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Continuity or discontinuity in the European Early Pleistocene human settlement: the Atapuerca evidence

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ABSTRACT

The nature, timing, pattern, favourable circumstances and impediments of the human occupation of the European continent during the Early Pleistocene are hot topics in Quaternary studies. In particular, the problem of the (dis) continuity of the settlement of Europe in this period is an important matter of discussion, which has been approached in the last decade from different points of view. The Gran Dolina (TD) and Sima del Elefante (TE) cave sites in the Sierra de Atapuerca, (Spain) include large and quasi-continuous stratigraphic sequences that stretch back from at least 1.2 million years ago (Ma) to the Matuyama/Brunhes boundary. The archaeological and paleontological record from these sites can help to test different hypotheses about the character of the human settlement in this region and period. Furthermore, the TD6 level has yielded a large collection of human fossil remains attributed to *Homo antecessor*. According to different geochronological methods, as well as to paleomagnetic and biostratigraphical analyses, these hominins belong to an age range of 0.96–0.80 Ma. Unfortunately, the finding in 2007 of some human fossil remains in the TE9 level, dated to about 1.22 Ma, was not enough to conclude whether *H. antecessor* had deep roots in the European Early Pleistocene. A set of derived features of *H. antecessor* shared with both the Neanderthal lineage and modern humans suggests that this species is related, and not far, from the most recent common ancestor (MRCA) of *Homo neanderthalensis* and *Homo sapiens*. If we assume that there was a lineal biological relationship between the TE9 and TD6 hominins, we should reconsider many of the conclusions achieved in previous paleontological and genetic studies. In addition, we would be obliged to build a highly complicated paleogeographical scenario for the origin of the MRCA. Although continuity in the settlement of Europe during the entire late Early Pleistocene is not discarded (e.g. in refuge areas), it seems that this Western extreme of Eurasia, and the Iberian Peninsula in particular, was occupied by at least two different hominin populations.

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1. Introduction

During the last decade, and after the publication of a significant number of new sites, the early occupation of Europe has entered in a renewed debate, now focused in the Early Pleistocene (e.g. Dennell and Roebroeks, 1996; Carbonell et al., 1999a,b; Roebroeks, 2006; Shchelinsky et al., 2010; Dennell et al., 2011; MacDonald et al., 2012). As argued by Dennell (2003), the discussion of early hominin dispersals into Europe is centred on when (timing) this/these event/s occurred, as well as how (success) and often (frequency) hominins were able to colonise the European landscapes. According to Dennell (2003), these are three important key issues that need to be tested in future studies.

In relation to the timing of the first dispersal into Europe, there are hypotheses as extreme as those exposed by Bosinski (2006) or Leroy et al. (2011). For the first, the South of Europe could be already inhabited by 1.8 million years ago (Ma). Even more extreme is the suggestion of Leroy et al. (2010) who speculate, based on a

Abbreviations: TD, Gran Dolina; TE, Sima del Elefante; MRCA, Most recent common ancestor; Ma, Million years ago; TE-LRU, Sima del Elefante Lower Red Unit; MIS, Marine Isotope Stage; EMPT, Early-Middle Pleistocene Transition; CADE, Central area of dispersal to Eurasia; SWA, Southwestern Asia.

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theoretical model (Climatic Amplitude Method), that there were up to 42 possible narrow windows of opportunity for hominins to disperse into Europe along the entire Early Pleistocene (2.58–0.78 Ma), coinciding with particular ecological conditions of the glacial and interglacial cycles forced by obliquity. In contrast, Muttoni et al. (2010) propose that the first colonisation of Europe may have occurred after the Jaramillo event, most probably in relation to the extreme conditions of the MIS 22 (at ca 0.9 Ma), the first intense cold stage of the Early-Middle Pleistocene transition (EMPT). According to Muttoni et al. (2010), the aridification of Northern Africa and Eastern Europe was the cause that triggered the migration pulses of large herbivores (particularly elephants) out of their refuges in Southern Europe. Between these two positions, and waiting for additional evidences, there is a general consensus in assuming that humans dispersed to Western Europe at the beginning of the second half of the Early Pleistocene, probably at 1.5–1.4 Ma.

Concerning the possible success of the early colonisation of Europe, Bosinski (2006) is persuaded of the increasing ability of hominins to control the environment. Climatic changes and their possible competitors, in particular *Megantereon*, *Homotherium* and *Pachychrocuta*, would not have been a problem for a successful expansion into Southern Europe. In contrast, Turner (1992) and Hemmer (2000) argue that these large felids and the early giant short-faced Pleistocene hyena were a biological barrier for the expansion of hominins in the European continent. This aspect is also related to the question of the ecological niche of ancient hominins. Although early *Homo* was once catalogued as an opportunistic and passive scavenger (e.g. Binford, 1981), other authors have supplied evidence that suggests a more aggressive role in their ecosystems, either as predators of ungulates or as active scavengers (e.g. Domínguez-Rodrigo, 2002). Apart from depending on plant foods for themselves, the active scavenging and hunting of hominins in competition with other predators is related to open landscapes, with grasslands and/or forested steppes. According to Agustí et al. (2009) a sharp climatic deterioration before 1.8 Ma could be a possible barrier for the settlement of Western Europe after the "Dmanisi episode".

The simulation of Leroy et al. (2011) focuses on the climatic barriers and the environment during the Early Pleistocene. For these authors, the hominin dispersals in Europe occurred only during the transitions from glacial to interglacial periods. During glacial periods, the climate was too cold for hominins that were not yet adapted, and during the transition from interglacial to glacial periods, the environment was too forested for these hominins' lifestyle. Thus, Leroy et al. (2011) consider that hominins disappeared from Europe as soon as the climate and vegetation deviated too much from the ideal conditions. Therefore, and in agreement with other colleagues (Bar-Yosef and Belfer-Cohen, 2001; Dennell, 2003; Agustí et al., 2009; Blain et al., 2009; Moncel, 2010; Dennell et al., 2011; Bar-Yosef and Belmaker, 2011; Hughes et al., 2011; MacDonald et al., 2012), Leroy et al. (2011) think that the earlier occupation of Europe was probably discontinuous.

Some recent findings have enriched the European archaeological record (Parfitt et al., 2005, 2010; Arzarello et al., 2007; Scott and Gibert, 2009; Despriée et al., 2010, 2012; Martínez et al., 2010; García et al., 2013), increasing the list of sites with evidence of artefacts and/or hominins (Martínez-Navarro et al., 1997; Oms et al., 2000; Carbonell et al., 2005, 2008; de Lumley et al., 2009; Toro-Moyano et al., 2013). In the light of all this new information, the state of the art concerning the colonisation of Europe includes, among other questions: 1 – the possibility of rapid extinctions during the glacial periods due to the climatic worsening (discontinuity), 2 – the possibility of a continuous settlement, at least in the refuges of Southern Europe (continuity), and 3 – the capacity of adaptation of hominins to the changing conditions marked by the glacial and interglacial cycles forced by obliquity (continuity). To answer these questions we would need long and well-dated sequences. The aim of this article is to discuss the arguments in favour or against the alternative hypotheses by using the growing evidence from two key cave sites of the Sierra de Atapuerca complex: Sima del Elefante and Gran Dolina.

2. The Sierra de Atapuerca sites

The Sierra de Atapuerca is situated 15 km east of the city of Burgos, in northern Spain (Fig. 1), and contains a complex of karstic cavities. Sediments deposited from the Early Pleistocene to the Holocene filled some of these cavities (see Rodríguez et al., 2010 and references therein). The Sierra de Atapuerca has an area of 25 km^2 and it lies 1078 m above sea level, although the cave sites we deal with in this report are placed at an altitude of 1000 m. These sites, Sima del Elefante (TE) and Gran Dolina (TD), were exposed by the construction of a mining railway at the end of the 19th century in the western slope of the Sierra de Atapuerca. This railway was dismantled during the second decade of the 20th century, and systematic excavations begun in 1978 (Carbonell et al., 1999c). The latitude of the Sima del Elefante and Gran Dolina cave sites is 42° 21, and the longitude is 3° 31′.

The Sierra de Atapuerca is placed in a strategic position just between the limits of the basins of the Duero river and the Ebro river at its southwest and northwest limits, respectively. This position has favoured the passage of hominins near this enclave from the Early Pleistocene to the present day. In general terms, the Sierra de Atapuerca and surroundings are nowadays dominated by a continental Mediterranean climate, with cold winters and mild summers (Fig. 1). Extreme temperatures are not frequent, buy they may reach down to −20 °C in December–January and more than 40 °C in July–August.

2.1. The TE cave site

The TE site is a major cave infill, which blocks the exit of one of the galleries ("Galería Baja") of the "Cueva Mayor-Cueva del Silo" karst system. The stratigraphic exposed sequence is 27 m thick from the top to the present excavated surface and about 15 m wide

Fig. 1. Climatic map of the Iberian Peninsula, showing the location of the Sierra de Atapuerca and other relevant sites, as well as the Spanish cities quoted in Table 1.

(Fig. 2). This section has been divided into 21 lithostratigraphic units defined by major unconformities, 15 of which (TE7 to TE21) are exposed, whereas the lowermost part of the sequence is known from two core samples (Rosas et al., 2006). The evidence of the human presence in this site comes from levels TE19 (Mode 3 tools), TE14, TE12, TE11, and TE9 (Mode 1 tools, and some fossil human remains found in TE-9) (Rosas et al., 2006; Carbonell et al., 2008).

Our interest in this report is focused on the levels TE14 to TE7. These levels are known as Sima del Elefante Lower Red Unit (TE-LRU), and they contain the so-called Faunal Unit 1 (Cuenca-Bescós et al., 2007, 2010). Concerning micromammals, TE-LRU has the same taxa from TE7 to TE14, though their ecological structure varies in the relative number of specimens per species (Cuenca-Bescós et al., 2012). These authors indicate that the date of the last appearance of 77% of the species found at TE-LRU occur before the Jaramillo subchron. The presence of the arvicoline rodent *Allophaiomys* in TE-LRU is particularly significant. In TE-LRU we can find *Allophaiomys lavocati*, *Allophaiomys nutiensis*, and *Allophaiomys burgondiae*, together with *Castillomys rivas* and the insectivores *Asoriculus gibberodon*, *Beremndia fissidens*, and *Crocidura kornfeldi* (Cuenca-Bescós et al., 2012 and references therein). This assemblage constrains TE-LRU in the time interval of 1.5–1.1 Ma (*Allophaiomys lavocati* zone). The presence in TE-LRU (TE9 and TE10) of the large-sized mustelid *Pannonictis nestii* (García et al., 2008) supports the (Late Villafranchian or Early Biharian) age of this sequence in the range of 1.3–1.1 Ma. The presence of some fossils attributed to *Bison* sp. in some of the TE-LRU levels suggests that this stratigraphic assemblage is younger than 1.2 Ma (see Rosas et al., 2006), although the presence of *Bison degiulii* has been included in the faunal list of the Pirro Nord site, with an alleged chronological interval between 1.3 and 1.7 Ma (Arzarello et al., 2007).

The paleomagnetic study of TE reveals that stratigraphic layers TE7–TE16 have reverse magnetization directions only. These results are consistent with a Matuyama age of the sediments (1.78–0.78 Ma) and with the mammal assemblage (Carbonell et al., 2008) (Fig. 2). Two dates based on the radioactive decay of cosmogenic ^{26}Al and ^{10}Be obtained in the TE9 and TE7 (Fig. 2) suggest a range of 0.95–1.38 Ma (Carbonell et al., 2008) for these levels.

Blain et al. (2009) made a climatic reconstruction of the TE-LRU based on the presence of amphibian and squamate reptile species from each TE level (about 12,000 specimens), using the so-called Mutual Climatic Range method (Blain et al., 2009). The Spanish Pleistocene amphibians and squamates are specifically identical to those of present times. Thus it is possible to use the current distribution and environmental conditions of these species to obtain inferences about the climate at the time of deposition of the TE levels from TE-LRU.

According to the results of Blain et al. (2009), it seems that all the levels have been deposited during a warm-humid climate, suggesting a patchy landscape with a large representation of humid meadows and woodland. Through the entire sequence, the landscape shows little variation, with the development of open-dry meadows related to a regression of open-humid and woodland areas in a sublevel of TE9 (TE9b), TE11, and TE12. The estimated climatic conditions were similar in all levels, with values for the mean annual temperature 0.8°–2.6° warmer than today in Burgos (10.1°) and a mean annual precipitation of 800–1000 mm, greater than that of present times (700 mm) (see Table 1). The results reported by Blain et al. (2011) for TE-LRU agree with those for large and small mammals. In TE14, the results of Blain et al. (2009) suggest a climatic deterioration, similar to that observed in other Spanish sites at the beginning of the Jaramillo subchron.

2.2. The TD cave site

The Gran Dolina cave site (TD) fills up a large cavity 17 m deep and with a maximum width of 17 m (Fig. 3). The stratigraphic section of the site (cut and exposed by the construction of the railway trench) was first divided by Gil and Hoyos (1987) into eleven levels, TD1 to TD11 from bottom to top. The stratigraphy has been revised by Pérez-González et al. (2001), although the work is under continuous refinement as there is a vertical cut of the section in progress (e.g. Bermúdez de Castro et al., 2008a). Parés and Pérez-González (1995, 1999) observed a polarity reversal between TD7 and T8, interpreted as the Matuyama/Brunhes boundary, meaning that levels TD8–TD11 were deposited during the Middle

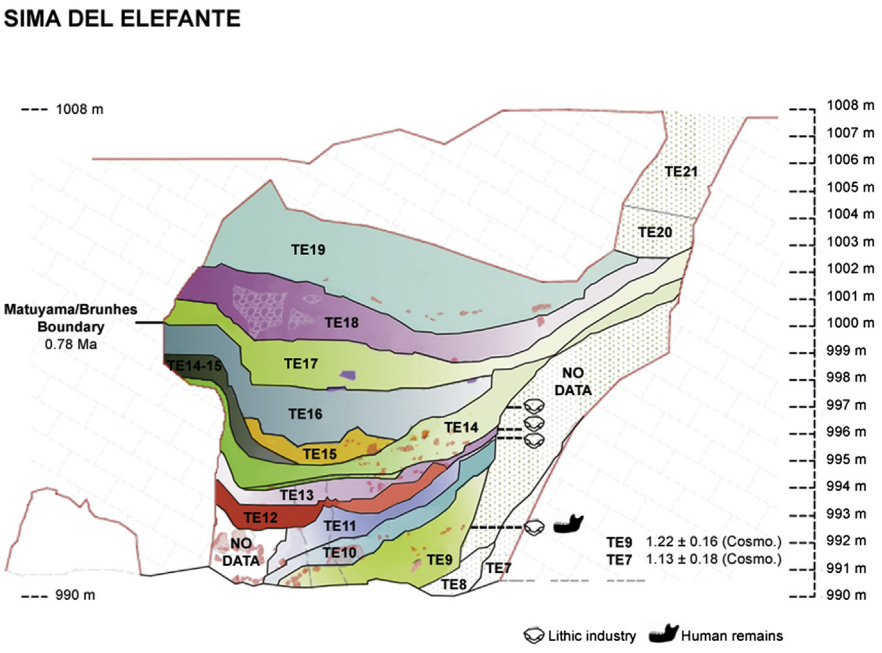

Fig. 2. Stratigraphic profile of the Sima del Elefante cave site. Cosmogenic burial ages in TE7 and TE9 are also shown, with the standard error given at the 68% confidence interval.

Table 1
Climatic parameters in some Spanish localities obtained in the 1791–2000 period.[a]

	Altitude[b]	MAT[c]	MAT January	MAT July/August	MAP[d]
Barcelona[e]	4	15.5	8.9	23.6	640
Burgos	891	10.1	2.7	18.9	555
Granada	567	15.1	6.7	24.5	357
Santander[f]	5	14.1	9.5	19.9	1246

[a] Source: "Agencia Estatal de Meteorología", Spanish Ministry of "Agricultura, Alimentación y Medio Ambiente".
[b] Metres above sea level.
[c] Mean annual temperature.
[d] Mean annual precipitation.
[e] Mediterranean sea.
[f] Cantabric sea, in northern Spain.

Pleistocene, whereas levels TD7–TD1 were attributed to the Early Pleistocene. This finding is consistent with the change in the fossil record of large- and micromammals, with a transition in TD7–TD8 (Faunal Unit 5) and drastic change in TD9–TD11 (Faunal Unit 6) (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010).

A large sample of human fossil remains, macro- and micromammals, and artefacts of Mode 1 were recovered in the 1994–1996 period, during the excavation of a biostratigraphic test pit of about 6 m^2 (Carbonell et al., 1995, 1999a,b). The combination of paleomagnetic data and US-ESR ages suggest a range between 780 and 857 ka for TD6 (Falguères et al., 1999). Thermoluminiscence (TL) ages (Berger et al., 2008) on samples taken one meter below the Brunhes–Matuyama boundary (0.78 Ma) give an age of 0.96 ± 0.12 Ma for TD6. Because this age is consistent with the biostratigraphic and paleomagnetic evidence, Berger et al. (2008) proposed a likely chronological interval of 0.90–0.95 Ma for the TD6 hominins. The last systematic dating of the Gran Dolina sequence has been made by Moreno (2011). Moreno took several samples for the entire TD sequence in order to apply the ESR dating method on optically bleached quartz. The dating of the TD1 level has been estimated at 1.18 ± 0.15 Ma. This level is sterile from the archaeological and paleontological point of view and is formed by sediments of an interior facies characteristic of a closed cave. Parés and Pérez-González (1999) have determined a normal magnetic polarity in TD1. It was tentatively correlated to the Jaramillo subchron but without any other reference to confirm this hypothesis. No samples were obtained by Moreno in TD2, which is also formed by sediments of interior facies, although well differentiated from those of TD1 (Parés and Pérez-González, 1999). Moreno selected five samples for the TD3/4 and TD5 levels, and her results suggest an age range between 0.94 and 1.0 Ma. It is interesting to mention that some artefacts were found in the 1990–1991 field seasons at the base of TD4 (Carbonell and Rodríguez, 1994). Finally, Moreno (2011) analysed six samples for TD6 and TD7, obtaining an age range of 0.8–0.88 Ma for these levels.

All evidence clearly suggests that neither archaeological nor palaeontological support for the Jaramillo event is present in the Atapuerca stratigraphical record. Cuenca-Bescós et al. (2010) conclude that most components of the faunal assemblage of the Sima del Elefante Lower Red Unit are not present in the Atapuerca Faunal Unit 2, which is characteristic of levels TD3/4. Apart from the presence of *Allophaiomys chalinei*, as representative of the Biozone of the Jaramillo–Matuyama/Brunhes interval, Cuenca-Bescós et al. (2010) also refer to the earliest occurrence of a large venomous shrew, *Dolinasorex glyphodon*, the earliest occurrence of *Marmota* in Western Europe, as well as the earliest occurrence of *Stenocranius*, *Iberomys* and *Terricola* for the Faunal Unit 2. The local appearance of *Cervus elaphus*, *Sus scrofa*, and the first European record of the spotted hyaena *Crocuta crocuta* also characterize Faunal Unit 2 (Made, 2001). Atapuerca Faunal Unit 3 corresponds to levels TD5 and TD6a. Concerning micromammals species, Faunal Unit 2 and Faunal Unit 3 are very similar in their composition, with some exceptions such as the first appearance of *Micromys minutus* and some species of snakes. The upper limit of Faunal Unit 3 is marked by the highest stratigraphical occurrence of *A. chalinei*. Faunal Unit 4 corresponds only to the upper part of TD6 (TD6b), and is characterized specially by the highest occurrence of *Castor fiber*, *D. glyphodon*, *Stenocranius gregaloides*, and *Hystrix refossa* (Cuenca-Bescós et al., 2010). Finally, Atapuerca Faunal Unit 5, which includes TD7 and the lower part of TD8 (TD8a) points to another hiatus in the Atapuerca stratigraphical record. The most significant aspect of this Faunal Unit is the highest occurrence of *A. bursae*, *Iberomys*

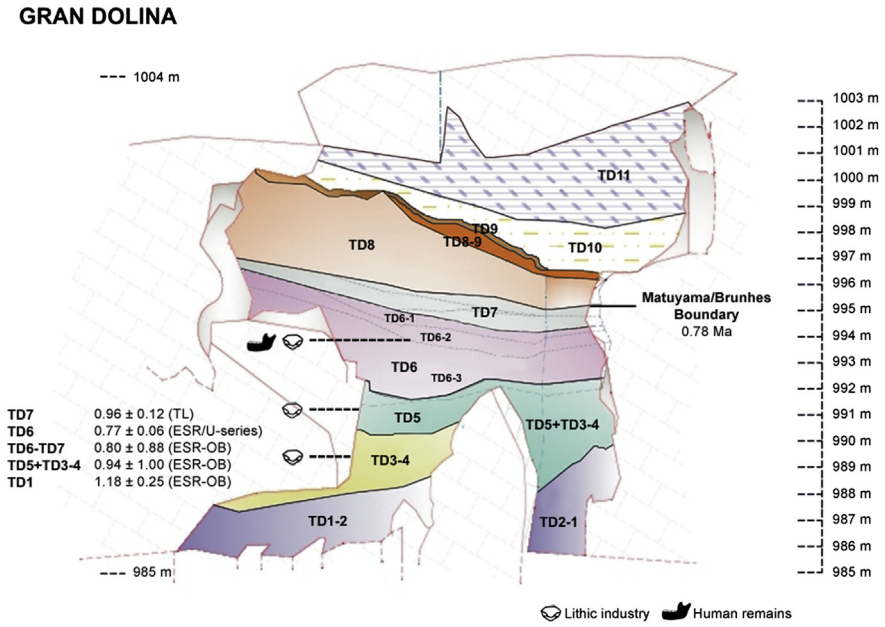

Fig. 3. Stratigraphic profile of deposits and levels at the Gran Dolina cave site. The TL dates in TD7 are from Berger et al. (2008), the ESR/U series dates are from Falguères et al. (1999), and the ESR-OB dates from Moreno (2011). Chronological dates for the upper levels have been deleted for simplification.

huescarensis, *P. episcopalis*, *M. savini* and *Lepus* (Cuenca-Bescós et al., 2010). In sum, the lower levels of the TD site seem to include a significant part of the Matuyama reverse period, possibly between the Jaramillo and the Matuyama/Brunhes boundary.

Blain et al. (2009) studied the amphibian and squamate reptile fossil record recovered from the test pit opened between 1993 and 1999 in the south part of the TD sequence, in which TD3/TD4 is not represented. For TD5, Blain et al. (2009) found an evolution from temperate-wet conditions towards colder humid conditions near the top of the level. In TD6 there is an evolution from a colder climate from TD6a to a warmer climate in TD6b and TD7. The estimations made by Blain et al. (2009) suggest that the mean annual temperature (10–13°) was always slightly warmer than nowadays in the TD5–TD7 sequence. Furthermore, the mean annual precipitation (800–1000 mm) was also greater than in present times in the Burgos area (Table 1). Concerning TD3–TD4, the small mammals suggest open moist conditions, whereas the amphibian and reptile assemblage preclude the existence of very extreme conditions (Rodríguez et al., 2010). In conclusion, climatic differences between "glacial" and "interglacial" periods seem to be poorly marked during the later period of the Early Pleistocene at 42° latitude, and about 1000 m about sea level (Blain et al., 2009).

Most Atapuerca levels exhibit a very low concentration of pollen and spores, probably due to a highly oxidative sedimentary environment of the karstic infillings (Carrión et al., 2009). Thus, the pollen record in the lower levels of the TE cave site is extremely low and no information on vegetal cover during the deposition of these levels is available. For the lower levels of Gran Dolina, García-Antón (1989) collected data from the TD5–TD7 levels. In TD5 the most abundant pollen record suggests the presence of conifers and *Poacea*, with some Mediterranean taxa. An increase of the mesic and Mediterranean taxa is observed in TD6 and, especially, in TD7, suggesting steppe habitats and an environment with a balanced supply of moisture.

In summary, and concerning the climatic conditions and environment of the Early Pleistocene periods represented in the Atapuerca cave sites, all the available information suggests the absence of extremely harsh conditions (Rodríguez et al., 2010). Concerning this conclusion, Carrión et al. (2011) note the major extinction of *Arctotertiary* plants in the Iberian Peninsula after MIS 36 up to MIS 33, coinciding with the fall of temperatures and precipitation related to the glacial cyclicity of 41,000 years. Carrión and Fernández (2009) and Carrión et al. (2011), also remember that the EMPT (1.4–0.7 Ma) represents the period with highest rates of phytodiversity loss within the last 65 Ma in the Iberian Peninsula. However, and in spite of the high altitude, available information supports the continuous presence of Mediterranean and mesothermophilus elements in the Sierra de Atapuerca through the early Pleistocene stratigraphical sequence.

3. The TE9 and TD6 hominins

The TE9 mandible and most of the TD6 human specimens have been described in detail in previous papers (e.g. Arsuaga et al., 1999; Bermúdez de Castro et al., 1999a,b; Rosas and Bermúdez de Castro, 1999; Carbonell et al., 2005; Bermúdez de Castro et al., 2011; Bermúdez de Castro et al., 2012). Thus, we will only highlight some of the most outstanding features to the extent they are relevant to the aims of this report.

Unfortunately, the human fossil evidence of the TE9 level is limited to a proximal hand phalanx, a small humerus fragment and an incomplete mandible. The mandibular fragment (ATE9-1) (Carbonell et al., 2008; Bermúdez de Castro et al., 2011; Martinón-Torres et al., 2011a) is not enough to have a good picture of the early hominins living in Europe before the Jaramillo subchron. The anterior face of the symphysis exhibits a conspicuous *incisura submentalis*, a faint mental trigone, a visible mental protuberance, and well-developed anterior marginal tubercles below the C/P3. These features are primitive with regard to the *Homo* clade, and thus, they are not useful for taxonomic or phylogenetic purposes. In contrast, the ATE9-1 mandible presents four derived traits relative to African early *Homo* on the internal face of the symphysis: a minimal inclination of the planum alveolare, absence of the superior transverse torus, a limited thickness of the mandibular body, as well as a parabolic shape of the dental arch. The presence of these features in ATE9-1 suggests that the European hominins of the Sima del Elefante must have diverged from their African ancestors, as well as from those of Dmanisi, for a long period. However, we do not have enough information to include this fragment in a previously named taxon (Bermúdez de Castro et al., 2011). Furthermore, is not possible to establish a reliable comparison with the mandibles of the TD6 hominin hypodigm published by Rosas and Bermúdez de Castro (1999), Carbonell et al. (2005), and Bermúdez de Castro et al. (2008a), in which a complete symphysis is not represented. However, we have enough information about the TD6 human remains to draw some important conclusions about their phylogenetic position. The TD6 hominins present a mosaic of primitive and derived features with regard to the *Homo* clade, and they were attributed to the species *Homo antecessor* (Bermúdez de Castro et al., 1997). The TD6 hominins exhibit a set of morphological traits in the postcranial skeleton that are similar to those displayed by modern humans (Carretero et al., 1999; Lorenzo et al., 1999). Among the most outstanding cranial features it is important to mention the modern human face morphology of the specimens ATD6-69 (immature) and ATD-58 (adult), the convex superior border of the temporal squama (ATD6-20), and the nearly vertical trajectory of the incisive canal (ATD6-69). The two latter features are shared with Neanderthals and modern humans (Arsuaga et al., 1999). All these data were compatible with the hypothesis of *H. antecessor* representing the most recent common ancestor (MRCA) of Neanderthals and modern humans (Bermúdez de Castro et al., 1997). Furthermore, the facial growth pattern of the specimen ATD6-69 also confirms the modern character of the face of *H. antecessor* (Lacruz et al., 2013) which, according to these authors, may be related with both a modern human pattern of dental development (Bermúdez de Castro et al., 1999b; Bermúdez de Castro et al., 2010) and the increase of the brain over 1.000 cc^3 (Arsuaga et al., 1999). Some researchers have identified mediofacial traits in later fossils from Asia such as Nanjing (Arsuaga et al., 1999; Wang and Tobias, 2000; Vialet et al., 2010), Dali and Zhoukoudian (Pope, 1992) that could be interpreted as "modern" and similar to that of *H. antecessor*.

On the other hand, with regard to the anterior teeth Ramirez-Rozzi and Bermúdez de Castro (2004) reported that *H. antecessor* had shorter periods of dental growth than *Homo sapiens*. This result is not incompatible with the observation that *H. antecessor* exhibits a modern pattern of dental development. The latter feature does not necessarily imply that the time of development of the crown of the anterior teeth in *H. antecessor* was similar to *H. sapiens*. Time and pattern of development can be two independent aspects of the dental growth. The important fact is that nearly one million years ago, at least one hominin paleodeme shows a clear trend towards "modernity".

A new excavation in TD6b of about thirteen square meters near the archaeological test pit performed between 1993 and 1999 has allowed the recognition of a clearer and finer stratigraphical sequence (the so-called "Aurora archeostratigraphic set [AAS]": Bermúdez de Castro et al., 2008a), which was not evident in the Aurora Stratum excavated during the nineties. This excavation has also contributed to a significant increase in the hominin hypodigm.

From this new information and additional investigations of the mandibular, dental, and postcranial remains, we first changed our previous hypothesis about the phylogenetic position of *H. antecessor* (Bermúdez de Castro et al., 2003), and we later reconsidered the interpretation of the TD6 hypodigm (e.g. Bermúdez de Castro and Martinón-Torres, 2012).

The mandibular sample (ATD6-5, ATD6-96, and ATD6-113) exhibits a derived pattern with regard to the *Homo* clade. Thus, clear differences with the early Pleistocene specimens from *Homo habilis*, *Homo rudolfensis*, *Homo ergaster*, as well as with those of the Dmanisi and Sangiran sites are observed. However, the TD6 mandibles do not share apomorphic features that characterize the European Middle and Early Pleistocene lineages (Rosas and Bermúdez de Castro, 1999; Carbonell et al., 2005; Bermúdez de Castro et al., 2008a).

As far as the dental sample is concerned, most features of the TD6 specimens are primitive with regard to the *Homo* clade (Bermúdez de Castro et al., 1999a). However, geometric morphometric analyses of the teeth have revealed some aspects that deserve attention. The three permanent first upper molars (ATD6-18, ATD6-69, and ATD6-103) show a distal displacement of the lingual cusps and a protrusion in the external outline of a large and bulging hypocone. This morphology is similar to that of the European Middle Pleistocene hominins, like Atapuerca-Sima de los Huesos, Steinheim, Pontnewydd and Arago (although less pronounced in the latter), and Neanderthals (Gómez-Robles et al., 2007). Likewise, the morphology of the permanent second premolars (ATD6-4 and ATD6-96) is not as derived as in *H. sapiens*, but these teeth have lost the primitive pattern of the *Homo* clade. The TD6 lower second premolars exhibit a trend towards dental reduction with a diminished occlusal polygon and decreased lingual occlusal surface, as in the European Middle and early Upper Pleistocene hominins (Martinón-Torres et al., 2006). Again, Arago specimens would cluster with European Middle Pleistocene fossils, but their morphologies are in general less pronounced than in SH and Neanderthals (see also Bermúdez de Castro et al., 2003). The TD6 lower and upper canines (ATD6-1, ATD6-13, and ATD6-69) do not show the primitive features described, for instance, in Dmanisi specimens and other Pliocene and Early Pleistocene hominins (Martinón-Torres et al., 2008). Instead, these teeth exhibit a morphology which resembles that observed in European Middle Pleistocene hominins. In addition, upper lateral incisors from TD6 display an incipient triangular shovel shape, with pronounced labial convexity (Martinón-Torres et al., 2007). This feature is part of the Eurasian dental pattern (Martinón-Torres et al., 2007) shared with Asian and European Early and Middle Pleistocene hominins and Neanderthals. These features are absent in the Pleistocene populations found in Africa, including the Middle Pleistocene hypodigms from Rabat, Tighenif and Jebel Irhoud (Martinón-Torres et al., 2007; Bermúdez de Castro et al., 2008b).

Finally, the study of two humeri, ATD6-121 and ATD6-148, has shown that these specimens share some derived features in the distal epiphysis with the Atapuerca-Sima de los Huesos hominins and Neanderthals (Bermúdez de Castro et al., 2012).

4. Discussion

4.1. Hominin adaptations

An obvious statement is that early hominins were able to colonize a specific region only if they had biological, technological and/or social capabilities to do so. Although geographic barriers were not a particular problem for the settlement of Europe, climatic, cultural, and ecological barriers undoubtedly had an important role in the progressive colonization of increasingly higher latitudes (Dennell, 2003; Parfitt et al., 2005, 2010; Agustí et al., 2009), particularly during glacial periods. It is also obvious that we cannot fall into an actualistic vision and to conceive the Early Pleistocene hominins as the inhabitants of the XXI century in terms of their physiological adaptations. Due to seasonality, it is important to consider that meat and marrow consumption was crucial in the colonisation of the northern hemisphere. In East Africa, hominins were able to regularly access the ungulate carcasses to obtain meat, fat and marrow (Selvaggio, 1994; Domínguez-Rodrigo and Pickering, 2003), until the point of developing typical diseases caused by the lack of animal proteins (Domínguez-Rodrigo et al., 2012). This aspect of the ecological niche of hominins was essential during their first European expansion. In the absence of vegetal resources during the cold seasons, early European hominins were able to survive either as effective hunters of ungulates or as active scavengers (Martínez-Navarro and Palmqvist, 1995; Arribas and Palmqvist, 1998; Dennell, 2003). Some researchers have suggested that the presence in Europe of the saber-toothed felids (particularly the genus *Megantereon*) probably favoured the ecological niche of scavengers. Due to its great killing capabilities and peculiar dental characteristics, these felids were probably unable to consume all the meat they obtained by hunting large ungulates. Thus, they were unintentionally sharing some of the meat of their prey with hominins and other scavengers (Turner, 1992; Martínez-Navarro and Palmqvist, 1996; Palmqvist et al., 1996, 2005). However, the behaviour of these hominins seems to have been more generalist than perceived by these authors and therefore may not be exclusively based on scavenging (Domínguez-Rodrigo and Barba, 2006; Huguet et al., 2013). In order to target animal resources, hunting and scavenging may have been combined with episodes of small prey procurement, as can be deduced from the finding of some remains of lagomorphs, birds and tortoises with cut-marks at Sima del Elefante (Huguet, 2007; Blasco et al., 2011). These strategies of adaptation to the environment can be also recognized in early periods in Africa (Braun et al., 2010) and in Asia (Wood and Strait, 2004; Joordens et al., 2009). The scarce evidence we have from the TE9 to the TE14 levels of the Sima del Elefante cave site, and the TD3/TD4 and TD5 levels of the Gran Dolina cave site suggest that hominins were sporadic visitors of the caves during the formation of these stratigraphic deposits, searching for animals fallen in natural traps, and that these hominins probably also lived in open air camp-sites. The presence of cut-marks and/or intentional bone breakage on large mammal bones is occasional. They probably had an opportunistic behaviour and dietary habits, with a wide range of size for the animals they consumed (Rosell, 1998; Huguet, 2007). The artefacts (Mode 1) suggest that knapping strategies were not complex, with the purpose of obtaining simple flakes using unidirectional knapping. Although several previous studies have shown that these early human populations were able to process carcasses (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Pickering, 2003, and references therein), the evidence provided by Early Pleistocene localities with human presence, such as Vallonnet, Fuente Nueva 3 and Barranco León D, suggests that most of the reported scavenging activity in the preserved bones from these localities does in fact correspond to *Pachycrocuta* (Echassoux, 2004; Espigares, 2010).

In contrast, the lithic assemblage recovered from the different levels of the AAS, composed of flint, quartzite, sandstone, limestone, and quartz, suggests a diversity of knapping strategies (Carbonell et al., 1999b). Although the artefacts are also classified as belonging to Mode 1, the finding of some refittings suggests that most of the “chaines opératoires” or reduction sequences were made inside the cave (Carbonell et al., 1999b). Furthermore, the faunal assemblage also suggests a different trophic behaviour, with

a high level of carcass processing, as well as primary and early access to animals (Díez et al., 1999; Huguet, 2007; Saladiè, 2009; Saladié et al., 2011). The TD6 human assemblage represents the earliest evidence of regular cannibalism so far described in human evolution (Fernández-Jalvo et al., 1999; Carbonell et al., 2010a), and can be linked to the isolated case of Stw 53 from Sterkfontein in South Africa, which represents the first known case of anthropogenic processing of a hominid carcass (Pickering et al., 2000).

Dennell (2003) is right to remember a literal cite of Gamble (1999: p. 125) in which this author considered that hominids "were not simply dancing to the rhythms of the Pleistocene". However, Dennell also notes the worsening of the climatic conditions during the EMPT, an aspect that we will discuss below. Furthermore, most colleagues ignore the increasing social abilities of early hominins. These abilities are related to a dramatic change in the life history pattern of hominins with regard to *Australopithecus* or *H. habilis* (e.g. Bogin and Smith, 1996; Wood and Collard, 1999). As it was mentioned above, *H. antecessor* had a modern human pattern of dental development (Bermúdez de Castro et al., 1999b; Bermúdez de Castro et al., 2010). Although this biological aspect does not necessarily imply a modern human somatic development for these hominins, it is evident that near 1 Ma ago, hominins were at least approaching the developmental characteristics of later *Homo*, including a significant increase in cranial capacity, and probably also in the cognitive capacities to survive in an adverse environment.

4.2. The first colonisation of Europe

The evidence of the hominin occupation in Europe during the Early Pleistocene between the 37° and 47° has increased in recent years (Fig. 4). Apart from the Atapuerca Sima del Elefante cave site

Fig. 4. Climatic units in Europe showing the place of the Early Pleistocene sites quoted in the text: 1) Sima del Elefante, 2) Gran Dolina, 3) Barranco León, 4) Fuente Nueva 3, 5) Vallparadís, 6) Hérault, 7) Vallonet, 8) Pirro Nord, 9) Monte Poggiolo, 10) Kozarnika Cave, 11) Saint-Hilaire-la Gravelle, 12) Lunery-Rosières, 13) Pont de Lavaud, 14) Untermassfeld, 15) Pakefield, 16) Happisburg.

and based either on paleomagnetism, numerical datations, and/or biostratigraphical information, some of these sites are claimed to be older than the Jaramillo subchron. Thus, the Kozarnika Cave, in Bulgaria, has presented evidence of the presence of hominins dated to 1.6–1.4 Ma (Sirakov et al., 2010). Crochet et al. (2009) have reported an association of a vertebrate fauna with lithic artefacts of Mode 1 from the Hérault Valley (France) dated around 1.57 Ma. Also in France, the alluvial formations of the Middle Loire Basin present numerous localities with Mode 1 artefacts in Pont de Lavaud in the Creuse River Valley, Lunery-Rosières in the Cher River valley, and Saint-Hilaire-la Gravelle in the Loir River Valley (Despriée et al., 2010) testifying a human presence in the Central Region of France at least from about 1.1 Ma (Voinchet et al., 2007; Voinchet et al., 2010). In Southern Italy, preliminary results based on biostratigraphy and paleomagnetism suggest a Pre-Jaramillo age (about 1.5–1.3 Ma) for the site of Pirro Nord, near Apulia, in the province of Fogglia (Arzarello et al., 2007; Pavía et al., 2012). Several thousand Mode 1 artefacts have been recovered from the Ca' Belvedere site of Monte Poggiolo, Emile-Romagne, Italy. No faunal remains have been found at this site, which magnetostratigraphic study indicates a reverse polarity (Peretto et al., 1998). In Southern Spain, the sites of Barranco León and Fuente Nueva 3 have presented dates between 1.1 and 1.4 Ma for the large assemblages of Mode 1 artefacts so far found in these sites (Oms et al., 2000; Agustí et al., 2009, 2010; Toro-Moyano et al., 2013).

The stratigraphic assemblage III from Le Vallonet, in Southern France, has provided some artefacts from the Mode 1 (Lumley et al., 2009) associated to an Epivillafranchian mammal assemblage and included in sediments with a normal polarity. Lumley et al. (2009) attribute this assemblage to the Jaramillo subchron. Landeck (2010) and García et al. (2013) have also reported human occupation at Untermassfeld, a site placed 50° N, near Thuringia, in central Germany, where a rich assemblage of the Epivillafranchian fauna, recently attributed to the Jaramillo event, has been recovered from several decades ago (Kahlke, 2000). The unit EVT7 (levels 10 and 10c) from the Vallparadís site (Barcelona, Spain) may be post-Jaramillo (ca 0.98 Ma) according to the ESR-U/Series and OSL dating (Martínez et al., 2010; García et al., 2012; Duval et al., 2011, 2012, but see also; Madurell-Malapeira et al., 2011). Scott and Gibert (2009) have reported the presence of Mode 2 artefacts in the open-air site of Solana del Zamborino and in the rock-shelter site of Cueva Negra del Estrecho del Quípar in Southern Spain. These authors date the first site from the Early Pleistocene (about 0.9 Ma), whereas Cueva Negra would be from the initial part of the Middle Pleistocene (about 0.76 Ma). However, these results have been seriously questioned by Jiménez-Arenas et al. (2011). Finally, the presence of hominins in northern Europe above 52° N at the beginning of the Middle Pleistocene (0.7 Ma) have been reported by Parfitt et al. (2005, 2010), from the findings of flint artefacts in Happissburg-3 (U.K.), dated from MIS 21 (about 0.84 MA) or MIS 25 (about 0.95 Ma), as well as in the Cromer Forest-bed Formation at Pakefield. All these sites are placed in Fig. 4, in their respective climatic domains.

4.3. The state of the art for (dis) continuity

First of all, it is necessary to define the concepts of continuity and discontinuity for European settlement. Discontinuity, assumed in literal terms, implies a repeated extinction caused by unfavourable climatic and/or ecological conditions (see for instance Dennell, 2003, or Agustí et al., 2009). Continuity implies that hominins were continually residents, even if they remained restricted to local refuges during cold periods. In this case, other waves of population could have settled large areas of the continent, genetically absorbing or mixing with previous residents. Another

possibility is that the European Early Pleistocene hominins were resilient to the adverse conditions of the glacial periods. Then it is possible that small groups of new settlers were integrated into the autochthonous population.

It is a matter of fact that we have enough proof to defend a settlement of Europe during the early Pleistocene, before the Jaramillo subchron. However, we have not yet reached a full consensus. Muttoni et al. (2010) made a severe critical assessment of the available magnetostratigraphic and/or radiometric age constraints on all European sites bearing hominin fossil remains and/or artefacts from Southern Europe (Italy, France, and Spain). According to these authors, the magnetostratigraphic data of some of the sites such as Le Vallonet, Soleilhac, and Ca'Belvedere of Monte Poggiolo do not meet the basic quality criteria. Furthermore, faced with the difficulty of matching the reverse magnetizations with a particular interval of the Matuyama, even when there is a stratigraphic upward succession of reverse to normal polarity, Muttoni et al. (2010) consider that some of the best-dated sites, presumably from the pre-Jaramillo period (Sima del Elefante cave site; Barranco León-D, and Fuentenueva 3) could be younger and dated between the Jaramillo subchron and the Brunhes period. Estrecho del Quípar and Gran Dolina-TD6, in Spain, may have a similar chronology; whereas other sites provisionally dated with biostatigraphy or numerical dating techniques (Ca'Belvedere, Notarchirico, Le Vallonet, and Pont de Lavaud) present high potential analytical errors, as well as several uncertainties in the application of the methods (Muttoni et al., 2010). The site of Pirro Nord in Italy is, according to these authors, still poorly known and, finally, other sites (Lèzignan-la-Cèbe, France) are simply ignored. In sum, the model presented by these authors does not contemplate a colonisation of Europe before the MIS 22, i.e., about 0.87 Ma.

We agree that the evidence of some sites is still limited (e.g. Untermassfeld, Pirro Nord, and Le Vallonet) and that additional information is required. In addition, evidence from some other sites has been also seriously questioned (e.g. Solana del Zamborino and Cueva Negra del Estrecho del Quípar). Furthermore, large sedimentary deposits with a clear stratigraphical context offer a better perspective than anthropic evidences in fluvial terraces.

On the opposite side and based on theoretical considerations, Leroy et al. (2011) consider that the presence of hominins during the early Pleistocene in Europe could have occurred possibly associated to a mammal migration from Africa to Eurasia around 2.58 Ma, coinciding with a major aridification in North Africa (the so-called Elephant-*Equus* dispersal event dispersal (Arribas and Palmqvist, 1999)). Leroy et al. (2011) assume that, for the moment, the first proofs of the early dispersal correspond to those obtained in the Dmanisi site. Using a climatic simulation, these authors consider that the presence of ancient hominins in the early Pleistocene was only possible at the transition from glacial to interglacial periods (obliquity–forcing cycles). The full glacials were too cold for these ancient (non-adapted) hominins, whereas the transition from interglacial to glacial periods was too forested for the lifestyle of these hominins. This way, Leroy et al. (2011) can admit an intermittent settlement of the European continent, a hypothesis they test with the available environmental data from several sites. Since the range of the numerical chronological data of these sites is too wide, it becomes practically impossible to match the narrow favourable time periods suggested by these authors with the theoretical presence of hominins in a specific place.

Although we cannot ignore the information obtained from some localities, which points to an early occupation of the European continent perhaps before 1.5 Ma, our aim is to debate if this settlement had a continuity, or if we are observing evidence of repeated incursions of very limited duration during the early Pleistocene (Leroy et al., 2011). These hypothetical incursions would probably have vanished without trace. For some, the sum of the evidence of scattered sites seems to be a non-convincing argument for continuity (Dennell, 2003; Moncel, 2010).

In order to test this hypothesis we need to explore large stratigraphical sequences, and to look for some kind of anthropic evidence. If the Leroy et al. (2011) predictions are correct, the probability of finding such evidence even in these large sequences is small or practically null, due to the lifestyle of these ancient hominins and the short interval of time of such occupations.

4.4. The large sequences from the TE and TD cave sites

The lower levels of the Sima del Elefante cave site (TE7 to TE14, the TE-LRU levels) and the lower levels of the Gran Dolina cave site (TD3/4 to TD7) represent relatively large periods of time in the Early Pleistocene. One important particularity of these sites is that they are placed about 1000 m above sea level. In Table 1 we can see a comparison of the present climatic conditions in Burgos with other Spanish localities of Southern Spain (Granada, near the Guadix-Baza basin), or placed at the sea level (Santander and Barcelona) (see Fig. 1). Even considering that the climatic conditions in the Sierra de Atapuerca were warmer than nowadays during the interglacial periods of the Early Pleistocene, the winters were probably as hard as today. Although it is not frequent, the temperatures near the Sierra de Atapuerca can reach extreme values as low as -20°, whereas the apparent temperature or body sensation of heat is frequently influenced by northerly winds. The Sierra de Atapuerca and surrounding areas are characterized by a Mediterranean climate. However, the altitude provokes a remarkable thermic amplitude, which is typical of continental weathers. Similar conditions would have occurred during the Early Pleistocene, in spite of the mean annual temperature being warmer today. Therefore the presence of hominins at the Sierra de Atapuerca during long time periods suggests that they were well-adapted to the hard and seasonal conditions of the northern hemisphere, at a latitude of 42° and at an altitude of 1000 m above sea level.

The archaeo-paleontological sites of Barranco León-D and Fuente Nueva 3 (Guadix-Baza basin) may be older than the TE-LRU levels from Sima del Elefante. Although the range of dates obtained in Barranco León-D using the ESR method are not as precise as desired (1.43 ± 0.38), thus overlapping the numerical dates obtained for the lower levels of Sima del Elefante, the biostratigraphic study suggest an older age, probably of about 1.4 Ma (Agustí et al., 2010). The climatic conditions in the Guadix-Baza basin (about 900 m above sea level) were similar to those of Atapuerca, with the presence of woodland and water-edge areas, but showing the same differences we know today between the north and south of the Iberian Peninsula (Blain et al. 2010). With present information, we cannot discard continuity in the presence of hominins in the Iberian Peninsula during a long period of at least 0.3 Ma in the Early Pleistocene before the Jaramillo subchron. This suggestion agrees with the conclusion of Agustí et al. (2009), who gave the name "phase 3" to this long period of human settlement of the Iberian Peninsula. Considering climatic and paleontological information from other sites of the Guadix-Baza Basin, these authors suggest that 1.4 Ma may be the oldest date for the presence of hominins in the European continent, if the Iberian sites chosen by these authors can be considered as representative of Western Europe.

In contrast, Agustí et al. (2009) suggest that after this phase and during a long period (including a part of the Jaramillo subchron and until MIS 22 [0.87–0.88 Ma]) hominins may have disappeared from Western Europe. The extreme decrease in the mean annual temperature, which is correlated with an increase in mean annual precipitation, could have caused an extinction of hominins. This is an interesting conclusion, which implies discontinuity in the

European hominin population. However, and although we will discuss this possibility in the next section based on the hominin evidence, it is important to note that dating results obtained by Berger et al. (2008) and Moreno (2011) for the TD3/4 to TD7 levels, as well as the paleomagnetic analyses (Parés and Pérez-González, 1999), suggest a chronological range of about 1.0–0.78 Ma. Thus, hominin presence in the period in question can be demonstrated at the Sierra de Atapuerca.

Cuenca-Bescós et al. (2010) distinguish the Atapuerca Faunal Unit 1 (TE-LRU) from the Atapuerca Faunal 2 (TD3/4) based on the microfaunal assemblage. However, the large mammal assemblage of the lower levels of TE is limited, and such a distinction between TE-LRU and TD3/TD4 is, for the moment, more problematic regarding both the faunal structure and composition. Although discontinuity of the hominin population at the Sierra de Atapuerca during the Jaramillo subchron and just after this event is possible, we cannot expand this conclusion to the entire Iberian Peninsula (e.g. Vallparadís), nor to Western Europe. Anyway, hominins with a behaviour similar to that inferred for those of the Sima del Elefante lower levels were present at the Sierra de Atapuerca in TD3/TD4, TD5, and TD6a. The Atapuerca Faunal Unit 4 (TD6b) is mainly characterized by the presence of *H. antecessor*, as well as some changes in the micromammal species, which we have mentioned above (Cuenca-Bescós et al., 2010). The amphibian and squamate reptile fossil record suggests an evolution from a cold and humid (TD5) to a warm climate in TD6b (Blain et al., 2009). The possible different behaviour of these hominins with regard to the previous Early Pleistocene European populations has already been mentioned in a previous section. Next, and in order to clarify the aims of this report, we will deal with some phylogenetic questions regarding *H. antecessor*.

4.5. What human fossils tell us?

The new information yielded by the AAS during the 2003–2005 field seasons moves the TD6 hominins away from the earlier Pleistocene African populations, and points to closer links with the Eurasian hominins (Carbonell et al., 2005; Martinón-Torres et al., 2007; Bermúdez de Castro et al., 2008a,b; Martinón-Torres et al., 2011b). Thanks to these new findings and new studies, we have also found additional links of the TD6 hominins with the European Middle and early Upper Pleistocene lineages which, as stated above, could lead us to reconsider the position of *H. antecessor* as the MRCA of Neanderthals and modern humans. However, there could be another explanation of our results. It could be that some of the traits, previously considered as Neanderthal apomorphies, are indeed derived features that appeared in the Early Pleistocene and were retained by Neanderthals and their ancestors (Bermúdez de Castro et al., 2012). This hypothesis has two important implications. First, *H. antecessor* would be a species related to the MRCA of Neanderthals and modern humans and secondly, this MRCA may be older than the present genetic estimates (e.g. Noonan et al., 2006; Endicott et al., 2010; Krause et al., 2010). The molecular analyses of Endicott et al. (2010) for the MCRA support the hypothesis of a widely-dispersed ancestral species during the middle part of the Middle Pleistocene, and a split that would have occurred in a time range between 0.34 and 0.54 Ma, with a mean age of 0.43 Ma. According to these authors, the split might have coincided with the severe climatic of MIS 12 (ca 0.48–0.42). However, other estimations place the time of the MRCA at a mean age of more than 0.6 Ma, in a range of between 0.36 and 0.85 (Ovchinnikov et al., 2002), and between 0.52 and 0.80 (Green et al., 2008). The oldest dates of these ranges would cover the chronology of the TD6 hominins (but see a recent article by Fu et al., 2013). Although this debate will continue during next years, it is important to taking into account the well-known uncertainties of both the geological time calibration and the assumption that the molecular clock was ticking at a constant speed since two particular lineages diverged (Green and Shapiro, 2013).

Therefore our problem is to reconcile the fact that we have a hominin population with an Eurasian/European identity that shares some features with modern human and Neanderthals with the fact that, according to the genetic analyses, this population predates or is at the oldest extreme of variation of the presumed existence of the MRCA of Neanderthals and modern humans. In addition, this population lived at the most extreme edge of the European continent.

In a recent report (Bermúdez de Castro and Martinón-Torres, 2012) we proposed a new theoretical model to explain the evolution of the Eurasian populations. We hypothesize the existence of a central area of dispersal of Eurasia (CADE) closely related to the Levantine Corridor and continuously inhabited by a "source population". This source population could be the origin of the hominins that settled the eastern and western territories of Eurasia, probably at different moments of the Early and Middle Pleistocene and taking advantage of favourable climatic and ecological conditions, as well as of intense interaction between different human groups. In relation to this hypothesis, it is interesting to mention that "… the keys for the activation of evolutionary change in hominins may have been geological instabilities, and a shifting physiographical heterogeneity combined with high biodiversity and ecological interaction" (Carrión et al., 2011, p. 281).

Our model is compatible with the existence of a hominin population, perhaps no older than 1.0 Ma and probably placed in Southwestern Asia (SWA), as the source of both *H. antecessor* and the MRCA of Neanderthals and modern humans. We cannot forget the Eurasian identity of *H. antecessor*, and that the genetic impact of Asia in the colonization of Europe during the Early Pleistocene was probably stronger than that of the African continent (Martinón-Torres et al., 2007). This hypothetical Eurasian population would have been characterized by a mosaic of primitive features for the *Homo* clade together with a set of polymorphic derived features, which are first inherited by *H. antecessor* and later by the Neanderthal lineage. If this hypothesis is correct, there would have been a return to Africa of populations that later gave rise to modern humans. Although the Saharan–Arabian desert is presently the largest hyperarid region of the planet, there is evidence for episodes of significantly more humid conditions over much of the Sahara desert in the past, driven by orbital insolation-induced African monsoon maxima (Osborne et al., 2008). The lacustrine sediments recovered from the Fazzan Basin, in Southwest Libya, have yielded relevant information concerning palaeohydrological changes in this region (Armitage et al., 2007). Sedimentary evidence of these humid episodes was obtained using OSL dating techniques, suggesting changes during the MIS 5 and the Holocene. These humid periods have been confirmed by other studies (Vaks et al., 2007; Osborne et al., 2008; Castañeda et al., 2009; Drake et al., 2011). Furthermore, Armitage et al. (2007) described an older lacustrine event during MIS 11, and suggested at least two additional humid phases, which unfortunately are beyond the age range over which the conventional OSL method is applicable (Armitage et al., 2007). Therefore, the "door" of the Levantine Corridor could have been open during short periods, probably lasting no more than 0.01 Ma (DeMenocal, 2008), but enough to allow genetic interchange and/or population migrations between SWA and east Africa at least during the Middle Pleistocene. Unfortunately, the East African early Middle Pleistocene fossil record is certainly scarce (apart from the Bodo and Kapthurin Formation specimens) and we need more fossil evidence to test this hypothesis. Alternatively, the MRCA could have entered Africa before the

total aridification, ca 0.9 Ma (Bermúdez de Castro et al., 2011; Martinón-Torres et al., 2011b).

On the other hand, if we assume that Europe was continuously inhabited and that the TD6 hominins were a part of an old European lineage, then we need to assume that the first settlers had a morphology not very different from that described for *H. antecessor*. This hypothesis might push the minimum date for the divergence of the *H. sapiens* and *Homo neanderthalensis* lineages back to more than one million years ago. Therefore it is more parsimonious to assume that the TD6 hominins reached Europe after the first settlement of the continent. That is, the TE9 and the TD6 hominins would represent two different migrational waves into Europe likely coming from the same source population in SWA (Bermúdez de Castro et al., 2011; Bermúdez de Castro and Martinón-Torres, 2012). It remains to elucidate if *H. antecessor* found an "empty" territory and a vacant ecological niche, or if the members of this species were mixed and they assimilated the resident hominins. Although the evidence suggests a phylogenetic link between TD6 hominins and the Middle Pleistocene populations of Europe (see above), the exact geometry of this relationship is still unknown. Anyway, the possible continuity between the Early and the Middle Pleistocene populations of Europe is out of the scope of this work and will be tackled in further studies.

Finally, and concerning the origin of the TD6 hominins, it is important to remember that this level has yielded Mode 1 lithic tools. Although Mode 2 back from 1.76 Ma from the Kokiselei 4 archaeological site from the Nachukui Formation, in West Turkana, Kenya (Lepre et al., 2011), the generalization of the use of Mode 2 probably occurred in African populations about 1.4 Ma (Carbonell et al., 2010b). If the TD6 hominins came directly from the African continent they would have colonized Europe provided with a Mode 2 technology and not with Mode 1. Thus, the hypothesis of an Eurasian origin for these hominins seems to gain strength. Future studies can help to know the precise source of this species in the Eurasian continent.

5. Conclusions

In the absence of large and well-dated stratigraphical sequences containing unequivocal anthropic evidence, we cannot conclude that the European continent was settled before 1.4–1.5 Ma. The Barranco León and Fuentenueva 3 sites, in the Guadix-Baza basin, and the lower levels (TE LRU) of the Sima del Elefante cave site in Sierra de Atapuerca have reliable information to suggest a continuous hominin population during a large time period before the Jaramillo subchron, independently of the climatic conditions of a certain number of glacial and interglacial conditions forced by obliquity. Thus, hominins were resilient to harsh climatic and ecological conditions, at least in the Mediterranean-influenced areas. Since the Sierra de Atapuerca sites are situated 1000 m above sea level (like most of the territories of the Northern Plateau), we cannot rule out seasonal movements (or a long stay in refuge areas) between the warmer coastal areas and the interior of the Iberian Peninsula.

Unfortunately, we only have a handful of human fossils from this period, and we do not know if Europe was settled by one or more migratory pulses to Western Europe from the same source population.

The lower levels of the Gran Dolina cave site also offer the opportunity of testing the hypothesis of (dis) continuity of the hominin population between the Jaramillo subchron and the Matuyama/Brunhes boundary. There are still some uncertainties regarding the chronology of the TD3/4-TD7 levels. The TD6b level (Aurora archaeostratigraphic set) could be posterior to the extreme cold of MIS 22 (0.88–0.87). The biostratigraphic data, with some changes in the micro- and macro-mammal composition (three different Faunal Units) agree with this scenario. *H. antecessor* would represent a different hominin migratory pulse to the (or those) previous one/s, probably coming from SWA, and coinciding with MIS 21. If TD6b level is anterior to the MIS 22 (e.g. MIS 25) then it is necessary to give a reasonable explanation for the biostratigraphical characteristics of the TD3/TD4–TD6b levels in a relatively short time period (about 0.04 Ma), since the Jaramillo event has not been found at all in this sequence.

In either of these scenarios, the detailed morphological study of the TD6 human hypodigm is consistent with the arrival of new emigrants to the European continent. If we assume a continuity of the European lineage during the Early Pleistocene, then we should review the present paradigm of human evolution, including the timing of Neanderthal and modern human origins, and genetic estimates for the time to the MRCA of *H. neanderthalensis* and *H. sapiens.*

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