



## Evolution of the hominin knee and ankle



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### ABSTRACT

The dispersal of the genus *Homo* out of Africa approximately 1.8 million years ago (Ma) has been understood within the context of changes in diet, behavior, and bipedal locomotor efficiency. While various morphological characteristics of the knee and ankle joints are considered part of a suite of traits indicative of, and functionally related to, habitual bipedal walking, the timing and phylogenetic details of these morphological changes remain unclear. To evaluate the timing of knee and ankle joint evolution, we apply geometric morphometric methods to three-dimensional digital models of the proximal and distal tibiae of fossil hominins, Holocene *Homo sapiens*, and extant great apes. Two sets of landmarks and curve semilandmarks were defined on each specimen. Because some fossils were incomplete, digital reconstructions were carried out independently to estimate missing landmarks and semilandmarks. Group shape variation was evaluated through shape- and form-space principal component analysis and fossil specimens were projected to assess variation in the morphological space computed from the extant comparative sample. We show that a derived proximal tibia (knee) similar to that seen in living *H. sapiens* evolved with early *Homo* at ~2 Ma. In contrast, derived characteristics in the distal tibia appear later, probably with the arrival of *Homo erectus*. These results suggest a dissociation of the morphologies of the proximal and distal tibia, perhaps indicative of divergent functional demands and, consequently, selective pressures at these joints. It appears that longer distance dispersals that delivered the Dmanisi hominins to Georgia by 1.8 Ma and *H. erectus* to east-southeast Asia by 1.6 Ma were facilitated by the evolution of a morphologically derived knee complex comparable to that of recent humans and an ankle that was morphologically primitive. This research sets the foundation for additional paleontological, developmental, and functional research to better understand the mechanisms underlying the evolution of bipedalism.

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### 1. Introduction

While terrestrial bipedalism initially evolved at, or soon after, the split with the last common ancestor of *Homo* and *Pan*, ~6–7 Ma (Brunet et al., 2002; Zollikofer et al., 2005; Richmond and Jungers, 2008; Almécija et al., 2013), fossil evidence suggests that the

evolution of skeletal characteristics associated with bipedal locomotion was a ‘mosaic’ process (Harcourt-Smith and Aiello, 2004; Zipfel et al., 2011) and that early hominins, and even some early members of the genus *Homo* (Antón et al., 2014), may have adopted a diverse array of locomotor behaviors (Clarke and Tobias, 1995; Harcourt-Smith and Aiello, 2004; Lovejoy et al., 2009; Zipfel et al., 2011; Haile-Selassie et al., 2012; Harcourt-Smith et al., 2015; Harcourt-Smith, 2016). Despite the complexity of this evolutionary transition, the postcranial morphology indicative of obligate terrestrial bipedalism and increased locomotor efficiency is

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typically thought to have evolved as part of a suite of morphological, behavioral, and life history characteristics during the transition from *Australopithecus* to *Homo*, at least 2–2.5 Ma (Aiello and Wheeler, 1995; Bramble and Lieberman, 2004; Antón et al., 2014) or earlier (Villmoare et al., 2015). More recent fossil and archaeological evidence, however, suggest that the “suite” of traits typically associated with *Homo ergaster/erectus* in fact may have appeared over a prolonged period and across multiple species spanning australopithecids and early *Homo* (Haile-Selassie et al., 2010; Pontzer, 2012; Antón et al., 2014; Harmand et al., 2015).

Determining an accurate timeline for the evolution of derived skeletal features indicative of modern human-like bipedal locomotion is critical for understanding the functional implications of morphological changes in the locomotor skeleton of hominins and the nature of adaptive and ecological shifts that led early *Homo* to disperse out of Africa (Antón, 2012; Antón et al., 2014). Among the suite of morphological traits associated with efficient bipedal locomotion, derived ankle and knee joints that effectively stabilize the lower limb during walking, functioning in a manner comparable to that seen in later Pleistocene hominins and modern *Homo sapiens*, are key features (Tardieu, 1999; DeSilva, 2008; Zipfel and Berger, 2009; Zipfel et al., 2011; Sylvester and Pfisterer, 2012; Sylvester, 2013). Most studies of the knee and ankle joint, however, focus on tibiofemoral and talocrural morphology (Lovejoy, 2007; Harcourt-Smith et al., 2008)—the proximal and distal morphology of the tibia are rarely analyzed within a phylogenetic and functional context.

Differences between human and ape tibiae have often been noted (Table 1). These are attributed mainly to variations in locomotor mode—bipedalism versus arboreal and terrestrial quadrupedalism (including climbing). The relative positions of articular surfaces, degree of curvature of the tibial condyles, muscle and ligament attachment areas, diaphyseal morphology, overall proportions, and torsion of the shaft are among the features commonly analyzed. These same features are also commonly used for the diagnosis of hominin fossil specimens (Davis, 1964; Trinkaus, 1975; Tardieu, 1981, 1999; Stern and Susman, 1983; Latimer et al., 1987; Berger and Tobias, 1996; Wood et al., 1998; Organ and Ward, 2006; DeSilva, 2008, 2009, 2010; Lovejoy et al., 2009; Zipfel and Berger, 2009; DeSilva and Throckmorton, 2010; Zipfel et al., 2011; Tallman et al., 2013). Nevertheless, despite the functional significance of many of these morphological features, it remains unclear precisely when and in which hominin species the functionally-relevant changes in ankle and knee morphology evolved in relation to bipedal locomotion.

Turning to the hominin fossil record, although the degree of habitual terrestrial bipedalism in early hominins remains a subject of debate (Richmond and Jungers, 2008; Lovejoy et al., 2009; White et al., 2009; Sarmiento and Meldrum, 2011; Almécija et al., 2013; White et al., 2015; Harcourt-Smith, 2016), most studies agree that habitual terrestrial bipedalism appeared with the genus *Australopithecus* (McHenry, 1986; Latimer et al., 1987; Leakey et al., 1995; Berger and Tobias, 1996; Ward et al., 1999; Harcourt-Smith and Aiello, 2004; Green et al., 2007; Haile-Selassie et al., 2010; Zipfel et al., 2011). East African taxa such as *Australopithecus anamensis* and *Australopithecus afarensis* provide the best evidence for habitual terrestrial bipedalism (Ward et al., 1999; Kimbel et al., 2006; Haile-Selassie et al., 2010; Prang, 2015), perhaps with similar locomotor efficiency as seen in later hominins (Haile-Selassie et al., 2010; Pontzer, 2012). Locomotor behavior in South African species such as *Australopithecus africanus* are less clear, as this taxon may exhibit several ape-like features in the postcranial skeleton (Berger and Tobias, 1996; Harcourt-Smith and Aiello, 2004; Green et al., 2007; Harcourt-Smith, 2016). More recently, the discovery and descriptions of *Australopithecus sediba* (Berger et al.,

2010; Zipfel et al., 2011; DeSilva et al., 2013), *Homo naledi* (Berger et al., 2015; Harcourt-Smith et al., 2015; Marchi et al., 2016), and the foot from Burtele, Ethiopia (Haile-Selassie et al., 2012) have confirmed what appears to have been significant locomotor diversity in the hominin fossil record. Evidence for locomotor adaptations in the earliest members of the genus *Homo* is relatively scant, but fossil evidence for *Homo erectus* from eastern Africa starting about 1.8 Ma provides clear evidence for derived skeletal traits indicative of modern human like limb proportions and obligate terrestrial bipedal locomotion (Ruff, 1993, 2008; Bramble and Lieberman, 2004; Harcourt-Smith and Aiello, 2004; Bennett et al., 2009; Haeusler et al., 2011; Boyle and DeSilva, 2015; Harcourt-Smith, 2016; Hatala et al., 2016).

To evaluate the timing of this morphological transition in the lower limb, we apply geometric morphometric (GM) methods to three-dimensional digital models of the proximal and distal epiphyses of tibiae belonging to Plio-Pleistocene fossil hominins, Holocene *H. sapiens*, and extant great apes. Group shape variation was evaluated through shape space and form space principal component analysis (PCA), and Procrustes distances of fossils to the human mean shape were used to compare evolutionary trends in proximal and distal tibial morphologies.

## 2. Material and methods

### 2.1. Sample

The comparative sample used in this study included proximal and distal tibiae from 49 great apes (19 *Pan*, 20 *Gorilla*, and 10 *Pongo*) and 34 recent *H. sapiens*. The non-human sample consisted of wild-collected and zoo animals with recorded sexes and no apparent pathologies (Table 2), most of them housed at the Anthropological Institute and Museum, University of Zurich (Switzerland), while the rest came from the Department of Zoology, Natural History Museum of Vienna (Austria). Because articular surface morphology is less plastic than diaphyseal structure (Lieberman et al., 2001), the morphological differences between wild and captive apes in the characters we analyzed should be minimal. The human skeletal sample was derived from two behaviorally distinct populations. The first consisted of the Late Prehistoric North American village agriculturalists ( $n = 16$ , Norris Farm, Illinois, USA) from the Illinois State Museum (USA) and the second comprised Holocene hunter-gatherers ( $n = 18$ , Black Earth, Illinois, USA) housed at the Center for Archaeological Investigation, Southern Illinois University (USA). Sex and age-at-death were taken from museum records (Table 2). A taxonomically and temporally diverse sample of 18 fossil hominin specimens representing *A. anamensis*, *A. afarensis*, *A. africanus*, *A. sediba*, *Paranthropus boisei*, early *Homo*, *H. erectus*, *Homo neandertalensis*, and Upper Paleolithic *H. sapiens* was included in our analyses (Table 3). The fossil material derives from a variety of sources as listed in Table 3.

### 2.2. Data acquisition

Virtual reconstructions were obtained using either high-resolution CT or three-dimensional (3D) laser scanning of right tibiae (Table 3), but in some cases it was necessary to consider the left bone and mirror the data. The non-human sample was scanned using a triTOS surface scanner (Breuckmann GmbH), resulting in dense 3D surface representations of the whole tibia. The human sample was scanned using an industrial microCT at the Center for Quantitative Imaging at the Pennsylvania State University. Scans were collected for the entire tibia from each individual using source energy settings of 180 kV and 300  $\mu$ A, with pixel sizes of 0.110 mm

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