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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.

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

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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

MIS 21.

The last radiometric dating of the German Mauer mandible is 609 ± 40 ka (Wagner et al., 2010). These authors have applied the ESR/U-series method to the mammal teeth presumably associated to the human specimens, and infrared radiofluorescence to the sands grains that have been related to the site where the mandible was recovered. The French Arago mandibular sample is formed by five specimens: Arago II (hereinafter we prefer to use the Arabic numbers), Arago 13, Arago 89, Arago 118–119, and Arago 130–131. We have studied the originals of Arago 2, Arago 13, and Arago 89. The other specimens are still unavailable and the information published is very limited so they will not be included here (M.A de Lumley, 2015). It is important to mention that the mandible Arago 13 was obtained from the archaeostratrigraphic unit (AU) F (subunit Fm3), Arago 2 was discovered in the AU G (Gm3), and Arago 89 also comes from the AU G (Gs1) (H. de Lumley, 2015). This mean that the three specimens fall within the age range of 400 and 450 ka, the youngest of them being Arago 13 (de Lumley, 2015).

Concerning the Atapuerca-SH site there is a large mandibular sample formed by eleven almost complete specimens and a certain number of fragmentary specimens (see Rosas, 1995; Rosas, 2001; Bermúdez de Castro et al., 2014). U-series dating of a cave raft speleothem deposited directly on a hominin cranium (Cranium 4) from LU-6 yielded a mean age of 434 + 36/−24 ka. Furthermore, luminiscence dating by means of thermally transferred OSL and post-infrared IRSL, as well as ESR quartz of the sediments containing the fossils have yielded similar values which range between 395 ± 35 and 443 ± 90 ka (Arsuaga et al., 2014). These values are consistent with paleomagnetic analyses and the associated macro- and micromammal species (Arsuaga et al., 2014). Summarizing, apart from the Early Pleistocene TD6-2 specimens, the Middle Pleistocene mandibles included in this study belong to populations that lived in Europe between MIS 11 and MIS 15.

The list of morphological features we will examine in search of Neanderthal traits can be found in Table 3 of Rosas (2001) and includes:

- Position of mental foramen
- Place of M3 in relation to the ramus (retromolar space)
- Length of the retromolar space
- Position of the lateral prominence
- Inclination of the retromolar area
- Position of the mylohyoid line in relation to the alveolar margin at M3 level
- Trajectory of the mylohyoid line in relation to the alveolar margin
- Relief of the masseteric fossa
- Relief of the pterygoid fossa
- Gonion profile
- Place of the condyle in relation to the mandibular notch

Furthermore, two mandibular metrical variables and indices proposed in Rosas and Bermúdez de Castro (1998) are also used: the relationship between the M3-LIN/total length of the mandible (LIN = lingula landmark); the distance FOR-M3 (FOR = mental foramen landmark). See Rosas and Bermúdez de Castro (1998) for additional explanations.

3. Results

The left hemimandible ATD6-96 recovered from the TD6 level exhibits a primitive structural pattern, shared with other African and Asian Pleistocene hominins (Carbonell et al., 2005; see also Bermúdez de Castro et al., 2015). This pattern includes a lateral prominence at the M2 level, absence of retromolar space, a short and an inclined trigonum postmolare. The small M3 is partially covered by the ramus, and the mylohyoid line is almost parallel to the alveolar border. These features are also present in ATD6-113. Furthermore, in ATD6-96 the mental foramen is placed at the level of P3 and there is a medial intersection between the mandibular notch and the condyle. However, ATD6-96 also shows a well-developed medial pterygoid tubercle (MTP), which is characteristic of the Neandertals (ca. 89%) and is also very frequent (55%) in the Sima de los Huesos (SH) hominins (Bermúdez de Castro et al., 2014; see also Weaber, 2009) (Table 1). Following Rosas and Bermúdez de Castro (1998), we have obtained the distance between the posterior-lingual corner of the M3 alveoli and the lingula (LIN) in ATD6-96. This distance (in absolute terms) has a little taxonomic significance (Rosas and Bermúdez de Castro, 1998). However, when the distance is corrected by maximum length of the mandible, the European Middle hominins (particularly the SH hominins) and the Neandertals are out of the range of variation of *H. erectus* s.s., *H. ergaster* and *H. sapiens* (Rosas and Bermúdez de Castro, 1998). In ATD6-96 the M3-LIN value is 24.0 mm. This is a small value in accordance to the size of the specimen, but when it is corrected by the total length of the mandible (Bermúdez de Castro et al., 2015) we obtain a value of 0.24, which is included in the range of the Middle Pleistocene hominins and the Neandertals and far from the smaller values of *H. erectus* s.s., the Tighenif hominins and *H. sapiens* (Rosas and Bermúdez de Castro, 1998). Finally, the distance between the posterior-lingual corner of the M3 alveoli and the mental foramen (FOR) obtained in ATD6-96 (46.0 mm) is at the lower limit of the East African Middle Pleistocene mandibles and out of the range of variation of the Middle Pleistocene hominins and the Neandertals (Rosas and Bermúdez de Castro, 1998).

In the Mauer mandible we note the following features (Table 1): the strong anterior lateral tubercle and the mental foramen are both placed at the P4-M1 level, the lateral prominence is located at

Table 1
List of the mandibular morphological and metrical derived "Neandertal" features present in specimens and samples of European Pleistocene hominins. See text, Rosas and Bermúdez de Castro (1998) and Rosas (2001) for a detailed explanation of the mean of these features. LIN: Lingula landmark; FOR: Mental foramen landmark.

Specimen/ sample	Feature
ATD6-96	Presence of medial pterygoid tubercle M3-LIN distance/total lenght
Mauer	Mental foramen at the level of P4-M1 Anterior lateral tubercle at the level of P4-M1 Lateral prominence at the M3 level Truncated gonion profile M3-LIN distance/total length Distance FOR-M3
Arago	Mental foramen at the level of M1 or P4-M1 Anterior lateral tubercle at the level of M1 or P4-M1 Lateral prominence at the level of M3 or M2-M3 Medial position of the condyle in relation to mandibular notch Truncated gonion profile (in Arago 13) M3-LIN distance/total length Distance FOR-M3
Atapuerca-SH	Presence of medial pterygoid tubercle (55%) Mental foramen at the level of M1 (65%) or P4-M1 Anterior lateral tubercle at the level of P4-M1 Lateral prominence at the M3 level Medial position of the condyle in relation to mandibular notch Diagonal/intermediate trajectory of the mylohyoid line Large retromolar space and uncovered M3 by the ramus M3-LIN distance/total length Distance FOR-M3

the M3 level, and the gonial angle is truncated. In all these features the Mauer mandible recall the lateral aspect of Neandertals (Rosas, 2001; Mounier et al., 2009). Mounier et al. (2009) also consider that the posterior location of the deepest point of the mandibular notch is also a Neandertal-like feature of the Mauer specimen (Rosas, 1992; Creed-Miles et al., 1996; Rak et al., 2002; but see also Wolpoff and Frayer, 2005). The relationship between the M3-LIN/total length is between the range of variation of the SH hominins and the Neandertals. Similarly, the distance FOR-M3 is in the range of variation of all the European Middle Pleistocene hominins and the Neandertals (Rosas and Bermúdez de Castro, 1998). Other key morphological features, not related to Neandertals, are the following: 1- the trigonum postmolare is short and horizontal; 2- the M3 is partially covered by the ramus; 3- the position of the condyle in relation to the mandibular notch is lateral; and 4- the mylohyoid line is horizontal or subhorizontal. No medial pterygoid tubercle is present in this specimen.

The Arago mandibles exhibit the following features shared with Neandertals (Table 1): 1- the anterior lateral tubercle is placed at the level of M1 (Arago 2), and P4-M1 (Arago 13 and Arago 89); 2- the lateral prominence is located at the M3 level in Arago 2 and Arago 89, and M2-M3 in Arago 13; 3- the position of the mental foramen lies at the M1 in Arago 2 and the P4-M1 in Arago 13 and Arago 89; 4- the position of condyle in relation to the mandibular notch is medial in the three specimens; 5- the pterygoid fossa is deep in Arago 2 and Arago 89, but it is shallow in Arago 13; 6- the masseteric fossa is variable; it is flat in Arago 2, shallow in Arago 89, and deep in Arago 13. Furthermore, the relationship between the M3-LIN/total length in Arago 2 and Arago 13 is within the range of variation of SH hominins and Neandertals. The same is valid for the distance FOR-M3, which is within the range of variation of Neandertals and the SH hominins, and out of the range of variation of the African and Asian Early and Middle Pleistocene hominins. The Arago mandibles are different from Neandertals in the presence of a parallel or subhorizontal mylohyoid line, the absence of retromolar space; an M3 partially covered by the ramus, the absence of medial pterygoid tubercle and a regular profile of the gonion. The trigonum postmolare is horizontal in Arago 2 (like in Neandertals), but it is inclined in Arago 13 and Arago 89. The trigonum postmolare in Arago 2 measures 10.0 mm, a value which is slightly lower than the average (11.8, $n = 12$) obtained in the SH hominins (Rosas, 2001), and is not within the maximum category (3) that, according to Rosas (2001), corresponds to a true retromolar space (>14.5) and is the derived feature for Neandertals.

The large mandibular sample from the SH site has the following Neandertal features (Table 1): 1- frequent expression of a medial pterygoid tubercle (55%); 2- mental foramen mainly at the level of M1 (65%) or at the level of P4-M1; 3- anterior lateral tubercle at the level of P4-M1; 4- lateral prominence at the level of M3; 5- medial position of the condyle in relation to the mandibular notch; 6- large retromolar space with an horizontal surface, which may reach a length near 19.0 mm; and 7- a diagonal (oblique) trajectory of the mylohyoid line. Furthermore, the relationship between the M3-LIN/total length in most SH specimens is within the range of variation of the Neandertals. The same applies for the distance FOR-M3, which is within the range of variation of Neandertals and out of the range of variation of the African and Asian Early and Middle Pleistocene hominins. However, in the SH hominins the profile of the gonion is regular, in contrast with the truncated shape exhibited by Neandertals. Besides, the relief of the pterygoid in the SH hominins is shallow, whereas in Neandertals is deep, and the relief of the masseteric fossa is deep whereas in Neanderthals is flat.

The mandibular body of the European Middle Pleistocene is generally low, with parallel alveolar and basal borders. In contrast, the African *Homo* specimens (particularly those of the Tighenif) and the Indonesian *H. erectus* exhibit a high and robust corpus. The height of the mandibular body the TD6-2 specimens is low and similar to the means obtained in most European Middle Pleistocene hominins, but also in the Zhoukoudian specimens, and Neandertals (Rosas, 1995; Carbonell et al., 2005; M.A. de Lumley, 2015). The thickness of the mandibular body of the European Middle Pleistocene and the TD6-2 mandibles is also moderate (except in Arago 13) and clearly lower than that of the Tighenif specimens, KGA 10-1, KNM-ER 730, KNM-ER- 1802, UR 501, OH 22, and Sangiran 9 (Schrenk et al., 1993; Rosas, 1995; Anton, 2003; Carbonell et al., 2005; Kaifu et al., 2005; Suwa et al., 2007; M.A.de Lumley, 2015). Interestingly, the thickness of the mandibular body of the Zhoukoudian hominins is also moderate (Carbonell et al., 2005).

On the other hand, it is noteworthy that the medial surface of the mandibular body of ATD6-96 lacks a torus mandibularis, and the slope of this surface at the level of the canine is moderately convex, suggesting an almost vertical planum alveolare. In the Mauer and SH specimens there is a moderate torus mandibularis and the planum alveolare is wide (Rosas, 1995). This plane is in lateral continuity with the planum subalveolaris. In contrast, the torus mandibularis is strongly developed in the Arago specimens, particularly in Arago 13 (M.A. de Lumley, 2015). The planum alveolare is conspicuous, especially in Arago 13. As a result, the planum subalveolaris is remarkable in the French specimens (M.A. de Lumley, 2015).

4. Discussion

Although this report deals with the hominin fossil record, we consider that evidence from other related fields can be useful to have a more complete and general picture of the human evolutionary scenario of the European continent during the Pleistocene. In fact, hominins cannot be seen as isolated entities, but rather as primates closely linked to their environment. Therefore, before discussing the paleoanthropological evidence, we will make a short review of the cultural and environmental evidence.

4.1. Which information we get from the archaeological record? Is this information totally reliable?

Although it is not the purpose of the authors to go into detail about the technological diversity of the European Pleistocene sites, we think that it is essential to present an overview of the archaeological record of late Early Pleistocene and the Early Middle Pleistocene. Tools can be well preserved even when the fossilization of organic remains is not possible. Hence, the presence, location and density of sites with lithic evidence are very important to answer numerous questions about the population of a given territory (e.g., Rocca, 2016). In Table 2 we show the most important European sites with reliable dating, along with the classification of the artefacts obtained from these localities.

The Pre-Jaramillo lithic assemblages comprise core and flake elements (cf. Doronichev, 2015). The few known sites between the Jaramillo event and the Matuyama/Bruhnes reversal have yielded assemblages formed by a core-flake-tool industry (Doronichev, 2015; but see below) and they are limited to southern Europe. These lithic assemblages can be included in Mode 1, cf. Clark (1969). However, it is important to note that, according to Doronichev (2015) the West European (or Eurasian) core-flake-tool technology is not necessarily a fully cultural analogous of the Africa Oldowan, but it might represent an independent cultural phenomenon. The presence of one handaxe in Estrecho de Quipar (Murcia, Spain) and one hand axe in Sola de Zamborino (Granada) have been claimed as the oldest presence of Large Cutting Tools (LCTs, or Mode 2) in Europe (Scott and Gibert, 2009). However, the

Table 2
List of some key Pleistocene European sites dated between MIS 25 and MIS 13.

Site	Age (ka)	Methods	Technology	Reference
Ca' Belvedere di Monte Poggiolo (Italy	700–1.400	Paleomagnetism ESR	PBC[1]	Gagnepain et al. (1998) Yokoyama et al. (1992) Bahain et al. (2007)
Gran Dolina-TD6 (Spain)	788–866	Biostratigraphy Paleomagnetism US-ESR	PBC	Cuenca-Bescós et al. (1999) Cuenca-Bescós et al. (2015) Falguères et al. (1999) Parés and Pérez-González et al. (1995; 1999)
	960 ± 0.120	TL-IRSL		Berger et al. (2008)
	601 ± 88 947 ± 90	ESR (OBQ)[2]		Moreno et al. (2015)
	846 ± 57 OSL	(TT-OSL)		Arnold et al. (2014)
	851 ± 46 OSL	(TT-OSL)		Arnold and Demuro (2015)
Pradayrol (France)	900	Biostratigraphy	PBC	Turq et al. (2012)
Vallaparadis (Spain)	790 ± 230	Biochronology Paleomagnetism	PBC	Martínez et al. (2010)
	830 ± 130	ESR-ESR/US		Duval et al. (2009, 2011)
Barranc de la Boella II (Spain)	960–780	Biochronoloy Paleomagnetism	LCT	Lozano-Fernández et al. (2014) Vallverdú et al. (2014) Mosquera et al. (2015)
Happisburg 3 (UK)	814–870 970–936	Biochronoloy Paleomagnetism	PBC	Parfitt et al. (2010)
Pakefield (UK)	700	Paleomagnetism & Amino-acid-Biostratigrafy	PBC	Parfitt et al. (2005)
Soleihac (France)	700–500	$^{39}K/^{40}K$ Paleomagnetism	PBC	Raynal et al. (1985)
Isernia-La Pineta (Italy)	602 ± 2 583–561	$^{39}K/^{40}K$ $^{39}K/^{40}K$	PBC	Coltorti et al. (2005) Peretto et al. (2015)
Notarchirico (Italy)	640 ± 40 640 ± 70	$^{39}K/^{40}K$ & Racemisation, TL	LCT[3]	Pilleyre et al. (1999) Lefèvre et al. (2010)
Brinay, La Noira (France)	655 ± 55	ESR	LCT	Despriée et al. (2010, 2011) Moncel et al. (2013)
Morandière (France)	610 ± 60	ESR	LCT	Despriée et al. (2011) Despriée et al. (2007) Voinchet et al. 2015
Arago, levels P, Q	550–580	Biostratigraphy ERS/US U series	LCT	Barsky et al. (2010)
Boxgrove (UK)	550	Biostratigraphy	LCT	Pope et al. (2009)
Mauer (Germany)	609 ± 40	Biostratigraphy ESR/US; IR/RF	–	Wagner et al. (2010)
Maidcross Hill (England)	529 ± 55 621 ± 56	ESR & ESR/U-series	LCT	Voinchet et al. (2015)
Brooksby (England)	294 ± 36 710 ± 64	E SR & ESR/U-series	LCT	Voinchet et al. (2015)
Warren Hill (England)	544 ± 53 539 ± 38	ESR & ESR/U-series	LCT	Voinchet et al. (2015)
Abbeville (France)	446 ± 44 757 ± 153	ESR & ESR/U-series	LCT	Voinchet et al. (2015)
Amiens Rue du Manège (France)	531 ± 61 570 ± 89	ESR & ESR/U-series	LCT	Voinchet et al. (2015)

chronology of both sites has been firmly contested by other authors (Jiménez-Arenas et al., 2011).

The Barranc de la Boella site, in the Spanish Mediterranean coast, has yielded clear evidence for LCTs during the LEP (Vallverdú et al., 2014; Mosquera et al., 2015). Besides the presence of *Mimomys savini*, *Victoriamys chalinei* and *Mammuthus meridionalis* (Lozano-Fernández et al., 2014; Mosquera et al., 2015), both paleomagntic and cosmogenic analyses of the Unit II of Barranc de la Boella support a human occupation during the Matuyama chron (Vallverdú et al., 2014). Concerning this site it is interesting the presence of only one LCT (one pick) among a total of 125 artefacts. Researchers wonder if this early European Acheulean was the logical evolution of the precedent technologies or may have been imported from the Near East or Africa (Mosquera et al., 2015). Whether this finding represents the tip of the iceberg of the expansion of the Acheulean technology in Europe, which coexists with the core-flake-tools technocomplex, is a matter of interest to test in other Pleistocene European sites. It is well known that composition of lithic assemblages (diversity of the heavy-duty components) may be explained by the duration of the occupation, raw materials, environments or regional variants, as well as by cultural traditions (specific behaviour) of local groups (e.g. Moncel et al., 2013). Therefore, it seems we should be prudent and wait for more evidence before changing the current paradigm. In fact, the presence of Acheulean begins to generalize in southwestern Europe around 700–600 ka ago (Barsky and de Lumley, 2010; Moncel et al., 2013). Furthermore, the absence of LCTs in Central Europe has promoted an interesting reflection on the methodological approaches and the accurate definition of lithic assemblages (Rocca, 2016).

Concerning Western Europe, two main traditions seem to have coexisted during the EMP. On one hand, pebble and core technology (BCT) can be recognized at sites as Soleihac in France (Raynal et al., 1985), Isernia-La Pineta, in Italy (Coltorti et al., 2005; Peretto et al., 2015), Happisburg and Pakefield, in UK (Parfitt et al., 2005, 2010) or Korolevo VII-VIII, in Ukrania (Koulakovska et al., 2010), all of them dated between the Matuyama-Brunhes Boundary and 500 Ka. On the other hand, putting aside the evidence from the Barranc de la

Boella site, the LCTs may have appeared in Europe 700 ka ago, as evinced by the sites of La Noira, in France (Coltorti et al., 2005; Moncel et al., 2013), and Notarchirico, in Italy (Lefèvre et al., 2010). Other sites are consistent with dates around 600 ka or a bit younger (see Table 1), such as levels P and Q from Arago, Boxgrove (UK), or the fluvial sandy levels of Mauer, the type site of *H. heidelbergensis*.

Moncel et al. (2013) argues that a few European sites have yielded some tentative bifacial elements, as it is also observed in developed Oldowan African sites. However, the Acheulan technology from La Noira is advanced and very different from the African basal Acheulan (Moncel et al., 2013). That is, the efforts of the hominins who inhabited La Noira seem to be aimed at systematically making LCTs. The dating of La Noira is 655 ± 55 ka (Despriée et al., 2010, 2011), similar to the dates obtained at the site of Notarchirico (Pilleyre et al., 1999; Lefèvre et al., 2010). Thus, the geochronological dates suggest that classic Acheulan could have entered in Europe during MIS 16 and/or MIS 17. In North-western Europe (Britain and northern France) a systematic dating of different site by means he ESR and EST/U-series confirm the presence of Acheulian between late MIS 15 and MIS 13 (Voinchet et al., 2015).

On the other hand, and according to some colleagues, the European Acheulean (or the LCTs technocomplex) seems to exhibit an African tradition (Lycett, 2009; Santonja and Pérez-González, 2010; Sharon, 2011; Doronichev, 2015). The absence of Acheulean sites in Eastern Europe has promoted the idea of a settlement of Europe through the Gibraltar strait (e.g. Santonja and Pérez-González, 2010; Sharon, 2011; Gibert et al., 2016; but see Rocca, 2016). However, and although the hominin fossil record is scarce, the comparison between the North African and European mandibles and teeth does not support this scenario (Bermúdez de Castro et al., 2007).

Summarizing, the lithic evidence seems to present a complex scenario, in which a different technology to that recorded in the late Early Pleistocene appeared in Europe during the early Middle Pleistocene. In addition, the technological variability observed in different regions of the European continent (Moncel et al., 2013; Rocca, 2016) seems to support complex dynamics within the European populations during the Pleistocene, rather the lineal evolution of a single and isolated hominin lineage.

4.2. The paleoenvironmental evidence

Severe climatic changes have affected the European hominin populations who colonized the continent during the Early Pleistocene (Carbonell et al., 2008; Toro-Moyano et al., 2013). These climatic changes affected the physical and biotic environment, and the structure of mammal communities (Rodríguez et al., 2011) thus reflecting the diversity and richness of fauna and flora at different times of the Pleistocene (Palombo and Mussi, 2006; Manzi et al., 2011). Rodríguez–Gómez et al. (2014) studied the faunal assemblage of the TD6 y TD8 levels of the Gran Dolina cave site. These levels were probably deposited during the periods we are dealing with. In fact, the ESR and U-series dates obtained from the middle part of TD8 suggest an average of 602 ± 52 ka (Berger et al., 2008) for this level. Besides *H. antecessor*, in TD6 it has been identified the presence of *Crocuta crocuta* and *Canis mosbachensis* as the main predators of the ecosystem (García and Arsuaga, 1999). The main predators identified in TD8 are *Crocuta crocuta*, *Hyaena* sp., and *Panthera gombaszoegensis*. So far neither artefacts nor human fossil remains have been found in TD8. It is possible that human access to the Gran Dolina cave during the deposition of TD8 was difficult (a narrow entrance) and that the sedimentation dynamics constituted a more favourable environment for the establishment of carnivore dens and shelters (Blasco et al., 2011). Alternatively, the mathematical model established by Rodríguez-Gómez et al. (2014) concerning the reconstruction of the trophic relationships in paleocommunities and the comparison of the intensities of intraguild competition suggests more adverse conditions for hominins during the deposition of TD8. Thus, the presence in this period of one panther and two species of hyena could have been a handicap for the presence of hominins, al least in this region of the Iberian Peninsula. The question is whether these results can be applied to other parts of Europe and whether the intraguild competition for resources may have played a major role in the distribution of the genus *Homo* in Europe (Rodríguez-Gómez et al., 2014). Was this intraguild competition a possible triggering factor of the demise/population decrease in the late Early Pleistocene in Europe? It is well-known the importance of the effective population size and its possible effect in the rate of evolution (see Lanfear et al., 2014 for a review). A small population size can affect the adaptation capacity, as well as to increase the genetic drift, thus contributing to the extinction of isolated groups. Although it is not possible to test this issue in the Pleistocene, this may have been a very common event during this long period of human evolution.

On the other hand, Dennell et al. (2011) used the concepts of "sink" and "source" for understanding the settlement history of Early and Middle Pleistocene Pleistocene Europe. According to these authors, "source" populations in glacial refugia in southern Europe would have provided a demographic growth necessary for the colonisation of northerly areas when weather conditions improve. In this regard we must remember that the altitude of the Sierra de Atapuerca is between 980 and 1074 m above sea level. Nowadays, the Sierra de Atapuerca and surroundings are dominated by a continental Mediterranean climate. This climate includes cold winters and mild summers. The average annual temperature is 10.5° and the precipitation reaches 600 mm. Presumably, conditions worsened significantly during glacial periods, with cold and dry climatic conditions. We can assume, for instance, that the regions of the Mediterranean coast were more feasible places for hominins' life. However, Rodríguez et al. (2011) have suggested that the absence of evidence for hominins in TD8 cannot be attributed to climatic deterioration. With regard to the environment, the main conclusion of these authors is that there was an absence of extremely harsh conditions at the region of Sierra de Atapuerca throughout the late Early Pleistocene to the late Middle Pleistocene. The presence of Mediterranean taxa was constant and the dominant landscape was a savannah-like open environment, probably with small forest patches (Rodríguez et al., 2011). In contrast, Cuenca-Bescós et al. (2011) point to a demise of the humid and forested habitats towards more open landscapes during the deposition of the levels TD8 and TD9. This interpretation is consistent with the results obtained by Blain et al. (2011) through the analysis of the amphibian and squamate reptile evidence.

4.3. The evidence of the human fossil record

Wagner et al. (2010) argue that the mandible ATD6-96 is not a good specimen to obtain solid arguments about the phylogenetic position of *H. antecessor*, since it belongs to a young adult. However, the occlusal surface of M3 of this mandible exhibits a wear facet at the mesial marginal ridge, suggesting that this molar was functional at the time of death of the individual. Furthermore, it has been shown that early in ontogeny, when dental development is still in progress, the differences in mandibular shape are already well established at the genus (Daegling, 1996) and the species level (Boughner and Dean, 2008). Thus, in modern humans, the definitive breadth of the mandible is reached early in ontogeny, since the maximum breadth of the cranium occurs at an age of about 2–3

years and no significant shape differences in the architecture of the mandible are expected after this age (Enlow and Harris, 1964; Enlow, 1990; Rosas, 1992). Therefore, we can use confidentially the information supplied by the ATD6-96 (contra Wagner et al., 2010). As we have shown, this mandible exhibits a well-developed MTP. Rak et al. (1994) were the first authors to note that the MTP could be a typical feature of the Neandertals. Given its high frequency of occurrence in Neandertals and the SH sample, its presence in *H. antecessor* is interesting. Since ATD6-96 is the only mandible that preserves a ramus in the TD6 hominin assemblage, it is possible that this represents an idiosyncratic feature of ATD6-96. Besides, the index M3-LIN/Total length relates ATD6-96 with the European Middle Pleistocene hominins and the Neandertals.

Howell (1960) was the first to recognize significant differences between the Mauer mandible and the Middle Pleistocene North African and Asian specimens. Later, some authors have noted similarities between the Mauer specimens and other European Middle Pleistocene hominins (Aguirre and de Lumely, 1977; Rosas, 1987) although. some colleagues do not agree with this conclusion (Wolpoff, 1980; Cook et al., 1982). The analysis of the morphology and some absolute and relative dimensions of the Mauer mandible, led to Rosas and Bermúdez de Castro (1998, p. 694) to conclude that this specimen "exhibits a set of features which are the structural basis on which Neandertal apomorphies will eventually fully developed". Condemi and von Koenigswald (1997) and Mounier et al. (2009) have also recognized the morphological similarities between the Mauer specimen and the Neandertals.

Concerning Arago, and leaving aside taxonomical assignments (e.g., Tattersall, 1986; Rightmire, 1998; Stringer, 2012; M.A. de Lumley, 2015), the mandibles found at this site exhibit some clear Neandertal features. There is a general consensus about the relationship between the Arago hominins and the Neandertal lineage. The same applies for the SH hominins, which exhibit clear Neandertal features not only in the mandibles (Rosas, 1997), but also in the neurocranium (Arsuaga et al., 1997, 2014; Martínez and Arsuaga, 1997), teeth (Bermúdez de Castro, 1993; Martinón-Torres et al., 2012) and the postcranial skeleton (e.g. Carretero et al., 1997; Pablos et al., 2013, 2014).

Rosas (2001) analysed the statistical relationship (chi-square test) between selected mandibular features in different hominin samples. As a result of his analyses, Rosas (2001) proposed that two different hypothetical processes occurred in the evolutionary development of the mandible during the Neandertal genealogy. One of the processes consisted of the backwards displacement of the structures of the corpus, namely the mental foramen, the lateral prominence and the anterior marginal tubercle, as well as the anterior border of the ramus. The second process would have involved the internal aspect of the corpus and ramus, fundamentally related to the inclination of the mylohyoid line and the alignement of the corpus and ramus. The latter would have resulted in the flattening of the masseteric fossa and the excavation of the pterygoid fossa. The first process is clearly observed in the Mauer, Arago and Sima de los Huesos mandibles, whereas the second one seems to have partially affected only the Arago and, especially, the Sima de los Huesos hominins. Thus, the derived state of all these features seems to represent an evolutionary novelty of the Middle Pleistocene lineage (Rosas, 2001), which is absent in the TD6 mandibles.

According to previous studies (Aguirre and de Lumley, 1977; Rosas, 1987) the presence of some morphological features in the Mauer, Arago and Sima de los Huesos mandibles suggest a close relationship between the hominins represented in these Middle Pleistocene sites. In contrast, the TD6-2 mandibles exhibit a generalized mandibular pattern, which apparently is not compatible with a direct relationship between *H. antecessor* and the European Middle Pleistocene hominins.

4.4. A plausible scenario

The presence of a unique and derived structural pattern in the mandibles of the Middle and Late Pleistocene suggests the existence of a particular evolutionary lineage, different from those of the African an East Asian continents. This pattern supports a scenario of continuity during the Middle and Late Pleistocene. In other words, we could assume that the European Middle and Late Pleistocene hominins belonged to and ancestral-descendant sequence of populations without rupture of the reproductive continuity (Eldredge and Cracraft, 1980). In contrast, the absence of this pattern in the TD6-2 hominin mandibles point to a demographic discontinuity between the late Early Pleistocene and the Middle Pleistocene.

However, we cannot exclude that *H. antecessor* had some kind of phylogenetic relationship with the European Middle Pleistocene lineage. The presence of a strong medial pterygoid tubercle is very frequent in Neandertals and the SH hominins, and the M3-LIN/total length index is within the range of the European Middle Pleistocene hominins and the Neandertals and out of the range of the African and Asian Pleistocene specimens. It is noteworthy that other cranial, dental and postcranial features observed in *H. antecessor* are also shared with Neandertals (Arsuaga et al., 1999; Carretero et al., 1999; Gómez-Robles et al., 2007; Bermúdez de Castro et al., 2012). Furthermore, the presence of a modern human-like facial morphology in the TD6-2 hominins (Bermúdez de Castro et al., 1997; Arsuaga et al., 1999; Lacruz et al., 2013; Bermúdez de Castro and Martinón-Torres, 2014) deserves attention.

Furthermore, the apparent continuity during the Middle and Late Pleistocene require a deep reflection. Three important questions ought to be considered in this issue: i, as stated above, *H. antecessor* (which is placed in the westernmost region of Europe) exhibits some Neandertal features. Obviously, these are not Neandertal autapomorphies, but traits that appeared during the late Early Pleistocene and were retained by classic Neandertals and their relatives from the Middle Pleistocene; ii, *Homo antecessor* also exhibits modern features; iii, the beginning of the Neandertal clade cannot be placed in Western Europe, since it shares a common ancestor with the modern humans clade. How to conciliate all these evidences?

The recent DNA analyses of some SH specimens demonstrate a clear relationship between these Middle Pleistocene hominins and the Neandertals (Meyer et al., 2016). Moreover, these authors suggest that the SH hominins could be considered as early Neandertals, although they not rule out the possibility that the SH hominins were a group closely related to them. However, to the light of the genetic data, the most parsimonious hypothesis would be to push back at least until the mid Middle Pleistocene (or even further back) the origins of the Neandertal lineage. According to previous paleogenetic results the geographic split of the Neandertals and modern humans could have occurred about 400.000 years ago (e.g., Noonan et al., 2006; Endicott et al., 2010). However and considering a human rate of mutation of $0.5 \times 10^{-}9$ per base pair per year, Meyer et al. (2016) suggest that the population split between archaic and modern humans occurred between 550 and 765 ka. The dating of the Mauer mandible (the holotype of *H. heidelbergensis*) is included in this temporal range and it represents the oldest specimen included in this species (i.e., Rightmire, 1998). Therefore, and in agreement with Meyer et al. (2016), we consider that with the present evidence it is difficult to accept that specimens included in the *H. heidelbergensis* species (like those from Arago or Petralona) can represent the population ancestral to

both modern humans and Neandertals. This is consistent with our results, since all the European Middle Pleistocene mandibles exhibit the characteristic Neandertal structural pattern.

Our results could be compatible with the hypothesis posed by Rightmire (1998). This author suggested that a set of African and Eurasian early Middle Pleistocene hominins fossils has clearly diverged from the *H. erectus/ergaster* "bauplan" and that these hominins could be related to *H. sapiens* and *H. neanderthalensis*. In our opinion *H. antecessor* does not share the *H. erectus/ergaster* bauplan, fitting the prediction of Rightmire (1998). The divergence from this bauplan would be older and could have occurred as far as the late Early Pleistocene. Although we initially suggested an African source for *H. antecessor* (Bermúdez de Castro et al., 1997), posterior reviews of additional fossil evidence in TD6-2 pointed to a Eurasian hallmark in this species (e.g., Carbonell et al., 2005; Martinón-Torres et al., 2006, 2007).

We have hypothesized that Southwestern Asia could be the best option for a cladogenetic event from hominins included in *H. erectus/H. ergaster* (Bermúdez de Castro and Martinón-Torres, 2013). This event would be the origin of several dispersals in different times not only to Europe, but also to Africa and Asia. In Europe, the TD6-2 hominins would be very close to this cladogenetic event and, for the moment, the best opportunity window to predict the aspect of this ancestor.

The new information supplied by the genetic analyses support a scenario as presented in Fig. 1, which could help to solve the dilemma. A cladogenetic event could have happened in Southwestern Asia about 700 ka ago, giving rise to the Neandertal clade (Bermúdez de Castro and Martinón-Torres, 2013). Specimens like those of the Mauer, Arago, Sima de los Huesos, Steinheim, Swanscombe, or Pontnewydd could evince different migrations from this region towards Europe. This may be one of the reasons for explaining the variability observed in the European Middle Pleistocene specimens. Of course, hibridyzation may be possible and probably very frequent between residents and new settlers. The archaeological record supports this scenario, since the LCTs technocomplex seems widespread in Europe about 700 ka ago, perhaps coinciding with the first expansion of a representative population of the Neanderthal genealogy. Although the hypothesis of the African origin for the LCTs is recurrent (i.e., Lycett, 2009), it is important to remember that this technology has been also found in the late Early Pleistocece site of Gesher Benot Ya'aqov, (Israel) (Goren-Inbar et al., 2000).

Noonan et al. (2006) suggested that the last common ancestor (LCA) to both modern humans and Neandertals could have lived about 700 ka. The new genetic evidence (Meyer et al., 2014) also forces us to push back this date. It would not be surprising that the LCA may be about one million years old (Martinón-Torres et al., 2011; Gómez-Robles et al., 2013). The TD6-2 hominins would be very close to the last common ancestor of Neandertal and modern humans, before the split of both genealogies (Fig. 1). The presence of a combination of modern human and Neandertal features in these hominins, as well as their chronology support this hypothesis. *Homo antecessor* was not necessarily extinct in the late Pleistocene, leaving the way clear for new settlers. As we have discussed above, glacial refugia in southern Europe could have allowed the persistence of this species during a long period (Dennell et al., 2011), without excluding the possibility of hybridization with the new settlers.

5. Conclusions

In this paper we have shown that there are interesting and hot debates about the distribution and characteristics of the European Pleistocene archaeological record. The same applies to the interaction of the hominins with other mammals, and the competence for the ecological niches. The dramatic Pleistocene climatic factors and the physical geography are important factors to consider in the models on the occupation of the European continent. We have posed some hypotheses, which ought to be tested in the future, especially if we have the luck of finding new sites with an abundant and informative hominin fossil record.

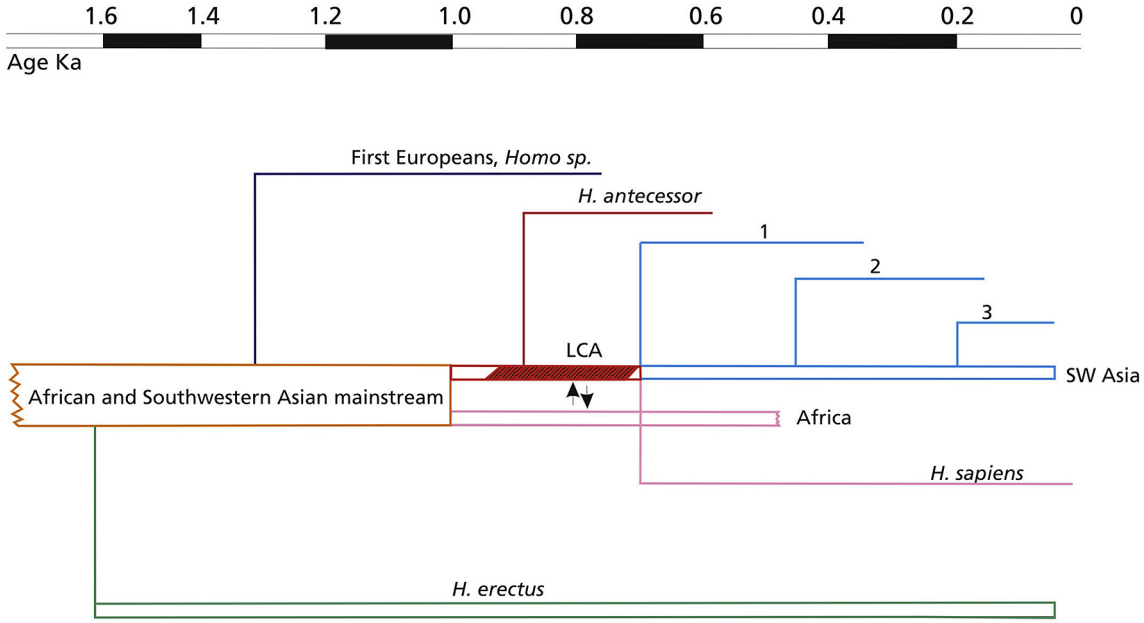

Fig. 1. This simplified scheme shows the hypothesis for and European evolutionary scenario, which could be compatible with the evidences of the fossil record and the paleogenetic data. *H. antecessor* would be an European branch closely related to the last common ancestor (LCA) of the Neandertal and modern human genealogies. According to Meyer et al. (2016), the geographic split of both genealogies would have occurred between 550 and 765 ka. Therefore, the species *H. heidelbergesis* should be removed of the hominin phylogeny, and the European Middle Pleistocene specimens could be tentatively included in two or more branches of the Neandertal clade (i.e. 1, 2, and 3 in the figure). In this review we prefer do not enter in the discussion about the taxonomic category of each of the branches.

We have confirmed the presence of a derived Neandertal pattern in the Mauer, Arago, and Sima de los Huesos mandibles, which is not present in the Gran Dolina TD6-2 specimens. The generalized and primitive morphology of the TD6 mandibles is apparently incompatible with a direct relationship between *H. antecessor* and the European Middle Pleistocene hominins (discontinuity). However, other skeletal parts of the TD6-2 assemblage exhibit a set of illuminating features, which support some kind of phylogenetic relationship with the Middle Pleistocene European hominins and the classical Neandertal, showing an unquestionable European hallmark in all these hominins.

We hypothesize that the specimens analysed in this review can be related through a common ancestor, which may have lived during the late Early Pleistocene. The evolution of this ancestor would have occurred in Southwestern Asia, a crossroad between Africa and Eurasia and a true hotspot for biodiversity during the entire Pleistocene (Hughes et al., 2007; Carrión et al., 2011). A first dispersal into Europe related to this ancestor could be represented at the Gran Dolina TD6-2 level (*H. antecessor*). According to the latest data provided by the paleogenetic analyses, a cladogenetic event would have led to the split of the Neandertal and modern human genealogies during the early Middle Pleistocene. This cladogenetic event may have also occurred from this common ancestor, giving rise to different migratory movements towards Europe.

H. antecessor could have occupied not only Southern Europe, but also higher latitudes, as shown by sites like Pakefield in the United Kingdom (Parfitt et al., 2005). Furthermore, there is no clear evidence that the Pleistocene populations ever got entirely extinct. Although the MIS 18 may have represented a window of opportunity for the settlement of a new population, residual groups occupying refuge areas may have formed a part of the European demography during the Middle Pleistocene. Hybridization between different populations cannot be discarded. Summarizing, we hypothesize that the European continent was settled in different moments, when conditions where favourable. Probably all of these populations shared a common origin, thus explaining the morphological derived similarities among them.

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