Cross-sectional properties of the lower limb long bones in the Middle Pleistocene Sima de los Huesos sample (Sierra de Atapuerca, Spain)

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ABSTRACT

The recovery to date of three complete and five partial femora, seven complete tibiae, and four complete fibulae from the Atapuerca Sima de los Huesos site provides an opportunity to analyze the biomechanical cross-sectional properties in this Middle Pleistocene population and to compare them with those of other fossil hominins and recent modern humans.

We have performed direct comparisons of the cross-sectional geometric parameters and reduced major axis (RMA) regression lines among different samples. We have determined that Atapuerca Sima de los Huesos (SH) fossils have significantly thicker cortices than those of recent modern humans for the three leg bones at all diaphyseal levels, except that of the femur at 35% of biomechanical length. The SH bones are similar to those of Neandertals and Middle Pleistocene humans and different from *Homo sapiens* in their diaphyseal cross-sectional shape and strength parameters.

When standardized by estimated body size, both the SH and Neandertal leg bones have in general greater strength than those of *H. sapiens* from the early modern (EMH), Upper Paleolithic (UP), and recent populations (RH). The Sima de los Huesos human leg bones have, in general terms, an ancestral pattern similar to that of Pleistocene humans and differing from *H. sapiens*.

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1. Introduction

Bone is a living and dynamic tissue that has the ability to model and remodel itself in response to loads placed on it during the lifetime, mainly during the growth period, and provides the mechanical integrity for locomotion. Bone's primary response to loading is material redistribution (changes in shape or cross-sectional geometry) rather than in its intrinsic properties (Larsen et al., 1995; Beck et al., 2001). In fact, compact cortical bone retains a broadly constant density across mammals and has less potential for altering its microstructural organization (Hayes, 1991). However, adjustments in the amount and distribution of cortical bone can alter the strength and stiffness of the skeletal structures, and differences in bone diaphyseal shape in recent human populations have been related to activity patterns (for example,

Trinkaus and Churchill, 1999; Trinkaus and Ruff, 1999a,b; Shackelford, 2007; Maggiano et al., 2008; Marchi, 2008; Shaw and Stock, 2009a,b). Other aspects, such as subsistence strategy, terrain conditions, sexual dimorphism, bilateral asymmetry, and changes during ontogeny, can also be analyzed, at least in modern humans, through diaphyseal cross-sectional analysis (Ruff and Hayes, 1983a,b; Ruff et al., 1993; Shackelford, 2007; Ruff, 2008; Sparacello and Marchi, 2008; Cowgill, 2010; Sparacello et al., 2011, 2014).

Trinkaus and Ruff (2012) have published femoral and tibial cross-sectional data for a large sample of Pleistocene *Homo*, revealing differences in shape and thickness between species and chronological groups. Their study includes most of the non-pathological and mature femora and tibiae attributable to the genus *Homo*.

The SH site is well-known for yielding the largest sample of pre-*Homo sapiens* hominin fossils representing a single biological population (Arsuaga et al., 2014, 2015). All the hominin fossils come

from a single stratigraphic level and have recently been dated to around 430 kya (Arsuaga et al., 2014). The SH hominins have been considered phylogenetically closely related to Neandertals (Arsuaga et al., 2014, 2015; Meyer et al., 2014, 2016). In addition to many ancestral traits, the Atapuerca SH hominins share numerous derived traits with the Neandertals in the cranium and face (Arsuaga et al., 2014), the teeth (Martinón-Torres et al., 2012), the mandibles (Rosas et al., 2002), and the postcranial bones (Arsuaga et al., 2015).

The present study reports on the main diaphyseal geometric properties of eight femora, seven tibiae, and four fibulae from the SH site. These data significantly augment the sample of Middle Pleistocene femoral and tibial specimens analyzed by Trinkaus and Ruff (2012) and include the biomechanical analysis of the fibula in a fossil hominin sample for the first time.

Trinkaus and Ruff (2012) found that Upper Paleolithic (UP) *H. sapiens* differed from all previous fossil hominins in cross-sectional shape. Nevertheless, the relative cortical area in all pre-Upper Paleolithic specimens was similar to the UP group. The SH geometric properties are compared with those from other fossil hominins and to a recent human sample. These data can help elucidate the patterns of femoral, tibial, and fibular diaphyseal robusticity and shape in the Atapuerca SH hominins, and to shed new light on Middle Pleistocene specimens and their implications for human evolution.

2. Material and methods

The original SH lower limb long bones analyzed in this study include eight femora. Three of them are complete or almost complete (F-X, F-XII, F-XIII), while four more are incomplete specimens that preserve part of the diaphysis and at least one epiphysis (AT-1020, F-IX, F-XI, F-XIV, and F-XVI). In addition, seven nearly complete tibiae (TIB-I, III, IV, VI, XI, XII, AT-848) and four virtually complete fibulae (Fib-I, II, III, and AT-1060) are also analyzed. The lower limb bones represent a minimum of five (femur), six (tibia), and four (fibula) individuals (see Carretero et al., 2012 and Supplementary Online Material [SOM] Fig. 1 for incomplete femoral specimens).

A comparative sample of recent modern humans (RH) has also been analyzed, consisting of 59 complete adult femora (26 females and 32 males) and 41 complete adult tibiae (25 males and 17 females) from the medieval cemetery at the San Pablo Monastery in Burgos, Spain. Sex assessment in the San Pablo individuals was based on the associated pelvic morphology following Phenice (1969). The sample includes only young and mature (non-elderly) adult individuals, estimated to be younger than 50 years of age based on different skeletal markers (Rodriguez et al., 2015).

Data on other fossil specimens from the Early Pleistocene (EP), Middle Pleistocene (MP), Neandertals, Early Modern Humans (EMH), and Upper Paleolithic (UP) are taken from the literature, specifically from Trinkaus and Ruff (2012) in the case of femora and tibiae (see SOM Table 1 for details), and from Marchi and Shaw (2011) in the case of the fibulae (only recent modern humans). The estimated sex of the specimens has also been taken into account in the comparisons even though all of these fossil samples, including SH, are apparently male-biased.

The SH and San Pablo (RH) data were calculated following Ruff and Hayes (1983a), using biomechanical long bone lengths and analyzing cross sections at different levels corresponding to percentages of the diaphyseal length. Computed tomography (CT) scans of all specimens were performed at the University of Burgos (Spain) with an YXLON Compact X-Ray industrial multi-slice CT scanner. To obtain cross-sectional slices, the specimens were aligned along the long bone axis with the proximal epiphysis superiorly. Scanner energy was 160 kV and 4 mA, slice thickness was

collimated to 0.5 mm, inter-slice spacing was 0.5 mm, and field of view was 18.52 cm, with a reconstruction interval of 0.5 mm. Slices were obtained as a 1024 × 1024 matrix of 32-bit Float format with a pixel size of 0.18 mm. The CT images were visualized using the Mimics™ (Materialise, NV., Belgium) software program, and selected cross sections were subsequently imported into Autocad (Autodesk, USA) to compute all cross-sectional parameters (Fig. 1 and see SOM Figs. 2–4 for the femora, tibiae, and fibulae respectively).

To avoid error in obtaining the geometrical parameters (Sládek et al., 2010), and to determine biomechanical shaft levels for the incomplete SH femora (AT-1020, F-IX, F-XI, F-XVI), it is necessary to estimate their biomechanical length. To reduce mathematical problems derived from differences in epiphyseal and diaphyseal proportions relative to bone length between fossils and extant humans, biomechanical lengths of the SH femora were estimated by digital 3D reconstructions. The 3D model of the complete F-X and F-XIII (which have quite different epiphyseal length proportions) were rescaled to the same femoral head size and/or distal epiphyseal breadth of the incomplete specimens. Considering various anatomical landmarks (e.g., the deepest point in the neck, the most projecting point of the greater trochanter, and the position of the lesser trochanter), we generated a complete 3D virtual model reconstruction of each incomplete SH specimen (Fig. 2 and SOM Fig. 5).

The cross-sectional geometric parameters include: a) total subperiosteal area (TA); b) cortical subperiosteal area (CA): provides a measure of resistance to axial loads (Ruff et al., 1993); c) anteroposterior (I_x), mediolateral (I_y), maximum (Imax), and minimum (Imin) second moments of area: assess bending rigidity in the reference planes; d) polar second moment of area (J): provide both an indication of resistance to torsion and a general reflection of overall rigidity; f) relative CA or cortical to total area index (%CA): reflects the differential subperiosteal deposition and endosteal resorption of bone, principally during development (Ruff and Hayes, 1983b; Ruff et al., 1994); g) I_x/I_y or Imax/Imin, showing the diaphyseal shape and bone distribution in femora and tibiae,
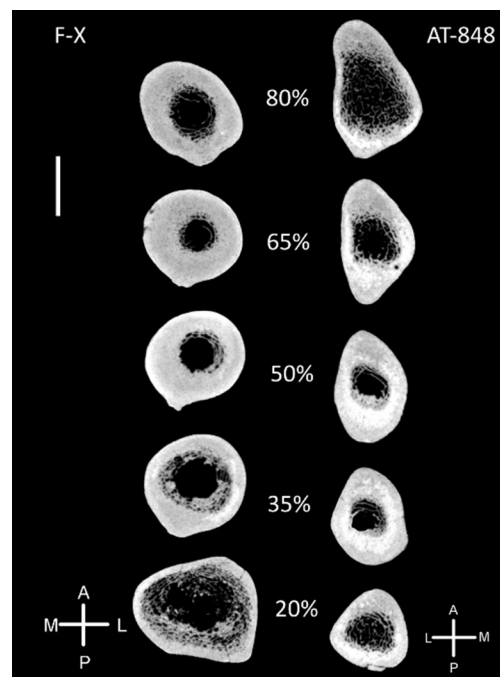

Figure 1. Cross-sectional levels for the Sima de los Huesos femur (F-X) and tibia (AT-848). Scale bar = 2 cm.