



Trabecular bone anisotropy and orientation in an Early Pleistocene hominin talus from East Turkana, Kenya

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ABSTRACT

Among the structural properties of trabecular bone, the degree of anisotropy is most often found to separate taxa with different habitual locomotor modes. This study examined the degree of anisotropy, the elongation, and primary orientation of trabecular bone in the KNM-ER 1464 Early Pleistocene hominin talus as compared with extant hominoid taxa. Modern human tali were found to have a pattern of relatively anisotropic and elongated trabeculae on the lateral aspect, which was not found in *Pan*, *Gorilla*, *Pongo*, or KNM-ER 1464. Trabecular anisotropy in the fossil talus most closely resembled that of the African apes except for a region of high anisotropy in the posteromedial talus. The primary orientation of trabeculae in the anteromedial region of KNM-ER 1464 was strikingly different from that of the great apes and very similar to that of modern humans in being directed parallel to the talar neck. These results suggest that, relative to that of modern humans, the anteromedial region of the KNM-ER 1464 talus may have transmitted body weight to the midfoot in a similar manner while the lateral aspect may have been subjected to more variable loading conditions.

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Introduction

It is well accepted that Plio-Pleistocene hominins frequently engaged in terrestrial bipedalism, but it remains contentious whether or not their bipedalism was mechanically different from that of modern humans (e.g., Lordkipanidze et al., 2007; Bennett et al., 2009; Haile-Selassie et al., 2012) and/or if they routinely practiced arboreal locomotion (e.g., Stern, 2000; DeSilva, 2009; Green and Alemseged, 2012; Venkataraman et al., 2013). Fossil tali have figured prominently in discussions of early hominin locomotor behavior because the shape and arrangement of the articular surfaces of the talus are thought to provide much information about the structure and function of the entire foot (e.g., Wood, 1974; Latimer et al., 1987; DeSilva, 2009). One aspect of talar morphology that may shed additional light on the locomotor behavior of early hominins is the architecture of the trabecular bone contained within the cortical shell. A recent study by DeSilva and Devlin (2012) concluded that trabecular architecture in the hominoid talus has little value in distinguishing among species. Here, we

report on data from a large sample of modern human, chimpanzee, gorilla, and orangutan tali, which in contrast does display significant differences among species that may relate to locomotor differences and therefore may be useful for inferring locomotor behavior from fossils.

In previous comparative studies of trabecular bone structure among primates, the degree of anisotropy (DA), which describes the extent to which trabeculae are aligned into one or more directions, has stood out as being most able to distinguish among species whose locomotor repertoires involve different habitual joint kinematics. In species with stereotypic locomotor repertoires with joint motion primarily within a particular plane, trabecular bone tends to display greater anisotropy, whereas in species with more diverse locomotor repertoires involving varied joint kinematics, trabecular bone tends to display greater isotropy (Fajardo and Müller, 2001; MacLatchy and Müller, 2002; Ryan and Ketcham, 2002; Maga et al., 2006; Griffin et al., 2010; Saporin et al., 2011; but see Carlson et al., 2008). The plate- or rod-like geometry of trabeculae may also be useful for inferring talar loading and locomotor patterns as plate-shaped trabeculae have been shown to develop primarily in joint regions that sustain high mechanical loads, whereas rod-shaped trabeculae tend to develop in regions that experience lower magnitude loads (Ding et al., 2002). In addition to differences in trabecular anisotropy, the

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specific primary spatial orientation of talar trabeculae might be expected to differ among species with different habitual joint loading patterns during locomotion (Odgaard et al., 1997; Ryan and Ketcham, 2005; Gosman and Ketcham, 2009). This expectation is based on multiple controlled loading experiments involving animal models that have demonstrated that altering joint loading orientation can cause corresponding adjustments in trabecular orientation (Pontzer et al., 2006; Barak et al., 2011).

The capacity of trabecular bone to adjust and realign itself throughout life according to its customary mechanical environment is well documented (Pontzer et al., 2006; Barak et al., 2011). However, it is not the case that trabecular architecture results solely from adaptation to habitual loads. Other factors such as genetics and developmental history can also influence trabecular structure (Judex et al., 2004; Wallace et al., 2012). Thus, trabecular architecture in fossils cannot be assumed a priori to reflect functional loading. Rather, it is necessary to first determine if talar trabecular structural parameters differ among extant hominoids in ways that are consistent with presumed differences in habitual ankle joint loading patterns. Insights gleaned from the results of such comparisons can then be used to interpret talar trabecular architecture in fossils.

If early hominins exhibited distinct forms of terrestrial bipedalism and/or engaged in diverse locomotor behaviors including both bipedalism and arboreal activities, then it is reasonable to infer that their talocrural joints would have been subject to different habitual loading patterns than modern humans. This should be detectable in talar trabecular structure given trabecular bone's responsiveness to mechanical signals. With this in mind, we compared the trabecular architecture of KNM-ER 1464, an Early Pleistocene hominin talus from East Turkana, Kenya, with the talar trabecular architecture of extant hominoids (modern humans, chimpanzees, gorillas, and orangutans) in order to gain insight into the habitual loads that this fossil may have experienced during life. This specimen has exceptional preservation (Fig. 1), and its external morphology displays a unique 'enigmatic' mosaic of primitive and derived features (Gebo and Schwartz, 2006), suggesting that this individual may have been adapted for mixed forms of locomotion and/or displayed a unique form of bipedalism.

We reasoned that if talar trabecular bone anisotropy and orientation are correlated with habitual patterns of ankle joint loading in extant hominoids, and therefore potentially useful for inferring locomotor behavior from fossils, then the following would be expected:

1. Humans have a greater overall degree of trabecular anisotropy than non-human hominoids and the regional pattern of anisotropy across the talus differs among species.
2. The primary trabecular orientation in the talus differs among species in ways consistent with observed differences in habitual ankle joint postures. Specifically, apes are expected to differ from humans in the anterior regions, based on observations of weight bearing on a highly dorsiflexed ankle during climbing (DeSilva, 2009). Also, apes are expected to differ from humans in the lateral regions, based on the varus angle of the ankle joint during terrestrial locomotion, and greater load transmission from the fibula (Marchi, 2007).

If the fossil talus belonged to a hominin with a bipedal gait like that of modern humans that did not frequently engage in arboreal activities, then it should display a similar pattern of anisotropy and primary trabecular orientation.

Materials and methods

KNM-ER 1464 was discovered in Area 6A of the Koobi Fora Formation, 8 m below the Lower Illet Tuff, and has been securely dated to 1.59 ± 0.05 Ma (millions of years ago) (McDougall et al., 2012). The specimen is typically assigned to *Paranthropus boisei* based on its stratigraphic association with craniodental remains characteristic of that species (Wood and Constantino, 2007). Primitive aspects of KNM-ER 1464 include its deeply grooved trochlea and strongly developed fibular facet; derived aspects include its overall large size and low talar angle (Gebo and Schwartz, 2006; DeSilva, 2009) (Fig. 1).

The comparative sample used in this study consisted of tali from adult modern humans (*Homo sapiens*; $n = 17$), chimpanzees (*Pan troglodytes*; $n = 20$), gorillas (*Gorilla gorilla*; $n = 14$), and orangutans (*Pongo pygmaeus*; $n = 13$) from collections at the Cleveland Museum of Natural History, the American Museum of Natural History, and the Smithsonian National Museum of Natural History. The modern human tali are from twentieth century Americans (Hamann–Todd Collection). The non-human tali are primarily from wild-shot specimens. We analyzed female hominoids in order to minimize body mass differences among the species. All specimens lacked signs of any skeletal pathology or traumatic injury to the limbs.

Talar trabecular architecture for all specimens, including the fossil, was assessed using high-resolution computed tomography (CT). KNM-ER 1464 was scanned using a XCT Research SA + scanner

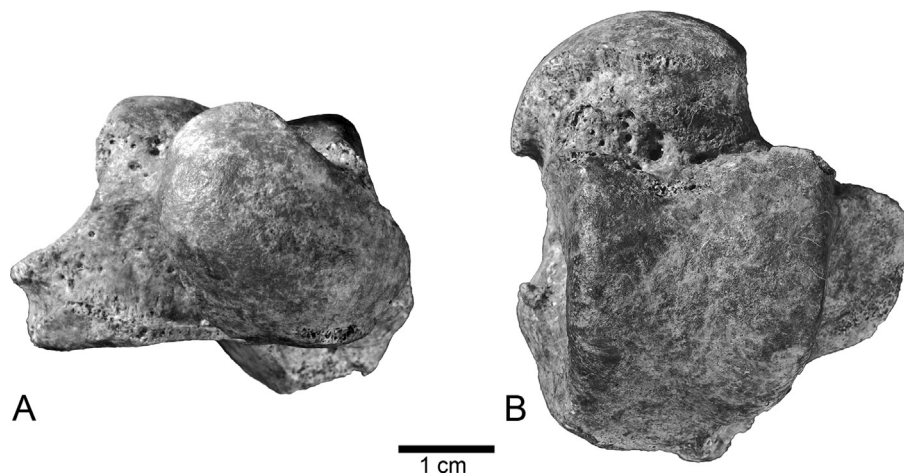


Figure 1. The KNM-ER 1464 talus is well preserved and displays a mixture of primitive features (deeply grooved trochlea, prominent fibular facet) and derived features (large size and low talar angle). (A) Anterior view, (B) Superior view.

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