

Early Pleistocene hominin deciduous teeth from the *Homo antecessor* Gran Dolina-TD6 bearing level (Sierra de Atapuerca, Spain)

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Abstract

Objectives: During the last 13 years, the late Early Pleistocene Gran Dolina-TD6-2 level (Sierra de Atapuerca, northern Spain) has yielded an additional sample of 26 dental specimens attributed to *Homo antecessor*. In this report, we present a descriptive and comparative study of the six deciduous teeth.

Methods: We provide external and internal morphological descriptions following classical terminology, as well as the mesiodistal and buccolingual measurements of the teeth. The internal morphology was described by means of micro-CT technique.

Results: The TD6 deciduous teeth preserve primitive features regarding the *Homo* clade, such as the presence of styles in lower and upper canines and developed anterior and posterior foveae in the dm₂. However, other features related to the complexity of the crown morphology (e.g., cingulum) are not present in this sample. Furthermore, the great reduction of the talonid of the dm_{1s} is also noteworthy. Despite the limited comparative evidence, the presence of a remarkably well-developed tuberculum molare in the dm¹ and dm_{1s} from TD6 can be also considered a derived feature in the genus *Homo*. The TD6 hominins exhibit dental dimensions similar to those of other Pleistocene hominins. The dm_{1s} are buccolingually elongated and the buccolingual diameter of ATD6-93 is the largest recorded so far in the *Homo* fossil record.

Conclusions: This study expands the list of plesiomorphic features of *H. antecessor*, and provides some information on the evolutionary status of this species. However, the identification of some advanced traits evinces a step towards the derived morphology of European Pleistocene teeth. The study of the deciduous dentition confirms the mosaic pattern of *H. antecessor* morphology revealed in previous studies of this hominin sample.

KEYWORDS

deciduous teeth, *Homo antecessor*, Sierra de Atapuerca

1 | INTRODUCTION

The presence in the hominin fossil record of deciduous teeth is limited in comparison with the larger collections of permanent specimens recovered from many African and Eurasian sites. Therefore, any information concerning the morphology and dimensions of the hominin deciduous teeth is always welcomed by the scientific community (e.g., Benazzi et al., 2011; Crevecoeur et al., 2010; Howell & Coppens, 1973; Hublin, 2006; Keyser, Menter, Moggi-Cecchi, Pickering, & Berger, 2000; Mallegni & Ronchitelli, 1989; Peretto et al., 2015; Toussaint et al., 2010; Tillier, Hardy, David, Girard, & Dłatchenko, 2013; Zanolli, Bayle, & Machiarelli, 2010, 2012). Several studies suggest that deciduous nonmetric dental traits are useful tools in assessing the biological relationships of human populations (Tocheri, 2002, and references therein). Furthermore, it is generally accepted that the deciduous dentition is more evolutionarily conservative than the permanent dentition “and are thus relatively more useful for distinguishing specimens at various taxonomic levels” (Bailey, Benazzi, Buti, & Hublin, 2016 and references therein; Keyser et al., 2000, p. 194).

Here we describe unpublished deciduous teeth recovered from the Gran Dolina-TD6 site in Sierra de Atapuerca (Spain) during the last decade. Our aim is to present a descriptive and comparative study of these teeth which, apart from the specimen recovered from Barranco León [Orce, Spain (Toro-Moyano et al., 2013)], represent the only available information on the deciduous dentition in the European Early Pleistocene.

The TD6 level (Bermúdez de Castro, Rosas, & Nicolás, 1999a) has been divided in three sublevels: TD6-1, TD6-2, and TD6-3 (Bermúdez de Castro et al., 2012; Campaña et al., 2016). The human fossils, as well as more than 300 artefacts and several thousand micro- and macromammal fossil remains (Carbonell et al., 1999; Cuenca-Bescós, Laplana, & Canudo, 1999; García & Arsuaga, 1999; van der Made, 1999), come from the sublevel TD6-2. Parés and Pérez-González (1995, 1999) observed a polarity reversal between TD7 and TD8, interpreted as the Matuyama/Brunhes boundary, meaning that levels TD8 to TD11 were deposited during the Middle Pleistocene, whereas levels TD7 to TD1 were deposited during the Early Pleistocene. A combination of paleomagnetic data and ESR/U-series ages suggests an age range between 0.78 and 0.86 million years ago (Ma) for the TD6 level (Falguères et al., 1999). Thermoluminescence (TL) dates on samples taken at the TD7 level, one meter below the Brunhes/Matuyama boundary give a weighted mean age of 0.96 ± 0.12 Ma for TD7 (Berger et al., 2008). The ESR dating applied to optically bleached quartz grains from TD6 gives dates between 0.60 ± 0.09 Ma and 0.95 ± 0.09 Ma (Moreno et al., 2015). These authors also obtained dates of 0.73 ± 0.13 Ma and 0.85 ± 0.14 Ma for the TD7 level from samples taken under the Matuyama/Brunhes boundary. Using thermally transferred OSL (TT-OSL) dating of individual quartz grains, Arnold et al. (2014) obtained a weighted mean age of 0.84 ± 0.06 Ma for the TD6 level. Finally, Arnold and Demuro (2015) have undertaken a series of TT-OSL suitability assessments on known-age samples from TD6. Using this method, they obtained a weighted average age of

0.85 ± 0.04 Ma for TD6-3. Summarizing, and taking into account the biostratigraphic information from TD6 (Cuenca-Bescós et al., 1999, 2015), we consider that the TD6 hominins could be assigned to the MIS 21.

2 | MATERIALS

The deciduous dental sample of the TD6 hominin assemblage includes eight *H. antecessor* specimens. In our first study of the TD6 teeth (Bermúdez de Castro et al., 1999a) we presented the description of the two deciduous teeth: the upper canine (dc^1) and the first molar (dm^1) preserved in situ in the maxilla ATD6-14. The other deciduous teeth are an upper lateral incisor (di^2), an upper second molar (dm^2), a lower canine (dc_1), two lower first molars (dm_1), and a lower second molar (dm_2). One of the dm_1 s and the dm_2 belong to the immature mandible ATD6-112 (Bermúdez de Castro et al., 2010).

In previous papers (Bermúdez de Castro et al., 1999a), we suggested a minimum number of eleven individuals (MNI) for the current TD6 hominin assemblage. Due to the considerable fragmentation of the hominin remains (see Carbonell et al., 2010; Fernández-Jalvo, Díez, Cáceres, & Rosell, 1999; Saladié et al., 2012) we have serious difficulties to ascertaining this estimate. In Table 1 we present the specimens described in this study and a re-evaluation of the MNI.

The so-called Aurora Archaeostratigraphic Set (Bermúdez de Castro et al., 2008), which corresponds to the TD6-2 sublevel, includes at least two strata with human fossil remains. These and other strata are condensed near the wall of the cave, where a test pit was made during the 1990s. A new stratigraphic study confirms not only the complexity of the TD6 level, but also that the fossils and artefacts were accumulated in the cave by geological processes, derived from the adjacent slope above the cave or the cave entry (Campaña et al., 2016). Therefore, it is possible that the current *H. antecessor* hypodigm includes a combination of various human occupations of the Gran Dolina cave. Although the time elapsed among these hypothetically different occupations was relatively short, we must be aware that the identified individuals may not correspond to the same event and the MNI may be as high as fifteen. Awaiting clarification from future excavations at the TD6 level, this demographic assessment must be considered preliminary. However, it is interesting to note that between 70% (for the MNI) and 80% (if the maximum number of individuals is fifteen) of the individuals are immature.

It must be kept in mind that although the TD6 hominins exhibit a modern human pattern of dental development (Bermúdez de Castro et al., 1999b), the rates of dental growth in *H. antecessor* may be faster than those of *H. sapiens* and therefore the ages at death given in Table 1 may be overestimated.

3 | METHODS

The external morphology is described from direct observation following both classic and more recent studies (e.g., Grine, 1984; Johanson, White, & Coppens, 1982; Moggi-Cecchi, Grine, & Tobias, 2006; Tobias,

TABLE 1 Individuals represented in the TD6 hominin assemblage

Hominin	A/I	Specimens	Age at death ^a
H1	Immature	ATD6-1 (LC ₁), ATD6-2 (LI ₂), ATD6-3 (RP ₃), ATD6-4 (RP ₄), ATD6-5 (R mandible fragment (M ₁ -M ₃), ATD6-6 (fragment of RLC ₁), ATD6-7 (RP ₃), ATD6-8 (RP ₄), ATD6-9 (LP ₄), ATD6-10 (RM ₁), ATD6-11 (LM ₁), ATD6-12 (RM ₂), ATD6-13 (Left maxillary fragment, C ¹ -P ³), ATD6-5a,b,c (some small isolated fragments of the mandible ATD6-5).	13.5–14.5
H2	Immature	ATD6-14: left maxillary fragment with dc ¹ -dm ¹ , and some permanent germs I ¹ , I ² , C ¹ , P ³ , and P ⁴ inside.	3.5–4.0
H3	Immature	ATD6-69: maxilla and left zygomatic bone with LP ³ , M ¹ , and unerupted M ² , M ³ , and R I ² to M ¹ .	10.0–11.0
H4	Adult	ATD6-48, LI ₂ .	Young
H5	Immature	ATD6-94 (RM ₁), ATD6-103 (RM ₁).	5.0–6.0
H6	Adult	ATD6-96, left hemimandible with C ₁ to M ₃	Young
H7	Adult	ATD6-113, left mandibular fragment with M ₂ -M ₃ .	Young
H8	Immature	ATD6-112, right mandibular fragment with dm ₁ , dm ₂ , and the germs of I ₂ , C ₁ , P ₃ , P ₄ , and M ₁ .	3.5–3.9
H9	Immature	ATD6-102 (di ²).	2.5–3.0
H10	Immature	ATD6-125, right LP ₄	13.5–14.5

A/I: Adult/Immature.

^aAccording to modern human standards.

1991; Zanolli, Grine, Kullmer, Schrenk, & Macchiarelli, 2015). When necessary, a binocular microscope was also used. Mesiodistal (MD) and buccolingual (BL) dimensions of the crowns were measured with a standard sliding caliper and recorded to the nearest 0.1 mm following the technique of Flechier, Lefèvre, and Verdère (Lefèvre, 1973). Morphological and metrical data were obtained from the literature, except in the case of the Arago sample and the dm₁ from Barranco León for which the originals were observed and measured by JMBC and MMT. A recent *H. sapiens* sample was also measured (CCG and JMBC). This sample is formed by naturally shed deciduous teeth of living Spanish children.

Concerning the internal morphology, we have made comparisons with two deciduous specimens of the Atapuerca-Sima de los Huesos (SH) dental collection, as well as with Neanderthal and *Homo sapiens* dental samples obtained from NESPOS, ESRF, and CENIEH databases. Additional information of the internal morphology (e.g., Barranco León, Qesem, and Sangiran) was obtained from the literature (Fornai et al., 2016; Toro-Moyano et al., 2013; Zanolli et al., 2012, 2015). It is a common practice that dental anthropologists use the expression of morphological features of both the permanent and deciduous teeth to study relationships between populations, assuming that this expression is genetically modulated. Usually, results based on permanent and deciduous morphology are very similar (see Edgar & Lease, 2007, for a review of the literature concerning this matter). Therefore, and as an orientation for the readers, in this report we have followed the Arizona State University Dental Anthropology System (ASUDAS; Turner, Nichol, & Scott, 1991) and Martínón-Torres, Bermúdez de Castro, Gómez-Robles, Prado-Simón, and Arsuaga, (2012) for the identification of morphological features. Additionally, for the trigonid crests we

employed Martínez de Pinillos et al. (2014) and for the assessment of the talonid crests and the entoconid mesial ridge we followed the standards by Martínón-Torres et al. (2014). Although these methods have been devised from permanent teeth we found they could be applied to the deciduous morphology as well.

In order to study the dentine morphological characteristics of *H. antecessor*, the sample was scanned with a microtomographic Phoenix v/tome/xs of GE Measurement, housed at the CENIEH with the following parameters: 130 kV, 150 μA, and 0.2 Cu filter resulting in an isometric voxel size of 18 μm. Tomographic data were segmented and visualized with Amira 6.0.0.

4 | RESULTS

4.1 | External morphology

4.1.1 | Deciduous left upper lateral incisor (ATD6-102)

The TD6 sample includes one specimen of this class (Figure 1A). ATD6-102 is remarkably well preserved. A thin flake, about 4 mm long, is missing from the lingual aspect of the root. Another thin enamel flake is missing from the mesiobuccal aspect of the crown. The latter probably occurred antemortem, since the edges of the damaged area are rounded and the surface shows fine striations, similar to those observed in the rest of the buccal surface. These striations are well visible under 5× magnification. ATD6-102 is slightly worn, showing a very narrow dentine strip on the incisal edge (degree 2 of Molnar's [1971] classification). In modern humans the di² finishes its formation (stage H2) at about 2.5 years of age (Liversidge & Molleson, 2004). Because this tooth exhibits minimal occlusal wear, the most probable age at

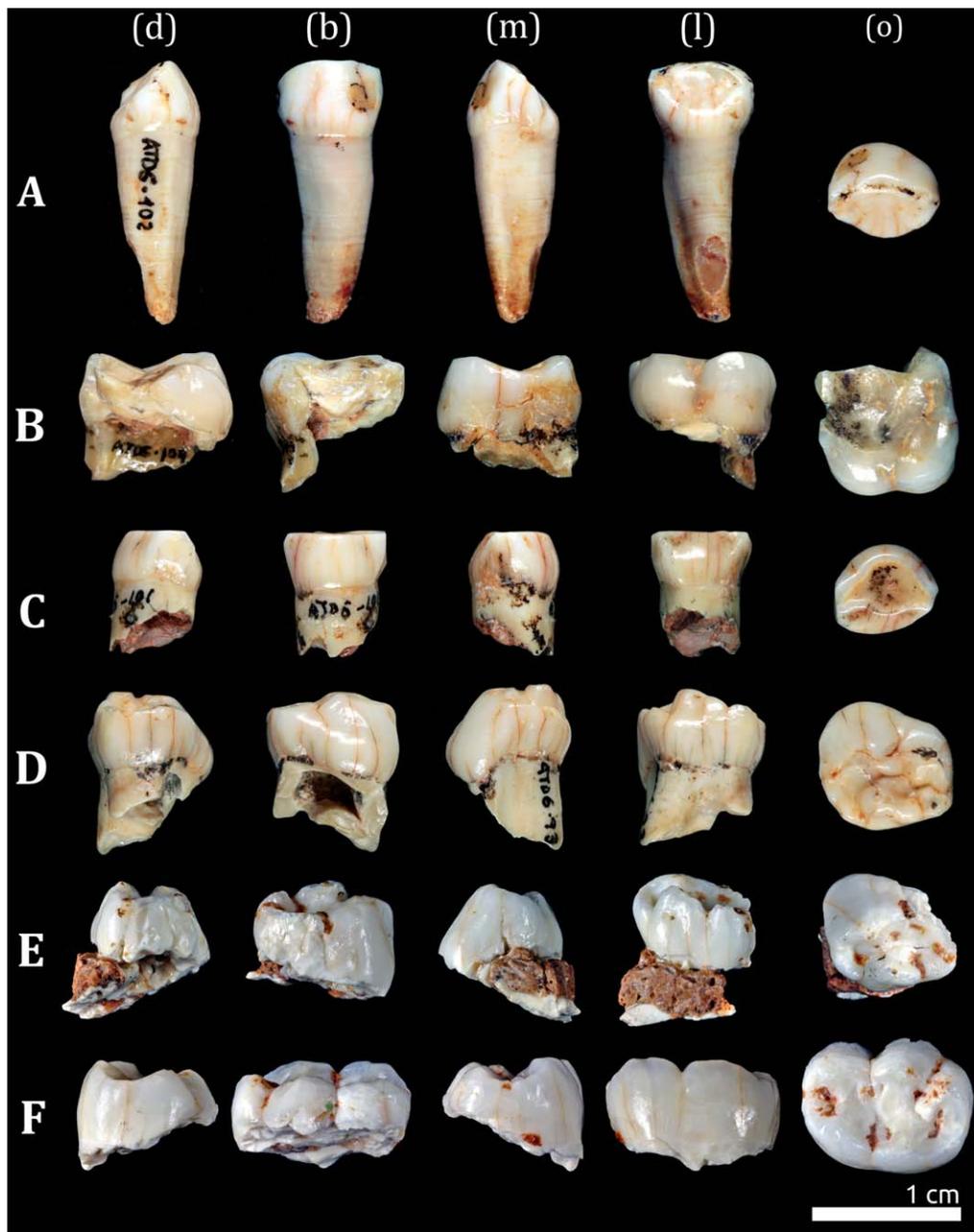


FIGURE 1 Distal (d), buccal (b), mesial (m), lingual (l), and occlusal (o) aspects of (A) ATD6-102 (di2); (B) ATD6-104 (dm2); (C) ATD6-101 (dc); (D) ATD6-93 (dm1); (E) ATD6-112 (dm1), and (E) ATD6-112 (dm2)

death of this individual was between 2.5 and 3.0 years according to the standards of modern humans. A small mesial interproximal wear facet is present, but there is no a distal interproximal facet. In lateral view, the labial surface of this tooth is gently convex from the cervical line to the incisal rim. From the occlusal aspect, the labial convexity is gentle (corresponding to ASUDAS grade 3). The mesial and distal marginal ridges are weakly developed conforming a moderate shovel shape, and they merge with a moderate lingual basal eminence (grade 2, according to Martín-Torres et al., 2012). Two barely perceptible grooves run vertically from this eminence and disappear in the lingual surface, delimiting a smooth central ridge. The root is complete, slightly curved towards distal. It measures 13.0 mm at the buccal aspect from

the cementum–enamel junction (CEJ) to the apex. The cross-section of the root at the cervical level is ovoid in shape, with the longer axis orientated in a mesiobuccal to distolingual direction. A wide developmental groove runs along the lower half of mesial aspect of the root.

The comparative *di*² hominin sample is small. From the morphological point of view there are no key features to distinguish between different taxa, except for the smaller size and simplified morphology of the *H. sapiens* specimens. The prominence of the mesial and distal marginal ridges and the cervical eminence is variable in all taxa and the shovel-shape is generally not well developed. The crown dimensions of ATD6-102 are somewhat smaller than in the Neandertal sample (Table 2).

TABLE 2 Mesiodistal (MD) and buccolingual (BL) measurements of the deciduous upper lateral incisor, ATD6-102, the lower canine ATD6-101, the lower first molars ATD6-93 and ATD6-112, and the lower second molar ATD6-112 compared with those of other deciduous teeth from different hominin specimens and samples

Species/specimen	N	di ²			dc ₁			dm ₁			dm ₂										
		MD		BL	MD		BL	MD		BL	MD		BL								
		X	SD	X	n	X	SD	X	n	X	SD	X	n	X	SD	X	n	X	SD	X	n
Early Homo (SA) ^a	1	(4.6)	-	4.1	-	1	6.0	-	5.8	-	2	8.75	-	7.50	-	2	11.25	-	9.55	-	
Early Homo (EA) ^b						2	8.95	-	7.30	-	2	11.45	-	9.35	-						
Chinese <i>H. erectus</i> ^c						3	6.16	0.06	5.26	0.06	2	8.75	-	6.80	-	5	11.30	0.66	9.26	0.71	
PCG.2 Kabuh formation ^d											1	10.05	-	8.48	-						
BL02-J54-100 ^e																					
<i>H. antecessor</i> ^f	1	6.0	-	5.1	-	1	7.0	-	6.0	-	2	8.95	-	8.55	-	1	11.4	-	(9.2)	-	
<i>H. heidelbergensis</i> ^g						3	6.56	0.87	6.13	0.72	3	9.43	0.66	8.03	0.40	3	10.36	0.30	9.56	0.50	
<i>H. neanderthalensis</i> ^h	9/11	6.43	0.61	5.52	0.43	13	6.77	0.61	6.06	0.54	24	8.83	0.44	7.56	0.47	32	10.55	0.52	9.40	0.48	
Qesem QC2, QC3 ⁱ											1	9.10	-	7.10	-	1	11.3	-	9.5	-	
<i>H. sapiens</i> (pooled sex) ^j	32	5.17	0.29	4.75	0.27	21	5.82	0.45	5.40	0.33	18	7.91	0.36	6.90	0.39	18	10.03	0.40	8.67	0.41	

^aThis sample (SA: South Africa) includes specimens from Sterkfontein and Drimolen (Keyser et al., 2000; Moggi-Cecchi et al., 2015, 1995).

^bThis sample (EA: East Africa) includes specimens from Koobi Fora (Leakey & Wood, 1973, 1974; Wood, 1991).

^cThis sample includes specimens from Zhoukoudian (Weidenreich, 1937).

^dFrom Zanolli et al. (2012).

^eFrom Toro-Moyano et al. (2013).

^fThis study.

^gThis sample includes the original specimens from the Arago site. Measurements taken by JMBC.

^hThis sample includes specimens from the following sites: Amud, Archi, Arcy-sur-Cure, La Chaise (Bourgeois Delauney), Chateaufneuf, Combe-Grenal, Cova Negra, Ehringsdorf, Engis, Gibraltar 2, Kebara, Krapina, La Ferrassie, Roc de Marsal, Pech de l'Azé, Placard, Saleman, Shanidar, Spy, Staroselje, Subalyuk, Taubach, Teshik-Tash, Uluzzo, Zaskalnaya. Data taken from: (Arsuaga et al., 1989; Bailey and Hublin, 2006; Crevecoeur et al., 2010; Madre-Dupouy, 1985; Tillier, 1979; Wolpoff, 2012).

ⁱFrom Hershkovitz et al. (2016).

^jRecent human sample. Measurements taken by JMBC and CGC.

4.1.2 | Deciduous left upper second molar (ATD6-104)

The only dm^2 of the TD6 assemblage is poorly preserved (Figure 1B). A substantial part of the buccal cusps and the mesial crown of ATD6-104 are missing, and it is not possible to obtain the MD and BL measurements. Only a minimal part of the distal root is still preserved. The occlusal surface is worn, showing wide dentine patches (degree 4 of Molnar's [1971] classification). A wide and well-marked distal interproximal facet is present. According to modern human standards of dental development the owner of this tooth died between about 6.0 and 12.0 years (Al Qahtani, Hector, & Liversidge, 2010). In spite of the bad preservation, it is possible to see that the occlusal outline is a regular and symmetrical square, with a well-developed hypocone (grade 4 of ASUDAS). No metaconule is present. The lingual cusps of ATD6-104 are aligned transversely with the buccal cusps forming an approximately squared occlusal polygon and a regular contour. In contrast, the two preserved Arago dm^2 s (Arago 12 and 27) show a relatively distal displacement of the lingual cusps forming a rhomboidal occlusal polygon. The same morphology is present in the rest of the Neandertals analysed (Chateaufort 2, Roc de Marsal, and in all the Krapina dm^2 s), as well as in the Pontnewydd PN4 specimen (Compton & Stringer, 2015). In ATD6-104 a crista obliqua connecting the protocone and metacone is present (grade 1 of Martín-Torres et al., 2012). This tooth shows two small ridges and a small depression at the mesiolingual corner of the protocone (Carabelli's complex grade 3 of ASUDAS), whereas a well-developed Carabelli's cusp is observed in the Krapina dm^2 s.

4.1.3 | Deciduous left lower canine (ATD6-101)

The TD6 sample includes one deciduous left lower canine (Figure 1C). This tooth is severely worn (degree 5 of Molnar's [1971] classification) showing a broad dentine patch, as well as marked mesial and distal interproximal wear facets. At the buccal aspect, the preserved height of the crown measures about 3.5 mm. It is not possible to ascertain if the root resorption process began in this tooth. Without additional data we can only speculate that the age at death of the individual was between 6 and 10 years, following the modern human standard. Only about 4 mm of the root is preserved at the buccal aspect. The occlusal outline of the crown is ovoid in shape and asymmetrical. In spite of its advanced wear, the mesial and distal marginal ridges are still visible, suggesting a moderate shovel-shape. The lingual basal eminence is also moderate. A lingual central ridge is barely developed. In lateral view, the labial surface is gently convex from the cervical line to the incisal rim. From the occlusal aspect, the labial convexity is moderate. The expression of mesial and distal vertical grooves along the labial surface (ASUDAS grade 1) suggests the possible presence of mesial and distal cusplets or styles, as in the deciduous upper canine of ATD6-14 (Bermúdez de Castro et al., 1999a).

The morphology of ATD6-101 is not very different from that of Arago and Neandertal specimens. The lingual basal eminence and the mesial and distal marginal ridges in all these canines exhibit a moderate development, whereas the essential ridge can be present (Arago 50) or absent (Spy 645a). The main difference is the presence in ATD6-101 of

potential mesial and distal styles. At least a distal style seems to be present in the deciduous canines from Zhoukoudian (Weidenreich, 1937), as well as in some Neandertals such as Combe Grenal and Pech de LAzé (Madre-Dupouy, 1985). We have not noted the same features in our visual inspections of the Arago specimens. At the buccal face, the Zhoukoudian deciduous canines present a swollen rim at the basal aspect of the buccal face. It is well-differentiated from the rest of the buccal surface, and ascends to a higher level on both the mesial and distal borders forming an arch-like cingulum (Weidenreich, 1937, Plate XXI, Fig. 190). This primitive feature is not present in the deciduous canine of TD6. At the cervical level, the cross-section of the root of ATD6-101 is circular in shape.

Despite the marked interproximal wear facets, the MD dimension of ATD6-101 is larger than the mean values of the Arago, Neandertals, and Zhoukoudian samples (Table 2), whereas the BL dimension of ATD6-101 is similar to that of these samples.

4.1.4 | Deciduous lower first molars (ATD6-93 and ATD6-112)

The TD6 sample includes two specimens of this class. ATD6-93 is an isolated right dm_1 preserving the crown and a minimum part of the roots (Figure 1D). Nevertheless, we can observe that bifurcation of the mesial and distal roots occurs at about 2.0 mm under the cemento-enamel junction (CEJ). ATD6-112 lost a fragment of the distobuccal cusp (Figure 1E), as well as some of the enamel and dentine at the level of CEJ. For this reason, and although the two roots remain included in the mandible, it is not possible to fit the crown and roots. ATD6-93 exhibits small dentine patches in all cusps (degree 3 of Molnar's [1971] classification), whereas in ATD6-112 wear affects only the enamel, except that there is an almost negligible dentine patch at the protoconid (degree 2-3). A well-marked distal interproximal wear facet is present in ATD6-93, but the possible contact of this tooth with the deciduous canine is not apparent. In ATD6-112 there is no mesial interproximal facet and the distal part of the crown is broken. In modern humans the dm_1 finishes its formation (stage H2) about 2.5 years (Liversidge & Molleson, 2004), whereas the dm_2 finishes its formation about 2.9 years. Given the occlusal wear of ATD6-93, the owner of this tooth probably died between 4.0 and 6.0 years according to the standards of modern humans. ATD6-112 belongs to an immature individual (Bermúdez de Castro et al., 2010) who died at about 3.5–4.0 years according to the modern human standards. In both molars the occlusal outline is strongly asymmetrical, exhibiting a trapezoidal shape due to the marked buccal flaring of the tuberculum molare and the receding mesiolingual corner. The tuberculum molare is well-developed, being expanded both buccally and strongly cervically. Four cusps are present in ATD6-93 and ATD6-112. In these two specimens the protoconid is the largest and it is mesially displaced, followed by the metaconid, the hypoconid, and the entoconid, which is almost vestigial in ATD6-93. The mesial cusps are clearly higher than the distal ones and they occupy a greater portion of the crown. The essential crests of the mesial cusps are joined forming a mid-trigonid crest (MdTC) (type A, continuous MdTC with an absent or discontinuous distal trigonid crest [DTC], from Martínez de Pinillos et al., 2014). The

essential crest of the hypoconid is conspicuous and swollen. The mesial marginal ridge is well marked. An incipient mesioconulid (Grine, 1984: 46) is formed at the mesial aspect of the mesial marginal ridge. In ATD6-93 this ridge is separated by a buccolingually large anterior fovea from the mesial cusps (grade 1 according to Martínón-Torres et al., 2012), whereas in ATD6-112 the anterior fovea is very deep, pit-like, and centrally placed (grade 2 according to Martínón-Torres et al., 2012). In ATD6-93 the groove pattern is well defined. There is a clear contact between the metaconid and the hypoconid (Y-pattern). In this tooth a pit-like posterior fovea is placed between this ridge and the groove which separates the hypoconid from the entoconid. The mesio-buccal groove between the protoconid and the hypoconid ends in a short longitudinal groove, which ascends by the distal slope of the protoconid. A pit is also observed at the lingual slope of the metaconid. In ATD6-112, the groove pattern is less conspicuous due to the dental wear, but it is possible to observe a contact between the metaconid and the hypoconid. Although the posterior part of the crown is damaged, the morphology in this area seems to be similar to that of ATD6-93.

General features of the TD6 dm_1 s fit well the morphology of the genus *Homo* (see Hillson, 1996). The trigonid is clearly larger than the talonid, in contrast to the Early Pleistocene dm_1 s from Sangiran (FS 67) (Putjangan Formation), Barranco León (BLO2-J54-100), the African early *Homo* specimens, and the dm_1 from Qesem where both regions show a similar area (Grine, 1984; Hershkovitz et al., 2016; Leakey & Wood, 1973, 1974; Toro-Moyano et al., 2013). The tuberculum molare is particularly conspicuous in the TD6 dm_1 s. This feature is weak or absent in early *Homo* (Grine, 1984; Leakey & Wood, 1973, 1974; Toro-Moyano et al., 2013). In the Zhoukoudian specimens there is a swollen cervical rim that, according to Weidenreich (1937), would correspond to the tuberculum molare. He also describes the presence of a vestigial paraconid in the mesial marginal ridge of the Zhoukoudian dm_1 s. The same feature has been described in BLO2-J54-100 from Barranco León, which is separated from the metaconid by a deep V-shaped groove that opens towards the lingual face. This groove is also observed in the dm_1 from ATD6-112. The tuberculum molare is not especially marked in the Arago specimens (A11, 34, and 55), and exhibits a variable development in Neandertals (Bailey and Hublin, 2006; Madre-Dupouy, 1985; Mallegni and Ronchitelli, 1989; Tillier, 1979, 1980, 1982; Tillier and Genet-Varcin, 1980; Wolpoff, 1979), as well as in modern humans. The presence of a mesioconulid has been reported in FS 67 from Sangiran (Grine, 1984). A similar incipient swelling of the mesial marginal ridge at the protoconid level is observed in Arago 11 and 34. No other reference to this feature has been noted in the available literature. In TD6 dm_1 s molars, as in other *Homo* specimens, the protoconid is generally the largest cusp. In the TD6 dm_1 s the mid-trigonid crest is high and very conspicuous. The presence of this feature is variable in the *Homo* fossil record. It is present in BLO2-J54-100 from Barranco León (Toro-Moyano et al., 2013) and in the unworn Zhoukoudian 125 (Weidenreich, 1937), but absent in FS 67 from Sangiran (Grine, 1984). Similarly, the feature is present in Arago 11 and 34, and less conspicuous in Arago 55. The mid-trigonid crest is generally

well developed in Neandertals (Bailey and Hublin, 2006; Madre-Dupouy, 1985; Mallegni & Ronchitelli, 1989; Tillier, 1979; Tillier & Genet-Varcin, 1980), but absent in specimens from the Upper Paleolithic assigned to *H. sapiens* (Bailey & Hublin, 2006). In the dm_1 from Qesem the anterior fovea is connected to the central basin by a longitudinal fissure (Hershkovitz et al., 2016). Interestingly, in the recent *H. sapiens* studied here 17 out of 18 specimens (94.5%) exhibit a well-developed mid-trigonid crest.

Regarding the size of these deciduous molars (Table 2), ATD6-93 is comparatively broader (breadth: 8.8 mm) and in the range of the larger *Homo* specimens due to its strong tuberculum molare. The BL breadth of ATD6-112 (BL: 8.3 mm) is somewhat less, whereas the MD dimension of both TD6 specimens is similar (MD: 9.0 mm for ATD6-93, and 8.9 mm for ATD6-112). These measurements are in the range of variation of the genus *Homo*, in which the largest specimens are represented by the dm_1 from Barranco León (BLO2-J54-100) and Arago 66 (see Table 2). Surprisingly, the BL dimensions of the Zhoukoudian dm_1 s are low and similar to those obtained in the modern human sample. Although Weidenreich (1937, p. 5) clearly explains the method he used to obtain the dental measurements, there is no scale in the Plates to check his results.

4.1.5 | Deciduous lower second molars (ATD6-112)

The TD6 assemblage includes one specimen belonging to the right hemimandible ATD6-112 (Figure 1F). The lower part of the crown at the mesial and buccal sides is missing, and it is not possible to fit the crown to the roots, which are included in the alveoli of the mandible. Wear has erased a part of the enamel in all cusps, but the dentine is only visible at the hypoconid (degree 2–3 of Molnar's [1971] classification). ATD6-112 shows the five principal cusps. They are well-developed and clearly separated. The buccal face is bilobed in occlusal view. The size of the protoconid, metaconid and hypoconid is similar, followed by a well-developed entoconid and a small hypoconulid (corresponding to ASUDAS grade 2). There is a deeply incised narrow mid-trigonid crest connecting the essential crest of protoconid and metaconid, crest type A from Martínez de Pinillos et al. (2014). An incised mid-trigonid crest, similar to that present in the dm_2 of ATD6-112 is observed in three specimens (16.6%) of the modern human sample, whereas one specimen exhibits a well-developed mid-trigonid crest. That is, the different expressions of mid-trigonid crest is present in 22.2% dm_2 s of the modern human sample used in this study. Metaconid and hypoconid of ATD6-112 show a minimum contact (Y-pattern). The mesial marginal ridge is well developed, and its central aspect forms a small cuspule or mesioconulid. The anterior fovea is particularly deep and broad due to the small development of the mid-trigonid crest. The essential crest of the hypoconulid joins with the essential crest of the entoconid. This crest and the broad distal marginal ridge delimit a deep, groove-like, and lingually placed posterior fovea. A pit-like posterior fovea is observed in 9 out of 18 modern human specimens (50%). The cusps tips of the dm_2 of ATD6-112 are not especially internally compressed, as reported in other fossil specimens (Bailey & Hublin, 2006; Toussaint et al., 2010; Weidenreich, 1937). There are no signs of buccal cingulum in the TD6 dm_2 sample.

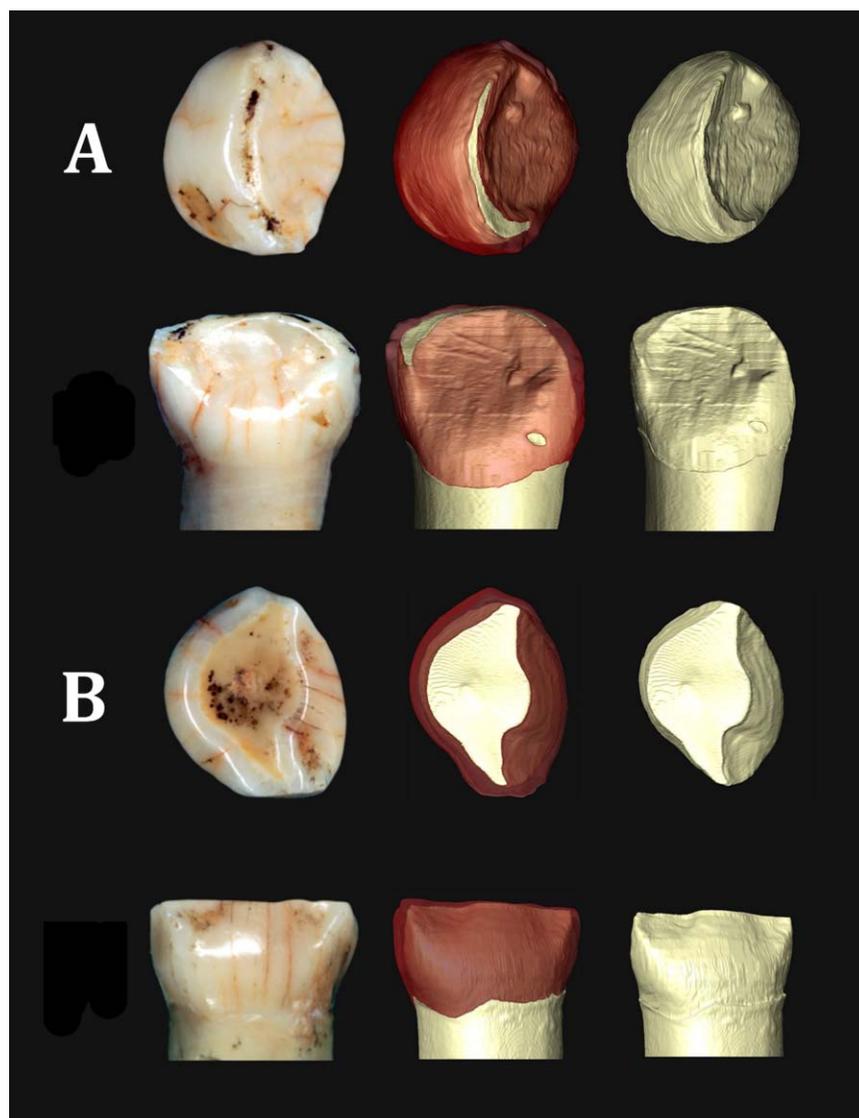


FIGURE 2 Inner morphology of A) ATD6-102 (di2); and B) ATD6-101 (dc)

The MD dimension (11.4) is large and similar to that of other Early Pleistocene *Homo* specimens (Table 2), and larger than the mean values of the Neandertal and Arago samples. The crown fracture of ATD6-112 prevents a precise measurement of its BL dimension.

4.2 | Internal morphology

4.2.1 | Deciduous left upper lateral incisor (ATD6-102)

The labial surface of ATD6-102 (Figure 2A) exhibits a pronounced convexity (grade 4 of ASUDAS) and the elevation of the marginal ridges is marked (grade 3 of ASUDAS). The mesial marginal ridge of the di² is more developed compared to the distal one. On the lingual surface of the EDJ we observed a small protuberance barely perceptible at the enamel to the naked eye.

4.2.2 | Deciduous left upper second molar (ATD6-104)

In the ATD6-104 EDJ (Figure 3A) the crista obliqua is present and continuous (grade 1 of ASUDAS). There are two small depressions delimit-

ing faint ridges at the mesiolingual corner of the protocone. They correspond to a Carabelli's complex grade 3 of ASUDAS that is less marked than at the enamel. There is a well-developed hypocone (grade 4 of ASUDAS) whereas the metaconule is absent.

4.2.3 | Deciduous left lower canine (ATD6-101)

In ATD6-101 (Figure 2B) the expression of features at the EDJ corresponds to that observed at the enamel. The occlusal outline of the crown is asymmetrical. The mesial and distal marginal ridges are still visible. The mesial ridge is larger than the disto-lingual (grade 1, according to Martín-Torres et al., 2012). On the contrary the distal accessory ridge is weakly developed (grade 1, according to Martín-Torres et al., 2012). The lingual basal eminence is moderate and the lingual surface also exhibits a mesial and a distal marked grooves. Finally, from the occlusal aspect, the labial and lingual surfaces exhibit moderate convexity.

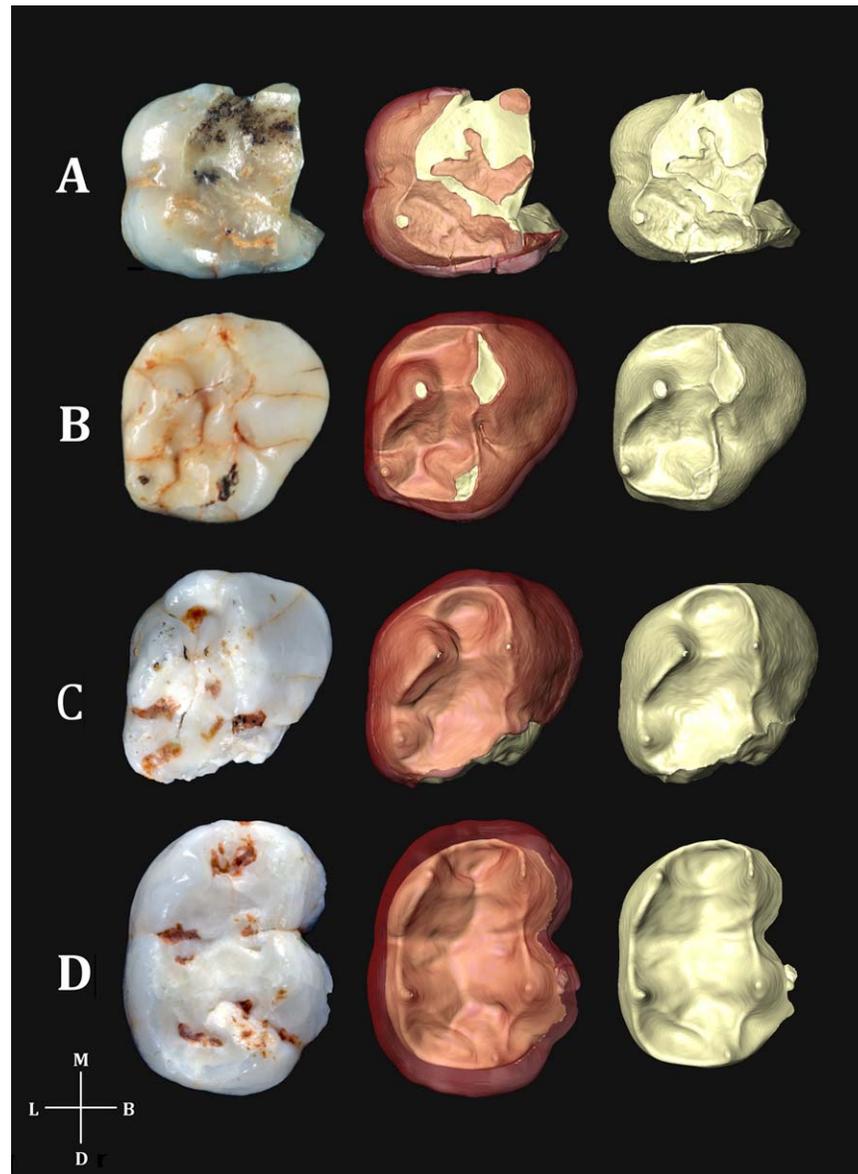


FIGURE 3 Inner morphology of (A) ATD6-104 (dm₂); (B) ATD6-93 (dm₁); (C) ATD6-112 (dm₁); and (D) ATD6-112 (dm₂)

4.2.4 | Deciduous lower first molars (ATD6-93 and ATD6-112)

The right dm₁ ATD6-93 (Figure 3B; Table 3) exhibits a well-developed tuberculum molare in the buccal part of the protoconid, giving a strongly asymmetrical shape to the occlusal outline of the molar. The tooth exhibits a marked mesial marginal ridge, with a small protuberance, which may correspond to a vestigial paraconid. The mesial marginal ridge is separated from the metaconid by a deep groove that extends lingually. This feature has also been identified the Barranco León specimens (Toro-Moyano et al., 2013). The anterior fovea forms a slight linear depression (grade 1 according to Martínón-Torres et al., 2012). Following Martínez de Pinillos et al. (2014) trigonid crest scoring system, we classified the crest exhibited by ATD6-93 as type 1, or continuous middle trigonid crest. There is no expression of talonid crest in the EDJ. Finally, on the disto-buccal surface of the protoconid there is

a ridge running distally. This trait could correspond to a moderate protostylid at the EDJ (grade 4 of ASUDAS), or to a mesial protoconid ridge *sensu* Hlusko (2004), the latter being mostly identified so far in permanent molars of Asian *H. erectus* (Xing, Martínón-Torres, Bermúdez de Castro, Xiuji, & Liu, 2015, 2016) and some isolated Sima de los Huesos (Martínez de Pinillos et al., 2014).

The fracture exhibited by the right dm₁ of ATD6-112 (Figure 3C; Table 3) at its disto-buccal surface prevents the assessment of the hypoconid size, the presence of hypoconulid and the outline shape of the molar. The expression of the tuberculum molare is clear, but less developed than in ATD6-93. The anterior fovea is deep (grade 2 according to Martínón-Torres et al., 2012) and the mesial marginal ridge, in contrast to that of ATD6-93, follows the occlusal outline and ends up in the metaconid. The expression of the trigonid crest corresponds to type 1 (Martínez de Pinillos et al., 2014) and we did not identify a talonid crest.

TABLE 3 Expression of some features of the EDJ in the dm₁s and dm₂s of *H. antecessor* and other hominin specimens

Site	Species	Specimen	Tooth	TgC	TM	C5	C6	C7	TIC	Protostylid	AF	Asy	EMR
Sangiran	<i>H. erectus</i>	PCG.2	dm ₂ L	1	-	x	x	-	-	x	x	NA	-
Barranco León		BL02-J54-100	dm ₁ L	1	-	x	-	-	-	-	-	x	-
Gibraltar	<i>H. neanderthalensis</i>	HA-40.26	dm ₁ R	1	-	x	-	-	-	-	x	-	-
		HA-40.26	dm ₂ R	1	-	x	x	-	-	-	x	-	x
Abri Suard	<i>H. neanderthalensis</i>	S14 5	dm ₂ R	1	-	x	x	-	-	-	x	-	x
Krapina	<i>H. neanderthalensis</i>	d62	dm ₂ L	1	-	x	-	-	-	-	x	-	x
		d63	dm ₂ L	1	-	x	-	-	-	-	x	-	x
		d64	dm ₂ L	1	-	x	-	-	-	-	x	-	x
		d65	dm ₂ L	1	-	x	-	-	6	-	x	-	x
		d66	dm ₂ L	1	-	x	-	-	-	-	x	-	x
		d67	dm ₁ L	1	-	x	-	-	-	-	x	x	x
		d68	dm ₂ R	10	-	xx	-	-	-	-	x	-	x
Atapuerca-Sima de los Huesos ^a		AT-2398	dm ₂ L	1	-	x	-	-	-	-	x	-	x
		AT-947 ^b	dm ₂ R	1	NA	NA	NA	NA	NA	-	x	-	NA
Mirador	<i>H. sapiens</i>	MIR4_P22_294	dm ₁ L	1	x	NA	-	-	-	-	NA	x	-
		MIR4_P22_294	dm ₂ L	NA	x	x	-	-	-	-	-	-	-
Qafzeh	<i>H. sapiens</i>	15	dm ₁ R	1	x	x	-	-	-	-	x	x	-
		15	dm ₁ L	1	x	x	-	-	-	-	x	x	x
		15	dm ₂ R	-	-	x	-	-	-	-	-	-	x
		15	dm ₂ L	-	-	x	x	-	-	-	-	-	x
Lagar Velho	<i>H. sapiens</i>		dm ₂ R	-	-	x	-	-	3	-	-	x	
La Madeleine	<i>H. sapiens</i>	4	dm ₁ R	-	-	-	-	-	-	-	x	x	-
		4	dm ₁ L	1	x	x	x	x	x	x	x	x	x
		4	dm ₂ R	-	-	x	-	-	1	-	-	-	-
		4	dm ₂ L	-	-	x	-	-	-	-	-	-	-
Qesem		QC2	dm ₂ L	6	-	x	x	-	-	-	-	x	
Gran Dolina	<i>H. antecessor</i>	ATD6-93	dm ₁ R	1	x	-	-	-	-	-	x	x	-
		ATD6-112 ^c	dm ₁ R	1	x	NA	NA	-	-	-	x	NA	-
		ATD6-112 ^d	dm ₂ R	1	NA	x	-	-	-	-	x	NA	x

x: present; -: not present; NA: not assessed.

TgC: trigonid crest; TM: tuberculum molare; C5: cusp 5; C6: cusp 6; C7: cusp 7; TIC: talonid crest; AF: anterior fovea; Asy: asymmetry; EMR: entoconid mesial ridge.

^aThis hominin sample has been excluded from *H. heidelbergensis* (Arsuaga et al., 2014), but no other species has been proposed so far.

^bAT-947: tooth heavily worn.

^cATD6-112: teeth fractured on the distal side.

^dATD6-112: teeth broken on buccal side.

4.2.5 | Deciduous lower second molars (ATD6-112)

The right dm₂ of ATD6-112 (Figure 3D; Table 3) presents a fracture that has damaged the buccal side of the crown. The five main cusps are expressed and the occlusal outline is symmetrical with a well-developed mesial marginal ridge. The EDJ presents a pronounced ante-

rior fovea (grade 2 according to Martín-Torres et al., 2012) and a mid-trigonid crest type 1 (Martínez de Pinillos et al., 2014), although it is lower than those of the dm₁s. This type of crest is a common finding in the comparative sample, except for d68 (type 10) and QC2 (type 6) (see Table 3 and Fornai et al., 2016; Zanolli et al., 2012, 2015). The

distal fovea is well-developed, lingually displaced, and delimited by the distal marginal ridge and a continuous crest that joins the entoconid and the hypoconulid. We observed a mesial entoconid ridge that, according to Martín-Torres et al. (2014), could be interpreted as a "trace" of Korenhof's talonid crest type 4.

The comparison of some morphological features of the EDJ in the deciduous first and second lower molars of *H. antecessor* and other available hominins is presented in Table 3. A continuous mid-trigonid crest like that of the *H. antecessor* deciduous molars is present in Barranco León and Qesem specimens, as well as in the totality of the Sangiran dm_2 (Zanoli et al., 2012), *H. neanderthalensis* and Atapuerca-Sima de los Huesos samples, whereas only 4 out of 11 Pleistocene and Holocene *H. sapiens* specimens present a continuous mid-trigonid crest. The type 1 of this crest is also the most frequent in the comparative sample. The expression of tuberculum molare in the dm_1 s and the concomitant asymmetry of the occlusal outline are shared with several fossil specimens, such as Qafzeh, La Madeleine and the modern *H. sapiens* specimen from El Mirador (Spain). The absence of a C6, C7, and protostylid is the common condition in our comparative sample, with the exception of the Sangiran specimens and the left dm_1 from La Madeleine that express a protostylid. The expression of an entoconid mesial ridge in the dm_2 s is common in all Neandertals, Atapuerca-Sima de los Huesos, and in *H. antecessor*, whereas this feature is absent in the two Sangiran specimens and in some Pleistocene and Holocene *H. sapiens* specimens.

5 | DISCUSSION AND CONCLUDING REMARKS

Some authors have emphasized the diagnostic value of the deciduous teeth (e.g., Bailey & Hublin, 2006; Benazzi et al., 2012; Keyser et al., 2000; Leakey, Feibel, McDougall, Ward, & Walker, 1998; White, Suwa, & Asfaw, 1994). Thus, it is advisable to further explore the utility of the features outlined in this study in larger hominin samples. Regarding the dm^2 ATD6-104 the lingual cusps are aligned transversally with the buccal cusps forming an approximately squared occlusal polygon and a regular contour. According to Gómez-Robles et al. (2007), this is the plesiomorphic condition of the *Homo* clade for the M^1 s, whereas a relatively distal displacement of the lingual cusps forming a rhomboidal occlusal polygon in which lingual cusps are distally displaced and the hypocone protrudes in the external outline is a derived condition in *H. antecessor*, *H. heidelbergensis*, and *H. neanderthalensis*. If we consider a theoretical genetic correlation between the morphology of the dm^2 s and that of the M^1 s (see Bailey, Benazzi, & Hublin, 2014 for a discussion on this matter; Edgar & Lease, 2007), it is interesting to observe that this derived condition is observed in the available Neandertal dm^2 specimens, in Pontnewydd PN4, as well as in Arago 12 and Arago 27. Therefore, the possible correlation of this feature between the dm^2 s and the M^1 s of different hominin species/paleodemes should be explored in the future.

It has been stated that the size of the talonid and the trigonid is similar in the dm_1 s of *Australopithecus* and early *Homo* (Hillson, 1996;

Leakey et al., 1998; White et al., 1994). However, this is not the case of later *Homo*, like TD6 dm_1 s, where the talonid is greatly reduced in comparison to the size of the trigonid (derived condition). It is interesting to note that the trigonid and the talonid of the 1.4 Ma old dm_1 from Barranco León display a similar size. Thus, this specimen would be more primitive than TD6 in this regard (Toro-Moyano et al., 2013).

The tuberculum molare is extremely developed in the upper and lower dm_1 s from TD6 (see Bermúdez de Castro et al., 1999a), whereas it is weak or absent in early *Homo* (Grine, 1984; Leakey & Wood, 1973, 1974; Toro-Moyano et al., 2013). The absence or weak presence of this feature would be the primitive condition in hominins (see Keyser et al., 2000), whereas a well-developed tuberculum molare in the dm_1 s could be a derived feature of later *Homo*. Regarding the mid-trigonid crest, Bailey and Hublin (2006) have emphasized the presence of this feature in the dm_1 s of the Neandertals. According to these authors, this feature allows the distinction between these hominins and the Upper Paleolithic sample they observed. However, it is interesting to remark that the mid-trigonid crest in the dm_1 s is an extremely variable feature in hominins, and its pattern of expression may be less clear-cut than previously thought. A mid-trigonid crest is present in Taung and Stw 296, but it is absent in Stw 104 (Moggi-Cecchi et al., 2006). Similarly and as we stated above, the presence of this feature is variable in Pleistocene *Homo* and extremely frequent in the modern sample studied here. Therefore, we must be very cautious regarding the taxonomic value of this trait.

The dm_2 of ATD6-112 lacks any structure related to the buccal cingulum. Thus, ATD6-112 seems more derived than the Plio-Pleistocene specimens in this aspect, although more evidence would be necessary to evaluate the polarity of this feature in the genus *Homo*. The dm_2 of ATD6-112 exhibits mid-trigonid crest and well-developed anterior and posterior foveae. Again, a mid-trigonid crest in the dm_2 has been considered as a diagnostic feature of Neandertals in comparison to modern humans (Bailey & Hublin, 2006). This feature is only occasionally absent in Neandertals, like Chateaufort 2 and Combe-Grenal (Madre Dupouy, 1985). The mid-trigonid crest is also absent in the dm_2 -QC2 from Qesem (Hershkovitz et al., 2011). A well-developed mid-trigonid crest has also been described in *A. afarensis* (e.g., A.L. 333 43b), and *A. africanus* (e.g., Stw 67, 97, 104, 315, and 428, as well as in Taung), (Johanson et al., 1982; Moggi-Cecchi et al., 2006) or in PCG.2 from Sangiran (Zanoli et al., 2012). In the absence of enough information about the dm_2 variability in early *Homo* and modern humans, we suggest that the continuous mid-trigonid crest could be the primitive condition in the hominin clade. This feature could have been retained by Neandertals and probably lost in the dm_2 of *H. sapiens* (Bailey & Hublin, 2006). In the dm_2 sample studied here ($n = 18$) we have found only one specimen with a continuous mid-trigonid crest (5.5%). It would be interesting the study of larger modern human samples to make an evaluation of this feature. We could ascertain if this feature is as diagnostic as in the permanent molars (Bailey, Skinner, & Hublin, 2011, and references therein). The presence of a pit-like posterior fovea in 50% of the recent dm_2 also raises questions about the polarity of this trait.

The presence of mesial and distal styles in the deciduous upper and possibly in the lower canines (see Bermúdez de Castro et al., 1999a), as well as the large root of the di^2 can be considered as primitive features of the TD6 deciduous teeth. Furthermore, and in agreement with the previous study of the permanent teeth (Bermúdez de Castro et al., 1999a), the size of the deciduous dentition remains within the range of variation of early *Homo*. The limited evidence points to a reduction of the deciduous molars, at least in the European Middle Pleistocene hominins and the Neandertals.

In general we can observe that there is a positive correspondence between the enamel (external) and the EDJ (internal) morphology. Specimen ATD6-102 presents similar morphology on both surfaces except for the small protuberance on the distal aspect of the lingual surface that is not reflected in the external enamel surface. The traits described for the external enamel surface on the mandibular molars (ATD6-93 and ATD6-112) are also found at the EDJ surfaces (e.g., a similar pattern of foveae, or number of cusps and crests). To fully understand the polarity of the traits expressed at the EDJ, however, it is desirable that more data on more hominin specimens is recovered in future studies.

The present study is a new contribution to our understanding of the TD6 hominins. Fieldwork in the coming years will allow to excavation of a surface of more than seventy square meters in each of the different sublevels of TD6. Until then, this study enlarges the list of primitive features of *H. antecessor* regarding the *Homo* clade, as well as the number of traits that this species shared with other *Homo* species including *H. sapiens* and *H. neanderthalensis*. Thus, the study of the deciduous dentition confirms the mosaic pattern of *H. antecessor* morphology revealed in previous studies of this hominin sample (e.g., Bermúdez de Castro et al., 2015).

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