



Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Homo antecessor: The state of the art eighteen years later



José-María Bermúdez-de-Castro ^{a,*}, María Martín-Torres ^a, Laura Martín-Francés ^a,
 Mario Modesto-Mata ^a, Marina Martínez-de-Pinillos ^a, Cecilia García ^a,
 Eudald Carbonell ^{b,c}

^a Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo de la Sierra de Atapuerca 3, 09002, Burgos, Spain

^b Institut Català de paleoecologia Humana i Evolució Social (IPHES), Marcel·li Domingo s/n, 43007, Tarragona, Spain

^c Laboratory of Human Evolution, Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, 100044, Beijing, China

ARTICLE INFO

Article history:

Available online 23 May 2015

Keywords:

Human evolution
Homo antecessor
 Sierra de Atapuerca
 Gran Dolina

ABSTRACT

It is eighteen years since the human fossils recovered from the TD6 level of the Gran Dolina cave site, in Sierra de Atapuerca (Burgos, northern Spain) were assigned to a new hominin species, *Homo antecessor*. This review summarizes the main results obtained from the study of these fossils during this period. The increase of the African and Eurasian fossil record, as well as the application of new methodological approaches, has led to competing interpretations about its hypothetical phylogenetic position and possible evolutionary scenarios. At present, we can argue that this species is defined by a unique mosaic of primitive traits for the *Homo* clade, a certain number of derived features present in modern humans, a significant suite of derived features shared with Neandertals and their ancestors in the European Middle Pleistocene (in particular with the Atapuerca-Sima de los Huesos hominins), and some derived features shared with the Chinese Middle Pleistocene hominins. From this evidence, we suggest that a speciation event could have occurred in Africa/Western Eurasia, originating a new *Homo* clade. *Homo antecessor*, most probably dated to the MIS 21, could be a side branch of this clade placed at the westernmost region of the Eurasian continent.

© 2015 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

During the 1994 and 1995 field seasons, an assemblage of near ninety human fossil remains and about 150 Mode 1 artifacts were recovered from the so-called Aurora stratum of the TD6 lithostratigraphic unit (LU) of the Gran Dolina cave site in Burgos (Fig. 1), northern Spain (Carbonell et al., 1995, 1999). These findings occurred during the excavation of an archaeological test pit of about six square meters, made in order to evaluate the potential of the site. The first paleomagnetic studies revealed the presence of the Matuyama/Bruhnes reversal at the top of the TD7 LU, about 117 cm (cm) above the Aurora stratum (Parés and Pérez-González, 1995, 1999). The study of these human fossils evinced a unique combination of primitive and derived features regarding the *Homo* clade,

and we proposed a new *Homo* species, *H. antecessor* (Bermúdez de Castro et al., 1997).

It has been nearly 18 years since this proposal. In this period, another sixty human fossils were obtained in TD6 from a small area near the test pit made during the nineties of the twentieth century. During this excavation, the stratigraphic sequence of TD6 was refined (see Bermúdez de Castro et al., 2008a,b and Figs. 2 and 3) and new additional geochronological information is available from the Gran Dolina site (see below). Furthermore, new studies have been made from the TD6 human fossils. These studies, the finding of new African and Eurasian human remains (e.g. Abbate et al., 1998; Manzi et al., 2001; Asfaw et al., 2002; Gabunia et al., 2002; Macchiarelli et al., 2004; Lumley and Lordkipandize, 2006; Carbonell et al., 2008; Kappelman et al., 2008; Carretero et al., 2009; Krause et al., 2010; Viala et al., 2010; Bermúdez de Castro et al., 2011; Roksandic et al., 2011; Liu et al., 2013; Toro-Moyano et al., 2013; Arsuaga et al., 2014; Xing et al., 2014, 2015) as well as the reinterpretation of specimens recovered in the past (e.g. Manzi et al., 2003; Mounier et al., 2009; Manzi et al., 2010; Stringer, 2012; Liu et al., 2013) have offered a considerable amount of information to reconsider our first proposal and to look for alternative and

* Corresponding author.

E-mail addresses: josemaria.bermudezdecastro@cenieh.es (J.-M. Bermúdez-de-Castro), maria.martinon@cenieh.es (M. Martín-Torres), laura.martinfrances@fa.cenieh.es (L. Martín-Francés), mario.modesto@cenieh.es (M. Modesto-Mata), marina.martinezdepinillos@cenieh.es (M. Martínez-de-Pinillos), cecilia.garcia@cenieh.es (C. García), valtes@iphes.cat (E. Carbonell).



Fig. 1. The Gran Dolina cave site is about 27 m deep. The lower two thirds of the sequence belong to the Lower Pleistocene. A test pit made between 1993 and 1999, as well as a vertical cut of the entire sequence allowed to find the human fossils from the TD6 level (see arrow and Fig. 2).

possibly complementary hypotheses (e.g. Bermúdez de Castro et al., 2003; Martínón-Torres et al., 2007; Bermúdez de Castro et al., 2008a,b; Endicott et al., 2010; Martínón-Torres et al., 2011; McDonald et al., 2012; Bermúdez de Castro and Martínón-Torres, 2013).

In this review, we present a summary of the main results presented so far about the TD6 hypodigm, as well as the different interpretations made on the meaning of these hominins in the context of the African and Eurasian human evolution. It is important to note that a certain number of new analyses of the TD6 hominins are in progress, which undoubtedly will offer additional information to test our hypothesis. Furthermore, in a near future the present Atapuerca Research Team will have access to a wide area of the different thin sublevels forming the Aurora archaeostratigraphic set (also named TD6-2). This will be an opportunity to increase our knowledge of this hominin population, who lived in Western Europe during the late Early Pleistocene.

2. The TD6 level

The Gran Dolina cave site (TD) fills up a large cavity about 27 m deep and with a maximum width of 17 m (see Fig. 3 in Bermúdez de Castro et al., 2013). The stratigraphic section of the site was cut and exposed by the construction of a railway trench. Gil and Hoyos

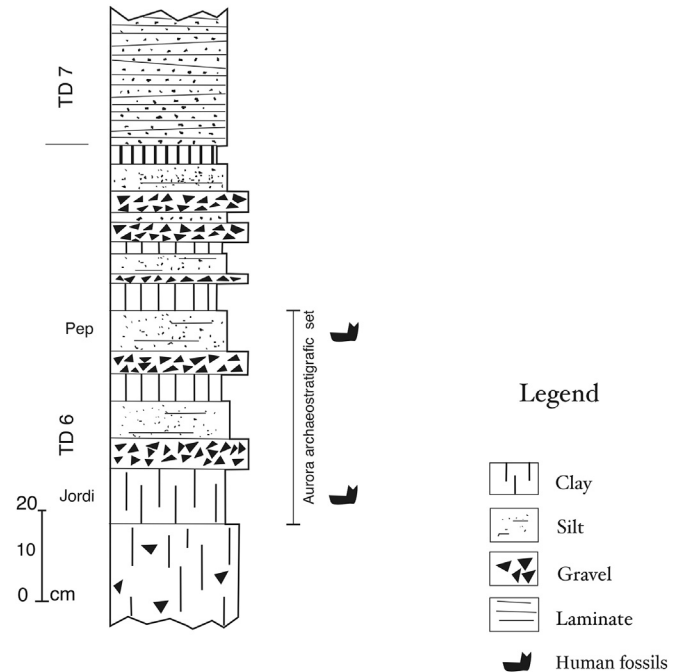


Fig. 2. Upper sequence of the lithostratigraphic unit TD6 from the Gran Dolina cave infilling (Matuyama Chron), which includes the “Aurora archaeostratigraphic set” (AAS), also known as TD6-2. All the human fossils of the *H. antecessor* hypodigm have been recovered from this section of the unit TD6. The AAS is not well defined as a sequence of different layers on the test pit performed in the 1994–1996. Thus, the AAS corresponds to what was named “Aurora stratum” during the first excavations (Carbonell et al., 1995). Modified from Bermúdez de Castro et al., 2008a).

(1987) divided this section from bottom to top into eleven levels: TD1 to TD11. However, the stratigraphy of the Gran Dolina site is under continuous refinement. There is a vertical cut of the section in progress, (e.g. Bermúdez de Castro et al., 2008a). In addition, we are currently studying a wide pit about 10 m deep excavated below the present level of the ancient railway (see Fig. 1). 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 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 TD6-2 (Faunal Unit 4), TD7–TD8 (Faunal Unit 5) and drastic change in TD9–TD11 (Faunal Unit 6) (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010). Pollen analysis of TD6 (García-Antón, 1989) suggests a Mediterranean climate for this level, whereas the study of the amphibian and squamate reptile fossil record (Blain et al., 2009) of TD6-2 also suggests a slightly warmer temperature than today in Burgos.

The combination of paleomagnetic data and US–ESR ages suggest a range between 0.78 and 0.86 Ma (million years ago) for TD6-2 (Falgüeres et al., 1999). Thermoluminescence (TL) ages (Berger et al., 2008) on samples taken 1 m below the Brunhes/Matuyama boundary (0.78 Ma) give an age of 0.96 ± 0.12 Ma for TD6, which may correspond to MIS 25. The last systematic dating of the Gran Dolina sequence has been made by Moreno (2011) using the ESR dating method on optically bleached quartz. This author analysed six samples for TD6 and TD7, obtaining an age range of 0.80–0.88 Ma for these levels, which is consistent with the biostratigraphic and paleomagnetic analyses and suggest that the human assemblage was deposited during MIS 21.

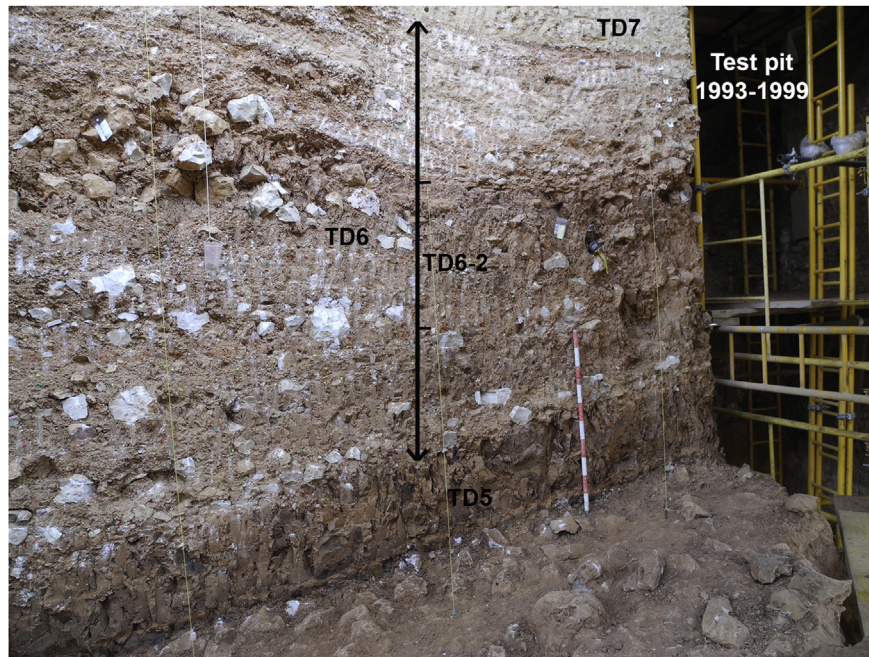


Fig. 3. Vertical cut of the Gran Dolina site, pointing the position of the TD7, TD6, and TD5 levels. The scaffold is placed in the hollow left by the test pit made between 1993 and 1999.

3. Materials and methods

3.1. The TD6 human remains

The human remains from TD6b are in good preservation, although the majority of them are fragmentary due to clear events of cannibalism (Fernández-Jalvo et al., 1999; Carbonell et al., 2010). Nevertheless, we recorded and analyse a number of cranial and postcranial features, mainly from the teeth, the mandibles and the face. Postcranial remains are also numerous and represent different anatomical elements, including nearly twenty-five hand and foot remains.

In this synthetic review we provide an overview of the information obtained from the study of the different cranial, and postcranial features observed in *H. antecessor*, carried out by Arsuaga et al. (1999), Carretero et al. (1999), Lorenzo et al. (1999), Rosas et al. (1999), Carbonell et al. (2005), Bermúdez de Castro et al. (2008a,b), Bermúdez de Castro et al. (2012) and Pablos et al. (2012). Concerning teeth, their crown and root morphology have been analysed in previous studies (Bermúdez de Castro et al., 1997; Bermúdez de Castro et al., 1999; Bermúdez de Castro et al., 2003; Carbonell et al., 2005; Bermúdez de Castro et al., 2008a,b; Martín-Torres et al., 2006, 2007; Gómez-Robles et al., 2007, 2008, 2011, 2011, 2012).

3.2. Minimum number of individuals (MNI)

In previous studies we assessed the possible minimum number of individuals (MNI) currently represented in the TD6 hypodigm (e.g. Bermúdez de Castro et al., 2006). However, due to the considerable fragmentation of the hominin remains, this aspect remains difficult. Furthermore, the six sublevels (generally less than 10 cm) identified during the last excavations (Bermúdez de Castro et al., 2008a,b) are condensed near the wall of the cave, where the test pit was made during the nineties. Then, it was not possible to state the precise provenance of each of the human remains found in the test pit in correlation with the six levels, which were deposited in at least two different time events. Although we suspect that the MNI is higher than the estimation presented in Table 1, in this paper we prefer to be conservative and to avoid speculations with the association of some isolated permanent and deciduous specimens. The present TD6 hypodigm includes four isolated deciduous teeth, two permanent Incisive germs and two permanent complete lower incisors, some of which could represent additional immature or adult individuals. Summarizing, and considering that we have excavated only a small area of the TD6 level, our conclusions on the MNI are preliminary, except for the remarkable presence of a high percentage of immature individuals in the TD6 hypodigm (75%). The age at death of the individuals presented in Table 1 is only an indicative approach. We have used modern human standards with the aim of determining the MNI, but we are aware that this model may not apply for this Early Pleistocene population.

Table 1
List of the individuals represented in the TD6 hominin hypodigm.

Hominin	Inventory number	Specimen	Age at death ^a
H1	ATD6-1	Left lower C	13.5–14.5
	ATD6-2	Left I ₂	
	ATD6-3	Right P ₃	
	ATD6-4	Right P ₄	
	ATD6-5	Right mandible fragment with M ₁ –M ₃ in-situ	
	ATD6-6	Fragment of crown of right lower C	
	ATD6-7	Right P ³	
	ATD6-8	Right P ⁴	
	ATD6-9	Left P ⁴	

Table 1 (continued)

Hominin	Inventory number	Specimen	Age at death ^a
	ATD6-10	Right M ¹	
	ATD6-11	Left M ¹	
	ATD6-12	Right M ²	
H2	ATD6-14	Left maxillary fragment, with dc–dm ¹ in-situ	3.5–4.0
H3	ATD6-69	Maxilla and left zygomatic bone, including: left P ³ , M ¹ , and unerupted M ² , and right I ² –M ¹	10.0–11.0
H4	ATD6-125	Right P ₄	13.5–14.5
H5	ATD6-94	Right M ₁	about 6.0
	ATD6-103	Right M ¹	
H6	ATD6-96	Left half mandible, including P ₃ –M ₃ in-situ	About 17.0
H7	ATD6-113	Fragment of the left half of a mandible including M ₂ and M ₃ in-situ.	About 17.0
H8	ATD6-112	Right part of the mandibular corpus, from the symphysis to the crypt of the M ₂	3.5–3.9

^a In years, and according to modern human patterns of dental development (see Bermúdez de Castro et al., 1999).

4. Results of the main studies performed in the TD6 human fossils

In Tables 2, 3, and 4 we present the state (primitive or derived) of the main features identified so far in the TD6 hypodigm. The state of these features is evaluated in relation to the *Homo* clade.

associated anterior flexion of the maxillary surface near the nasal aperture. This last feature suggests that nose was projecting in ATD6-69. Arsuaga et al. (1999) conclude that the derived *sapiens*-like midfacial topography of ATD6-69 is not present in early *Homo* (i.e. *H. habilis*, *H. rudolfensis*) and *H. ergaster* (or African *H. erectus*). Interestingly, ATD6-69 shows a modern human pattern of dental

Table 2

Derived features shared by *H. antecessor* with modern humans.

- *Face*: – coronal orientation of the infraorbital surface, inferoposterior slope of this surface (with the canine fossa), anterior flexion in the maxillary surface and arcing of the zygomatico-alveolar crest, a projecting nose, and a zigomaxillary tubercle.
- *Face*: – modern (*H. sapiens*) growth remodelling pattern.
- *Skull*: – convex superior border of the temporal squama.
- *Maxilla*: – anterior position and almost vertical trajectory of the incisive canal.

Table 3

Primitive features of *H. antecessor* regarding the *Homo* clade.

- *Lower premolars*: – complex occlusal and root morphology, asymmetry of the crown, large talonid, and presence of cingulum.
- *Permanent upper and lower molars*: M₂ > M₁.
- *Permanent upper second molar*: four well developed cusps.
- *Permanent molars*: complex occlusal enamel crenulation pattern.
- *Mandible*:
 - position of the mental foramen.
 - position of the lateral prominence.
 - position of the mylohyoid line in relation to alveolar margin at M₃ level.
 - trajectory of the mylohyoid line in relation to alveolar margin.
 - relief of the pterygoid fossa.
 - intersection between mandibular notch and condyle.
- *Radius*: absolutely and relatively long radial neck.

Table 4

Derived features shared by *H. antecessor* with Neandertals and Middle Pleistocene Atapuerca-SH hominins.

- *Mandible*: presence of the medial pterygoid tubercle.
- *Mastoid region*: small and minimally projecting mastoid process and the anteriorly obliterated digastric groove.
- *Permanent lateral upper incisors*: marked shovel shaped (Eurasian pattern).
- *Permanent lower fourth premolars*: reduced occlusal polygon.
- *Permanent upper first molar*: rhomboidal and compressed occlusal polygon and a skewed external outline with a bulging protrusion of the hypocone.
- *Clavicle*: – absolutely very long (maximum length), relatively slender (low robusticity index), pronounced shaft curvature, and relatively small epiphyses.
- *Humerus*: – large olecranon fossa and very thin medial and lateral pillars.
- *Talus*: – relatively narrower trochlea (only shared with Neandertals).

The finding that the TD6 hominins exhibit a *sapiens*-like midfacial morphology was surprising (Bermúdez de Castro et al., 1997; see Table 2). Arsuaga et al. (1999) made the first detailed study of the midface of the immature specimen ATD6-69 (H3). These authors described this specimen as having a coronal orientation of the infraorbital surface, an inferoposterior slope of this surface (with the development of a canine fossa), arcing of the zygomatico-alveolar crest, a forward position of the nasal aperture, and

development (Bermúdez de Castro et al., 1999b). Lacruz et al., (2013) have showed close similarities between ATD6-69 and *H. sapiens* regarding the facial growth remodeling pattern. This pattern is totally different from the presumed primitive pattern of the *Homo* clade, observed in the specimen KNM-WT 15000. Another subadult specimen, ATD6-38, which is similar in size and shape to ATD6-69, also presents canine fossa (Arsuaga et al., 1999). Furthermore, the adult specimen ATD6-58, represented by a left

large zygomaxillary fragment, exhibits a remarkable canine fossa, as well as a great zygomaxillary tubercle placed in a maxillary position, that projects out about 3.3 mm (Arsuaga et al., 1999). Finally, an adult small zygomaxillary fragment (ATD6-19) also shows a zygomaxillary tubercle in the same position, which projects out about 2.0 mm (Arsuaga et al., 1999). These authors suggest that the zygomaxillary tubercle may be present in the Zhoukoudian maxilla II. Thus, the Zhoukoudian and the TD6 hominins would represent the unique presence of this facial feature prior to the Late Pleistocene (Arsuaga et al., 1999). Furthermore, Vialet et al. (2010) have identified a facial pattern in the Chinese Middle Pleistocene specimens, Yunxian II and Nankin 1, that is similar to that presented by modern humans. Regarding all these results and since the African origin of our species seems to be undisputed for the majority of paleoanthropologists, the presence of a modern-like human face in *H. antecessor* has been the subject of interest of some other researchers (e.g., Freidline et al., 2013). The latter made an interesting theoretical ontogenetic study of the ATD6-69 face by means of 3D geometric morphometric analyses, with reference data mainly from Neandertals and modern humans. Freidline et al. (2013) concluded that ATD6-69 exhibits a modern-like human midfacial morphology, although their analyses placed ATD6-69 near the margin of modern human variation and intermediate between the modern humans and Middle Pleistocene human samples. According to these authors, the face of this individual would not have been significantly altered in the course of the subsequent development.

Finally, and concerning the skull features, the TD6 hominins share with Neandertals and modern humans a convex superior border of the temporal squama, as well as an anterior position of the incisive canal, which is nearly vertical (Arsuaga et al., 1999). These authors also concluded that the TD6 hominins show a small and minimally projecting mastoid process and the anteriorly obliterated digastric groove, a feature shared with Neandertals (Table 4).

Some of the mandibular features are primitive regarding the *Homo* clade (Table 3). However, in ATD6-96 and ATD6-113 the M3 is only partially covered by the ramus, the retromolar area is oblique, the relief of the masseteric fossa is shallow, and the posterior subalveolar fossa is moderately hollowed. In these mandibles, as well as in ATD6-5 there is no alveolar prominence and the angle of inclination of the mylohyoid groove is clearly lesser than 50°. In all these features, the *H. antecessor* mandibles are derived in relation to the earliest African *Homo* mandibles, as well as in relation to the earliest Javanese *H. erectus*. Furthermore, the small height and breadth of the *H. antecessor* mandibles contrast with the large dimensions of most African *Homo* specimens (except KNM-ER 1501 and OH 13), as well as with those of Sangiran 5, 8, 9, Hexian, Tighenif 1, 2, and 3, Sidi Abderrahman, and Arago 13. Moreover, the height of TD6 mandibles is lower than in the European Middle Pleistocene hominins and the Neandertals (see Table 2 in Rosas and Bermúdez de Castro, 1999). In this respect, *H. antecessor* is clearly derived, sharing their gracility with most Chinese Middle Pleistocene hominins (Carbonell et al., 2005). The mandible ATD6-96 exhibits a hypertrophied medial pterygoid tubercle (Carbonell et al., 2005; Bermúdez de Castro et al., 2012), a feature that has been included in the list of Neandertal apomorphies (Rak et al., 1994; Weaver, 2009).

Concerning teeth, the *H. antecessor* permanent lower and upper canines are derived regarding the *Homo* clade (see Martínón-Torres et al., 2008). However, they retain a vestigium of a cingulum and present conspicuous essential ridges, unlike European Middle Pleistocene hominins and *H. neanderthalensis*. The two *H. antecessor* P³s (ATD6-7 and ATD6-69) show an incipient derived morphology regarding the *Homo* clade. These teeth show a relatively reduced lingual cusp and a nearly symmetric shape, although

not as pronounced as in the Middle and Late Pleistocene hominins (Gómez-Robles et al., 2011). The P⁴ in *H. antecessor* (ATD6-8, ATD6-9, and ATD6-69) is more derived than the P³, similar to that of Asian *H. erectus*, *H. neanderthalensis* and Atapuerca-SH hominins, but primitive regarding *H. sapiens*. The buccal surface of upper premolars show also a vestigium of a cingulum and several longitudinal grooves that resemble that of other Early and Middle Pleistocene fossils from Asia (except for Panxian Dadong, see Liu et al., 2013) and Africa but not from Europe (Martínón-Torres et al., 2011; Xing et al., 2014, 2015). Both the crown and root of the P₃ are remarkably primitive (Bermúdez de Castro et al., 1999; Gómez-Robles et al., 2008) and different from the European Middle Pleistocene hominins, Neandertals and *H. sapiens*. Although the *H. antecessor* P_{4s} (ATD6-4 and ATD6-96) exhibit a primitive morphology, with an elongated, subrectangular outline and a mesially displaced metaconid, they also show a reduced occlusal polygon. *H. antecessor* shares this feature with *H. neanderthalensis* and the European Middle Pleistocene hominins (Martínón-Torres et al., 2006; see Table 4). The permanent upper first molars (ATD6-18, ATD6-69, and ATD6-103) share their conformation with Neandertals and some (but not all, e.g. Arago) European Middle Pleistocene hominins (but see Martínón-Torres et al., 2013 for differences in cusp proportions). This morphology includes a rhomboidal and compressed occlusal polygon and a skewed external outline with a bulging protrusion of the hypocone (Gómez-Robles et al., 2007). The reduced occlusal polygon of the P₄ in *H. antecessor* is another feature shared with *H. neanderthalensis* and the European Middle Pleistocene hominins (Martínón-Torres et al., 2006). In addition, upper lateral incisors from TD6 display a triangular shovel shape, with pronounced labial convexity (Martínón-Torres et al., 2007). This feature is part of the Eurasian dental pattern (Martínón-Torres et al., 2007) shared with Asian and European Early and Middle Pleistocene hominins and Neandertals (Table 4). Finally, and although the primitive M₂ > M₁ is the standard in both the maxillary and mandibular molar series, the strong size reduction of the lower M₃ is remarkable in the ATD6-96 mandible.

Lorenzo et al. (1999)'s conclusions about the study of the hand and foot remains suggest that the TD6 hominins exhibit a morphology more similar to modern humans than that of Neandertals and their predecessors from the European Middle Pleistocene. The long bones are fragmentary and their study (Carretero et al., 1999; Pablos et al., 2012) yielded some interesting indications about the phylogenetic position of the TD6 hominins (Tables 2 and 4). Thus, the clavicle ATD6-50 is described by Carretero et al. (1999) as "absolutely very long (maximum length), relatively slender (low robusticity index) and with pronounced shaft curvature and relatively small epiphyses", sharing its morphology with Neandertals. Similarly, the humeri ATD6-121 (subadult) and ATD6-148 (adult) exhibit a large olecranon fossa and very thin medial and lateral pillars, sharing these features with European Middle Pleistocene hominins, Neandertals and, interestingly, with the Bodo Middle Pleistocene humerus (Carretero et al., 2009; Bermúdez de Castro et al., 2012). Finally, the talus shows relatively narrower trochlea, a feature only shared with Neandertals (Pablos et al., 2012).

5. Discussion

Although the number of specimens of the TD6 hypodigm is still limited, there is enough information to offer proposals about the hypothetical phylogenetic position of *H. antecessor*. We expect that this information will be greatly increased in a near future, when we excavate the majority of the TD6-2 level (about 80 square meters).

The former hypothesis that *H. antecessor* could represent the last common ancestor of *H. neanderthalensis* and *H. sapiens* (Bermúdez de Castro et al., 1997) was formulated mainly due to the presence of a modern-like face in the TD6 hypodigm. However, the geographic position of the Iberian Peninsula in the westernmost extreme of the Eurasian continent, as well as the geological age of the TD6 level pose some difficulties to conciliate with the present paradigm about the origin of our species. In fact, genetic data point to a more recent divergence of modern humans and Neandertals (e.g. Noonan et al., 2006; Endicott et al., 2010; Krause et al., 2010). The molecular analyses made by 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 climate of MIS 12 (ca. 0.48–0.42 Ma). Other results, however, suggest dates near to the MIS 21 (Ovchinnikov et al., 2002; Green et al., 2008; Langergraber et al., 2012). Concerning the genetic approach there is no consensus about the best method. Thus, recent analyses by Fu et al. (2013) suggest a nuclear substitution rate that is approximately half that of previous estimates based on fossil calibration. Therefore, and according to these authors, major events in human evolution occurred far earlier than previously thought. However, other specialists consider that the rate of mutation is slower than assumed so far and thus, it would affect the hypothetical split of hominin lineages (Hawks, 2012; Scally and Durbin, 2012). In consequence, it may be recommendable to wait for an agreement before using genetics arguments favouring or rejecting hypotheses on the split time of Neandertals and modern humans.

Concerning the modern-like face of *H. antecessor*, Freidline et al. (2013) proposed that evolution of modern-like facial morphology occurred independently in Africa, Asia and Europe and several times during the Early and the Middle Pleistocene. Freidline et al. (2013)'s evolutionary interpretation of ATD6-69 is clearly influenced by the most commonly accepted paradigm that the root of *H. sapiens* lies in the African Middle Pleistocene populations (e.g., Stringer and Andrews, 1988). However, their interpretation has been replied by Bermúdez de Castro and Martín-Torres (2014). As we have previously explained (Bermúdez de Castro et al., 2003) and we also defend in this review, we agree that Gran Dolina-TD6 hominins may not represent the origin of modern human populations but a side branch restricted to Western Europe. However, from a cladistic point of view this lineage would stem out very close to the last common ancestor of *H. sapiens* and *H. neanderthalensis*.

On the other hand, we have showed that the hominins recovered from the Sima del Elefante cave site (TE9 level), dated to about 1.1–1.2 Ma (Carbonell et al., 2008) and only 500 m far from Gran Dolina, may represent a previous and different population dispersal than that represented in TD6. Since the TE hominin sample is very limited (Bermúdez de Castro et al., 2011; Martín-Torres et al., 2011; Prado-Simón et al., 2011, 2012; Lorenzo et al., 2015) it is not possible to draw sound conclusions from the anatomical comparisons with the TD6 hominins. However, differences in the inferred behaviour and knapping strategies has led us to propose that the TE9 and TD6 hominins can belong to two different migrations into Western Europe (Bermúdez de Castro et al., 2013). Waiting for new evidence, the TE9 hominins have been assigned to *Homo* sp. (Bermúdez de Castro et al., 2011). In contrast to TE remains, the TD6 hominins exhibit enough information to posit phylogenetic hypotheses. They show a certain number of derived features, mainly shared with Eurasian hominins and, in particular, with the Middle Pleistocene and early Late Pleistocene populations. In this context, it is surprising the relatively high number of features exclusively

shared with Neandertals and with the Atapuerca-SH hominins (Table 4).

Gómez-Robles et al. (2013) have studied the dental morphology of a large sample of hominins by combining 2D geometric morphometrics method with the GLM method for estimating ancestral traits (e.g. Martins and Hansen, 1997; Polly, 2008). These authors concluded that no known fossil species is a suitable candidate for being the last common ancestor of Neandertal and modern humans. Thus, they exclude *H. antecessor*, but also other species like *H. heidelbergensis*. Since all the European hominins posterior to 1.0 Ma exhibit “Neandertal features” they consider the possibility that molecular estimates of the divergence between Neandertals and modern humans may be underestimated. We agree with this conclusion although, as we stated above, the time of divergence of different lineages using genetic estimations ought to be considered with caution. A second hypothesis suggested by Gómez-Robles et al. (2013) points to the possibility that the divergence in dental features between Neandertals and modern humans significantly predates the complete speciation. This decoupled phenotypic differentiation would have affected the dentition, but no other cranial and postcranial features. However, we have confirmed that *H. antecessor* shares some neurocranial, mandibular, and postcranial features with the Atapuerca-SH hominins and the Neandertals (Table 4). These features would be not Neandertal apomorphies, but traits appeared in an ancestral and polymorphic population during the Early Pleistocene (Bermúdez de Castro et al., 2012; Bermúdez de Castro and Martín-Torres, 2013; Bermúdez de Castro et al., 2014).

The TD6 hominins exhibit a suite of features lost in their African ancestors and in the Dmanisi hominins (e.g. Martín-Torres et al., 2008; Rightmire et al., 2008; Bermúdez de Castro et al., 2014). Moreover, the dental features are in line with the Eurasian pattern suggested by Martín-Torres et al. (2007). Although the TD6 hominins show a significant number of derived features shared with Neandertals and modern humans, the hypothesis that *H. antecessor* represent the last common ancestor of both hominin lineages is not fully supported according to the dental morphology (Gómez-Robles et al., 2013), or the geographic location of the Sierra de Atapuerca. Nevertheless, all the evidences need to be reconciled in a credible scenario. Bermúdez de Castro and Martín-Torres (2013) have presented this scenario considering geographic and climatic factors (see also Dennell et al., 2011; Martín-Torres et al., 2011). Since it seems unlikely that Neandertal roots can stretch back as deep as 1.0 Ma, we favour the existence of a Eurasian clade. This clade would be the origin of some waves of populations into Europe during the late Early Pleistocene and the Middle Pleistocene. We also suggest that the settlement of Europe was complicated by climatic and geographic factors, favouring isolation and possible hybridation between paleodemes, including the first residents. This scenario would explain the considerable diversity observed in the European fossil record, evinced in the human samples recovered from Ceprano, Arago, Sima de los Huesos or Mala Balanica (e.g. Manzi, 2001; Roksandidic et al., 2011).

Since the most accepted theory in the present paradigm is that modern humans originated in Africa and the lineage of Neandertals developed in Europe, the physical and genetic divergence of the two populations might have occurred either in Europe or in Africa. The latter has been the preferred option of many colleagues, perhaps because Africa has been traditionally considered as the source of different migrations towards the Eurasian continent (e.g. Stringer and Hublin, 1999; Hublin, 2009; Mounier et al., 2009; Abbate and Sagri, 2011). In parallel with the current paradigm concerning the origin of modern humans (Stringer and Andrews, 1988) it has also been suggested that the ancestors of

Neandertals come from a significant out of Africa dispersal during the Middle Pleistocene (Krause et al., 2010).

Nevertheless, and as we have stated in previous studies (Martinón-Torres, 2011; Bermúdez de Castro and Martinón-Torres, 2013), Southwest Asia represents a suitable region for the evolution of hominins during the entire Pleistocene (Hughes et al., 2007, 2008; Almogi-Labin, 2011). Furthermore, the Levantine Corridor is a geographical crossroad between continents, and has been identified as a true biodiversity hotspot (Carrión et al., 2011). This means that this region can be a source of phylogenetic diversity, inducing speciation and reduced extinction rates (Kingston, 2007; Spathelf and Waite, 2007; Ricklefs, 2010). Western Eurasia could be then the homeland of an early hominin population, origin of several migrations into Europe during the late Early and Middle Pleistocene. Rightmire (1998) suggested that a speciation event occurred in Africa during the very early Middle Pleistocene from *Homo erectus* s.l. This author identified the speciation event with the *H. heidelbergensis* species, and stated that it would be represented in both Africa (e.g., Bodo) and Europe (e.g., Petralona). During the late Middle Pleistocene, either in Africa or Western Eurasia, *H. heidelbergensis* species would have separated in would have splitted into two branches, leading to the modern humans and Neandertal lineages in Africa and Europe, respectively (Rightmire, 1998).

We agree with Rightmire (1998) in the general idea that there was an early speciation process during the Pleistocene. However, evidence from TD6 would push back in time this event. Also interesting in this topic, is the inclusion of Western Eurasia in the Rightmire's scenario as the possible region for the splitting of modern humans and Neandertals. In our view, the Western Eurasian–African region could have been connected at least until the so-called Middle Pleistocene Transition (MPT: 1.25–0.7 Ma) throughout the Levantine Corridor, yielding support to the physical and genetic continuity of this hypothetical African–Western Asian population. This is a prerequisite for the splitting sometime of the modern human and Neandertal lineages. According to new evidences (e.g. Arnold, 2014; Arsuaga et al., 2014) and putting aside the ongoing debates about the interpretation of the genetic data (see above), this splitting might have occurred earlier than assumed by Rightmire (1998). Furthermore, the Rightmire (1998)'s scenario might be more complex, with the possible formation of different Eurasian lineages during the Middle Pleistocene. Moreover and regarding these questions, future comparative studies with African late Early Pleistocene human fossils (Abbate et al., 1998; Manzi et al., 2003; Macchiarelli et al., 2004; Zanolli et al., 2014) would shed light to test this evolutionary scenario.

Concerning the geographic aspect of this scenario, it is very interesting the O'Regan et al. (2011)'s review on the Afro-Eurasian large-mammals dispersals during the Plio-Pleistocene. In their review, these authors conclude that the majority of the large-mammals migrations out of Africa occurred prior to 3.0 Ma or between 1.8 and 1.3 Ma. Later mammal movements out of Africa were possibly sporadic. The faunal record of Western Europe from 1.2 Ma onwards suggests transversal dispersals of large mammals originating in Asia (Crégut-Bonnoure, 1992 a,b; Kahlke, 1992; Kalkhe et al., 2011, 2011; Carrión et al., 2011; van der Made, 2011), obviously favoured by similar climatic conditions in Eurasia during the late Early and Middle Pleistocene. O'Regan et al. (2011) also conclude that a relatively small number of African Pleistocene taxa emigrate into Eurasia, and *viceversa*. The suggestion made by Clarke (2000) that the first Eurasian hominins could have moved back into Africa is a very interesting idea, also considered by Manzi (2004), Dennell and Roebroeks (2005), Rightmire et al., (2006), Martinón-Torres et al. (2007, 2008). These hypothetical population movements in both directions through the Levantine Corridor may have

diminished or ceased due to the worsening climate occurred during the MTP (see a detailed discussion in Bermúdez de Castro and Martinón-Torres, 2013 and references therein on geographical and climatic aspects of the region). The climatic changes associated to the MTP might be the main mechanism behind the physical separation of the African/Western Eurasian population, previously connected through the Levantine Corridor during the Early Pleistocene. This separation would have preceded the genetic divergence leading to modern humans and Neandertals.

6. Concluding remarks

H. antecessor exhibits a unique and very interesting mosaic of primitive and derived features. A significant number of derived features in this species points to a certain relationship with the modern human and Neandertal lineages. In order to reconcile these observations with the present fossil record, we suggest that *H. antecessor* could represent one of the successive waves of populations, which settled Europe during the Pleistocene and splitted away from an early population probably living in Western Eurasia or in Africa/Western Eurasia. This early population would be the result of a cladogenetic event occurred during the late Early Pleistocene. For this review, we prefer to avoid taxonomical questions about this hypothetical population, and we are aware that some colleagues may identify this cladogenetic event with *H. erectus* s.l.

Palaeogenetic studies ought to be refined in order to reduce the time range for the physical and genetic divergence of the modern humans and Neandertal lineages. However, we consider that this event occurred during the evolution of this hypothetical population. Independently from the name we could assign to the last common ancestor of Neandertals and modern humans, and according to the present evidence observed in the TD6 hominins, both lineages would belong to the same clade of *H. antecessor*. The recent genetic and morphological observations on the Atapuerca-Sima de los Huesos hominins (Meyer et al., 2014; Arsuaga et al., 2014) are very promising for understanding the evolutionary scenario in Europe.

As a corollary of this report, we consider that the variability observed in Asia (Anton, 2003; Vialet et al., 2010; Liu et al., 2013; Xing et al., 2014, 2015) ought to be reconsidered. Independently from taxonomical questions, the settlement of the Asian continent might have occurred during the Early and Middle Pleistocene from some successive migration population waves, some of them probably coming from Western Eurasia as well. Future comparative studies between *H. antecessor* and other Middle Pleistocene European hominins with the Chinese fossil record could shed light on these open questions.

Acknowledgements

The authors are grateful to all members of the Atapuerca Research Team for their effort over decades recovering information from the Sierra de Atapuerca sites and their superb research work. We keep a special and grateful memory to Jaume Guiu whose dedication and expert work in the TD6 excavation will be always remembered. This article has been sponsored by the Dirección General de Investigación of the Spanish Ministry of Economía y Competitividad, Grant numbers CGL2012- 38434-C03-02, the Consejería de Cultura y Turismo and the Consejería de Familia e Igualdad de Oportunidades of the Junta de Castilla y León, the Fundación Atapuerca, and the Leakey Foundation through the support of Gordon Getty and Dub Crook. Fig. 1 has been kindly granted by Ana Isabel Ortega. The image processing was carried out by Susana Sarmiento. Authors are also grateful to the reviewers, who have contributed to improve the first manuscript.

References

- Abbate, E., Sagri, M., 2011. Early to Middle Pleistocene Homo dispersals from Africa to Eurasia: geological, climatic and environmental constraints. *Quaternary International* 267, 3–19.
- Abbate, E., Albianelli, A., Azzaroli, A., Benvenuti, M., Tesfamariam, B., Bruni, P., Cipriani, N., Clarke, R.J., Ficarelli, G., Macchiarelli, R., Napoleone, G., Papini, M., Rook, L., Sagri, M., Teclé, T.M., Torre, D., Villa, I., 1998. A one-million-year-old *Homo* cranium from the Danakil (Afar) Depression of Eritrea. *Nature* 393, 458–460.
- Almogi-Labin, A., 2011. The paleoclimate of the Eastern Mediterranean during the transition from early to mid Pleistocene (900 to 700) based on marine and non-marine records: an integrated overview. *Journal of Human Evolution* 60, 428–436.
- Anton, S.C., 2003. Natural history of *Homo erectus*. *Yearbook of Physical Anthropology* 46, 126–170.
- Arnold, L.J., Demuro, M., Parés, J.M., Arsuaga, J.L., Aramburu, A., Bermúdez de Castro, J.M., Carbonell, E., 2014. Luminescent dating and paleomagnetic age constraint on hominins from Sima de los Huesos, Atapuerca, Spain. *Journal of Human Evolution* 67, 85–107.
- Arsuaga, J.L., Martínez, I., Lorenzo, C., Gracia, A., Muñoz, A., Alonso, J., Gallego, J., 1999. The human cranial remains from Gran Dolina Lower Pleistocene site (Sierra de Atapuerca, Spain). *Journal of Human Evolution* 37, 431–457.
- Arsuaga, J.L., Martínez, I., Arnold, L.J., Aramburu, A., Gracia-Téllez, A., Sharp, W.D., Quam, R.M., Falguères, C., Pantoja-Pérez, A., Bischoff, J., Poza-Rey, J., Parés, J.M., Carretero, J.M., Demuro, M., Lorenzo, C., Sala, N., Martínón-Torres, M., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Gómez-Olivencia, A., Moreno, D., Pablos, A., Shen, C.-C., Rodríguez, L., Ortega, A.I., García, R., Bonmatí, A., Bermúdez de Castro, J.M., Carbonell, E., 2014. Neandertal roots: cranial and chronological evidence from Sima de los Huesos. *Science* 344, 1358–1363.
- Asfaw, B., Gilbert, W.H., Beyene, Y., Hart, W.K., Renne, P.R., WoldeGabriel, G., Vrba, E.S., White, T.D., 2002. Remains of *Homo erectus* form Bouri, middle Awash, Ethiopia. *Nature* 416, 317–320.
- Berger, G.W., Pérez-González, A., Carbonell, E., Arsuaga, J.L., Bermúdez de Castro, J.M., Ku, T.-L., 2008. Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain. *Journal of Human Evolution* 55, 300–311.
- Bermúdez de Castro, J.M., Rosas, A., Nicolás, M.A., 1999a. Dental remains from Atapuerca-TD6 (Gran Dolina site, Burgos, Spain). *Journal of Human Evolution* 37, 523–566.
- Bermúdez de Castro, J.M., Martínón-Torres, M., 2013. A new model for the evolution of the human Pleistocene populations of Europe. *Quaternary International* 295, 102–112.
- Bermúdez de Castro, J.M., Martínón-Torres, M., 2014. Evolutionary interpretation of the modern-like facial morphology of the Atapuerca Gran Dolina-TD6 hominins. *Anthropological Science* 122. <http://dx.doi.org/10.1537/ase.140827>.
- Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I., Mosquera, M., 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science* 276, 1392–1395.
- Bermúdez de Castro, J.M., Rosas, A., Carbonell, E., Nicolás, M.E., Rodríguez, J., Arsuaga, J.L., 1999b. A modern human pattern of dental development in Lower Pleistocene hominids from Atapuerca-TD6 (Spain). *Proceedings of the National Academy of Sciences USA* 96, 4210–4213.
- Bermúdez de Castro, J.M., Martínón-Torres, M., Sarmiento, S., Lozano, M., 2003. Gran Dolina-TD6 versus Sima de los Huesos dental samples from Atapuerca: evidence of discontinuity in the European Pleistocene population? *Journal of Archaeological Science* 30, 1421–1428.
- Bermúdez de Castro, J.M., Carbonell, E., Gómez-Robles, A., Mateos, A., Martínón-Torres, M., Muela, A., Rodríguez, J., Sarmiento, S., Varela, S., 2006. Paleodemografía del hipodigma de fósiles de homínidos del nivel TD6 de Gran Dolina (Sierra de Atapuerca, Burgos): estudio preliminar. *Estudios Geológicos* 62, 145–154.
- Bermúdez de Castro, J.M., Pérez-González, A., Martínón-Torres, M., Gómez-Robles, A., Rosell, J., Prado, L., Sarmiento, S., Carbonell, E., 2008a. A new Early Pleistocene hominin mandible from Atapuerca-TD6, Spain. *Journal of Human Evolution* 55, 729–735.
- Bermúdez de Castro, J.M., Martínón-Torres, M., Gómez-Robles, A., Prado, L., Sarmiento, S., 2008b. Comparative analysis of the Gran Dolina-TD6 and Tighennif hominin mandibles: taxonomical implications. *Bulletins et Mémoires de la Société d'Anthropologie* 19, 149–167. Paris.
- Bermúdez de Castro, J.M., Martínón-Torres, M., Gómez-Robles, A., Prado-Simón, L., Olejniczak, A., Martín-Francés, L., Lapresa, M., Carbonell, E., 2011. The Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): a comparative morphological study. *Journal of Human Evolution* 61, 12–25.
- Bermúdez de Castro, J.M., Carretero, J.M., García-González, R., Rodríguez-Gracia, L., Martínón-Torres, M., Rosell, J., Blasco, R., Martín-Francés, L., Modesto, M., Carbonell, E., 2012. Early Pleistocene human humeri from the Gran Dolina-TD6 site (Sierra de Atapuerca, Spain). *American Journal of Human Evolution* 147, 604–617.
- Bermúdez de Castro, J.M., Martínón-Torres, M., Blasco, R., Rosell, J., Carbonell, E., 2013. Continuity or discontinuity in the European Early Pleistocene human settlement: the Atapuerca evidence. *Quaternary Science Reviews* 76, 53–65.
- Bermúdez de Castro, J.M., Martínón-Torres, M., Sier, M.J., Martín-Francés, L., 2014. On the variability of the Dmanisi mandibles. *PLOS One* 9, e88212.
- Blain, H.-A., Bailon, S., Cuenca-Bescós, G., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina-Cave, Atapuerca, Spain. *Journal of Human Evolution* 56, 55–65.
- Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., Díez, J.C., Rosas, A., Cuenca-Bescós, G., Sala, R., Mosquera, M., Rodríguez, X.P., 1995. Lower Pleistocene hominids and artifacts from Atapuerca-TD6 (Spain). *Science* 269, 826–830.
- Carbonell, E., Esteban, M., Martín-Nájera, A., Mosquera, M., Rodríguez, X.P., Ollé, A., Sala, R., Vergès, J.M., Bermúdez de Castro, J.M., Ortega, A.I., 1999. The Pleistocene site of Gran Dolina, Sierra de Atapuerca, Spain: a history of the archaeological investigations. *Journal of Human Evolution* 37, 313–324.
- Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., Allue, E., Bastir, M., Benito, A., Cáceres, I., Canals, T., Díez, J.C., van der Made, J., Mosquera, M., Ollé, A., Pérez-González, A., Rodríguez, J., Rodríguez, X.P., Rosas, A., Rosell, J., Sala, R., Vallverdú, J., Vergès, J.M., 2005. An early Pleistocene hominin mandible from Atapuerca-TD6, Spain. *Proceedings of the National Academy of Sciences USA* 102, 5674–5678.
- Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Ollé, A., Mosquera, M., Cuenca-Bescós, G., García, N., Granger, D.E., Huguet, R., van der Made, J., Martínón-Torres, M., Rodríguez, X.P., Rosas, A., Sala, R., Stock, G.M., Vallverdú, J., Vergès, J.M., Allue, E., Benito, A., Burjachs, F., Cáceres, I., Canals, A., Díez, J.C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. *Nature* 452, 465–469.
- Carbonell, E., Cáceres, I., Lozano, M., Saladié, P., Rosell, J., Lorenzo, C., Vallverdú, J., Huguet, R., Canals, T., Bermúdez de Castro, J.M., 2010. Cultural cannibalism as a paleoeconomic system in the European Lower Pleistocene. *Current Anthropology* 51, 539–549.
- Carretero, J.M., Lorenzo, C., Arsuaga, J.L., 1999. Axial and appendicular skeleton of *Homo antecessor*. *Journal of Human Evolution* 37, 459–499.
- Carretero, J.M., Haile-Selassie, Y., Rodríguez, L., Arsuaga, J.L., 2009. A partial distal humerus from the middle pleistocene deposits at Bodo, middle Awash, Ethiopia. *Anthropological Science* 117, 19–31.
- Carrion, J.S., Rose, J., Stringer, C., 2011. Early human evolution in the Western Palearctic: ecological scenarios. *Quaternary Science Reviews* 30, 1281–1295.
- Clarke, R.J., 2000. Out of Africa and back again. *International Journal of Anthropology* 15, 185–189.
- Crégut-Bonnoure, E., 1992a. Les Caprinae (Mammalia, Bovidae) du Pléistocène d'Europe: Intéret biostratigraphique, paléocologique et archéozoologique. n.s Mémoires de la Société géologique de France 150, 85–93.
- Crégut-Bonnoure, E., 1992b. Dynamics of bovid migration in Western Europe during the middle and late Upper Pleistocene. *Courier Forschungs-Institut Senckenberg* 153, 177–185.
- Cuenca-Bescós, G., García, N., 2007. Biostratigraphic succession of the Early and Middle Pleistocene mammal faunas of the Atapuerca cave site (Burgos, Spain). *Courier Forschungsinstitut Senckenberg* 259, 99–110.
- Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.A., De Marfá, R.J., Galindo-Pellicena, M.A., Bennásar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Biochronology of Spanish Quaternary small vertebrate faunas. *Quaternary International* 212, 109–119.
- Dennell, R.W., Roebroeks, W., 2005. An Asian perspective on early human dispersal from Africa. *Nature* 438, 1099–1104.
- Dennell, R.W., Martínón-Torres, M., Bermúdez de Castro, J.M., 2011. Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. *Quaternary Science Reviews* 30, 1511–1524.
- Endicott, P., Ho, S.Y.W., Stringer, C.B., 2010. Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins. *Journal of Human Evolution* 59, 87–95.
- Falguères, C., Bahain, J.-J., Yokoyama, Y., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., Bischoff, J.L., Dolo, J.-M., 1999. Earliest humans in Europe: the age of Atapuerca fossils, Spain. *Journal of Human Evolution* 37, 343–352.
- Fernández-Jalvo, Y., Díez, J.C., Cáceres, I., Rosell, J., 1999. Human cannibalism in the Early Pleistocene of Europe (Gran Dolina, Sierra de Atapuerca, Burgos, Spain). *Journal of Human Evolution* 37, 591–622.
- Freidline, S.E., Gunz, P., Harvati, K., Hublin, J.-J., 2013. Evaluating developmental shape changes in *Homo antecessor* subadult facial morphology. *Journal of Human Evolution* 65, 404–423.
- Fu, Q., Mittnik, A., Johnson, P.L.F., Bos, K., Lai, M., Bollongino, R., Sun, C., Giemsch, L., Schmitz, R., Burger, J., Ronchitelli, A.M., Martini, F., Cremonesi, R.G., Svoboda, J., Bauer, P., Caramelli, D., Castellano, S., Reich, D., Pääbo, S., Krause, J., 2013. A revised timescale for human evolution based on ancient mitochondrial genomes. *Current Biology* 23, 553–559.
- Gabunia, L., de Lumley, M.A., Vekua, A., Lordkipanidze, D., de Lumley, H., 2002. Dé couverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). *Comptes Rendus Palevol* 1, 243–253.
- García-Antón, M., 1989. Estudio paleontológico de los yacimientos mesopleistocenos de Atapuerca (Burgos): reconstrucción paisajística y paleoclimática (PhD thesis). Universidad Autónoma de Madrid.
- Gil, E., Hoyos, M., 1987. Contexto estratigráfico. Junta de Castilla y León, Valladolid. In: Aguirre, E., Carbonell, E., Bermúdez de Castro, J.M. (Eds.), *El Hombre Fósil de Ibeax y el Pleistoceno de la Sierra de Atapuerca*, pp. 47–55.
- Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M., Margvelashvili, A., Bastir, M., Arsuaga, J.L., Pérez-Pérez, A., Esteban, F.,

- Martínez, L.M., 2007. A geometric morphometric analysis of hominin upper first molar shape. *Journal of Human Evolution* 53, 272–285.
- Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M., Prado, L., Sarmiento, S., Arsuaga, J.L., 2008. Geometric morphometric analysis of the crown morphology of the lower first premolar of hominins, with special attention to Pleistocene Homo. *Journal of Human Evolution* 55, 627–638.
- Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M., Prado-Simón, L., Arsuaga, J.L., 2011. A geometric morphometric analysis of hominin upper premolars. Shape variation and morphological integration. *Journal of Human Evolution* 61, 688–702.
- Gómez-Robles, A., Martínón-Torres, M., Prado, L., Bermúdez de Castro, J.M., 2012. A geometric morphometric analysis of hominin upper second and third molars, with particular emphasis on European Pleistocene populations. *Journal of Human Evolution* 63, 512–526.
- Gómez-Robles, A., Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Polly, P.D., 2013. No known hominin species matches the expected dental morphology of the last common ancestor of Neanderthals and modern humans. *Proceedings of the National Academy of Sciences USA* 110, 18196–18201.
- Green, R.E., Malaspina, A.-S., Krause, J., Briggs, A.W., Johnson, P.L.F., Uhler, C., Meyer, M., Good, J.M., Maricic, T., Stenzel, U., Prüfer, K., Siebauer, M., Burbano, H.A., Ronan, M., Rothberg, J.M., Egholm, M., Rudan, P., Brajkovic, D., Kucan, Z., Gusic, I., Wikström, M., Laakkonen, L., Kelso, J., Slatkin, M., Pääbo, S., 2008. A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing. *Cell* 134, 416–426.
- Hawks, J., 2012. Longer time scale for human evolution. *Proceedings of the National Academy of Sciences USA* 109, 15531–15532.
- Hublin, J.J., 2009. The origin of Neandertals. *Proceedings of the National Academy of Sciences USA* 106, 16022–16027.
- Hughes, J.K., Haywood, A., Mithen, S.J., Sellwold, B.W., Valdes, P.J., 2007. Investigating early hominin dispersal patterns: developing a framework for climate data investigation. *Journal of Human Evolution* 53, 465–474.
- Hughes, J.K., Elton, S., O'Reagan, H.J., 2008. Theropithecus and "Out of Africa" dispersal in the Plio-Pleistocene. *Journal of Human Evolution* 54, 43–77.
- Kahlke, R.-D., 1992. Repeated immigration of Saiga into Europe. *Courier Forschungs-Institut Senckenberg* 153, 187–195.
- Kahlke, R.D., García, N., Kostopoulos, D.S., Lacombe, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersals in Europe. *Quaternary Science Reviews* 30, 1368–1395.
- Kappelman, J., Alçiçek, M.C., Kazanci, N., Schultz, M., Ozkul, M., Sen, S., 2008. First *Homo erectus* from Turkey and implications for migrations to temperate Eurasia. *American Journal of Physical Anthropology* 135, 110–116.
- Kingston, J.D., 2007. Shifting adaptive landscapes: progress and challenges in reconstruction early hominid environments. *Yearbook of Physical Anthropology* 50, 20–50.
- Krause, J., Fu, Q., Good, J.M., Viola, B., Shunkov, M.V., Derevianko, A.P., Pääbo, S., 2010. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature* 464, 894–897.
- Lacruz, R.S., Bermúdez de Castro, J.M., Martínón-Torres, M., Paine, M.L., Carbonell, E., Arsuaga, J.L., Bromage, T.G., 2013. First evidence for modern human facial morphogenesis nearly one million years ago. *PLOS One* 8 (6), e65199.
- Langergraber, K.E., Prüfer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, J.K., Inoue, E., Inoue-Muruyama, M., Mitani, J.C., Muller, M.N., Robbins, M., Schubert, G., Stoinski, T.S., Viola, B., Watts, D., Witting, R.M., Wrangham, R.W., Zuberhühler, K., Pääbo, S., Vigilant, L., 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences USA* 109, 15716–15721.
- Liu, W., Schepartz, L.A., Xing, S., Miller-Antonio, S., Trinkaus, E., Martínón-Torres, M., 2013. Late Middle Pleistocene Hominin Teeth from Panxian Sadong, South China.
- Lorenzo, C., Arsuaga, J.L., Carretero, J.M., 1999. Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). *Journal of Human Evolution* 37, 501–522.
- Lorenzo, C., Pablos, A., Huguet, R., Vallverdú, J., Martínón-Torres, M., Arsuaga, J.L., Carbonell, E., Bermúdez de Castro, J.M., 2015. Early Pleistocene human phalanx from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain). *Journal of Human Evolution* 78, 114–121. <http://dx.doi.org/10.1016/j.jhevol.2014.08.007>
- Lumley, M.A., de Lordkipanidze, D., 2006. L'Homme de Dmanisi (*Homo georgicus*), il y a 1810000 ans. *Comptes Rendus Palevol* 5, 273–281.
- Macchiarelli, R., Bondioli, L., Chech, M., Coppa, A., Fiore, I., Russom, R., Vecchi, F., Libsekal, Y., Rook, L., 2004. The late early Pleistocene human remains from Buia, Danakil Depression, Eritrea. *Rivista Italiana di Paleontologia e Stratigrafia* 110, 133–144.
- MacDonald, K., Martínón-Torres, M., Dennell, R., Bermúdez de Castro, J.M., 2012. Discontinuity in the record for hominin occupation in south-western Europe: implications for occupation of the middle latitudes of Europe. *Quaternary International* 271, 84–97.
- Manzi, G., 2004. Human evolution at the Matuyama-Brunhes boundary. *Evolutionary Anthropology* 13, 11–24.
- Manzi, G., Mallegni, F., Ascenzi, A., 2001. A cranium for the earliest Europeans: phylogenetic position of the hominid from Ceprano. *Proceedings of the National Academy of Sciences USA* 98, 10011–10016.
- Manzi, G., Bruner, E., Passarello, P., 2003. The one-million-year-old *Homo* cranium from Bouri (Ethiopia): a reconsideration of its *Homo erectus* affinities. *Journal of Human Evolution* 44, 731–736.
- Manzi, G., Magri, D., Milli, S., Palombo, M.R., Margari, V., Celiberti, V., Barbieri, M., Barbieri, M., Melis, R.T., Rubini, M., Ruffo, M., Saracino, B., Tzedakis, P.C., Zarattini, A., Biddittu, I., 2010. The new chronology of the Ceprano calvarium (Italy). *Journal of Human Evolution* 59, 580–585.
- Martinón-Torres, M., Bastir, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Sarmiento, S., Muela, A., Arsuaga, J.L., 2006. Hominin lower second premolar morphology: evolutionary inferences through geometric morphometrics analysis. *Journal of Human Evolution* 50, 523–533.
- Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Arsuaga, J.L., Carbonell, E., Lordkipanidze, D., Manzi, G., Margvelashvili, A., 2007. Dental evidence on the hominin dispersals during the Pleistocene. *Proceedings of the National Academy of Sciences USA* 104, 13279–13282.
- Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Margvelashvili, A., Lordkipanidze, D., Vekua, A., 2008. Dental remains from Dmanisi: morphological analysis and comparative study. *Journal of Human Evolution* 55, 249–273.
- Martinón-Torres, M., Dennell, R., Bermúdez de Castro, J.M., 2011. The Denisova hominin need not be an out African story. *Journal of Human Evolution* 60, 251–255.
- Martinón-Torres, M., Spěváčková, P., Gracia-Téllez, A., Martínez, I., Bruner, E., Arsuaga, J.L., Bermúdez de Castro, J.M., 2013. Morphometric analysis of molars in a Middle Pleistocene population shows a mosaic of "modern" and Neanderthal features. *Journal of Anatomy* 223, 353–363.
- Martins, E.P., Hansen, T.F., 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* 149, 646–667.
- Meyer, M., Fu, Q., Aximu-Petri, A., Glocke, I., Nickel, B., Paabo, S., Arsuaga, J.L., Martínez, I., Gracia, A., Bermúdez de Castro, J.M., Carbonell, E., 2014. A mitochondrial genome sequence of a hominin from Sima de los Huesos. *Nature* 505, 403–406.
- Moreno, D., 2011. Datation par ESR de quartz optiquement blanchis (ESR-OB) de la région de Atapuerca (Burgos, Espagne). Application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviaux quaternaires de l'Arlanza et l'Arlanza (PhD. dissertation). Universitat Rovira i Virgili, Tarragona, Spain and Muséum National d'Histoire Naturelle, (MNHN, Paris, France).
- Mounier, A., Marchal, F., Condemi, S., 2009. Is *Homo heidelbergensis* a distinct species? New insight on the Mauer mandible. *Journal of Human Evolution* 56, 219–246.
- Noonan, J.P., Coop, G., Kudaravalli, S., Smith, D., Krause, J., Chen, J.A.F., Platt, D., Pääbo, S., Pritchard, J.K., Rubin, E.M., 2006. Sequencing and analysis of Neandertal genomic DNA. *Science* 314, 1113–1118.
- ÓRegan, H.J., Turner, A., Bishop, L.C., Elton, S., Lamb, A.L., 2011. Hominins without fellow travellers? First appearances and inferred dispersals of Afro-Eurasian large-mammals in the Plio-Pleistocene. *Quaternary Science Reviews* 30, 1343–1352.
- Ovchinnikov, I.V., Götherström, A., Romanova, G.P., Kharitonov, G.P., Liden, K., Goodwin, W., 2002. Molecular analysis of Neandertal DNA from the northern Caucasus. *Nature* 404, 490–493.
- Pablos, A., Lorenzo, C., Martínez, I., Bermúdez de Castro, J.M., Martínón-Torres, M., Carbonell, E., Arsuaga, J.L., 2012. New foot remains from the Gran Dolina-1D6 Early Pleistocene (Sierra de Atapuerca, Burgos, Spain). *Journal of Human Evolution* 63, 610–623.
- Parés, J.M., Pérez-González, A., 1995. Paleomagnetic age for hominid fossils at Atapuerca Archaeological site, Spain. *Science* 269, 830–832.
- Parés, J.M., Pérez-González, A., 1999. Magnetochronology and stratigraphy at Gran Dolina section, Atapuerca (Burgos, Spain). *Journal of Human Evolution* 37, 325–342.
- Polly, P.D., 2008. Adaptive zones and the pinniped ankle: a three-dimensional quantitative analysis of carnivoran tarsal evolution. In: Sargis, E., Dagosto, M. (Eds.), *Mammalian Evolutionary Morphology, A Tribute to Frederick S. Szalay*. Springer, Dordrecht, The Netherlands, pp. 167–196.
- Prado-Simón, L., Martínón-Torres, M., Baca, P., Gómez-Robles, A., Bermúdez de Castro, J.M., 2011. A morphological study of the tooth roots of the Sima del Elefante mandible (Atapuerca Spain): a new classification of the teeth, biological and methodological considerations. *Anthropological Science* 120, 61–72.
- Prado-Simón, L., Martínón-Torres, M., Baca, P., Olejniczak, A.J., Gómez-Robles, A., Bermúdez de Castro, J.M., 2012. Three dimensional evaluation of root canal morphology in lower second premolars of early and middle Pleistocene human populations from Atapuerca (Burgos, Spain). *American Journal of Physical Anthropology* 147, 452–461.
- Rak, Y., Kimbel, W.H., Hovers, E., 1994. A neandertal infant from Amud Cave. *Journal of Human Evolution* 26, 313–324.
- Ricklefs, R.E., 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences USA* 107, 1265–1272.
- Rightmire, G.P., 1998. Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. *Evolutionary Anthropology* 6, 218–227.
- Rightmire, G.P., Lordkipanidze, D., Vekua, A., 2006. Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *Journal of Human Evolution* 50, 115–141.

- Rightmire, G.P., Van Arsdale, A.P., Lordkipanidze, D., 2008. Variation in the mandibles from Dmanisi, Georgia. *Journal of Human Evolution* 58, 492–504.
- Roksandic, M., Mihailović, D., Mercier, N., Dimitrijević, V., Morley, M.W., Racocevic, Z., Mihailovic, B., Guibert, J.B., Babb, J., 2011. A human mandible (BH-1) from the Pleistocene deposits of Mala Balanica cave (Sićevo Gorge, Niš, Serbia). *Journal of Human Evolution* 61, 185–196.
- Rosas, A., Bermúdez de Castro, J.M., 1999. The ATD6-5 mandibular specimen from Gran Dolina (Atapuerca, Spain). Morphological study and phylogenetic implications. *Journal of Human Evolution* 37, 567–590.
- Sally, A., Durbin, R., 2012. Revising the human mutation rate: implications for understanding human evolution. *Natural Review Genetics* 13, 745–753.
- Spathelf, M., Waite, T.A., 2007. Will hotspots conserve extraprimates and carnivore evolutionary history. *Diversity and Distributions* 13, 746–751.
- Stringer, C., 2012. The Status of *Homo heidelbergensis* (Schoetensack 1908). *Evolutionary Anthropology* 21, 101–107.
- Stringer, C.B., Andrews, P., 1988. Genetic and fossil evidence for the origin of modern humans. *Science* 239, 1263–1268.
- Stringer, C.B., Hublin, J.J., 1999. New age estimates for the Swanscombe hominid, and their significance for human evolution. *Journal of Human Evolution* 37, 873–877.
- Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J.M., Martínón-Torres, M., Fajardo, B., Duval, M., Falguères, C., Oms, O., Parés, J.M., Anadón, P., Juliá, R., García-Aguilar, J.M., Moigne, A.-M., Espigares, M.P., Ros-Montoya, S., Palmqvist, P., 2013. The oldest human fossil in Europe from Orce (Spain). *Journal of Human Evolution* 65, 1–9.
- van der Made, J., 2011. Biogeography and climatic change as a context to human dispersal out of Africa and within Eurasia. *Quaternary Science Reviews* 30, 1353–1367.
- Vialet, A., Guipert, G., Jianingc, H., Xiaobo, F., Zunec, L., Youpingc, W., Tianyuane, L., de Lumley, M.A., de Lumley, H., 2010. *Homo erectus* from the Yunxian and Nankin Chinese sites: Anthropological insights using 3D virtual imaging techniques. *Comptes Rendus Palevol* 9, 331–339.
- Weaver, T.D., 2009. The meaning of Neandertal skeletal morphology. *Proceedings of the National Academy of Sciences USA* 106, 16028–16033.
- Xing, S., Martínón-Torres, M., Bermúdez de Castro, J.M., Xiujie, W., Liu, W., 2015. Hominin teeth from the early Late Pleistocene site of Xujiayao, Northern China. *American Journal of Physical Anthropology* 156, 224–240. <http://dx.doi.org/10.1002/ajpa.22641>.
- Xing, S., Martínón-Torres, M., Bermúdez de Castro, J.M., Zhang, Y., Fan, X., Zheng, L., Huang, W., Wu, L., 2014. Middle Pleistocene hominin teeth from Longtan Cave, Hexian, China. *PLOS One*. <http://dx.doi.org/10.1371/journal.pone.0114265>.
- Zanolli, C., Bondioli, L., Coppa, A., Dean, C.D., Bayle, P., Candilio, F., Capuani, S., Dreossi, D., Fiore, I., Frayer, D.W., Libsekal, Y., Mancini, L., Rook, L., Tkle, T.M., Tuni, C., Macchiarelli, R., 2014. The late Early Pleistocene human dental remains from Uadi Aalad and Mulhuli-Amo (Buia), Eritrean Danakil. Macromorphology and microstructure; *Journal of Human Evolution* 74, 96–113.