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News and Views

Bone architecture of the hominin second proximal pedal phalanx: a preliminary investigation

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Introduction

Trinkaus (Trinkaus, 1975, 1983a; Trinkaus et al., 1991; Trinkaus and Hilton, 1996; Trinkaus, 2005) has proposed that diaphyseal and musculoligamentous hypertrophy of Neandertal proximal phalanges that distinguish them from those of modern humans indicates a higher frequency and/or level of loading in the forefoot during life. In their 1996 study, Trinkaus and Hilton used diaphyseal dimensions as measures of bending moments and determined that Neandertal pedal phalanges (2-5) have significantly greater midlength mediolateral (ML) breadth with respect to midlength dorsoplantar (DP) height than those of habitually unshod and shod samples of Holocene humans. Neandertals and combined Middle and Upper Paleolithic anatomically modern humans had a similar pattern of bending moments; however, Neandertals had only significantly larger relative ML breadths for the second proximal phalanx (PP2).

Given these data, Trinkaus and Hilton (1996) suggest that higher magnitudes of loading during locomotion explain why Neandertal lateral proximal pedal diaphyses are more ovoid than those of modern humans. It is noteworthy that Trinkaus and Hilton's (1996) modern human sample exhibits a trend of a decrease in mediolateral breadth relative to dorsoplantar height with an increase in both skeletal gracility and reported use of footwear. The correlation between relative mediolateral strength and behavior is also supported by a more recent study. Griffin et al. (in press) found that a sample of habitually unshod

individuals that inhabited an island characterized by steep terrain had hallucal proximal phalanges (phalanges from other rays not included in this study) with greater measures of mediolateral bending strength (higher Zy/Zx) than a shod industrial population sample.

Despite this support, other evidence questions the interpretation of pedal diaphyseal shape as a clear measure of mechanical demand witnessed by the anterior foot. For example, while the lateral proximal phalanx of *Homo antecessor* ATD6-32, is mediolaterally broad, the hallucal phalanges belonging to this hominin contrast with both modern humans and Neandertals in that they are more wide dorsoplantarly than mediolaterally (Lorenzo et al., 1999). Also, it has been found that there are significant differences between size-adjusted bending strength values of 20th century African American and European American metatarsals despite a lack of differences documented for activity level or use of footwear (Griffin and Richmond, 2005). All in all, level of loading may not be the only factor driving shape differences in the pedal diaphyses.

For the first part of this study, second pedal phalanges of the Neandertal specimen, Shanidar 3 and modern humans are compared to validate the external measurements (Trinkaus and Hilton, 1996). It is predicted that Shanidar 3 will have a larger ML breadth relative to DP height, greater relative bending rigidity in the mediolateral plane (Iy), and greater overall bending rigidity (J) than the modern human specimens. The same comparisons will then be made between the African American and European American males. I expect that there should be no diaphyseal shape differences between the two human groups because activity level and use of footwear are assumed to be held constant.

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I then investigate whether properties of the trabecular bone at the base of the Shanidar 3 phalanx indicate greater mechanical demand as has been proposed by the external morphology (i.e., pronounced musculoligamentous attachment sites; Trinkaus, 1975, 1983a; Trinkaus and Hilton, 1996). It is expected that compared to the human sample, the Shanidar 3 trabeculae will exhibit a more plate-like structure, a higher degree of anisotropy, and a greater trabecular bone volume (BV/TV) because these structural properties have been shown to correlate with Young's modulus, a measure of a bone's stiffness (Ulrich et al., 1999; Ding et al., 2002).

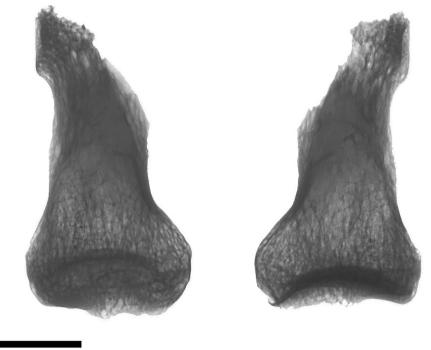
Materials and methods

The chronological age of the presumed male, Shanidar 3 has been estimated to be between 35-50 years and its stratigraphical context suggests a geological age of at least 45 ka (Thompson and Trinkaus, 1981). Due to the fragmentary nature of the Shanidar 3 skeleton, a body mass estimate using its femoral head diameter is impossible. The PP2, consisting of a complete base and diaphysis and small part of distal articular surface, belongs to the right foot (Trinkaus, 1983b; Figs. 1 and 2). Though what remains of the PP2 is not pathological, evidence of degenerative joint disease is found around the talocalcaneal and talocrural joints. Trinkaus and Zimmerman (1982) suggest these signs may be due to trauma from either a severe sprain or healed fracture. They predict that Shanidar 3 may have suffered from a locomotor disability with the onset of pain and/or restricted movement from his injury. Despite this, Shanidar 3 will be regarded as an appropriate representative Neandertal specimen because Trinkaus and Hilton included it in their 1996 study and Shanidar 3 exhibits the external morphology (i.e., the wide shaft relative to bone length and large musculoligamentous attachment areas at the base) that distinguishes Neandertals from modern humans (Trinkaus, 1983a; Fig. 2).

The comparative modern human sample (n = 40) of 20th century African American (n = 20) and European American (n = 20) males is part of the Terry Collection (National Museum of Natural History, Washington, D.C.). PP2s from the right foot lacking any obvious signs of pathological conditions were selected from specimens encompassing the age range predicted for Shanidar 3. The mean age of the sample used here is 42.5 years.

For each PP2 (n = 41), one scan at midlength was taken using a Siemens Somatom Emotion CT scanner (100 kV, 83 mA, 1 mm slice thickness) housed at the National Museum of Natural History in Washington, D.C. Proximal phalanges were set on the scanner in anatomical position by resting each on both its plantar tubercles. Cross-sectional geometric properties were obtained from a Microsoft Windows computer using a Scion Image macro, courtesy of Drs. Christopher Ruff and Valerie Burke DeLeon.

Due to limited access to the microCT scanner, high resolution scanning of trabecular bone could only be completed for Shanidar 3 and 10 of the Terry Collection males. The scanner used was a desktop fan-beam microCT 20 model (Scanco USA, Inc., Pennsylvania) that had been temporarily housed at the Smithsonian for another research project. Specimens were scanned with a source energy of 160 kV and at a slice thickness 0.34 millimeters.



1 centimeter

Fig. 1. Digital X-ray images of Shanidar 3's second pedal proximal phalanx (left, dorsal view; right, plantar view).

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