



## Fossil hominin radii from the Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain)



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### ABSTRACT

Complete radii in the fossil record preceding recent humans and Neandertals are very scarce. Here we introduce the radial remains recovered from the Sima de los Huesos (SH) site in the Sierra de Atapuerca between 1976 and 2011 and which have been dated in excess of 430 ky (thousands of years) ago. The sample comprises 89 specimens, 49 of which are attributed to adults representing a minimum of seven individuals. All elements are described anatomically and metrically, and compared with other fossil hominins and recent humans in order to examine the phylogenetic polarity of certain radial features. Radial remains from SH have some traits that differentiate them from those of recent humans and make them more similar to Neandertals, including strongly curved shafts, anteroposterior expanded radial heads and both absolutely and relatively long necks. In contrast, the SH sample differs from Neandertals in showing a high overall gracility as well as a high frequency (80%) of an anteriorly oriented radial tuberosity. Thus, like the cranial and dental remains from the SH site, characteristic Neandertal radial morphology is not present fully in the SH radii. We also analyzed the cross-sectional properties of the SH radial sample at two different levels: mid-shaft and at the midpoint of the neck length. When standardized by shaft length, no difference in the mid-shaft cross-sectional properties were found between the SH hominins, Neandertals and recent humans. Nevertheless, due to their long neck length, the SH hominins show a higher lever efficiency than either Neandertals or recent humans. Functionally, the SH radial morphology is consistent with more efficient pronation-supination and flexion-extension movements. The particular trait composition in the SH sample and Neandertals resembles more closely morphology evident in recent human males.

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### 1. Introduction

A distinctive radial morphology in Neandertals was recognized more than 100 years ago (Gorjanović-Kramberger, 1906; Boule, 1911). When compared to recent humans, the Neandertal radius

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has been described as more laterally curved, with a more medially oriented radial tuberosity and a longer neck length (Trinkaus, 1983; Trinkaus and Churchill, 1988; De Groot, 2011), and each of these traits has functional implications. A longer radial neck is related to a higher lever efficiency of the forearm (Trinkaus, 1983), while more medial orientation of the radial tuberosity and increased shaft curvature (which places the bone mass farther from the rotational axis) provide greater efficiency in pronation–supination (Trinkaus and Churchill, 1988; Galtés et al., 2008, 2009). Thus, the functional interpretation of this suite of anatomical features in the Neandertal radius is consistent with very powerful forearms and pronation–supination movements (Trinkaus and Churchill, 1988; De Groot, 2011). Fossil hominin radii can also provide useful information regarding manipulative abilities, complementing analyses of humeri (Trinkaus et al., 1994), scapulae (Carretero et al., 1997) and ulnae (Trinkaus et al., 1994; Churchill and Rhodes, 2009). In addition, it has long been argued that Neandertals have lower brachial indices than do modern humans, indicating a radius that is short relative to the humerus, perhaps reflecting adaptation to cold climates (Trinkaus, 1981), although this interpretation has been questioned (Holliday, 1999).

Prior to the Neandertals, radial remains attributed to the genus *Homo* are scarce (Tobias, 1978; Pearson and Grine, 1997; Carretero et al., 1999; Ward et al., 2015), and the phylogenetic polarity of some of these features remains to be clarified. Although incomplete, the Cave of Hearths (CH) radius combines thick cortical bone in its neck and shaft and a rather slender neck (as in archaic members of the genus *Homo*) with an anteromedially oriented tuberosity (as in modern humans) (Pearson and Grine, 1997). The Klasies River Mouth (KRM) radius also shows thick cortical bone in the radial neck, but, externally, the KRM radial neck is rather stout, resembling recent humans (Pearson and Grine, 1997). The Early Pleistocene radius from the site of the Gran Dolina (ATD6-43) in the Sierra de Atapuerca resembles recent humans in its anteriorly oriented radial tuberosity and relatively straight shaft, but departs from them in showing a long radial neck (Carretero et al., 1999). The Early Pleistocene radius KNM-ER 48100 suggests the presence of large-bodied individuals at this time period (Ward et al., 2015), while the incomplete SK 18b early *Homo* radius from Swartkrans in South Africa does not show a relatively slender neck (Tobias, 1978). A more medially oriented radial tuberosity is present in some early hominins, suggesting this may represent the primitive condition for the hominin clade (Carretero et al., 1999).

Given this dearth of radial fossils in the genus *Homo*, the site of the Sima de los Huesos (SH) in the Sierra de Atapuerca offers an important opportunity to study a large sample of Middle Pleistocene radii and to help clarify the phylogenetic polarity of radial features in the genus *Homo*. While the SH radii have been included in previous studies (Carretero, 1994; Carretero et al., 1999, 2012) they have not been fully described and analyzed. The principal aim of this study, then, is to present a complete inventory, morphological descriptions and metric analysis of the entire adult radial sample from the SH site.

The SH collection has increased significantly during years of controlled excavations, with more than 6500 human remains having been recovered to date. Careful restoration of the fossil collection over the years has resulted in the reconstruction of eight complete or nearly complete adult radii. Here we compare the SH radii with those of recent and Upper Paleolithic *Homo sapiens*, Neandertals and earlier fossil hominins to assess the phylogenetic polarity of some features. In addition, the cross-sectional properties of the radial diaphysis and neck, and their functional implications, are considered within a comparative framework.

## 2. Material and methods

### 2.1. The SH hominin radial sample

The Sima de los Huesos (SH) is a well-known Middle Pleistocene site in the Sierra de Atapuerca in northern Spain (Arsuaga et al., 1997a). The large sample of human remains represents at least 28 individuals of different ages and both sexes (Bermúdez de Castro et al., 2004) and represent the largest known repository of fossil hominins from the Middle Pleistocene. The SH hominin fossils have been recovered from a single stratigraphic level at the site (LU-6) and date to c.430 ky (thousands of years) ago (Arsuaga et al., 2014; Aranburu et al., in press). This new age estimate is internally consistent, revises previous ages proposed for the hominins (Bischoff et al., 1997, 2003; Arnold et al., 2014) and is congruent with the macro- and micro-mammal assemblages from the site (García et al., 1997; Cuenca-Bescós and García, 2007).

In addition to many primitive features, the SH hominins share some derived traits with Neandertals in the cranium and facial skeleton (Arsuaga et al., 1993, 1995, 1997b, 2014; Martínez and Arsuaga, 1997), dentition (Bermúdez de Castro, 1988; Bermúdez de Castro and Nicolás, 1995; Martinon-Torres et al., 2012), mandibles (Rosas et al., 2002) and postcranial skeleton (Arsuaga et al., 1991, 1995, 2015; Carretero, 1994; Carretero et al., 1997, 2004, 2005; Gómez-Olivencia et al., 2007; Bonmatí et al., 2010; Pablos et al., 2013, 2014). Based on these similarities, the SH hominins are considered to share a close phylogenetic relationship with the Neandertals (Arsuaga et al., 1991, 1997a,c, 2014; Carretero et al., 1997; Martínez and Arsuaga, 1997; Martinon-Torres et al., 2012).

The entire SH radial sample comprises 89 labelled fragments from both adult and subadult specimens. Of these, 49 labelled remains belong to adult individuals and are included in the present study. Some of these fragments fit together to comprise eight complete or virtually complete radii and portions of at least five other bones (Figs. 1–3). Taking into account the most frequently preserved region (the left midshaft), as well as size incompatibilities between specimens, we have determined that a minimum of seven adult individuals are preserved in the sample.

### 2.2. Comparative samples

For comparative purposes, we measured and analyzed a large sample ( $n = 384$ ) of recent human adult radii of known sex and age housed at the University of Coimbra (Portugal) (Table 1). In addition, the Upper Paleolithic specimens from Abri Pataud, Dolní Věstonice and Pavlov were included. Our Neandertal sample is based on observations of original specimens, high quality casts and data taken from the literature. We also included data on radii from the sites of Gran Dolina in Spain as well as the Cave of Hearths and Klasies River Mouth in South Africa (Table 1). Cross-sectional geometric properties of the SH radii were compared with additional modern human samples (San Pablo and Aranda de Duero) as well as a few Neandertal specimens.

### 2.3. Measurement definitions

Metric variables used in the present study (Fig. 4A) largely follow those defined by Martin and Saller (1957) and Maia Neto (1957). In order to calculate the radial curvature we defined three measurement points relying on digitized photos imported into the Autocad software program (Autodesk, USA). The point O is the point of intersection between the long axis of the neck and that of the diaphysis, taken in anterior view (Fig. 4A). Point A is defined as the point where a line perpendicular to the neck axis, with its origin in point O, intersects with the lateral radial margin. Point B is defined

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