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## Journal of Human Evolution

journal homepage: [www.elsevier.com/locate/jhevol](http://www.elsevier.com/locate/jhevol)

## The bony labyrinth in the Aroeira 3 Middle Pleistocene cranium

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## ARTICLE INFO

## Article history:

Received 25 April 2018

Accepted 13 August 2018

Available online xxx

## Keywords:

Evolution  
Inner ear  
Temporal bone  
Neandertal  
Atapuerca  
Iberian Peninsula

## ABSTRACT

The discovery of a partial cranium at the site of Aroeira (Portugal) dating to 389–436 ka augments the current sample of Middle Pleistocene European crania and makes this specimen penecontemporaneous with the fossils from the geographically close Atapuerca Sima de los Huesos (SH) and Arago sites. A recent study of the cranium documented a unique combination of primitive and derived features. The Aroeira 3 cranium preserves the right temporal bone, including the petrosal portion. Virtual reconstruction of the bony labyrinth from  $\mu$ CT scans provides an opportunity to examine its morphology. A series of standard linear and angular measures of the semicircular canals and cochlea in Aroeira 3 were compared with other fossil hominins and recent humans. Our analysis has revealed the absence of derived Neandertal features in Aroeira 3. In particular, the specimen lacks both the derived canal proportions and the low position of the posterior canal, two of the most diagnostic features of the Neandertal bony labyrinth, and Aroeira 3 is more primitive in these features than the Atapuerca (SH) sample. One potentially derived feature (low shape index of the cochlear basal turn) is shared between Aroeira 3 and the Atapuerca (SH) hominins, but is absent in Neandertals. The results of our study provide new insights into Middle Pleistocene population dynamics close to the origin of the Neandertal clade. In particular, the contrasting inner ear morphology between Aroeira 3 and the Atapuerca (SH) hominins suggests a degree of demographic isolation, despite the close geographic proximity and similar age of these two sites.

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## 1. Introduction

The European Middle Pleistocene is one of the most contentious periods in paleoanthropology, especially in terms of the evolutionary relationships between the fossils found in Africa and Europe. This situation is partly due to the fact that the Middle Pleistocene hominin record has long suffered from poor chronological control for key specimens, and the contrasting morphologies

observed in these fossils have clouded our understanding of the evolutionary process during this period.

Some authors prefer to group some European Middle Pleistocene fossils (e.g., Petralona, Mauer, Arago) with those from Africa (e.g., Kabwe, Bodo) into a single widespread, variable species, most often referred to as *Homo heidelbergensis* (Rightmire, 2008; Tattersall, 2011; Stringer, 2012). Focusing on the European fossil record, the recent analysis of the large sample of fossils from the Atapuerca (SH) site has revealed the presence of two main groups of fossils in the European Middle Pleistocene (Arsuaga et al., 2014).

On the one hand, there is a series of fossils, including Mauer, Arago, Ceprano and Mala Balanica, that lack clear Neandertal

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derived traits (Roksandic et al., 2011; de Lumley, 2015; Manzi, 2016), and which could reasonably be included in *H. heidelbergensis*. On the other hand, there is a series of fossils such as those from the sites of Atapuerca (SH), Swanscombe, Steinheim and Reilingen that show some clearly derived Neandertal features in their anatomy (Dean et al., 1998; Stringer and Hublin, 1999; Arsuaga et al., 2014) and, in the case of the Atapuerca (SH) hominins, in their nuclear DNA (Meyer et al., 2016). This anatomical and genetic evidence indicates that this latter group belongs to the same clade as the Neandertals of the Late Pleistocene.

Nevertheless, the full suite of Neandertal features only emerges towards the end of the Middle Pleistocene, perhaps around 200 ka (Hublin, 2009). The Atapuerca (SH) hypodigm, and by extension these other European Middle Pleistocene specimens, is sufficiently different from the Late Pleistocene Neandertals to be separated at least as different paleodemes (Martínez and Arsuaga, 1997; Tattersall, 2011; Arsuaga et al., 2014). Whether this difference is on the specific or subspecific level is currently an open question (Arsuaga et al., 2014). Regardless of the precise taxonomic allocation of these fossils, the existence of these two morphological groupings in the European Middle Pleistocene, one with a more primitive morphology and one with more clear affinities with the Neandertals, is recognized by many researchers (Tattersall, 2011; Stringer, 2012; Arsuaga et al., 2014; Manzi, 2016).

In this context, the recent discovery of a partial cranium from the Middle Pleistocene site of the Gruta da Aroeira (Portugal) is particularly relevant since it augments the still small non-SH European Middle Pleistocene sample (Daura et al., 2017). The Gruta da Aroeira is one of a series of Pleistocene archaeological and paleontological sites located in the Almonda karst system (Torres Novas). The Aroeira site was previously excavated between 1997 and 2002 and was designated as “Galerías Pesadas” (Marks et al., 2002a,b), while the more recent phase of fieldwork was resumed in 2013. The Aroeira site has yielded abundant archaeological materials, including Acheulean handaxes and three human fossils (Aroeira 1–3). Aroeira 1 and 2 are represented by isolated teeth (Trinkaus et al., 2003), while Aroeira 3 is a partial cranium (Daura et al., 2017). Three stratigraphic units have been identified at the Aroeira site, and the cranium was found in Unit 2 encased in very hard breccia. In addition, several hundred stone tools were recovered from this same unit (Daura et al., 2018), along with fragmentary and some burnt faunal remains. The age of the cranium was estimated relying on several radiometric dating techniques and likely falls between 389 and 436 ka, making Aroeira 3 one of the best dated crania from the European Middle Pleistocene and approximately contemporaneous with the Atapuerca (SH) sample (Daura et al., 2017).

In a recent study of the Aroeira 3 cranium, Daura et al. (2017) showed that it presents a unique combination of primitive and derived features among European Middle Pleistocene fossils. Based on the morphology of the glabellar and mastoid regions, as well as the presence of a well-developed postglenoid process, these authors concluded that Aroeira 3 was similar to the fossils from the Atapuerca (SH) site, Bilzingsleben and Steinheim. On the other hand, Daura et al. (2017) also indicated that the current evidence from the European Middle Pleistocene fossil hominin record is difficult to reconcile with a linear evolutionary model, and they suggested the existence of complex population dynamics, including population replacement, isolation and hybridization.

Although the Aroeira 3 cranium is incomplete, the right temporal bone, including the petrosal portion, is intact, providing the opportunity to examine its bony labyrinth morphology. Variation in bony labyrinth morphology among modern human populations has recently been shown to reflect population history below the species level (Ponce de León et al., 2018). In fossil hominins, the bony

labyrinth has been shown to contain phylogenetic information, and species-specific differences have been reported previously (Spoor, 1993; Spoor et al., 2003). In particular, Neandertals show several derived features in the bony labyrinth, including the relative canal proportions, a low position of the posterior canal, and distinct angular relationships of the lateral canal with the surrounding petrosal bone elements. While this suite of features occurs at high frequencies in Neandertals, some of the individual features can occasionally be found in other groups as well. In particular, fossils from two sites in China (Xujiayao and Xuchang) resemble Neandertals in the low position of the posterior canal and the canal proportions (Wu et al., 2014; Li et al., 2017). In the case of Xuchang, the additional presence of a suprainiac fossa in the occipital bone led Li et al. (2017) to suggest some degree of gene flow from Neandertal populations.

A recent study of the bony labyrinth in the Atapuerca (SH) hominins has provided insights into the emergence of these derived features during the course of evolution of the Neandertal clade (Quam et al., 2016). The Atapuerca (SH) hominins already show the derived canal proportions of Neandertals (Quam et al., 2016). While a few individuals do show a low placement of the posterior canal, most of the sample does not, differing from Neandertals in this regard. In addition, the Atapuerca (SH) hominins show a low shape index of the cochlear basal turn, due to a shortened cochlear height, and this may represent a derived feature in this sample. Limited data for other non-SH European Middle Pleistocene specimens suggest that these individuals largely show the derived canal proportions and lack a low placed posterior canal (except for Reilingen; Spoor et al., 2003; Quam et al., 2016). Thus, changes in the canal proportions apparently preceded the appearance of the low placement of the posterior canal in Neandertal evolution. Given their close geographic proximity and similar chronology, comparison of the Aroeira 3 and Atapuerca (SH) bony labyrinth may provide insights into hominin evolution at or near the origin of the Neandertal clade.

## 2. Materials and methods

### 2.1. Comparative samples

The bony labyrinth in Aroeira 3 is compared with a large sample of Pleistocene and recent humans (Table 1). Comparison with the Atapuerca SH sample is of particular interest, given the close similarity in chronology and geographic location between the SH site and Aroeira. Several additional European Middle Pleistocene individuals, as well as a sample of Neandertals, help to elucidate the phylogenetic affinities of Aroeira 3. In addition, the limited data for Early and Middle Pleistocene individuals from Africa and Asia are also included to provide information on earlier members of the genus *Homo*. Some authors prefer to separate these African and Asian specimens into two distinct species (*Homo ergaster*, in the case of Africa, and *Homo erectus*, in the case of Asia; Wood, 1991; Tattersall, 2007), while others prefer to recognize all these fossils as representing a single geographically widespread species (*H. erectus*; Rightmire, 1990; Antón, 2003). We have grouped these fossils together into a single sample of *H. ergaster/H. erectus*, since previous studies have suggested that a broadly similar bony labyrinth morphology, interpreted as reflecting the primitive condition for the genus *Homo*, characterizes all of these fossils (Spoor et al., 2003; Gilbert et al., 2008; Quam et al., 2016). Two sites in China, Xujiayao and Xuchang, have yielded fossils whose taxonomic affinities are currently unclear, but for which data on the bony labyrinth are available (Wu et al., 2014; Li et al., 2017). Finally, samples of fossil and recent *Homo sapiens* were also included in the comparative analyses.

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