, and *Homo*. In addition to characterizing the ontogenetic development of these morphologies, this study examines interspecific differences in morphology of the first tarsometatarsal joint across apes and humans and uses these data to re-interpret fossil medial cuneiforms (A.L. 333-28, StW 573, OH 8) from Plio-Pleistocene hominins.

2. Material and methods

2.1. Specimen selection

The study was approved by the Partners Healthcare Inc. Institutional Review Board and was Health Insurance Portability and Accountability Act compliant. A retrospective search was performed for foot computed tomography (CT) imaging obtained at Massachusetts General Hospital from January 2000 to January 2013 in subjects who were less than 21 years of age. Exclusion criteria included subjects with gross osteogenic deformity, fracture, or abnormality of the medial cuneiform or the adjacent tarsal bones. CT examinations from 46 feet were chosen that met the inclusion criteria. These included three scans per age group from age 9 to 20, two scans for ages 5 and 7, and one scan for ages 1, 2, 3, 4, 6, and 8. Age at time of scan was recorded for each subject.

Dry-bone medial cuneiforms were collected from wild-shot ape specimens from the Museum of Comparative Zoology (MCZ) at Harvard University and the American Museum of Natural History (AMNH) in New York (Table 1). All extant ape specimens had an associated skull cataloged with the medial cuneiforms at their respective museums. Stage of tooth eruption by visual inspection for all specimens was recorded; extant ape adults were defined by complete third molar eruption. Adult samples in *Homo* include specimens with absolute age greater than 17 years old. Dorsoplantar height of the medial cuneiform was used as a proxy for age given the different developmental schedules of the different species examined in this study.

High-quality research casts of A.L. 333-28 (*Au. afarensis*) and 3D surface scans (Next Engine scanner) of the original specimens OH 8 and StW 573 were used in this analysis (Table 2). Ten dry-bone adult *Homo* medial cuneiforms (Boston University biological anthropology laboratory) were also included in the specimen cohort. Because there were no significant differences ($p > 0.1$, all values) when comparing results of curvature or angulation between the adult *Homo* in vivo CT scans and the 10 additional dry-bone adult medial cuneiforms, these data were pooled in all subsequent analyses.

2.2. CT imaging

In vivo CT imaging of human subjects was performed using a GE LightSpeed Pro 16 scanner (General Electric, Milwaukee, WI): slice

Table 1
Medial cuneiforms examined in this study.

Species	Juvenile	Adult	Total
Gorilla gorilla	5	36	41
Pan troglodytes	20	36	56
Pongo pygmaeus	6	7	13
Homo sapiens	37	20	57
Total	**68**	**99**	**167**

In the extant apes, specimens were separated into juveniles and adults based on corresponding tooth eruption of the associated cranium. In *Homo*, juveniles were identified as younger than 18 years of age at time of CT.