



> 42 ka human teeth from El Castillo Cave (Cantabria, Spain) Mid-Upper Paleolithic transition

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Abstract

Three deciduous tooth crowns were found in Unit 18B in El Castillo Cave (Spain), considered a transitional Middle-Upper Paleolithic Unit with numerous ¹⁴C dates with means earlier than > 42–44 ka cal. BP. Our goal was to describe these teeth, compare them to Neanderthal, Mousterian Modern Humans, and Early-Mid Upper Paleolithic fossils (through scatterplots and Z-scores), and analyze their morphology. The teeth consist of deciduous and isolated crowns (one ULd₁¹, one ULdm₂², and one LRdm₂) corresponding to three children, and all of them were modified by heavy occlusal and interproximal wear. Their length and breadth diameters, shown in the bivariate scatterplots, were similar to those of the teeth of several young Neanderthals. The Z-scores of the two crown diameters with respect to the Late Neanderthal, Qafzeh and Skhul, and Aurignacian-Gravettian series had values of approximately 0, while those of the altered MDs of the ULdm₂² are just below -1, except in comparison to the last group; the Z-scores of the BL diameters fall within the range of variability of the three series. Qualitative morphological comparisons highlighted several characteristics that were consistent with a Neanderthal taxonomic assignment. The combined archeological and anatomical-comparative study suggested the presence of three Neanderthal children in Unit 18, in a location considered a primary butchery area. The chronology and morphology of these teeth in the framework of the Middle to Upper Paleolithic transition are outstanding in the debate about the last Neanderthals and the unconfirmed, but possible, presence of a few groups of modern humans in Western Europe.

Keywords Middle-Upper Paleolithic · MIS 3 · Deciduous teeth · Morphology · Neanderthal

Introduction

In the cultural sequence of the European Upper Pleistocene, there is an extraordinarily interesting period: the Middle to Upper Paleolithic transition, because of the biocultural changes reflected throughout it. As estimated by several authors, its duration ranged between ~2,600 and 5,400 years (at a 95.4% probability, Higham et al., 2014), characterizing a long period with a minimum of ~130 to ~270 human generations. Logically, the evolution, beginning, arrival, substitution, or disappearance of diverse lithic industries, as well as the biological and demographic changes that affected the human groups in this period, must have taken place with spatiotemporal differences that seem to have been reflected in some studies considering wide geographic extents (e.g., Higham et al. 2014). The new radiocarbon calibration curve (IntCal20) extends the chronology (older ages) of the possible overlap between Neanderthals and Modern Humans in certain European regions (Bard et al. 2020).

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From an anthropological point of view, it must be noted that, until today, all significant human remains found with Late Mousterian in Western Europe correspond to Neanderthals (N) and are also associated with different lithic industries, such as the French Châtelperronian (Leroi-Gourham 1958; Lévêque and Vandermeersch, 1980; Hublin et al., 1996; Trinkaus et al., 1999a; Del Prete & Vandermeersch 2001; Bailey & Hublin, 2006; David et al. 2009; Hublin et al. 2012; Tillier et al. 2012; Tillier et al. 2013; Welker et al., 2016; Maureille et al. 2019; Balzeau et al. 2020).

However, there is a crucial problem with the remains assigned to the first/earliest modern humans (MHs) in Western Europe since they are extremely scarce and fragmented. Two deciduous teeth found at Cavallo Cave, supposedly linked to the Uluzzian culture (Palma di Cesnola and Messeri 1967), have been assigned to MH (Benazzi et al. 2011, 2014, 2015; Zanolli et al. 2013). But due to controversy surrounding their stratigraphical position, it is difficult to reach an agreement about the authorship of the Uluzzian by N or MH (Zilhão et al. 2015; Villa et al. 2018). The Kent's Cavern 4 maxillary fragment still also with problematic chronostratigraphic data (Higham et al., 2011; White and Pettit 2012; Proctor et al. 2013).

To date, limited data exist about the makers of the Proto- and Early-Aurignacian, being mainly represented by a few isolated teeth from Brassempouy, Riparo Bombrini, and Grotta de Fumane (Henry-Gambier et al. 2004; Benazzi et al. 2015) as well as three bones from a perinate found at Le Piage (Beckouche and Poplin 1981). More representatives are the fragments of jaws, teeth, and some infracranial remains (generally considered later than ~40–38 ka cal. BP) and assigned to MH at the La Quina site (see Verna et al. 2012).

In Central Europe, the presence of MH is documented by the Mid or Late Aurignacian fossils (Oliva 2006) found at Mladeč (~31 ¹⁴C kyr BP, Wild et al. 2006) in the Czech Republic, or by the remains discovered at Cioclovina, Muierii, and Oase (Rougier et al. 2007; Soficaru et al. 2007; Dobos et al. 2010). Nevertheless, these Romanian fossils lack a secure archeological context, and only Oase 1 has been dated at ~40 ka cal. BP (Trinkaus et al. 2003; Bard et al. 2020). The last discovery is the presence of MH in the Bacho Kiro Cave (Bulgaria) identified by one molar and the mtDNA and nDNA sequences from several hominin bone fragments; these remains were directly dated at ~45 ka cal. BP and appeared with an Initial Upper Paleolithic (IUP) assemblage (Hublin et al. 2020; Hajdinjak et al. 2021).

Therefore, the human fossils assigned to this period, especially those from the Aurignacian and other early phases of the Upper Paleolithic, could partially correspond to MH individuals who seem to have immigrated into Europe, according to several authors (e.g., Villa and Roebroeks 2014; Hublin et al. 2020) bringing different cultural traditions, and

mixing with the indigenous Neanderthals, implying reciprocal cultural exchanges (e.g., Cabrera et al. 2006; Zilhão 2006; Villa and Roebroeks 2014; Greenbaum et al. 2019). These exchanges were also genetic, and for many years, some morphological characteristics of numerous fossils have been interpreted by various authors as traces of crossbreeding between the N and MHs (e.g., Frayer 1993; Wolpoff et al. 2000, 2001, 2004; Zilhão and Trinkaus 2002; Trinkaus et al. 2003; Bayle et al. 2010). The indisputable evidence of this interbreeding includes the aDNA analyses of some of the oldest European MH fossils (e.g., Oase 1: Fu et al. 2015; Kostenki 14: Seguin-Orlando et al. 2014; Sungir: Sikora et al. 2017; Goyet Q116-1, Muierii 2, Cioclovina 1, and 14 Gravettian skeletons mainly from Central Europe: Fu et al., 2016; Bacho Kiro: Hajdinjak et al. 2021, and possibly Zlatý kůň: Prüfer et al. 2021). On most of those fossils was identified higher amount of Neanderthal DNA than on more recent individuals or present-day Europeans.

Considering the questions, problems, and chronology summarized above, the interest in the three deciduous teeth found in Unit 18B of El Castillo Cave and repeatedly dated at more than 42 cal. kBP (with a 95% probability, Wood et al. 2018) appears evident. In our study, after presenting the site and the archeological context, we describe the dental remains by focusing on their morphometry, estimating the minimum number of individuals, and their age at death. Statistical and morphological comparisons with the teeth of N and MH children (of different periods) are followed by a discussion and interpretation of the results.

El Castillo Cave: Unit 18

El Castillo Cave, located on Mount Castillo near the village of Puente Viesgo (Cantabria, northern Spain, Fig. 1C), was discovered in 1903 by H. Alcalde del Río. Between 1910 and 1914, H. Obermaier carried out five excavation seasons in the hall of the cave, but it was only in 1980 that V. Cabrera and F. Bernaldo de Quirós initiated new excavations toward the cave entrance (Fig. 1A and B), where the stratigraphy was preserved. They focused their project on the earliest Upper Paleolithic level (Unit 16), a Middle-Upper Transitional level (Unit 18), and the underlying Late Mousterian (Unit 20). Below, we will summarize the most important archeological and environmental data.

The El Castillo stratigraphy is detailed in Table SI-1, where we see that Unit 18 is capped by Unit 17 (mainly sterile, but containing scarce lithic and faunal materials, especially at the bottom). Above it, Unit 16 corresponds to Obermaier's "Aurignacian gamma," now considered a Proto-Aurignacian (Maíllo-Fernández and Bernaldo de Quirós 2010). Unit 18 is also separated from the underlying Unit 20 (Obermaier's "Mousterian alpha") by a second sterile

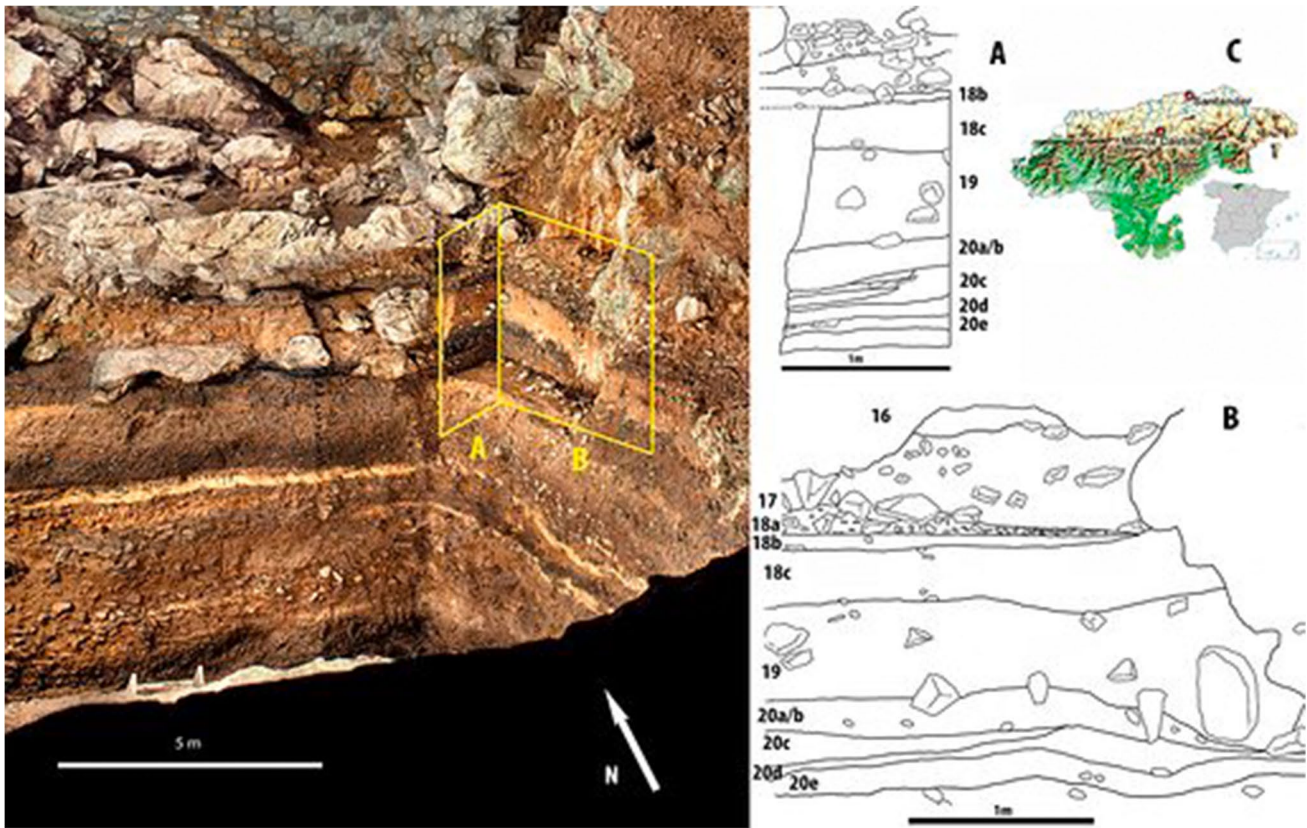


Fig. 1 El Castillo Cave. **A** East profile; **B** north profile; **C** location of El Castillo Cave

layer, Unit 19, which is a level of clays with blocks at the bottom. In the latest excavations, Unit 18 was subdivided into several levels based on its sedimentology: 18A (sterile), 18B, and 18C. Unit 18 is composed of brown clays that are rich in organic matter and includes subangular and dispersed limestone edges and blocks; units 18B and 18C also contain numerous archeological and faunal remains (Cabrera et al. 1993).

Unit 18 has been dated using ESR (Rink et al. 1997), AMS ^{14}C (Cabrera and Bischoff 1989), and ultrafiltration ^{14}C obtained from charcoal and humanly modified bones (Wood et al. 2018). These methods offer a consistent series of dates and place the antiquity of Unit 18 earlier than 42 cal. ka BP (44,940–42,110 cal. ka BP at 95% probability; Wood et al. 2018).

Unit 18 has not been without interpretation problems. It was considered to contain one of the oldest shreds of evidence of the Early-Aurignacian in Europe. This attribution was due, in part, to the batch of split-base points found during Obermaier's excavations (Cabrera and Bischoff 1989), which were provisionally assigned to Unit 18. Afterward, the Unit 18 lithic industry was interpreted as a transitional technocomplex between the Middle and Upper Paleolithic called "Transitional Aurignacian" (Cabrera et al. 2001;

Bernaldo de Quirós and Maíllo-Fernández 2009). The recent work carried out since the dating of materials found in old and new excavations and from different levels confirms that Obermaier's level 18 ("Aurignacian delta" according to him) cannot be directly related to Unit 18 of the current excavations taking place at the cave entrance (Wood et al. 2018).

Units 18B and 18C present very similar techno-typological characterizations suggesting that the industry was transitional between the Mousterian and the Upper Paleolithic. We previously indicated that initially this technocomplex was referred to as "Transitional Aurignacian" (Cabrera and Bernaldo de Quirós 1996; Cabrera et al. 1996, 2001; Bernaldo de Quirós and Maíllo-Fernández 2009), but at present, we consider that this denomination must be abandoned, and the Unit 18 culture simply referred to as a Transitional/Initial Upper Paleolithic assemblage (Wood et al. 2018). Technologically, the lithic production is dominated by discoid operational schemes with two well-defined methods: unifacial and bifacial (Fig. 2). To a lesser extent, laminar operational schemes used to obtain blade/bladelets by applying unipolar, burin-type, or prismatic methods on fine-grained quartzite have also been identified (Fig. 2). Typologically, both levels (18B and 18C) are dominated by substrate pieces (especially sidescrapers), although the most outstanding items are the

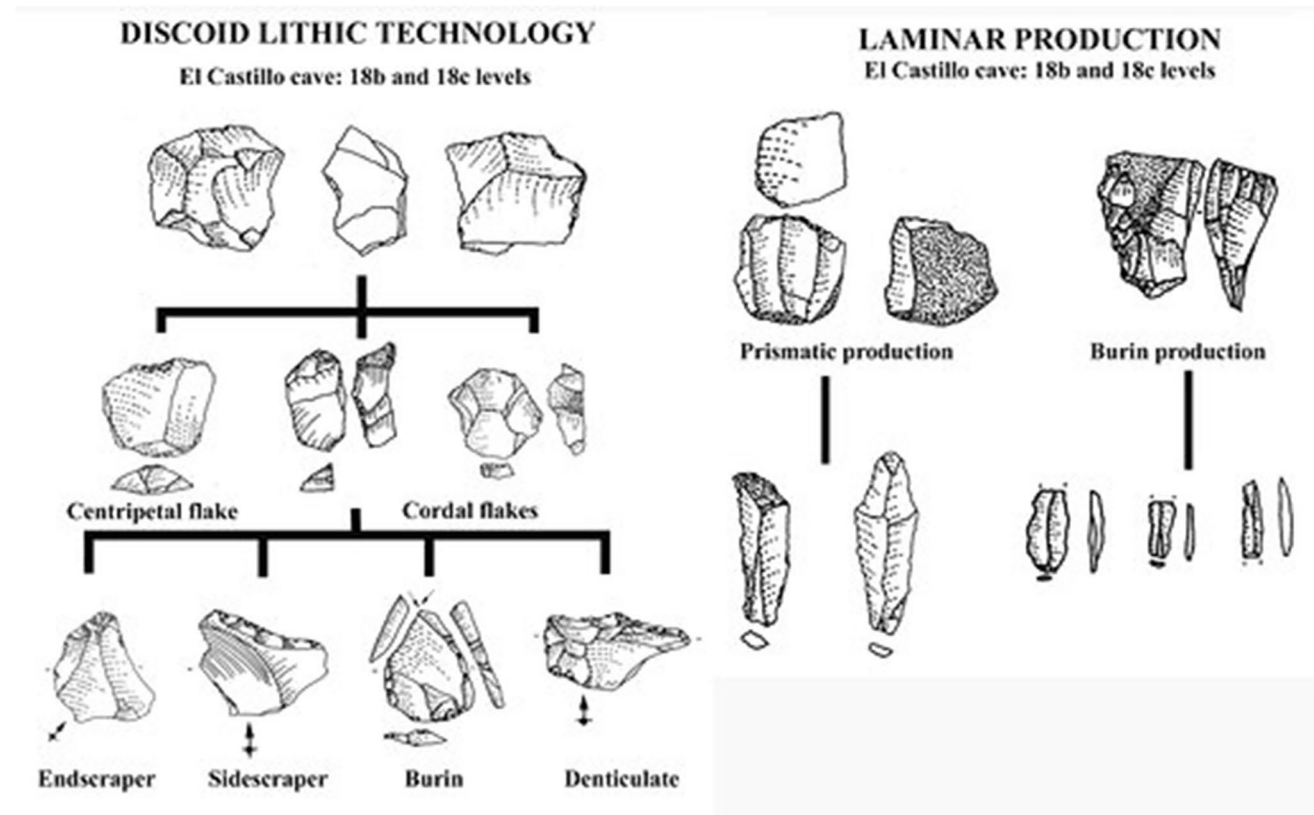


Fig. 2 Schematic process of the discoïd and blade/bladelet methods in Unit 18 at El Castillo Cave

Upper Paleolithic type tools (Fig. 3), specifically endscrapers and burins, many of them on discoïd blanks. Tools on bladelets are not very common, and only one Dufour bladelet appeared within level 18C.

In summary, the lithic assemblage of Unit 18 appears to be dominated by Discoïd/Levallois technology (Bernaldo de Quirós and Maïllo-Fernández 2009). However, what makes this unit different is that it has a high percentage of “Upper Paleolithic” pieces on Mousterian blanks, especially endscrapers and burins. This is not completely new, since in several Mousterian sites, especially those with “Moustérien de Tradition Acheuléenne B” (MTA B; Bordes and Sonneville-Bordes 1970) as La Plane (Turq 2000), tools such as endscrapers or burins have been found, although not in the proportions and variety as in the El Castillo Cave Unit 18.

Furthermore, the identified faunal remains indicate a change in the species hunted between the Late Mousterian (Unit 20) and Unit 18. The latter reveals a specialization in red deer, while during the Late Mousterian layers (Units 20, 21, and 22; Table S1), the hunting strategies were less specialized, and red deer, horse, and *Bos*/bison were hunted (Luret et al. 2020).

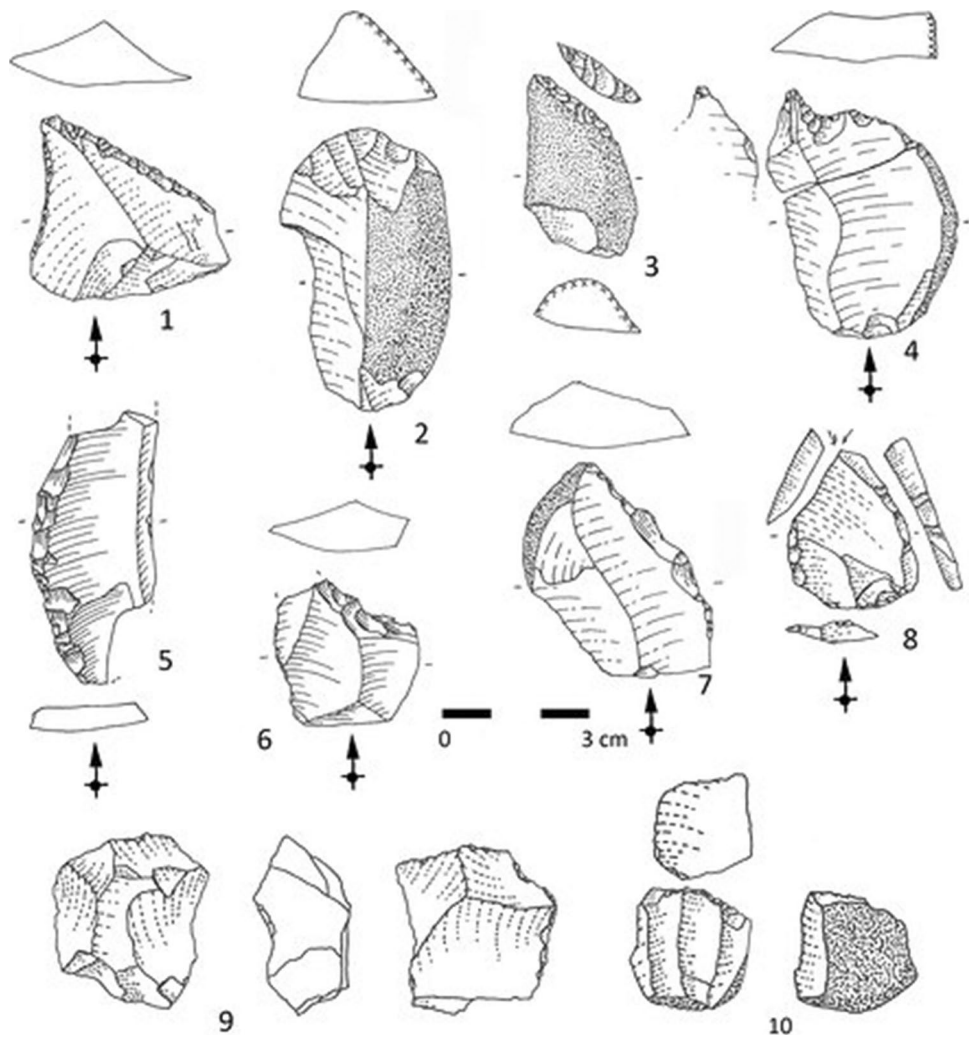
The bone industry discovered in Unit 18 is scarce, but significant (Fig. 4). Two distal fragments of bone points on a deer antler, a fishhook on a bone fragment, and an awl

on a bone splinter (Fig. 4: 3–5) have been found, as well as some pieces with incisions and engravings. There were also various objects probably related to the sphere of symbolism, such as a distal chisel fragment with a series of short, straight incisions, a mesial fragment of one ungulate metapod with incisions on the upper face, and a flattened bone fragment with painted lines on the upper side. Furthermore, Unit 18B also yielded the proximal fragment of one hyoid bone, possibly from *Cervus elaphus*, decorated with engraved lines on its upper surface representing a possible partial figure of cervid (Fig. 4: 2, red arrows), as well as a triangular-shaped sandstone plaque with four engraved lines on one of its faces and a bone with incisions (all the descriptions can be found in Cabrera et al. 2001; Tejero et al. 2005; Tejero and Bernaldo de Quirós 2007).

The human fossils

The excavations by V. Cabrera and F. Bernaldo de Quirós in El Castillo Cave led to the discovery in Unit 18B of three isolated deciduous teeth (not two, as indicated in Wood et al. 2018), found in two very close squares (Fig. 5) placed at the Cave entrance. The fossils are curated at the Museum

Fig. 3 Tools and cores from Units 18B and 18C at El Castillo Cave. **1, 5:** Sidescrapers; **2:** endscraper; **3:** truncation; **4:** borer; **6–7:** denticulates; **8:** burin; **9:** discoid core; **10:** prismatic core (all of them on quartzite)



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Methods of study

Morphology

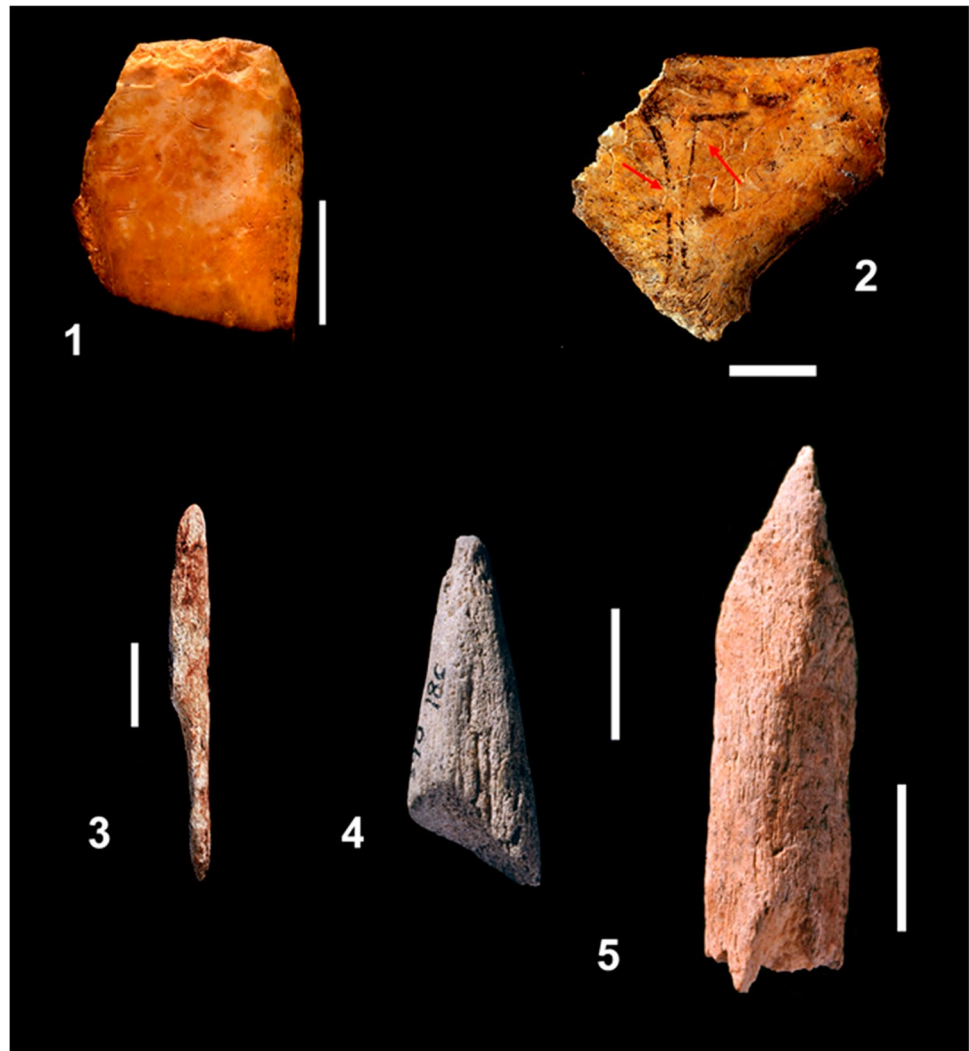
Tooth diameters were measured with a precision caliper three times by one of us (M. D. G.) and the average of these measurements is used in this paper. Crown diameters were recorded following Martin and Saller (1957): the greatest mesiodistal diameter was taken parallel to the occlusal and buccal surfaces, while the greatest buccolingual diameter was measured between the buccal and lingual surfaces, perpendicular to the plane in which the mesiodistal diameter was measured (Hillson, 1996). Occlusal and interproximal wear affected the crown height and the mesiodistal diameters, as indicated in Table 1. Based on the mesiodistal and buccolingual diameters, the crown index and crown area (Martin and Saller 1957) were calculated (Table 1).

Morphological characteristics were described using the Dahlberg (1956) and Hanihara (1961, 1963) explanations and plaques for deciduous teeth, where possible, as well as different traits found in the referred papers throughout the text. Age estimations were based on the Moorrees et al. (1963) formation stages, the Gustafson and Koch (1974) formation diagram, the Ubelaker (1989) schemes, and the AlQahtani et al. (2010) atlas, although all of them were based on samples with very different biological and environmental conditions than those of the El Castillo children. Wear was estimated through the Molnar (1971) scale.

Statistical analyses

For the statistical analyses, we used the adjusted (scaled) Z-scores method, considering three comparative fossil samples to evaluate the position of the El Castillo crown diameters, with respect to the comparative series (Maureille et al. 2001; Compton et al. 2021). The interval between -1 and $+1$ comprises 95% of the variation in

Fig. 4 Bone industry of El Castillo Unit 18: **1**: distal chisel fragment with marks; **2**: engraved proximal fragment of one cervid hyoid bone; **3**: fish-hook; **4**: bone point (fragment); **5**: awl on bone fragment. **1, 3–5** from 18C; **2** from 18B (photo credits: **1–2**, P. Saura; **3–5**, F. Bernaldo de Quirós)



each comparative sample, and a value of zero indicates that the dimension of the tooth is equal to the mean of the comparative series. A positive adjusted Z-score indicates a Castillo tooth dimension above the mean value and vice versa (Compton et al. 2021).

We also elaborated bivariate scatterplots of the buccolingual and mesiodistal crown diameters in Statistica 7 for each tooth type using modern-population samples from Spitalfields and Poundbury in the UK and Coxyde in Belgium (Historical Humans = HH; $n = 453$ individuals; Maureille 2001). In these scatterplots, we included the fossils from the Late Neanderthals (from MIS 4 = LN), Middle Paleolithic Modern Humans (MIS 5 = MPMH), and Early-Mid European Upper Paleolithic (Uluzzian, Aurignacian and Gravettian = UPMH). Given the small number of fossils, only the HH group's 95% confidence ellipse was provided (± 1.96 SD variation range). For these bivariate analyses, we also included a few Preneanderthal and Early

Neanderthal (PEN) fossils, to reflect the evolutionary trend of crown diameters within the Neanderthal lineage.

Metric and morphological comparisons with the equivalent PEN, LN, and MH (Mousterian and Early-Mid Upper Paleolithic) deciduous teeth were carried out using previously published specimens; although several original fossils were personally observed in various museums and institutions, while others were represented by high-quality casts (Table S2).

aDNA

Unfortunately, the MUPAC did not give us permission to micro-scan the teeth, as we did for another study (Garralda et al. 2019a, b), nor were we allowed to sample the teeth for aDNA investigations. Considering the preservation state of the fossils does not seem to have research potential; thus, we decided to analyze the sediments with the new techniques

Fig. 5 El Castillo Cave ground plan. The present excavations are placed at the cave entrance. The red arrows indicate the two squares where the presently studied teeth were found

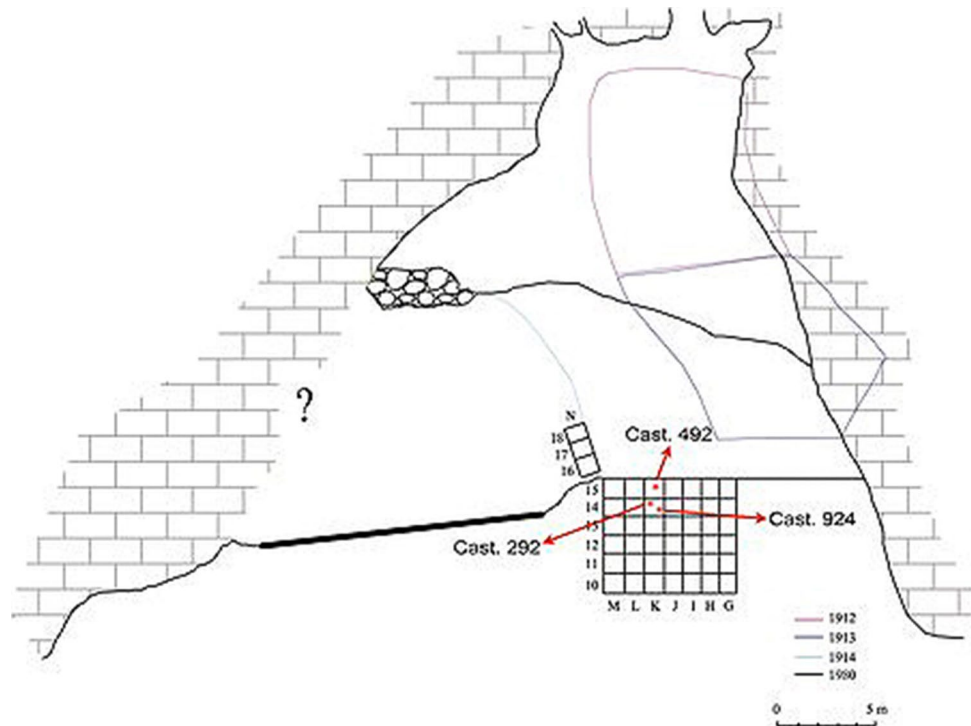


Table 1 El Castillo Unit 18 teeth diameters and indices

	Castillo 924 ULdi ¹	Castillo 492 ULdm ²	Castillo 292 dm ₂
M-D Ø (M81)	> 7.6	> 7.6	> 9.6
M-D Ø (estimated)			~ 10.4
B-L Ø (M81(1))	5.6	10.0	9.5
Crown index (M81(1)/M81 × 100)	73.7?	131.6?	91.3?
Crown area (M81 × M81(1))	42.6?	76.0?	98.8?

developed by our colleagues from the Max Planck Institute for Evolutionary Anthropology (Department of Evolutionary Genetics), work currently underway.

Results

Morphological description

Castillo 924 (Figure 6) Discovered in 1998 in grid K-14.3 (Fig. 5), the tooth corresponds to one upper left deciduous central incisor (ULdi¹). The fossil consists of the entire crown (exhibiting vertical microfractures) and the incomplete root broken obliquely from almost the cervix (on the lingual side) to between a third and a quarter of its height (on the labial side). A small chip of enamel is broken off at the center of the labial rim, probably due to masticatory pressures or other activities (Fig. 6: 1 and 3), and numerous

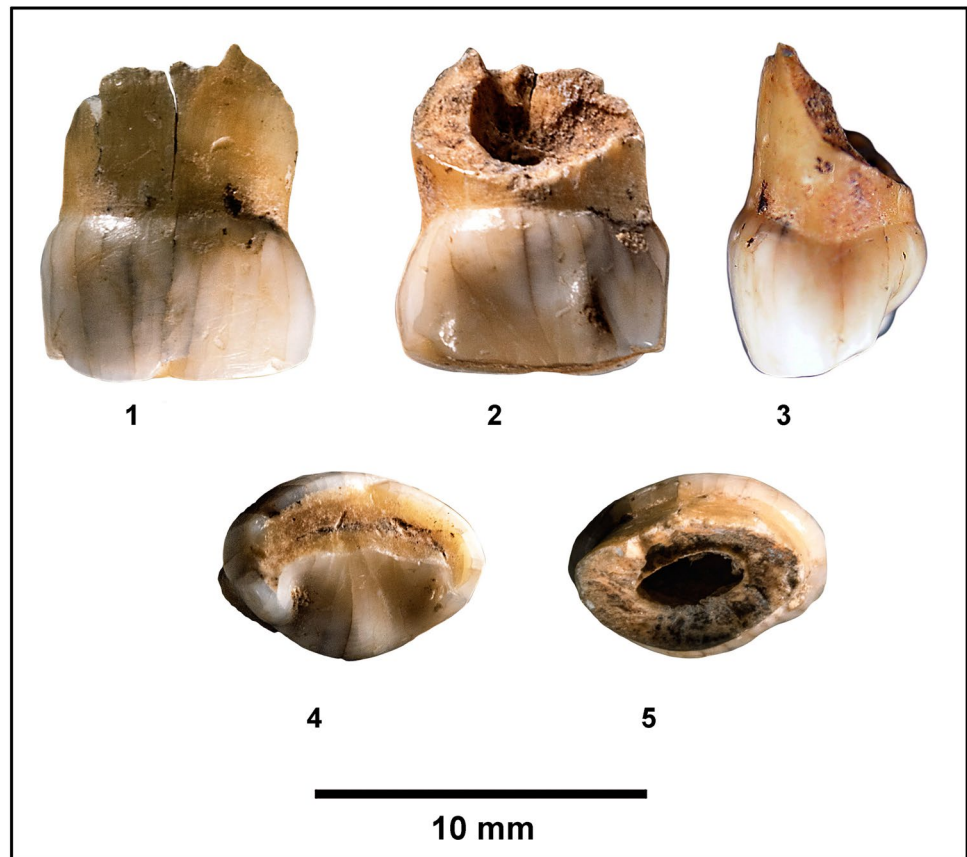
scratches right-oblique oriented are visible on the labial surface.

Crown height was reduced by intense wear, corresponding to Molnar’s (1971) stage 6/7 (Fig. 6: 3). The worn incisal surface is notable for its oblique orientation toward the lingual side. The occlusal plane is horizontal, and the dentine is exposed along its entire length.

There is a prominent lingual tubercle and two marked and well-developed marginal ridges (the mesial one more accentuated and individualized by a deep groove from the lingual tubercle), and the concavity of the lingual surface is distinct (Fig. 6: 2). The morphology of this tooth is “shovel-shaped” and corresponds to Hanihara (1961) type 2, being more accentuated than that of grade “m” (= maximum) of the Dahlberg plaque (1956) for deciduous incisors.

The labial surface is markedly convex, both mesiodistally and from the occlusal border to the cervix. The tooth is also asymmetric with a bulbous protruding mesially on the labial surface and a pronounced distal convexity (Fig. 6: 3). The

Fig. 6 Castillo 924 ULdi.¹. **1:** Labial; **2:** lingual; **3:** distal; **4:** occlusal; **5:** apical view. (Photo credits: P. Saura and R. Asiaín)



interproximal facets are developed, and the mesial one covers almost the entire crown height, but the crown diameters are still large (Table 1).

The incomplete root (Fig. 6: 4) has an oval section, flattened buccolingually. The root canal appears to have been large.

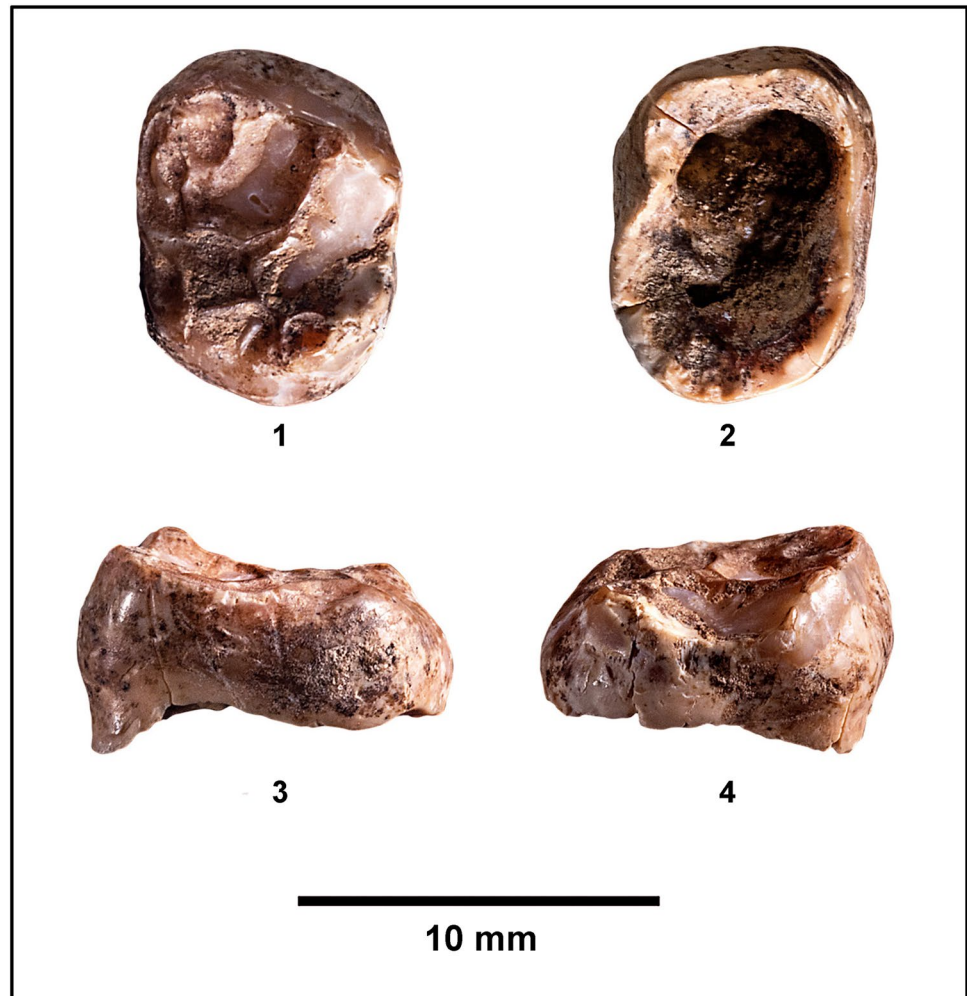
This tooth belonged to a child whose age could be estimated by considering the crown attrition and root stage. Resorption cannot be observed in the preserved part of the root. That process may have started near the apex or in the upper half, but the tooth was probably still in its alveolus. Consequently, the age at death of this child is estimated at ~ 4 years ± 12 months, based on Ubelaker's diagrams (1989) and ~ 5.5 years according to Al-Qathani et al. (2010) atlas. The tooth may not have fallen out naturally, but probably due to a traumatic avulsion from its alveolus, a relatively common incident in children's oral pathology (Neville et al. 2016), because the root was probably broken recently, lacking signs of the normal root resorption.

Castillo 492 (Figure 7) Found in 2001 in grid K-15.1 (Fig. 5), the fossil consists of an upper left deciduous second molar (ULdm²) crown. The occlusal face is very worn, the interproximal facets are wide, and the crown height is reduced to ~ 5.8 mm at its highest part. This fossil was first considered

as a ULdm¹ (Garraalda 2005, 2006a, b), but a detailed comparison with the crowns of numerous fossil children allowed us to reinterpret this altered crown. The roots are reabsorbed except for a thin band below the buccal side (Fig. 7: 3 and 4), suggesting that the crown was lost antemortem, a stage corresponding to ~ 10 years ± 30 months, based on the Ubelaker (1989) schemes and to ~ 10.5 according to the Al-Qahtani et al. (2010) atlas. Crown enamel is very thin, and best-preserved at the bottom of the main grooves.

The crown occlusal view is slightly trapezoidal and has four cusps (Fig. 7: 1), corresponding to Hanihara's (1963) type 4. The two buccal cusps (paracone and metacone) are larger than the lingual ones (protocone and hypocone). The occlusal view also shows a strong cingulum bulge near the crown base and a pronounced mesiobuccal projection at the base of the paracone. The mesial and distal margins are straight, with slight lingual convergence, and had marked interproximal facets altering the crown diameters (Table 1), which are underestimated. The buccal margin, which is also relatively straight and with a pronounced distal inclination, is longer than the lingual, which appears narrow and convex (Fig. 7: 1). There is a marked oblique crest (*crista obliqua*; degree 1, Martín-Torres et al. 2012), corresponding to a variant of type VI (Martin et al. 2017) where the *crista obliqua* joins the protocone and the metacone, and an additional

Fig. 7 Castillo 492 ULdm.². **1:** Occlusal (mesial view on the left); **2:** crown apical view; **3:** mesial; **4:** distal. (Photo credits: P. Saura and R. Asiaín)



crest runs from this crest to the distal marginal ridge between the paracone and the protocone in Castillo 492. The protocone is centrally located, and there is a notable development of the hypocone in relation to the metacone. The groove separating the two vestibular cusps must have been deep, similarly to the other grooves and the two mesial and distal fossae, judging by the reliefs remaining on the occlusal surface. No Carabelli cusp has been observed in the mesiolingual angle (Hanihara 1963, type 0).

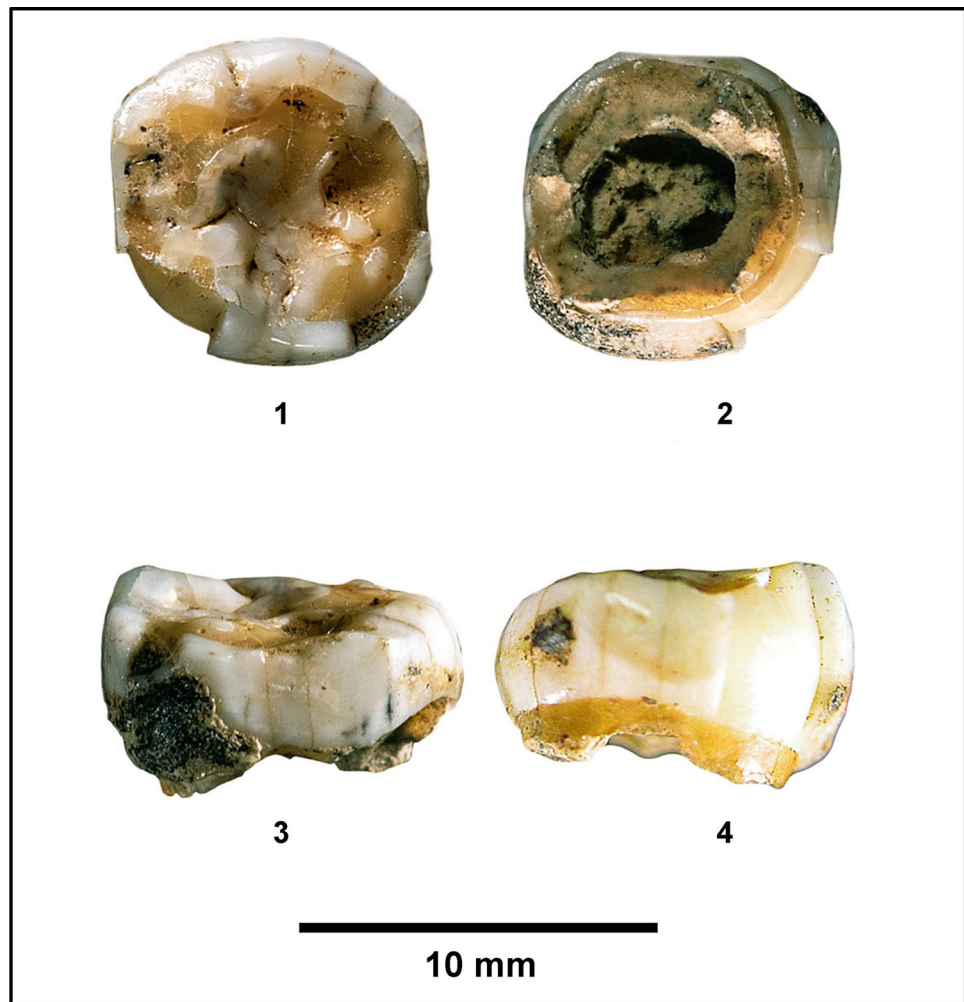
The buccal cusps are higher than the lingual ones (Fig. 7: 1), despite the intense attrition, corresponding to Molnar's type 3/4 (1971), with slight dentine exposure at the cusps. There is no evidence of caries. Numerous small calcite concretion deposits appear on and around the crown, as well as in the pulp chamber, due to taphonomic processes.

Castillo 292 (Figure 8) Found in 1998 in grid K-14.9 (Fig. 5), the fossil consists of a lower right deciduous second molar (LRdm₂), reduced to the incomplete crown, and lost antemortem.

The tooth has two postmortem enamel losses: the larger one is at the mesiolingual angle, affecting the crown's entire height, and it is a recent break (post-discovery). The smaller loss (colored by sediments) appears on the lingual view and is just mesial to the distolingual cusp. The occlusal plane is worn, and the wear corresponds to Molnar's type 7 (1971), with dentine appearing over a large occlusal surface.

This molar had an ovoid occlusal outline (Fig. 8: 1) with buccodistal expansion and four main cusps, with a marked groove between the protoconid and the hypoconid, and a small hypoconulid. There is no trace of the protostylid (Hanihara 1961, type 0). The fissure pattern is difficult to observe, but it seems that the metaconid and hypoconid were separated by a major and deep central fovea. Each major cusp presents a strong essential crest, as has been described in other fossils (Hanihara 1961, type 0). The possible presence of an anterior fovea and the mid-trigonid crest can be observed. The two best-preserved profiles, buccal and lingual, are convex inward. The molar is remarkable due to its large diameters (Table 1), despite the mesiodistal reduction

Fig. 8 Castillo 292 LRdm₂. **1**: Occlusal; **2**: crown apical view; **3**: distal; **4**: mesial. (Photo credits: P. Saura and R. Asiaín)



due to the two pronounced interproximal facets (especially the distal) that altered the rectangular contour of the crown. In the inferior view, the upper part of the preserved pulp cavity seems to reflect that its size should have been large.

The wear of the occlusal plane (Fig. 8: 1) and the importance of these interproximal facets permit the assignment of this fossil to an immature individual having the RM₁ already emerged and in use for some time before the shedding of this Rdm₂. On the lingual side, ~ 1 mm of the roots is preserved, and the resorption stage seems more accentuated than grade Res3/4 (Moorrees et al. 1963), suggesting that the tooth has been lost through dental development at approximately 13 years (Moorrees et al. 1963) or between 8/9 and ~ 11.5 according to Gustafson and Koch (1974), Ubelaker (1989), and AlQahtani et al. (2010). Consequently, Castillo 292 probably corresponded to an older immature in comparison to the younger children Castillo 924 and Castillo 492. A thin band of tartar is partially preserved around the crown cervical region.

Comparisons

Considering the chronology (> 42 cal. kBP, Wood et al. 2018) of El Castillo Cave Unit 18B, we decided to focus the comparisons on Late Neanderthal (LN) and Mousterian MH (MPMH), as well as European Early-Mid Upper Paleolithic children (UPMH), although the few available Pre- and Early Neanderthal (PEN) teeth were also used for the graphic representations (UPMH; Table S2).

The period covered by those comparative samples is very long (> 100 to ~ 25 ka), and the area of fossils distribution is very wide. Moreover, the children's living conditions, their genetic pools, and the influence of the micro-evolutionary factors on the diverse groups were probably very different. Such remarks, as well as the low number of individuals available for several groups (Tables SI-2 and SI-3) and the described alterations of the El Castillo teeth dimensions (especially because of interproximal

wear), imply necessary caution in the data management and interpretations.

Metric comparisons

Taking into account the strong wear altering the diameters of the three El Castillo Cave teeth, we made the comparisons using only the two crown diameters, because their combination (the crown index and area) exaggerates the metric differences among the tooth samples.

The comparative series parameters are shown in Table S3, and the adjusted Z-score values in Table 2. Considering its MD diameter, the ULdi¹ (Castillo 924) is very near the mean of the LN series, as well as that of the MPMH, falling in the range of > +2 standard deviations (from here: s. d.) with respect to the UPMH series. Although there were few individuals in the MPMH and UPMH series (n=4), the BL diameter of Castillo 924 was very similar to those of both groups, while it is smaller than the LN mean (in the range of < -2 s. d.).

Moreover, the bivariate plot of the ULdi¹ crown diameters (Fig. 9) shows that Castillo 924 falls out of the upper limit of the HH children’s 95% confidence ellipse, not far from several of the LN and MPMH teeth, many of which have marked *tubercula lingualia* and, consequently, thick buccolingual diameters. All the UPMH fossils fall inside the modern ellipse, even the largest, the Gravettian Pataud 4. The smallest UP tooth, Borsuka 1, is located at the center of the ellipse, while the three PN and four MPMH fossils are outliers.

The ULdm² (Castillo 492), due to its very small (and highly altered) MD diameter, is out of the 95% of the LN and MPMH variability, falling in that of the UPMH series. Its BL diameter is slightly smaller than the means of the three comparative series (within the LN, MPMH, and UPMH variability).

The ULdm² scatterplot (Fig. 10) presents a wide dispersion of the HH diameter values, and only several fossil individuals (3 LN, 3 PEN, 3 MPMH, and 3 UPMH) are out of the 95% confidence ellipse. Castillo 492 appears in the upper

Table 2 Reduced Z-score values of the three Castillo teeth with respect to the Late Neanderthals, Qafzeh-Skhul, and Aurignacian-Gravettian series

	Late Neanderthals		Qafzeh & Skhul		Aurignacian & Gravettian	
	M-D	B-L	M-D	B-L	M-D	B-L
Castillo 924	0.14	-0.62	0.02	-0.29	0.58	0.30
Castillo 492	-1.23	-0.38	-1.36	-0.38	-0.45	-0.10
Castillo 292	0.05	0.52	-0.47	0.04	0.07	0.29

Fig. 9 Scatterplot for the two crown diameters of the ULdi¹. In the three Figs. (9, 10, 11), the ellipse corresponds to the 95% confidence interval of the Historical Humans’ sample (HH) and the Castillo fossils are in red

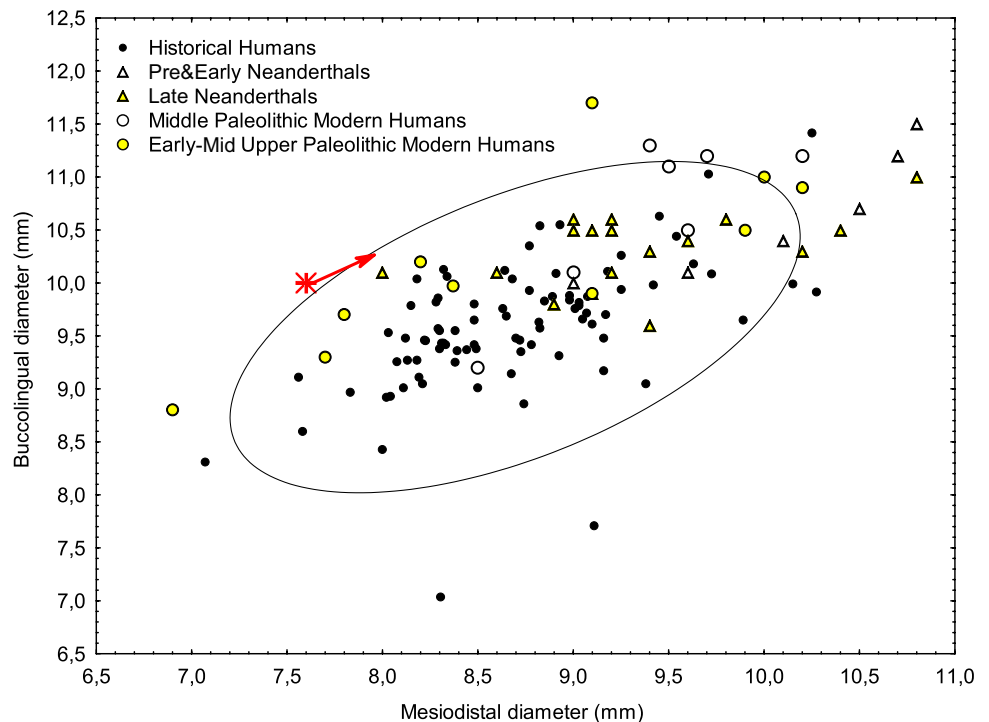
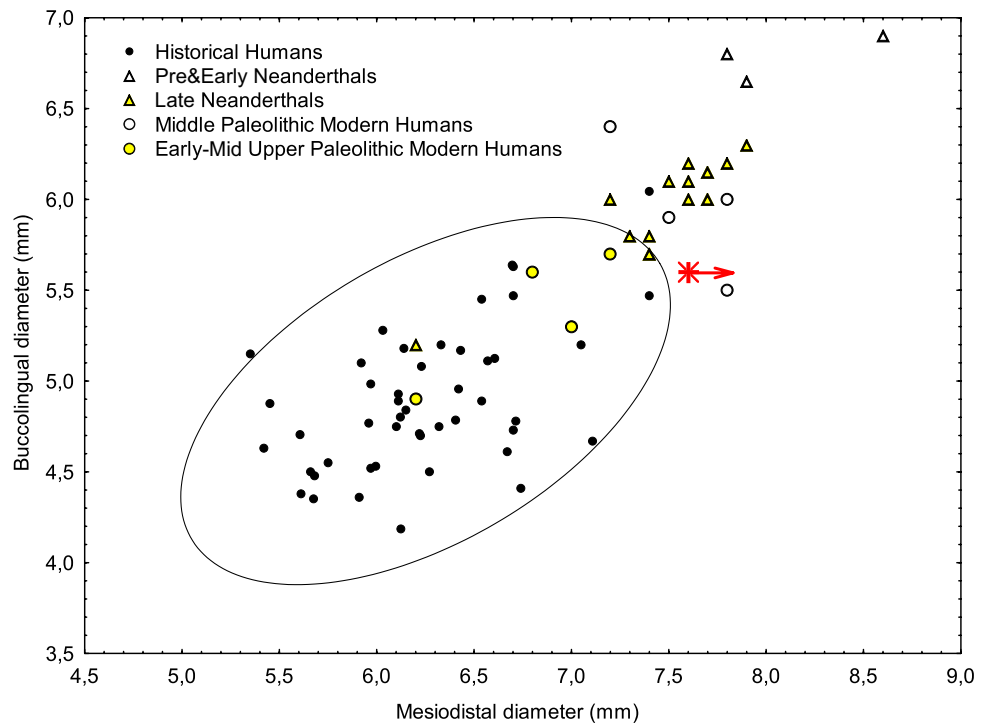


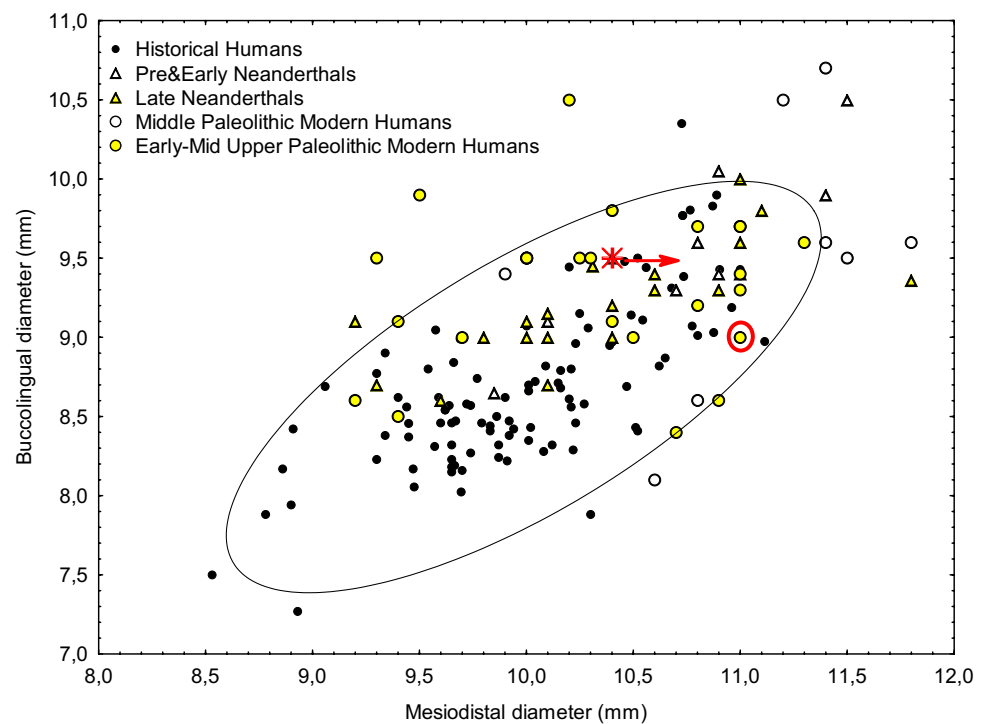
Fig. 10 Scatterplot for the two crown diameters of the ULdm²



border of the lower half of the ellipse, probably because of its reduced MD diameter due to interproximal wear. However, if we add 5 mm to that diameter, Castillo 492 will also remain in the same quadrant, very near the Neanderthal child Pñar-7 and the Gravettian Pavlov 06/2.

Considering the adjusted Z-score values, the LRdm₂ (Castillo 292) MD diameter falls within the LN and UPMH variability ranges and appears smaller than the MPMH mean but is still included in the variability of this series. The BL diameter offers positive and reduced

Fig. 11 Scatterplot for the two crown diameters of the LRdm₂. The Upper Paleolithic molar with a red circle is the Gravettian Castillo C



Z-score values (+/−0.5) with respect to the three comparative series.

Castillo 292 falls in the upper right quadrant of the HH children ellipse (Fig. 11) because of its large diameters (despite the interproximal facets), but the variable dimensions of this tooth in all the considered samples (from PEN to HH children) are obvious considering the dispersion of their positions in the graph. The three fossils appearing closest to Castillo 292 are the Neanderthal children Roc-de-Marsal 1, Archi, and Rescoundudou 1. As in the previous ellipses, the PEN and most of the MPMH fossils are distinguished by their high dimensions.

During his first excavation at El Castillo Cave, Obermaier found the incomplete mandible of an immature, Castillo 3, now directly dated to the Gravettian (Garralda, Mafillo-Fernández, Higham, Neira & Bernaldo de Quirós, 2019). The yellow spot with a red circle on the plot (Fig. 11) represents the LRdm₂ of this child, remarkable by its large MD diameter (not altered by wear), similar to other Early-Mid Upper Paleolithic fossils.

Qualitative morphological comparisons

ULdi.¹ Castillo 924 (Fig. 6)

The asymmetry of the Castillo 924 crown is a feature that has often been pointed out in the di¹ of Neanderthal children, as well as the lingual tubercles and marginal ridges (configuring the shovel-shaped morphology), the labial convexity, and crown thickness. These traits described in Castillo 924 were also depicted for Shanidar 7 (Senyürek 1959), Subalyuk 2 (Thoma 1963; Pap et al. 1996), Roc-de-Marsal 1 (Madre-Dupouy 1992), Krapina immatures (Wolpoff 1979), La Ferrassie 8 (Heim 1982), Engis 2 (Tillier 1983), G. des Cèdres (Vandermeersh 1995), Dederiyeh 1 (Mizoguchi 2002) and 2 (Kondo and Ishida 2002), Kebara 1, 4, and 15 (Tillier et al. 2003), G. du Renne 27 and 36 (Bailey and Hublin 2006), Spy VI (Crevecoeur et al. 2010), Piè Lombard (Texier et al. 2011), or Palomas 39 (Zapata 2017). To our knowledge, only Chateaneuf 2 (Tillier 1979) is cited as a Neanderthal child without a well-defined shovel-shaped Udi¹.

In comparison to the above-described morphology, the Qafzeh and Skhul children (MPMH) also have large diameters and, according to Tillier (1999), thick crowns (with high BL diameters) and pronounced lingual tubercles, although their prominent lateral ridges appear less marked than in most of the Neanderthal children.

No data on di¹ were found for the Aurignacian in the literature, and only four di¹ are available for different Gravettian sites: Dolní Vestonice 36a (Hillson 2006), Lagar Velho 1 (Hillson and Santos Coelho 2002), Borsuka (Wilczyński et al. 2014), and Satsurblia-2 (Margherita et al., 2017). The described morphology indicates that the incisors tend to

be labially flat, exhibiting only minor traces of marginal ridges and basal tubercles, except Satsurblia-2 (Wilczyński et al. 2014, Fig. 2) and (the remarkably small) Borsuka (Wilczyński et al. 2014, Fig. 5) which seem to have moderate labial convexity, concave lingual surface, marginal ridges, and a marked lingual tubercle. In Lagar Velho I, the di¹ have damage in their lingual faces, hindering the observation of the forms of the above-cited features (Hillson and Santos Coelho 2002, p. 342–343). Bayle et al. (2010), when studying the dental maturational pattern and endostructural tooth organization of Lagar Velho 1, remarked that some of the analyzed aspects are absent from extant populations and one Magdalenian child and are currently documented only among Neanderthals. This is also the case for the percent of the crown volume (dentine and pulp) for the deciduous upper central incisors of Lagar Velho 1 (Bayle et al. 2010, p. 1339).

ULdm.² Castillo 492 (Fig. 7)

The comparison of the Castillo 492 crown morphology is warranted by the occlusal and mesiodistal accentuated wear of the fossil. The occlusal outline is almost rhomboidal, with the distal cusps lingually displaced relative to the mesial cusps, as has been described for many Neanderthal fossils, while modern children have squarer outlines (Bailey and Hublin 2006; Bailey et al. 2014). The dm² cusps number shows variability independently of the taxonomic assignment of the compared fossils. Thus, Castillo 492 has four cusps as is the case for many of the Neanderthal children (Table S4), although some of them also have small metaconules. A similar cusps number appears on Skhul I (McCown and Keith 1939) and among the Qafzeh children, ranging from 4 (cusps) + 2 (metaconules) on Q12 to only four cusps (Tillier 1999). The few available UP fossils have 4 cusps (Table S4), with the possible exception of the heavily worn Dzudzuana 1 (Margherita et al. 2017), and the right molar of Lagar Velho 1 which has a small Cusp 5 (Hillson and Santos Coelho 2002).

Carabelli's trait appears as one fossa or cusp (more or less developed) on numerous Neanderthal children (Table SI-4), while Les Fieux and Les Pradelles 282 (pers. observation) lack this characteristic, as also does Castillo 492. All Qafzeh children (Tillier 1999) and Skhul I (McCown and Keith 1939) display a structure of different (no quantified) development ranging from a small fossa to a prominent cusp. One cusp is also described on four of the six Early-Mid Upper Paleolithic fossils (Table S4).

Few data exist for the *crista obliqua* (connecting protocone and metacone), often due to the intense wear of fossils. According to the available information (i.e., Bailey and Hublin 2006), this crest appears on many Neanderthal children (Table SI-4), in Castillo 492, and in Skhul I, Qafzeh 21, Předmostí 23, and Dolní Věstonice 36; however, it must be

considered that in many studies, this character has not been described. Considering its presence on those MH fossils, as well as in extant humans' permanent molars (i.e., Sakai and Hanamura 1971; Martin et al. 2017), the *crista obliqua* cannot be considered a Neanderthal autapomorphy.

LRdm₂ Castillo 292 (Fig. 8)

The intense wear of Castillo 292 complicates the observation and comparison of the occlusal morphological characteristics, although a mid-trigonid crest (perhaps slightly interrupted) seems visible, as it is in many Neanderthal molars, while is absent in the UP Ldm₂s (Bailey and Hublin 2006). Castillo 292 probably had four main cusps, plus one hypoco-nulid, but the known variability of this characteristic seems constant in both N and MPMH (Tillier 1999). Additionally, in Lagar Velho 1, these teeth bear a well-developed Cusp 5 (Hillson and Santos Coelho 2002).

Benazzi et al. (Hillson and Santos Coelho 2002) analyzed the cervical and crown outline of worn Neanderthal and Modern Human Ldm₂, demonstrating that the former showed buccodistal expansion and convex lingual outline shape, while MHs have buccodistal reduction and straight lingual outline shape. Although we could not use the same techniques (microcomputed tomography and morphometry), their Neanderthal molars shape results coincide with our description, and in Fig. 8, the buccodistal expansion (altered by wear) and the convex lingual outline shape are visible.

Discussion

The detailed analyses of the three deciduous crowns found in Unit 18B of El Castillo Cave permitted the identification of two or three children of indeterminate sex, aged between ~4/5 and ~9/11 years. The two nearby grid squares where they were found correspond to part of an area at the entrance of the cave where numerous faunal elements with cutmarks and lithic tools have appeared; this space is considered a primary butchery area (Cabrera et al. 2006; Wood et al. 2018).

The most likely taphonomic explanation for the presence of the three deciduous crowns in that zone is that the children were living around, not necessarily at the same time, and two of them (Castillo 492 and Castillo 292) had teeth fall out in the natural process of changing dentition. Perhaps the two deciduous molars, Castillo 492 and 292, with similar wear, could have belonged to the same individual, but the minor abrasion and the location of the incisor Castillo 492, without complete root resorption (contrary to the other two fossils), advises to attribute it to another child since the deciduous incisors are the first teeth to fall out in the process of deciduous tooth decay. The presence of part of the

root (broken) on this tooth allows us to consider a possible traumatic avulsion.

The crown diameters of Castillo teeth are not very large, except those of the ULdi¹ Castillo 92, who, in the scatterplot, falls outside of the HH ellipse, as do many Neanderthals, because of its lingual tubercle and marked shovel-shape. These features, as well as the strong and asymmetrical labial convexity and asymmetric crown, permit us to assign it to a Neanderthal child. Regarding the two other teeth, with a more intense mesiodistal and occlusal wear, the near-rhomboidal occlusal outline of the LUDm² Castillo 492 with lingually displaced distal cusps (relative to the mesial cusps) and a protruding hypocone (larger than the metacone, which is mesially and lingually oriented) has also been described for many Neanderthal fossils (Bailey and Hublin 2006; Bailey et al. 2014) as well as the *crista obliqua* (Bailey and Hublin 2006). If the position of the metacone and the morphology of the crown occlusal outline “can be used very successfully to identify the taxonomic assignment of isolated teeth when the choice is *H. neanderthalensis* versus *H. sapiens*” (Bailey et al. 2014), we should consider that this ULdm² Castillo 492 can also be attributed to a Neanderthal child, and its dimensions are not far from those of the young Carihuela 7 (García Sanchez et al. 1994) from the Granada region. Furthermore, the traces of a potential mid-trigonid crest on the Ldm₂ (Castillo 292) also permit its assignment to Neanderthals (although the presence of a mid-trigonid crest is present in 10% of the permanent LM₂ in some recent humans today and in 10% of early *H. sapiens*: Hublin et al. 2020).

We regret that we were not permitted to conduct a more detailed study (i.e., microstructural analyses), and we hope that the paleoproteomic analyses of the Unit 18 sediments by our colleagues at the Max Planck Institute (currently in progress) will help us to be more precise with this taxonomic assignment.

Conclusions

Unit 18 at the Castillo Cave entrance is extremely interesting from the chronological point of view given the numerous published ¹⁴C dates and their homogeneity, with an average value of > 42 ka. Furthermore, the archeological data provide the identification of a transitional industry between the end of the Middle and the beginning of the Upper Paleolithic, as summarized in the “El Castillo Cave: Unit 18” section.

Taking into account the solid chronology of El Castillo Cave Unit 18, we must consider that the human group, or groups, represented by the teeth of these children corresponds to recent Neanderthals (MIS 3), as do other fossils found in the Iberian Peninsula (e.g., Garralda 2005;

Rosas et al. 2006; Lorenzo et al. 2012; Wood et al. 2013; Garralda et al. 2014; Trinkaus and Walker 2017), many of which lack such solid chronostratigraphic data.

Given the antiquity of Unit 18 in El Castillo Cave, corresponding to the temporal range of the Middle-Upper Paleolithic transition in Iberia, it is very risky to think that the culture appearing in it could indicate the presence of MH groups who transmitted or promoted new technologies. To date, there are no fossil remains that allow us to confirm the presence of MH in the Iberian Peninsula, nor in France, until more recent times and associated with Aurignacian. The possibility that some bands (surely of reduced size) would have arrived at these expansive regions and mixed with the small groups of Neanderthals that they met, mixing during their displacements and through time, cannot be eliminated. However, the morphology and variability of the deciduous teeth of those children with a genetic patrimony resulting from such cross-breedings are unknown, and only the aDNA analyses could identify such a result.

It is now well acknowledged that the passage from the Middle to the Upper Paleolithic was not a clear break in Europe but more closely resembled a mosaic of innovations (art, ornaments, osseous industries) that first appeared during the Middle Paleolithic (Erwan et al. 2021). The transitional technologies or cultures recorded across Europe, as documented at El Castillo Cave, are diverse and widespread and could have resulted from local evolution or motivated or influenced by the presence of some bands of MH (Kuhn 2019; Hublin et al. 2020). The question of whether the El Castillo Cave Unit 18 children had exclusively Neanderthal ancestors or whether they represent a group with some interbreeding cannot, unfortunately, be answered with the available information; however, the new archeological excavations and the currently underway sediment analyses may help us find the answer to this question.

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Declarations

Consent to participate The authors declare that they agreed to participate in the present study.

Consent for publication The authors declare that they read and agreed to the publication of the present paper.

Conflict of interest The authors declare no competing interests.

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