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Human talus bones from the Middle Pleistocene site of Sima de los Huesos (Sierra de Atapuerca, Burgos, Spain)

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ABSTRACT

Here we present and describe comparatively 25 talus bones from the Middle Pleistocene site of the Sima de los Huesos (SH) (Sierra de Atapuerca, Burgos, Spain). These tali belong to 14 individuals (11 adult and three immature). Although variation among Middle and Late Pleistocene tali tends to be subtle, this study has identified unique morphological characteristics of the SH tali. They are vertically shorter than those of Late Pleistocene *Homo sapiens*, and show a shorter head and a broader lateral malleolar facet than all of the samples. Moreover, a few shared characters with Neanderthals are consistent with the hypothesis that the SH population and Neanderthals are sister groups. These shared characters are a broad lateral malleolar facet, a trochlear height intermediate between modern humans and Late Pleistocene *H. sapiens*, and a short middle calcaneal facet. It has been possible to propose sex assignment for the SH tali based on their size. Stature estimates based on these fossils give a mean stature of 174.4 cm for males and 161.9 cm for females, similar to that obtained based on the long bones from this same site.

RESUMEN

Aquí se presentan y describen comparativamente 25 astrágalos del yacimiento del Pleistoceno medio de la Sima de los Huesos (SH) (Sierra de Atapuerca, Burgos, España). Estos astrágalos pertenecen al menos a 14 individuos (11 adultos y tres inmaduros). Aunque la variación entre los astrágalos del Pleistoceno medio y superior tiende a ser sutil, este estudio ha identificado unas características morfológicas únicas en los fósiles de SH. En general, los astrágalos de SH son más bajos que los de los *Homo sapiens* del Pleistoceno superior, y muestran una cabeza más corta y una faceta maleolar lateral más ancha que todas las muestras consideradas. Además, unos pocos caracteres compartidos con los neandertales son consistentes con la hipótesis de que la población de SH y los neandertales representan grupos hermanos. Estos caracteres compartidos son una faceta maleolar ancha, una altura troclear intermedia entre los humanos modernos y los *H. sapiens* del Pleistoceno superior, y una faceta calcánea media corta. Por otro lado, ha sido posible proponer una asignación sexual a los astrágalos de SH basada en su tamaño. La estimación de la estatura a partir de estos fósiles ofrece una media de 174,4 cm para los individuos masculinos y 161,9 cm para los femeninos, valores similares a los obtenidos con los huesos largos del mismo yacimiento.

Introduction

The talus is an important bone in human evolution due its role in locomotion and weight transmission and because it acts as an index of body size (Morton, 1924; Wood, 1974; Rhoads and Trinkaus, 1977; Trinkaus, 1978; McHenry, 1992; Harcourt-Smith and Aiello, 2004;

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Pablos et al., 2013). Some tali from Pleistocene *Homo* have been previously studied, mainly belonging to *Homo habilis*, *Homo antecessor*, *Homo neanderthalensis*, *Homo sapiens* and *Homo floresiensis* (Day and Napier, 1964; Billy, 1975; Trinkaus, 1975a; Rhoads and Trinkaus, 1977; Vandermeersch, 1981; Lordkipanidze et al., 2007; Pearson et al., 2008; Jungers et al., 2009; Lu et al., 2011; Pablos et al., 2012). There are several tali from Koobi Fora (Kenya) and Olduvai (Tanzania), but there is current controversy about their assignment to the genus *Homo* (Day and Napier, 1964; Wood, 1974; Day et al., 1976; McHenry, 1992; DeSilva, 2009). For this reason, we do not consider these specimens in this study.

One of the largest talus known in the *Homo* fossil record is the Lower Pleistocene ATD6-95 from level TD6 of Gran Dolina (Atapuerca). This talus is long and tall and presents a wide and very long trochlea, with a proportionally short neck (Pablos et al., 2012). Considering other Pleistocene *Homo* tali, both the foot and talus of Jinniushan reveals a degree of robusticity that clearly distinguishes it from modern humans, and it resembles the well-represented Neanderthal foot (Lu et al., 2011). The talus of Omo-Kibish 1 is vertically short and presents a fairly small trochlea, significantly shorter than the populations of the Upper Pleistocene (Pablos et al., 2012). Moreover, the head is disproportionally large (Pearson et al., 2008).

A study of Neanderthal tali revealed that they are indistinguishable from those of modern humans in their implied locomotor capabilities and similar in overall size and proportions (Rhoads and Trinkaus, 1977). However, the Neanderthal tali present a relatively large trochlea, especially its lateral malleolar facet (Trinkaus, 1975a; Rhoads and Trinkaus, 1977; Heim, 1982). These characteristics have generally been associated with a high degree of biomechanical stress, and related to the greater general robustness of the postcranial skeleton (Trinkaus, 1975a, 1983, 2000; Rhoads and Trinkaus, 1977; Vandermeersch, 1981).

The species *H. floresiensis* from Liang Bua (Flores, Indonesia) preserves two quite complete tali comparable in size with 'Lucy' (AL 288-1). Although the height of the talar body is greater than in AL 288-1, the talus from Flores is similar to modern humans in some features, but the trochlear groove is shallow, and it is considered intermediate between humans and African apes in other respects (Jungers et al., 2009).

It has been proposed that the general morphology of the talus is similar across the genus *Homo* (Trinkaus, 1975a; Rhoads and Trinkaus, 1977; Pablos et al., 2012). However, the size of the talus has increased during the evolution of genus *Homo* mainly due to robusticity and biomechanical stress (Trinkaus, 1975a, 1983, 2000; Rhoads and Trinkaus, 1977; Vandermeersch, 1981; Pablos et al., 2012). Some characters, such as the trochlear morphology, offer taxonomic information since they differ among some fossil samples (Pablos et al., 2012).

Due to the paucity of human tali in the fossil record of the Lower and Middle Pleistocene, the sample from the Sima de los Huesos (SH) is very important to characterize the morphology and evolution of the talus during this period. Important information can be extracted from the Sima de los Huesos tali that is relevant to understanding the evolution of the Neanderthal foot due to the evolutionary relationship between Neanderthals and the SH sample (Arsuaga et al., 1993, 1997c, 2007; Carretero et al., 1997; Martínez and Arsuaga, 1997; Gómez-Olivencia et al., 2010).

Table 1
Inventory and description of the talus bones from Sima de los Huesos.

Specimen	Side	Age	Taphonomic and anatomical description
AT-575	R	A	Nearly complete talus formed by at least seven fragments. It shows an oblique fracture with erosion and the resulting exposure of cancellous bone. Eroded in medial-plantar area, on the trochlear surface and on the posterior calcaneal articulation.
AT-859	L	A	Trochlear fragment. It preserves a small fragment of the posterior calcaneal facet and the flexor hallucis longus groove.
AT-860	L	A	Complete. It displays a puncture (7.71 × 3.32 mm) and a pit (2.72 × 2.04 mm) in the sulcus tali, but the origin of both is not due to carnivore action. Slight erosion of the articular facets especially on the posterior calcaneal facet and the head.
AT-964	L	I	Complete. Slight erosion at the edges of the articular surfaces.
AT-965	L	A	Complete. Slight erosion at the edges of the articular surfaces.
AT-966[a]	R	A	Complete and intact.
AT-980[a]	L	A	Complete and intact.
AT-1322	L	A	Nearly complete. It displays some erosion on the posterior calcaneal facet and on the head. This talus presents a 2.93 mm-wide score, in which the carnivores' action cannot be ruled out as possible origin.
AT-1477	R	A	Nearly complete. It consists of at least seven fragments divided by net rectilinear fissures with irregular borders. There is a marked erosion and loss of internal spongy bone tissue particularly around the main fissures.
AT-1480	L	A	Quite complete. Longitudinal fracture with spongy bone tissue exposed. It also shows evidence of trampling on the trochlea.
AT-1498	L	I	Lateral half. Longitudinal fracture with spongy bone tissue exposed. Eroded.
AT-1700	R	A	Nearly complete. It presents furrowing in the medial zone of the trochlea. Moreover this talus displays a longitudinal score (breadth = 1.07 mm), the action of carnivores cannot be excluded.
AT-1716	L	A	Complete. Slightly eroded.
AT-1822	R	A	Complete. Slight erosion at the vertices of the articular facets of the head and trochlea.
AT-1832	R	A	Posterior half of talus (trochlea). Talar head is not preserved.
AT-1930	R	A	Complete. Slight erosion of the posterior side prevents the determination of whether the lateral tubercle, typical in adult individuals, was present.
AT-1931	R	A	Complete. It displays deformation of the upper zone of the trochlea. Currently, this is the smallest talus in the SH sample. Slight erosion at the edges of the articular facets.
AT-2495	R	A	Complete. Slight erosion at the superior edge of the head.
AT-2751	L	I	Complete.
AT-2803	L	A	Complete.
AT-2844	L?	?	Head fragment.
AT-3132	L	A	Complete with slight erosion in the plantar and dorsal zone of the head. It displays two parallel scores (maximum breadth = 2.43 and 0.66 mm) and two conspicuous marks (4.74 × 4.74 mm and 5.03 × 2.65 mm) on the trochlea. The origin of these marks does not seem to be due to carnivores.
AT-3133	L	A	Complete. Marked erosion of the trochlea which largely exposes trabecular tissue. The edges of the head are also eroded.
AT-4425	R	A	Complete. Displays slight erosion of the margins of the articular surface of the head.
AT-4445	R	A	Posterior half of talus (trochlea). Talar head is not preserved.

A = Adult, I = Immature, R = Right, L = Left.
[a] These tali belong to the same individual (Lorenzo et al., 1998).