

Evolutionary interpretation of the modern human-like facial morphology of the Atapuerca Gran Dolina-TD6 hominins

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Abstract The Early Pleistocene human fossil remains recovered from the TD6 lithostratigraphic unit of the Gran Dolina cave site in the Sierra de Atapuerca, northern Spain, show a mosaic of primitive and derived features. Among the latter, the modern human-like midfacial topography, as well as several synapomorphies shared with some European Middle Pleistocene hominin and Neanderthals, represents a challenge for the phylogenetic interpretation of *Homo antecessor*. Using an ontogenetic approach of the maxilla ATD6-69, Freidline et al. (Journal of Human Evolution, 65: 404–423 (2013)) have confirmed previous observations that *H. antecessor* adults had a set of facial features characterizing *H. sapiens*. However, Freidline and collaborators proposed that the evolution of modern-looking facial morphology occurred independently in Africa, Asia, and Europe and at several times during the Early and the Middle Pleistocene. Following their line of reasoning, the presence in *H. antecessor* of some features shared with the European Middle Pleistocene hominins and the Neanderthal lineage could also be interpreted as convergences. However, instead of supposing multiple, parallel evolution, we suggest that a more parsimonious interpretation envisages the hypothetical existence of an Early Pleistocene hominin population, from which several hominin lineages originate and inherit particular combinations of derived features. The TD6 hominins probably represent a side branch of this cladogenetic event, which evolved in Western Europe.

Key words: Early Pleistocene, Sierra de Atapuerca, *Homo antecessor*, facial morphology

Introduction

During the 1994 and 1995 field seasons an assemblage of nearly 90 human fossil remains and about 150 Mode 1 artefacts were recovered from the so-called Aurora Stratum of the TD6 lithostratigraphic unit (LU) of the Gran Dolina cave site in Burgos, northern Spain (Carbonell et al., 1995, 1999). These findings occurred during the excavation of a biostratigraphic test pit. The first paleomagnetic studies revealed the presence of the Matuyama/Bruhnes reversal at the top of the TD7 LU, about 117 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).

Among the features we recognized in the *H. antecessor* hypodigm, the remarkably modern pattern of midfacial to-

pography of the adolescent represented by the specimen ATD6-69 was surprising (Bermúdez de Castro et al., 1997; Arsuaga et al., 1999). Similarly, the subadult specimen ATD6-38 is very similar in size and shape to ATD6-69, and its topography clearly suggests the presence of a canine fossa (Arsuaga et al., 1999). The adult specimen ATD6-58, represented by an adult left large zygomaxillary fragment, exhibits a remarkable canine fossa, as well as a great zygomaxillary tubercle placed in a maxillary position, that projects out 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). All these data indicate that *H. antecessor* represents the oldest species having a modern-like human face.

On the other hand, and in addition to some cranial synapomorphies shared with both modern human and Neanderthals (Arsuaga et al., 1999), the study of an increased *H. antecessor* hypodigm has revealed the presence of some synapomorphies shared with some Middle Pleistocene hominins and Neanderthals. Thus, it seems interesting to explore the interpretation of the particular combination of features in the European Early Pleistocene assemblage recovered from the Gran Dolina cave site. In particular, the recent proposal that some of the facial features characterizing the recent modern humans may have developed multiple times during human evolution (Freidline et al., 2013) deserves attention. The aim

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of this report is to examine this hypothesis to the light of the information provided by the TD6 human assemblage.

The TD6 lithostratigraphic unit

At the end of the 1990s, we began to flatten the exposed section of the Gran Dolina site by vertically cutting the different LUs. Since the TD7 and TD6 LUs presented marked projecting areas at the middle and the north end of the section, we had the opportunity to excavate the section formed by these LUs. From 2003 to 2007 the excavation of a small area of about 13 m² of the TD6 LU, most of them near the test pit explored during the 1990s, led to new important findings. First, the stratigraphy of the TD6 LU was remarkably refined. At the upper sequence of the TD6 LU the so-called 'Aurora Archaeostratigraphic Set' was recognized (Bermúdez de Castro et al., 2008), formed by six sublevels, two of which yielded new human fossil remains and artefacts. The current hominin assemblage includes about 160 human fossil remains belonging to at least 11 individuals (Carbonell et al., 2005; Bermúdez de Castro et al., 2006, 2008, unpublished data).

Concerning the dating there are two alternative hypotheses. First analyses by Falguères et al. (1999) using the ESR and U-series methods, the biochronological study of the Atapuerca sites (Cuenca-Bescós et al., 1999; Cuenca-Bescós and García, 2007), and the stratigraphic position of these hominins below the Matuyama/Bruhnes geomagnetic boundary suggested a chronology of about 850 ka for the Aurora Archaeostratigraphic Set (Bermúdez de Castro et al., 2008), probably corresponding to the MIS 21. Further studies from Berger et al. (2008) using the TL and IRSL multi-aliquot dating methods and the latest paleomagnetic analysis of the Gran Dolina-TD7 LU (Parés et al., 2013) pointed to an interval of 900–950 ka for the TD6 hominins. Thus, the hominin-bearing sediments from TD6 could have been deposited during the MIS 25.

The ATD6-69 specimen

ATD6-69 preserves most of the left side of the face, except the frontal apophyses of the zygomatic and maxillary bones. The entire maxillary alveolar process is intact, and it also preserves the anterior part of the hard palate with part of the vomer attached to it, and a portion of the left pterygoid fossa of the sphenoid bone (Figure 1). ATD6-69 also preserves in situ the permanent right lateral incisor (I2), canine (C), third and fourth premolars (P3, and P4), and first molar (M1), as well as the left permanent P3, M1, M2, and M3 (Arsuaga et al., 1999; Bermúdez de Castro et al., 1999a). The right C and P4 were just ending the eruption process, but they were not yet in occlusion with the lower counterparts. The left M2 was still included in his crypt, whereas the germ of the third molar was kept attached to the bone through the process of fossilization and placed below the crypt of the M2. In Table 1 we present the mineralization stages of these teeth according to the classification of Moorrees et al. (1963). ATD6-69 is considered to represent Individual 3 of the TD6 hominin assemblage (Bermúdez de Castro et al., 2006). According to modern human standards (see Table 1), the dental age of Individual 3 from TD6 has been estimated to be between 10 and 11 years (Bermúdez de Castro et al., 1999b). In order to refine this information a histological study of the preserved teeth is in progress.

The definition and identification of the main features that shape the *sapiens*-like face has been the subject of much discussion in recent years (see Maddux, 2011, for a detailed review). The plesiomorphic morphology of the *Homo* clade, identified in specimens such as KNM WT 15000 (an immature individual with a dental age slightly advanced with regard to ATD6-69), KNM ER 3733, KNM ER 1470, and SK 847, includes an anteroinferiorly inclined infraorbital surface, absence of true canine fossa, and a maxillary flexion. Particularly in *H. habilis* and *H. rudolfensis* (KNM ER 1470) the midface is flat and the lateral nasal margin is



Figure 1. Original of the specimen ATD6-69 from the TD6 level of the Gran Dolina cave site, Sierra de Atapuerca.

Table 1. Mineralization stages, according the Moorrees et al. (1963) classification, of teeth of Individual 3 from the TD6 LU (Aurora Archaeostratigraphic Set) of the Gran Dolina site and chronological ages (years) associated with those stages in living humans.

Tooth	Stage	Age: Anderson et al. (1976);	Harris and McKee (1990)
Right			
I2	A1/2–Ac	10.5	>9.7
C	R3/4–Rc	10.3	11.0
P3	R3/4–Rc	10.5	11.5
P4	R2/3	10.1	10.8
M1	Complete	>10.1	>9.5
Left			
M1	Complete	>10.1	>9.5
M2	R1/3	10.0	11.2
M3	Cr2/3	11.9	11.8

situated only slightly in front of the zygomatic root (Arsuaga et al., 1999), evincing the lack of projecting nose. In the first detailed morphological study of ATD6-69, Arsuaga et al. (1999) observed that this specimen exhibits a coronal orientation of the infraorbital surface, an inferoposterior slope of this surface (with the canine fossa), arcing of the zygomaticoalveolar crest, a forward position of the nasal aperture, and associated anterior flexion of the maxillary surface near the nasal aperture. This last feature suggests that nose was projecting in ATD6-69. According to these authors, this 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 development (Bermúdez de Castro et al., 1999b), and Lacruz et al., (2013) have showed close similarities between the facial growth remodeling pattern between ATD6-69 and *H. sapiens*. Finally, Neanderthals exhibit very specialized facial morphology, as detailed by Rak (1986). These hominins show a parasagittal orientation of the infraorbital surface, without a concavity (canine fossa) seen in *H. sapiens*, and lack an incurvation (or malar notch) along the zygomaticoalveolar crest. Arsuaga et al. (1999) hypothesized that these autoapomorphic features derived from a *sapiens*-like morphology, i.e. the latter morphology is primitive with regard to Neanderthals, but derived relative to early *Homo* and *H. ergaster*.

ATD6-69 from a developmental point of view

In a very interesting report, Freidline et al. (2013) present the study of a cast of the ATD6-69 specimen from a developmental perspective and within an evolutionary context. These authors conclude that ATD6-69 exhibits a modern-like human midfacial morphology, although their 3-D geometric morphometric analyses placed ATD6-69 near the margin of modern human variation and intermediate between the modern humans and Middle Pleistocene human samples. The additional conclusion that the shape of the face of this individual would not have been significantly altered in the course of the subsequent development (Freidline et al., 2013) is particularly important, since the interpretation of its morphology has been controversial for many years due to

the young age of the specimen (see Table 1).

Freidline et al. (2013)'s evolutionary interpretation about the modern-like facial morphology of ATD6-69 is clearly influenced by a popular paradigm that the root of *H. sapiens* lies in the African Middle Pleistocene populations (e.g. Stringer and Andrews, 1988). Freidline et al. (2013) discussed several important features present in ATD6-69, including a coronal orientation of the infraorbital plate, a curved zygomaticoalveolar crest, and the infraorbital depression. These features are also present in Dali and Jebel Irhoud from the late Middle Pleistocene of Asia and Africa, respectively. Freidline et al. (2013) noted a possibility that these features represent synapomorphies shared by these hominins and *H. antecessor*. However, since the modern facial morphology did not fully appear in Kabwe and Bodo, which are interpreted by them as “the immediate ancestors of Neanderthals and modern humans” (p. 420), Freidline et al. (2013) preferred to explain the above similarities as convergences instead of synapomorphies.

On the other hand, Freidline et al. (2013) consider that the *sapiens*-like features present in ATD6-69 can be interpreted as being part of an ancestral (primitive) facial architecture that, for instance, is shared with KNM-ER 1813 (Rak, 1986; Arsuaga et al., 1999). The results of Freidline et al. (2013) agree partially with those of Maddux (2011), who has shown that most aspects of human infraorbital morphology are significantly correlated with infraorbital and facial size. For this reason, Maddux (2011) called into question the reliability of infraorbital features as independent morphological characters to infer phylogeny. Freidline et al. (2013) contended that the coronal orientation of the infraorbital plate and the curved zygomaticoalveolar crest were lost in the African and European Middle Pleistocene hominins, but were retained by Asian *H. erectus* (Nanjing, Dali, Zhoukoudian, and Yunxian 1 and 2, see below). Finally, this morphology evolved again during the late Middle Pleistocene in the African population, presumably ancestors of modern humans. Thus, Freidline et al. (2013) invoked evolutionary convergence for the above modern *sapiens*-like facial morphology in several places and times during the Pleistocene. These authors further support their conclusion by reference to a notion discussed by some researchers (see references in Freidline et al., 2013) that the facial region is more susceptible of convergence being affected by both mastication and climate.

As we explained above, the conclusions from Freidline et al. (2013) also imply that there is not necessarily a close relationship between the European and Asian hominins, since their facial similarities would have been acquired independently. Moreover, we think it is important to note that their interpretation is mainly based in the absence of a fully modern face in one of the only two Middle Pleistocene fossils from Africa they could examine, Kabwe and Bodo. Although the whole assemblage of features that compose the modern face is absent in Kabwe, Freidline et al. (2013) point to some infraorbital features in Bodo that would align it with *H. sapiens*. The lack of a representative sample for the African Middle Pleistocene calls for caution and suggests that an increased fossil sample from this region and period may potentially show varying degrees of facial “modernity.” Given the scarcity of the fossil record for that continent and

period, it is important to remember that the absence of evidence is not necessarily evidence of absence. Thus, the absence of “modern-like” features in Kabwe would imply a case of possible genetic polymorphism in the small (and thus, hardly representative) Middle Pleistocene record from Africa versus at least four episodes of convergent evolution in the facial topography (*H. antecessor*, Asian Middle Pleistocene, African late Middle Pleistocene and *H. sapiens*) in all continents and throughout the entire Pleistocene. In our opinion, the latter would be a less parsimonious model.

Freidline et al. (2013) also state that many of the facial features that ATD6-69 shares with modern humans can be considered to be part of what Rak (1986) called a generalized pattern of architecture. According to Rak (1986), this facial conformation was present in hominins such as Skhul IV and V, Zuttiyeh, Jebel Irhoud 1, and Qafzeh 6 and 9, and some of the features could be also identified in the Chinese *H. erectus* specimens from Zhoukoudian reconstructed by Weidenreich (see Pope, 1992), as well as in African Middle Pleistocene African specimens such as Bodo I and Kabwe, and the European cranium from Petralona (Rak, 1986), although the identification of these modern-looking facial traits could be obscured by the extreme pneumatization of the maxillary sinus that probably had obliterated much of the canine fossa in these specimens (but see Arsuaga et al. (1999) for the interpretation of Petralona facial morphology). Later, other authors have also noted a modern-like pattern of midfacial topography in the Chinese Middle Pleistocene record, such as in the partially distorted specimen from Dali (Arsuaga et al., 1999), in the two Yunxian skulls (Etler, 1994, 1996; Vialet et al., 2010) dated from the late Early Pleistocene or early Middle Pleistocene (Chen et al., 1997), and in the Chinese Middle Pleistocene specimen from Nanjing (Liu et al., 2005; Vialet et al., 2010). In the same line, Freidline et al. (2013) also recognize that this modern-like pattern can be present in varying degrees of expression in some later Asian *H. erectus*. In addition, and as we stated above, it is interesting to mention that ATD6-69, ATD6-19 (adult), and ATD6-58 (adult) show a zygomaxillary tubercle, a feature that is possibly also present in the Zhoukoudian Maxilla II (Arsuaga et al., 1999). According to these authors, these would be the only populations to present a zygomaxillary tubercle before the Upper Pleistocene, emphasizing the facial similarities shared by European and Asian groups. Interestingly, ATD6-69 would be the earliest specimen to show the features that Rak termed as generalized. However, the use of the term generalized (*sensu* Rak) in Freidline et al. (2013) can be rather equivocal since it means ‘unmodified’ (and therefore bears a connotation of primitive), whereas they also agree that the ATD6-69 face is clearly different from that of the early *Homo* (i.e. *H. habilis*, *H. rudolfensis*) or *H. ergaster* (or African *H. erectus*), which display indeed the primitive or plesiomorphic state of the *Homo* clade.

The derived *sapiens*-like midfacial topography of ATD6-69, including the projecting nose, the maxillary flexion, and the canine fossa, is not present in the earliest representatives of the genus *Homo* (Arsuaga et al., 1999). Freidline et al. (2013) state that with the exception of some isolated aspects of the infraorbital plane orientation in Sangiran 17, Dmanisi 2700, and KNM-ER 1813, *H. antecessor* represents the ear-

liest example of modern-like face.

In addition, and beyond morphometric aspects, there are ontogenic and developmental notions that need to be considered. In this context, the facial growth remodeling pattern is essential to achieve a particular adult facial architecture (Lacruz et al., 2013). Freidline et al. (2013) suggest that *H. antecessor* probably expresses a unique facial growth pattern. However, and as we stated above, Lacruz et al., (2013) have showed close similarities between the facial growth remodeling patterns of *H. antecessor* and *H. sapiens*. In contrast, KNM-WT 15000 specimen exhibits a facial remodeling pattern, which resembles the pattern seen in earlier hominins such as *H. habilis* and *Australopithecus* (Lacruz et al., 2013). Therefore, and as we stated above, we suggest that the facial morphology of KNM-WT 15000 represents the primitive condition of the *Homo* clade, whereas *H. antecessor* exhibits a derived condition shared with *H. sapiens*. The midfacial prognathism, recognized as a unique facial topography of classic Neanderthals (Rak, 1986) that is also present in the European Middle Pleistocene hominins (Arsuaga et al., 1999), would represent another derived condition that could have emerged from a modern-like face (Arsuaga et al., 1999).

It is interesting to remember that many facial features discriminating Neanderthals and modern humans are already established early in the ontogeny, and that subsequent growth will emphasize the facial differences between both taxa (Freidline et al., 2013 and references therein). This implies that the genetic changes determining the facial shape are expressed early in development and are decisive for the facial shape of the adults. Freidline et al. (2013) extrapolated the results obtained for the development trajectories from two samples, Neanderthals and modern humans, to estimate the adult shape of the ATD6-69 individual. Their results suggest that “facial morphology of ATD6-69 would not have been significantly altered in the course of subsequent development” (Freidline et al., 2013: 404). From this conclusion we infer that *H. antecessor* would have shared with other hominins not only a similar modern-like facial morphology but also the same genetic pattern of facial development.

In addition, *H. antecessor* exhibits a modern (derived) human pattern of dental development (Bermúdez de Castro et al., 1999a, 2010), perhaps related to their derived midfacial topography (Lacruz et al., 2013).

Other non-facial evidences in *H. antecessor*

Regarding the postcranial skeleton of *H. antecessor*, most of the features are more similar to modern humans than to European Middle and Late Pleistocene hominins (Carretero et al., 1999; Lorenzo et al., 1999), although some traits are also shared with the latter (Pablos et al., 2012). We have identified a few features in the TD6 hominins that are also present in Neanderthals and some European Middle Pleistocene hominins. 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 Neanderthals. 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, Neanderthals, and, interestingly, with the Bodo Middle Pleistocene humerus (Carretero et al., 2009; Bermúdez de Castro et al., 2012). In addition, the ATD6-96 mandible exhibits a hypertrophied medial pterygoid tubercle (Carbonell et al., 2005), a feature included in the list of Neanderthal apomorphies (Rak et al., 1994; Weaver, 2009). Finally, *H. antecessor* permanent upper first molars (M1s) (ATD6-18, ATD6-69, and ATD6-103) share their conformation with Neanderthals and some (but not all, e.g. Arago) European Middle Pleistocene hominins. 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).

All these derived features could have been inherited from an earlier ancestor or, if we follow the line of reasoning of Freidline et al. (2013), they would have appeared as a result of repeated convergences. We believe that the most parsimonious explanation is that all these features are derived features that appeared in an ancestral population during the Early Pleistocene and were retained by Neanderthals (synapomorphies) (Gómez-Robles et al., 2007; Bermúdez de Castro and Martínón-Torres, 2012; Martínón-Torres et al., 2013).

As an alternative to the interpretations made by Freidline et al. (2013), we propose a cladogenetic event of the genus *Homo* during the Early Pleistocene but previous to the chronology of *H. antecessor*, from which gradual branching of hominin lineages (species) would have occurred throughout time. This cladogenesis would have been characterized, among other features, by a cranial size increase and the appearance of a derived modern-like face morphology. The different clades resulting from this evolutionary process would have inherited this new facial morphology. Logically, we do not expect that this new face is identical to that of present *H. sapiens* as we are dealing with different and earlier hominin lineages and we can also expect a certain degree of regional variability due to the temporal and spatial distance. *H. antecessor* probably derived from this cladogenesis and, as we have suggested in previous reports (Bermúdez de Castro et al., 2003; Carbonell et al., 2005; Martínón-Torres et al., 2007; Bermúdez de Castro et al., 2012), this species would represent a side branch confined to Western Europe.

Concluding remarks

H. antecessor is characterized by a unique combination of plesiomorphic and derived features. Most plesiomorphic features are present in the dentition (Bermúdez de Castro et al., 1999a). In contrast, *H. antecessor* exhibits most of the derived morphological features related to the modern-like face (Arsuaga et al., 1999), as well as a derived (*sapiens*) facial growth remodeling pattern (Lacruz et al., 2013) and modern pattern of dental development (Bermúdez de Castro et al., 1999b, 2010). Furthermore, *H. antecessor* exhibits some features that were previously considered Neanderthal apomorphies and shares with Neanderthals and modern humans a convex superior border of the temporal squama, and an anterior position of the incisive canal, which is nearly

vertical (Arsuaga et al., 1999). Finally, the mastoid region of the TD6 hominins (ATD6-57) is reminiscent of those of Neanderthals, both in its small and minimally projecting mastoid process and the anteriorly obliterated digastric groove (Arsuaga et al., 1999 and references therein). According to these authors, this feature could be a polymorphism also present in other *Homo* species.

Recently, Freidline et al. (2013) concluded that *H. antecessor* expresses a primitive but unique facial growth pattern, particularly reminiscent of modern humans and earlier Pleistocene humans. In contrast, we suggest that *H. antecessor*, a species that for the moment is confined to an edge of the Eurasian continent, could represent a side branch originated in the cladogenesis of an ancestral Early Pleistocene population. Other Eurasian hominin branches of the cladogenetic event would have inherited a modern-like facial morphology, but not necessarily all the mosaic of features that characterize *H. antecessor*. Each new branch could exhibit a combination of the synapomorphic features shared with the evolutionary ancestor, such as the modern face, and other unique characteristics that are a consequence of the evolutionary changes that occur as they disperse from the source area where the ancestral population evolves (Lohmueller et al., 2008). Thus, in the Bodo assemblage we can observe a coronal orientation of the infraorbital plate (one of the derived *sapiens* facial features), as well as a particular morphology of the humeral distal epiphysis that is similar to that of *H. antecessor* and *H. neanderthalensis* (Carretero et al., 2009). The Bodo specimen could be part of one of the sister lineages of the cladogenesis that in Africa gave rise to *H. sapiens* and in Europe to *H. neanderthalensis* and presents some of the common (synapomorphic) features in varying degrees. In all cases, an expanded fossil sample for the African Middle Pleistocene is deemed necessary to ratify/falsify one or another interpretation. Summarizing, rather than supposing multiple evolution of modern facial morphologies, we consider that the most parsimonious interpretation of the available fossil evidence is that the *sapiens*-like morphology, as well as other derived features, could have appeared in an ancestral Early Pleistocene *Homo*. This population would have been the origin of new hominin branches by cladogenesis. Each new branch would exhibit a combination of features inherited from the ancestral population together with other traits that would be unique to that cladogenetic event.

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References

- Anderson D.L., Thompson G.W., and Popovich F. (1976) Age of attainment of mineralization stages of the permanent dentition. *Journal of Forensic Sciences*, 21: 191–200.
- Arsuaga J.L., Martínez I., Lorenzo C., Gracia A., Muñoz A., Alonso O., and Gallego J. (1999) The human cranial remains from Gran Dolina Lower Pleistocene site (Sierra de Atapuerca, Spain). *Journal of Human Evolution*, 37: 431–457.
- Berger G.W., Pérez-González A., Carbonell E., Arsuaga J.L., Bermúdez de Castro J.M., and Ku T.-L. (2008) Luminiscence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain. *Journal of Human Evolution*, 55: 300–311.
- Bermúdez de Castro J.M. and Martínón-Torres M. (2012) A new model for the evolution of the human Pleistocene populations of Europe. *Quaternary International*, 295: 102–112.
- Bermúdez de Castro J.M., Arsuaga J.L., Carbonell E., Rosas A., Martínez I., and 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., and 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., Rosas A., Carbonell E., Nicolás M.E., Rodríguez J., and 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., and Lozano M. (2003) Gran Dolina-TD6 versus Sima de los Huecos dental samples from Atapuerca: evidence of discontinuity in the European Pleistocene population? *Journal of Archaeological Sciences*, 30: 1421–1428.
- Bermúdez de Castro J.M., Carbonell E., Gómez A., Mateos A., Martínón-Torres M., Muela A., Rodríguez J., Sarmiento S., and 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., and Carbonell E. (2008) 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., Rosell J., Gómez-Polín L., Arsuaga J.L., and Carbonell E. (2010) New immature hominin fossil from European Lower Pleistocene shows the earliest evidence of a modern human dental development pattern. *Proceedings of the National Academy of Sciences, USA*, 107: 11739–11744.
- 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., and Carbonell E. (2012) Early Pleistocene human humeri from the Gran Dolina-TD6 site (Sierra de Atapuerca, Spain). *American Journal of Physical Anthropology*, 147: 604–617.
- Carbonell E., Bermúdez de Castro J.M., Arsuaga J.L., Díez J.C., Rosas A., Cuenca-Bescós G., Sala R., Mosquera M., and 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., Vergés J.M., Bermúdez de Castro J.M., and 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., and Vergés J.M. (2005) An early Pleistocene hominin mandible from Atapuerca-TD6, Spain. *Proceedings of the National Academy of Sciences, USA*, 102: 5674–5678.
- Carretero J.M., Lorenzo C., and 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., and Arsuaga J.L. (2009) A partial distal humerus from the Middle Pleistocene deposits at Bodo, Middle Awash, Ethiopia. *Anthropological Science*, 117: 19–31.
- Chen T.-M., Yanh Q., Hu Y.-Q., Bao W.-B., and Li T.-Y. (1997) ESR dating of tooth enamel from Yunxian *Homo erectus* site, China. *Quaternary Science Reviews*, 16: 455–458.
- Cuenca-Bescós G. and 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., Laplana C., and Canudo J.I. (1999) Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). *Journal of Human Evolution*, 37: 353–373.
- Etler D.A. (1994) The Chinese Hominidae: new finds, new interpretations. Ph.D. dissertation, University of California at Berkeley.
- Etler D.A. (1996) The fossil evidence for human evolution in Asia. *Annual Review of Anthropology*, 25: 275–301.
- Falguères C., Bahain J.-J., Yokoyama Y., Arsuaga J.L., Bermúdez de Castro J.M., Carbonell E., Bischoff J.L., and Dolo, J.-M. (1999) Earliest humans in Europe: the age of Atapuerca fossils, Spain. *Journal of Human Evolution*, 37: 343–352.
- Freidline S.E., Gunz P., Harvati K., and Hublin J.-J. (2013) Evaluating developmental shape changes in *Homo antecessor* subadult facial morphology. *Journal of Human Evolution*, 65: 404–423.
- Gómez-Robles A., Martínón-Torres M., Bermúdez de Castro J.M., Margvelashvili A., Bastir M., Arsuaga J.L., Pérez-Pérez A., Esteban F., and Martínez L.M. (2007) A geometric morphometric analysis of hominin upper first molar shape. *Journal of Human Evolution*, 53: 272–285.
- Harris E.F. and McKee J.H. (1990) Tooth mineralization standards for blacks, and whites from the middle southern United States. *Journal of Forensic Sciences*, 35: 859–872.
- Lacruz R.S., Bermúdez de Castro J.M., Martínón-Torres M., Paine M.L., Carbonell E., Arsuaga J.L., and Bromage T.G. (2013) Facial morphogenesis of the earliest Europeans. *PLOS One*, 8: e65199. doi:10.1371/journal.pone.0065199.
- Liu W., Zhang Y., and Wu X. (2005) Middle Pleistocene human cranium from Tangshan (Nanjing), southeast China: a new reconstruction and comparisons with *Homo erectus* from Eurasia and Africa. *American Journal of Physical Anthropology*, 127: 253–262.
- Lohmueller K.E., Indap A.R., Schmidt S., Boyko A.R., Hernandez R.D., Hubisz M.J., Sninsky J.J., White T.J., Sunyaev S.R., Nielsen R., Clark A.G., and Bustamante C.D. (2008) Proportionally more deleterious genetic variation in European than in African populations. *Nature*, 451: 994–998.
- Lorenzo C., Arsuaga J.L., and 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.
- Maddux S. (2011) A quantitative assessment of infraorbital morphology in *Homo*: testing for character independence and evolutionary significance. Ph.D. dissertation, University of Iowa.
- Martínón-Torres M., Bermúdez de Castro J.M., Gómez-Robles A., Arsuaga J.L., Carbonell E., Lordkipanidze D., Manzi G., and 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., Spěváčková P., Gracia-Téllez A., Martínez I., Bruner E., Arsuaga J.L., and 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.
- Moorrees C.F.A., Fanning E.A., and Hunt E.E. (1963) Age variation of formation stages for ten permanent teeth. *Journal of Dental Research*, 42: 1490–1502.
- Pablos A., Lorenzo C., Martínez I., Bermúdez de Castro J.M., Martinón-Torres M., Carbonell E., and Arsuaga J.L. (2012) New foot remains from the Gran Dolina-TD6 Early Pleistocene site (Sierra de Atapuerca, Burgos, Spain). *Journal of Human Evolution*, 63: 610–623.
- Parés J.M. and Pérez-González A. (1995) Paleomagnetic age for hominid fossils at Atapuerca Archaeological site, Spain. *Science*, 269: 830–832.
- Parés J.M. and Pérez-González A. (1999) Magnetochronology and stratigraphy at Gran Dolina section, Atapuerca (Burgos, Spain). *Journal of Human Evolution*, 37: 325–342.
- Parés J.M., Arnold L., Duval M., Demuro M., Pérez-González A., Bermúdez de Castro J.M., Carbonell E., and Arsuaga J.L. (2013) Reassessing the age of Atapuerca-TD6 (Spain): new paleomagnetic results. *Journal of Archaeological Science*, 40: 4586–4595.
- Pope G.G. (1992) Craniofacial evidence for the origin of modern humans in China. *Yearbook of Physical Anthropology*, 35: 243–298.
- Rak Y. (1986) The Neanderthal: a new look at an old face. *Journal of Human Evolution*, 15: 151–164.
- Rak Y., Kimbel W.H., and Hovers E. (1994) A neandertal infant from Amud Cave. *Journal of Human Evolution*, 26: 313–324.
- Stringer C.B. and Andrews P. (1988) Genetic and fossil evidence for the origin of modern humans. *Science*, 239: 1263–1268.
- Vialet A., Guipert G., Jianing H., Xiaobo F., Zune L., Youping W., Tianyuan L., de Lumley M.-A., and 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.