Continuity *versus* discontinuity of the human settlement of Europe between the late Early Pleistocene and the early Middle Pleistocene. The mandibular evidence

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ABSTRACT

One of the most interesting aspects of the settlement of Europe is the possible continuity or discontinuity of the populations living in this continent during the Early and Middle Pleistocene. In this paper we present an analysis of the mandibular fossil record from four important Pleistocene European sites, Gran Dolina-TD6-2 (Sierra de Atapuerca), Mauer, Arago, and Atapuerca-Sima de los Huesos. We focus this study in the recognition of key derived mandibular features that may be useful to assess the relationship among the populations represented at these sites. In order to make an approach to the ecological scenario, we also present a short review and discussion of the archaeological and paleoenvironmental evidences at that time. Our results suggest that probably there was a demographic discontinuity between the late Early Pleistocene populations (MIS 21-MIS 19), and those dated to the MIS 15. Hybridization between residents and new settlers cannot be discarded. However, some features of the Gran Dolina-TD6 hominins point to some relationship between the population represented in this site (probably dated to the MIS 21) and the European Middle Pleistocene and early Late Pleistocene populations. A hypothetical scenario is presented in order to understand this apparent contradiction with the model of discontinuity.

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1. Introduction

There is growing interest in elucidating the evolutionary scenarios during the Pleistocene in Europe that are consistent with the archaeological, fossil, and genetic evidences (e.g., Muttoni et al., 2010; Endicott et al., 2010; Martinón-Torres et al., 2011; Bermúdez de Castro and Martinón-Torres, 2013; Fu et al., 2013; Gómez-Robles et al., 2013; Peretto et al., 2015; Mounier and Lahr,

2016; Meyer et al., 2016). The latest findings in Pleistocene deposits of Europe have added many uncertainties and complicated our understanding on human evolution in this continent (Ascenzi et al., 1996; Manzi, 2004; Roksandic et al., 2011; Peretto et al., 2015). Many of these uncertainties are related to difficulty in obtaining precise dating and/or the margin of error of the different geochronological methods (Martínez et al., 2010; Parfitt et al., 2010; Falguères et al., 2015). However, it is also true that the variability of the human fossil record is not always easy to interpret (Vlcek, 1978; Manzi, 2004; Roksandic et al., 2011; Skinner et al., 2016). With a few exceptions (Atapuerca-Sima de los Huesos site) the number of specimens and their fragmented nature are a handicap for the understanding of the settlement of Europe. Although the archaeological record is now larger than three or four decades ago, it also depicts a wide variability and promotes a higher number of

different interpretations (e.g. Dennell, 2008; Sharon, 2011; Doronichev, 2015; Mounier and Lahr, 2016; Rocca, 2016).

One of the most interesting issues in this debate is the possible continuity or discontinuity of the peopling of Europe during the Pleistocene (Arribas and Palmqvist, 1999; Bermúdez de Castro et al., 2003; Dennell et al., 2011; MacDonald et al., 2012; Bermúdez de Castro et al., 2013; Bermúdez de Castro and Martinón-Torres, 2013; Mosquera et al., 2013; Rodríguez-Gómez et al., 2014). In a previous study (Bermúdez de Castro et al., 2013) we discussed the possibility of continuity/discontinuity between the earliest recognized dates for the settlement of Europe (e.g. Carbonell et al., 2008; Toro-Moyano et al., 2013) and the MIS 21. The discussion of this issue may be extended for the entire Pleistocene, given the changing climatic and biogeographical conditions of this continent.

Thus, after the end of Marine Isotopic Stage 19 (MIS 19) and during a long period, climate changes may have been a very tough challenge for human populations in Europe. Alternating climate cycles would have likely caused a decrease in population size with repeated episodes of local extinctions and periods of prolonged isolation in some cases favoured by geographical barriers (Arribas and Palmqvist, 1999; Dennell et al., 2011; Bermúdez de Castro et al., 2013; Manzi et al., 2011; Rodríguez et al., 2013). Several hypothetical scenarios are possible: 1- Discontinuity: The human populations of the late Early Pleistocene (LEP) disappeared during the lapse of time between the isotopic stages 18 and 16 without descendants and were totally replaced by a new population; 2- Continuity: During the MIS 18 to MIS16, human population of the late Early Pleistocene retract to refuges and expands again in the Middle Pleistocene, when conditions allowed; 3- Continuity/ discontinuity: The human population of the late Early Pleistocene contracts during isotopic stages 18 and 16, and hybridized with a new population that came later to Europe.

We are aware that it is complicated to test these hypotheses since the archaeological and paleontological records are limited, and it is difficult to found definitive support for one or another of these scenarios. Here, we aim to add to this debate by analysing the paleoanthropological record and, in particular, the mandibular evidence This is an appropriate approach, since key European Pleistocene localities with hominin evidence are indeed represented by mandibles, such as the TD6 level of Gran Dolina and the Sima de los Huesos site (Sierra de Atapuerca, Spain), the locality of Mauer (Germany), and the Arago cave (France). The population represented in TD6 level of Gran Dolina has been attributed to *Homo antecessor* (Bermúdez de Castro et al., 1997) and most likely lived in the MIS 21 (see below). These are the only European fossil hominins recovered so far between the Jaramillo and Brunhes-Matuyama reversals. The remaining mandibles belong to the Middle Pleistocene (see below), and their most accepted taxonomical attribution is *H. heidelbergensis* (i.e. Rightmire, 1998; Arsuaga et al., 1999; but see Arsuaga et al., 2014). There are several studies that have described in great detail all these mandibular specimens (e.g. Carbonell et al., 2005; Bermúdez de Castro et al., 2008; Rosas, 1995, 2001; Rosas and Bermúdez de Castro, 1998; Mounier et al., 2009). In this study we aim to test if the TD6-2 mandibles can be unequivocally related to the European Middle Pleistocene mandibles. Since Middle Pleistocene mandibles seem to share some Neandertal derived features, our study will focus particularly in this aspect. The new study is pertinent because there are currently different interpretations of the fossil record representing the late Early Pleistocene and the early-middle Middle Pleistocene. As an example, Condemi (2007) considers that present evidence is not enough to establish a clear relationship between *H. antecessor* and Neandertals. In contrast, Wagner et al. (2010, p. 19728) have criticized the results of the study of the ATD6-mandible from Gran Dolina and they consider that the corpus

proportions and surface relief "do not unambiguously differentiate the Gran Dolina hominins from Middle Pleistocene specimens", and that "it is possible that *Homo heidelbergensis* as a paleospecies/ lineage is deeply rooted in the Early Pleistocene".

We aim to discuss the possible continuity or discontinuity between the populations living in Europe during MIS 21-MIS 19 and those during the MIS 15. The respective temporal ranges of these periods are 865—810 ka and 621—568 ka (Liesiecki and Raymo, 2005). The choice of these periods is not at random, but responds to what we know about the human fossil record. Our initial premise is that the mandibles of the European classic Neanderthals of the Late Pleistocene exhibit a unique and derived structural pattern non shared with other Pleistocene African and Asian specimens (Rosas, 2001). As stated by this author, some of the features of this pattern may be questioned as Neanderthal apomorphies (Trinkaus, 1993; Franciscus and Trinkaus, 1995) when the specimens are analysed individually. However, Rosas (2001) also states that the joint occurrence of these features can be considered as an evolutionary novelty. If a particular combination of these features (rather than the presence of an isolated feature) is present in the late Early and Middle Pleistocene hominins then we can reject the hypothesis of discontinuity.

In order to interpret our results we will present a general picture of the available archaeological and paleoenvironmental evidences of this period. Genetic results (i.e. Endicott et al., 2010; Meyer et al., 2016) represent an additional an important approach to the interpretation of the fossil record.

2. Materials and methods

The mandibular evidence of the TD6 hominin assemblage includes four specimens: ATD6-5, ATD6-96, ATD6-112, and ATD6-113. Unfortunately, the four specimens are incomplete, and ATD6-112 and ATD6-5 belong to immature individuals (Rosas and Bermúdez de Castro, 1999; Carbonell et al., 2005; Bermúdez de Castro et al., 2008; Bermúdez de Castro et al., 2010). Concerning the stratigraphic context, the TD6 level has been divided in three sublevels: TD6-1, TD6-2, and TD6-3 (Bermúdez de Castro et al., 2012). The human fossils, as well as more than 300 artefacts and several thousands of micro- and macromammal fossil remains (Cuenca-Bescós et al., 1999; van der Made, 1999; García and Arsuaga, 1999; Carbonell et al., 1999) come from the sublevel TD6-2. Parés and Pérez-González (1995, 1999) observed a polarity reversal between TD7 and TD8, interpreted as the Matuyama/ Brunhes boundary, meaning that levels TD8-TD11 were deposited during the Middle Pleistocene, whereas levels TD1-TD7 were deposited during the Early Pleistocene. The combination of the paleomagnetic data and ESR/U-series ages suggests an age range between 780 and 866 ka for the so-called Aurora Stratum (Falguères et al., 1999). Thermoluminiscence (TL) dates on samples taken at the TD7 level, one meter below the Brunhes/Matuyama boundary give a weighted mean age of 960 ± 120 ka for TD7 (Berger et al., 2008). The ESR dating applied to optically bleached quartz grains gives dates between 601 ± 88 ka and 947 ± 90 ka (Moreno et al., 2015). These authors also obtained dates of 734 ± 128 ka and 852 ± 144 ka for the TD7 level, from samples taken under the Matuyama/Brunhes boundary. Using thermally transferred OSL (TT-OSL) dating of individual quartz grains, Arnold et al. (2014) obtained a weighted mean age of 846 ± 57 ka for the TD6 level. Finally, Arnold and Demuro (2015) have undertaken a series of TT-OSL suitability assessments on known-age samples from TD6. Using this method, they obtained a weighted average age of 851 ± 46 ka for TD6-3. Summarizing, and taking into account the biostratigraphic information from TD6 (Cuenca-Bescós et al., 1999, 2015), we consider that the TD6 hominins could be assigned to the