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Mousterian human fossils from El Castillo cave (Puente Viesgo, Cantabria, Spain)

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Summary - *El Castillo cave is a well-known site because of its Paleolithic archaeology and parietal rock art. This paper is focused on the human remains found by V. Cabrera in the Mousterian Unit XX assigned to MIS 4 and early MIS 3. The fossils consist of one upper left second premolar (ULP4), one incomplete proximal hand phalanx, and one partial femoral head. The tooth and the phalanx were assigned to adults, whereas the femoral head belonged to an immature individual due to the absence of fusion traces to the metaphyseal surface. The external morphology and metrical characterization of the Castillo-1466 (ULP4) tooth crown was quantified and compared to the variability of other Neanderthal dental remains and a sample of modern human populations. We also quantified its 3D enamel thickness distribution, its roots morphology, as well as the presence of chipping, and their possible relation to masticatory or paramasticatory activities. Castillo-1466 shows crown dimensions compatible with middle-sized Neanderthal teeth, but with a remarkably thicker enamel than other Neanderthal premolars, such as Marillac 13. The femoral head and the hand phalanx fragment are compared to published values for Neanderthals, although both partial fossils lack diagnostic features precluding any clear taxonomic diagnostic. Therefore, their attribution to Neanderthals is assumed based on the dating of the layers in which they were discovered. El Castillo cave Mousterian fossils represent another contribution to the knowledge of the Middle Paleolithic populations of Northern Spain, where different sites along the Cantabrian mountains yielded several human remains assigned to MIS 4 and early MIS 3.*

Keywords – *Neanderthal, Tooth, Macro and micromorphology, Enamel thickness distribution, Hand phalanx, Femur head.*

Introduction

El Castillo Cave: a historical overview

El Castillo Cave opens on the mountain of the same name, near the village of Puente Viesgo (Cantabria, Northern Spain; Fig. 1). It is a well-known site because of its Paleolithic art and its well-preserved litho-archeological stratigraphic sequence, revealed by Hugo Obermaier's fieldworks at the beginning of the 20th century. His results remained unpublished till the

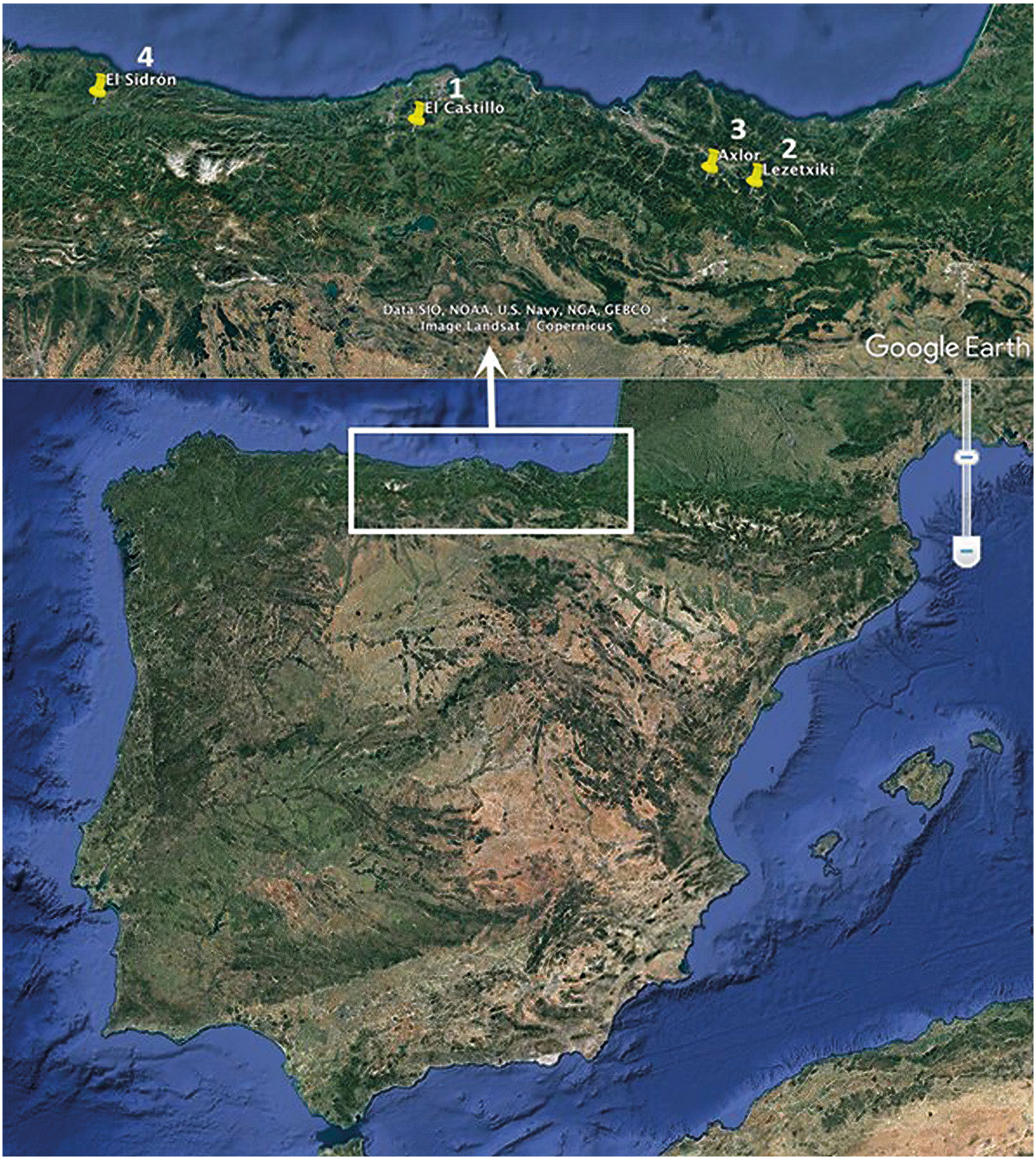

***Fig. 1** - The Iberian Peninsula and the Northern caves with Neanderthal adult teeth. 1: El Castillo C.; 2: Lezetxiki C.; 3: Axlor C.; 4: El Sidrón C. (Map source: Google Earth).*

eighties when Victoria Cabrera (1984) provided her analyses and interpretation of the site.

Indeed, in 1980, V. Cabrera and Federico Bernaldo de Quirós initiated new archeological excavations at the Cave entrance, concentrating their work on the Aurignacian, Middle-Upper Paleolithic Transition, and Mousterian levels (Cabrera et al. 2005; Bernaldo de Quirós et al. 2010a). During their research, several human remains have been found: three deciduous teeth

Obermaier 1924	Rink et al 1996 Wood et al. 2018	Martín-Perea et al 2023	Dates
f) Mousterian *alpha*	20a/b	XXa/b	34-53 ka cal BP (14C)
	20c	XXc	43-58 ka cal BP (14C)
	20d	XXd	44.2 ka BP ESR
	20e	XXe	38.6 ka BP (ESR) 69.3 ka BP (ESR)
	21	XXf	
	22	XXg	
		XXh	70.4 ka BP (ESR)
		XXi	
e) Clay layer	23	XXI	
d) Mousterian *Beta*		XXII	
c)Stalagmitic deposit		XXIIIa	
	Flowstone	XXIIIb	89 ka (U/Th)
	24	XXIIIc	
b) Acheulean		XXIV	
a) Clay	25	XXV	

***Fig. 2** - El Castillo cave. Stratigraphy and dates for the Mousterian Units XX-XXV.*

found on the Transitional Unit 18 (Garralda et al. 2022), and three human fossils in the Mousterian layers. The present study focuses on these latter Mousterian remains, with a summary of the main archeological characteristics of the Mousterian Units in which they were found, and their unprecedented morphometric description in comparison with other European Mousterian human fossils.

Mousterian occupations at El Castillo Cave

Three levels contain Mousterian occupations at El Castillo Cave, which were classified by Obermaier as Mousterian *alpha* on the top and Mousterian beta at the bottom, both separated by one clayey sterile level in between (Obermaier 1924; Cabrera 1984). After 1980, Cabrera and colleagues defined the Mousterian sequence, from the top to the base, within Units 20, 21, and 22 (Cabrera et al. 1992; Rink et al. 1997). They excavated Unit 20, which was divided into levels 20a/b, c, d and e, and the top of Unit 21 (Fig. 2; Supplementary Material Tab. S1). After a recent stratigraphic review, Martín-Perea et al. (2023) consider that Units 20-22, as defined by Cabrera and colleagues (1992), should be grouped within a single Unit XX (expressed in Roman numerals, Fig. 2), with eight sub-units ("a" to "h).

Unit XX has been dated several times using different methods (Fig. 2 and Supplementary Material Tab. S1). The ESR dates obtained from Obermaier's materials for Unit XX (Mousterian *alpha*) range around ~42-47 ka BP (Bernaldo de Quirós et al. 2006). The dates obtained with ^{14}C AMS and ^{14}C-Ultrafiltration from the materials found in the modern excavations range from ~39-49 ka BP to ~48-49 ka BP (~47 ka BP IntCal20) and are shown in Figure 2 and Supplementary Material Table S1. Several ESR dates fall in the same period, while those from the base are older (70.400±9.600 ka BP; Rink et al. 1997).

The lithic industry of Unit XX is overall classified as Mousterian. The most used raw material is quartzite, both fine- and coarse-grained. Sandstone and ophite were also used, while flint was very rare. Technologically, the most used operating scheme was the Discoid debitage in both unifacial and bifacial methods (Cabrera et al. 2006; Bernaldo de Quirós et al. 2010b). Other debitage methods, such as Levallois or Quina, are poorly represented in these collections.

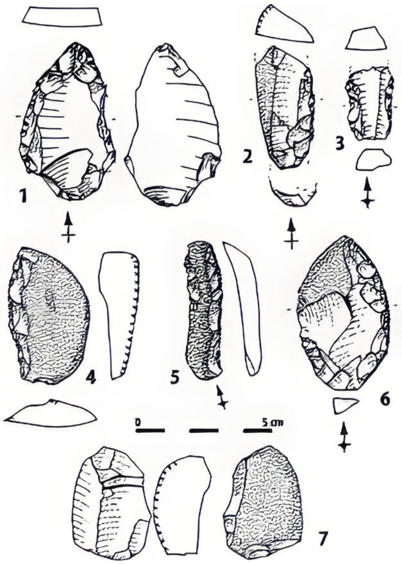

***Fig. 3** - Mousterian lithics from El Castillo Unit XX. 1: Flint point; 2-6: Sidescraper and denticulates on quartzite; 7: Levallois core on quartzite (drawings from Maíllo-Fernández).*

The retouched blanks are dominated by sidescrapers, denticulates, and notches (Fig. 3). Cleavers are also found in levels XXa/b and XXe, which led to the classification of the El Castillo Mousterian-*alpha* as "Vasconian", which was defined by Bordes (1953) as a regional Middle Paleolithic facies from western Cantabria and southwestern Pyrenees. Following Bordes' definition, Vasconian is also documented in other sites such as Cueva Morín, the Olha rock-shelter or Gatzarria. Moreover, the presence of cleavers and large format blanks is interpreted as a techno-functional aspect, and not so much anymore as a particular cultural entity (Cabrera 1984; Cabrera and Bernaldo de Quirós 1992; Deschamps 2017; Ríos-Garaízar 2017). A bladelet production from Levallois and prismatic cores seem to be qualitatively relevant because of their scarcity in the Middle Paleolithic, except in certain sites such as El Castillo, Combe-Grenal or Cueva Morín (Gutiérrez 2006; Cabrera et al. 2000; Maíllo-Fernández et al. 2004; Faivre 2012). Unit XXI is defined as sterile, and Unit XXII is only known through the Obermaier collection (Cabrera 1984).

Materials and methods

El Castillo Mousterian human remains

This paper reports on the three human remains found by Cabrera in Mousterian Unit XX (Martín-Perea et al. 2023).

The chronological assignment of these fossils is based on their conditions of finding and on the dates performed on the levels in which they were found. These human remains consist of a permanent maxillary left second premolar (later abbreviated as ULP4) Castillo-1466, which was found in Unit XXd and could be attributed to the end of MIS 4/beginning of MIS 3; an incomplete phalanx (Castillo-416) and a partial femoral head (Castillo-228) were also found in the middle of the same Unit XX, in a deeper level (XXf) and could be assigned to MIS 4. Because the three remains are isolated findings and were unearthed in different grid squares and levels (without evident bioturbation), they can be assigned to different individuals.

These fossils are curated at the Prehistory and Archeology Museum of Cantabria (MUPAC, Santander, Spain). Sampling for aDNA analysis was not granted for these fossils.

Macroscopic observation of Castillo-1466

The tooth was first examined with a Leica S8 APO stereomicroscope to identify pathological conditions (e.g., carious lesions), nonspecific stress markers (e.g., enamel hypoplasias), and any other kinds of modifications (e. g., totthpick grooves).

Micro-CT imaging and 3D model generation

The Castillo-1466 ULP4 was scanned using micro-computed tomography (μCT) on 13 May 2008, on the portable μCT scanner (SkyScan 1172 SN041, Bruker) of the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany). Technical parameters used for the μCT acquisitions are the following: 100 kV, 0.1 mA, metallic filters involving 0.04 mm Cu and 0.5 mm Al, 2065 ms of exposure time, 0.12° of rotation step, rotation over 360°, 3000 projections per scan, 2

Tab. 1 - Castillo-1466 ULP4 crown diameters and indices.

	M-D DIAMETER (M81)	B-L DIAMETER (M81(1))	CROWN INDEX (M81(1)/M81 X 100)	CROWN ROB. MODULE (M81 X M81(1))	CERVICAL M-D DIAMETER	CERVICAL B-L DIAMETER
LP4 CASTILLO-1466	>6.9 (~7.6?)	10.6	153.6	73.1	6.3	10.0

M-D: Mesiodistal; B-L: Buccolingual; Rob.: Robustness. Sign '>' refers to the minimal value affected by interproximal wear, while the value in parentheses is an estimate of the mesiodistal crown diameter corrected for wear

frame averaging, raw data saved in 16 bit TIFFs, pixel size of 17.39736 μm. The scans lasted each 5 h 08 mins. The raw μCT data were reconstructed in NRecon (version 1.4.4., Bruker) as a stack of 8-bit TIFFs, using the back-filtered projection algorithm, with some corrections for beam-hardening (30%) and ring artifacts (parameter: 3). To facilitate subsequent image processing (segmentation), the reconstructed datasets were resampled to 27 μm using the Triangle filter in Avizo 6.3 (www.vsg3D.com), and then filtered using a 3D median filter followed by a mean of least variance filter (each filter with a kernel size of 3; Kuwahara et al. 1976; Schulze and Pearce 1994; Wollny et al. 2013) for reducing the background noise while preserving and enhancing edges. The filtered TIFF stacks were imported into Avizo 6.3, where the enamel, dentine, and pulp chamber were segmented semi-automatically using region growing tools. Each dental component (i.e., enamel cap, enamel-dentine junction - EDJ -, dentine root surface, and pulp cavity) was visualized in 3D as a triangle-based surface model.

Tooth morphology and metrics

Dental linear measurements and discrete features. Standard dental measurements were taken with a digital caliper on the original Castillo-1466 premolar. These involved the crown diameters (Martin and Saller 1957; Bräuer 1988) which were measured to the nearest 0.1 mm. The greatest mesiodistal crown 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). Notably, both occlusal and interproximal wear affected the tooth's crown height and mesiodistal diameter (Tab. 1). Based on these crown diameters, the crown index and robusticity module were calculated (according to Martin and Saller 1957; results in Table 1). In addition, cervical diameters were measured following Hillson et al. (2005). All measurements were repeated three times on three different days, by one of the authors, and their average values were subsequently used for comparative analyses. The Arizona State University Dental Anthropology System (ASUDAS, Turner et al. 1991), or its expansion for Pleistocene humans (Bailey 2002a,b, 2005; Martinón-Torres et al. 2012) were used in the morphological description of Castillo-1466. Occlusal wear was scored using Molnar (1971) and Murphy (in Smith 1984) stages.

Morphological comparisons with other dental fossils were carried out using measurements either from the literature or from direct measurements on high-quality casts and specimens housed in curating institutions. A bivariate scatterplot (Statistica 7) enables comparing the buccolingual and mesiodistal crown diameters of Castillo-1466 with comparative data involving modern-population samples from Spitalfields, Poundbury and Coxyde (UK and Belgium respectively; n= 453 individuals in total; Maureille 2001). Most of the available European and Middle Eastern Neanderthal (n= 26), and European Upper Paleolithic humans (n = 24) dental measurements were obtained from their original publications (see details in Supplementary Material Tab. S2, and in Supplementary Material Tab. S3 in Garralda et al. 2020).

3D enamel thickness. The pronounced wear affecting the crown of Castillo-1466, and the lack of established methods to compensate for occlusal wear in premolars, preclude any quantitative assessment of the enamel thickness indices. For informative purposes, the 3D distribution of enamel thickness in Castillo-1466 was visualized in Avizo 6.3, using the 'Surface distance' module, and overlaying a color-coded map (modified after the 'physics.icol' colormap) onto the enamel surface.

Tooth root morphometrics. Using the μCT scans, the root length of the ULP4 Castillo-1466 was compared to Bailey's (2005) data since no other comparative data could be found in the literature. The μCT data enabled us to look at the root canals' morphology and compare it to Pan and Zanolli's (2019) data for Neanderthals. Adjusted-z scores (further abbreviated as 'Azs') were computed to compare the root length of Castillo-1466 to samples of Neanderthals and modern humans. An Azs close to 0 indicates that the specimen of interest is very close to the mean of the comparative sample. The specimen falls within the variation of the comparative sample when -1 ≤ Azs ≤ 1. When Azs > 1 or Azs > -1, the specimen falls outside of the Student test SD variation of the comparative sample. See Maureille et al. 2001, and Scolan et al. 2012 for details on the statistics, and SOM-S6 in Garralda et al. (2020) for an application on the Marillac teeth. The μCT data enabled to explore the root canals' morphology and compare it to Pan and Zanolli's (2019) data for Neanderthals.

Infracranial remains

Based on specimen preservation, only a few measurements could be performed for the femoral head, and the phalanx, following the methods described in Martin and Saller (1957) and Bräuer (1988).

Results

Tooth morphological description

The Castillo-1466 upper left second premolar (ULP4) was found in 1998 in Unit XXd (grid N16, sector 4). The tooth is well-preserved, although it has several cracks. Castillo-1466 lacks the typical Neanderthal condition (called "cyrtodontie" in French), in which there is a pronounced angle between the root and the crown and a labial convexity of the tooth median profile over its entire height. This condition was first described in Neanderthal incisors (Patte 1955; Brabant, Sally 1964) and later observed on the ULP3 of the Rochelot neanderthal (Couture and Tournepiche 1997), and to a lesser extent on the G. Boccard URP4 (Maureille et al. 2008) or the URP4 of Spy 2b (B. Maureille pers. obs.). The overall morphology of Castillo-1466 is close to that of the UP4 of other Neanderthals as can be observed in Figure 4 where Marillac 13G is shown (Garralda et al. 2020).

The crown shows an accentuated buccal prominence that should correspond to a well-developed buccal cusp in the original morphology (Fig. 4A; Supplementary Material Fig. S1). On the buccal side (Fig. 4A; Supplementary Material Fig. S1) the crown appears narrow, while the long root tilts distally. On the lingual aspect (Fig. 4B), the crown does not present any noticeable features due to occlusal and interproximal wear, but the distal inclination of the root is again easily visible (Supplementary Material Fig. S1).

On the mesial view, the cervical line is straight, the prominence of the outline of the buccal cusp should have been prominent (Fig. 4C) and there is a flat to concave, large, and elongated interproximal wear facet (5.5 mm long and 1.5 mm high), without subvertical grooves (Villa and Giacobini 1995; Garralda and Vandermeersch 2000; Poisson et al. 2002). The two roots are fused, with a shallow longitudinal groove in the middle of their surface breadth. The root is overall broad, with a clear dissimilarity between its buccal and lingual borders. The first is almost vertical, while the second one presents an angulation (at mid-height) towards the buccal side (Supplementary Material Fig. S1).

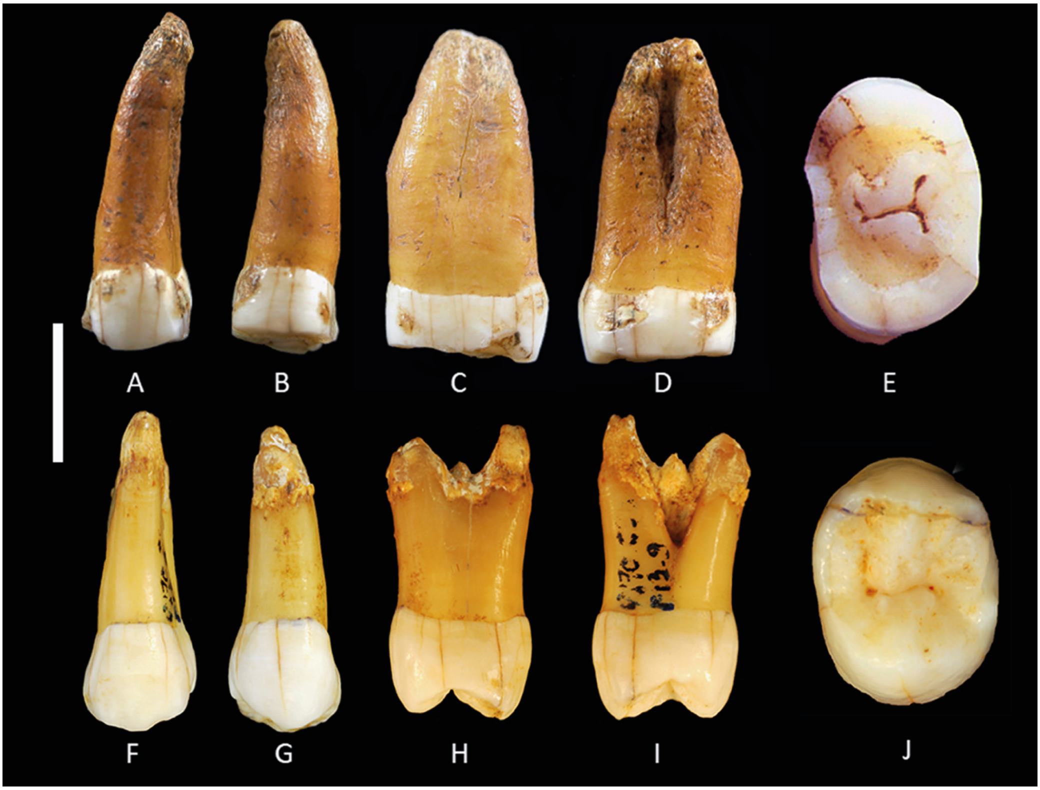

***Fig. 4** - Castillo-1466 (top) and Marillac 13G (bottom) ULP4s. A, F: Buccal. B, G: Lingual. C, H: Mesial. D, I: Distal (Scale = 10 mm). E, J: Occlusal (enlarged).*

On the distal view and the middle of the tooth cervix, the cervical line forms a slight convexity (Fig. 4D; Supplementary Material Fig. S1). The crown shows an elongated distal interproximal facet measuring at most 5.2 mm in length and 3.4 mm in height, which is slightly higher and convex than the mesial one. The distal interproximal facet is exempt from sub-vertical grooves. The convexity of the crown and the lateral prominence of the two cusps, especially the buccal one, are visible. The roots present a deep longitudinal and triangular depression on its two-third apical length and are joined by a thin layer of dentine and cementum up to the cervical root third (Fig. 4D; Supplementary Material Fig. S1 and S4). The buccal radical is vertical and shorter than the lingual one.

The general outline of the occlusal face (Fig. 4E; Supplementary Material Fig. S1) is slightly ovoid and altered by the accentuated interproximal facets (already described, see above) and by the pronounced occlusal wear (Murphy's advanced type 5, in Smith 1984). The attrition is stronger following the mesial half of the occlusal surface and over the whole height of both cusps. The distal and bifurcated fossa, the central groove, separating the main cusps, and a small trace of the mesial fossa (perhaps also bifurcate) are still visible at the crown center, but not the essential or accessory ridges (Supplementary Material Fig. S1).

The crown retains traces of tartar, especially on the mesial and distal sides (Fig. 4C-D). A small break in the enamel at the mesiobuccal angle could have been produced during the

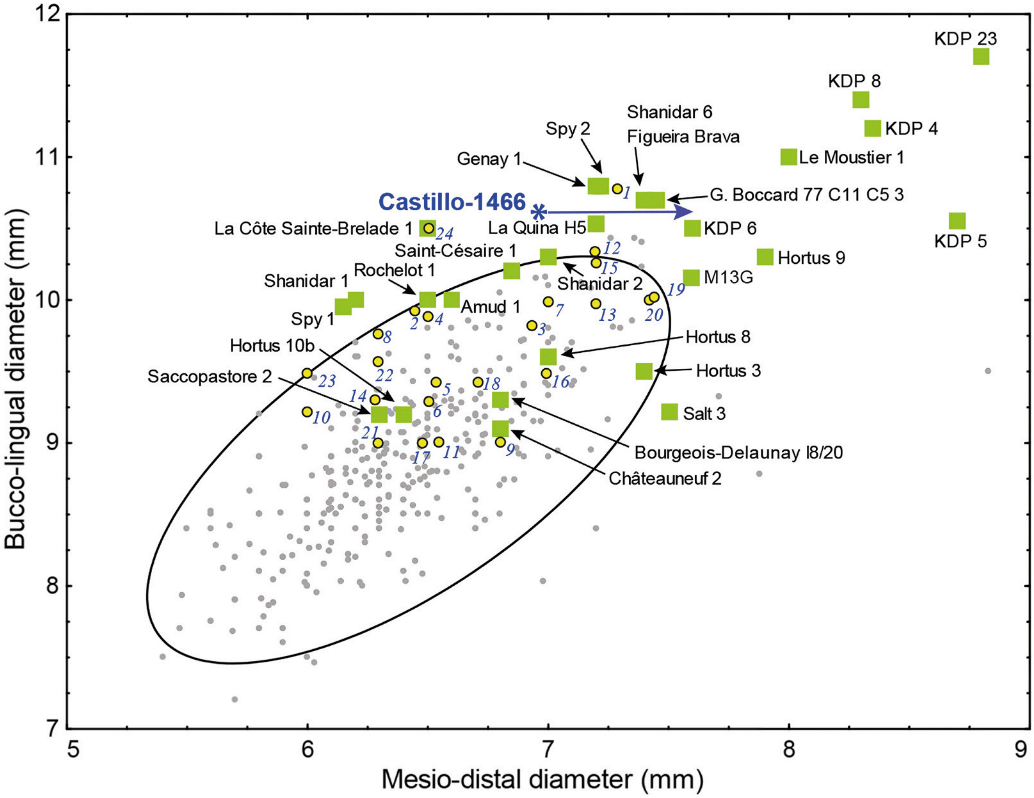

Fig. 5 - ***Scatterplots for both the mesiodistal and buccolingual crown diameters of the Castillo-1466 ULP4 (blue star) and comparative samples. The mesiodistal diameter being affected by interproximal wear, the blue arrow next to Castillo-1466 indicates the range of possibilities considering enamel reconstruction. Green-filled squares: Eurasian Neanderthals. Yellow circles: Upper Paleolithic humans (list of fossils in SOM Table S2). The black ellipse represents the 95% confidence interval of the sub-actual MH (grey dots) variation (± 1.96 SD).***

life of the individual since its edges are slightly rounded (Fig. 4C; red arrows on Supplementary Material Fig. S1). No enamel hypoplasias have been observed. The root has a marked hypercementosis visible, with more pronounced reliefs on the distal aspect of the root apex (SOM Fig. S1, S4, S5).

Castillo-1466 presents a long and large single pulp cavity. It only divides at the apical root third into a very thin buccal canal, and a larger bifid lingual canal (Supplementary Material Fig. S3). The lingual canal ends with a thin and small accessory canal opening laterally and close to the root apex through an accessory foramen (light blue arrows on Supplementary Material Fig. S1, S2). This morphology may be explained by the hypercementosis affecting the root apex of this tooth. The two cervical thirds of the pulp chamber can be described as a thin and convex blade-like structure linking the two root canals.

Such a pulp cavity morphology has yet never been described on a Neanderthal upper premolar. This increase in pulp volume may be interpreted as an overall enlargement of the pulp chamber, in comparison to premolars with divergent radicals. The apical pulp morphology described in Castillo-1466 explains the difference in height seen in the distal and mesial radicals.

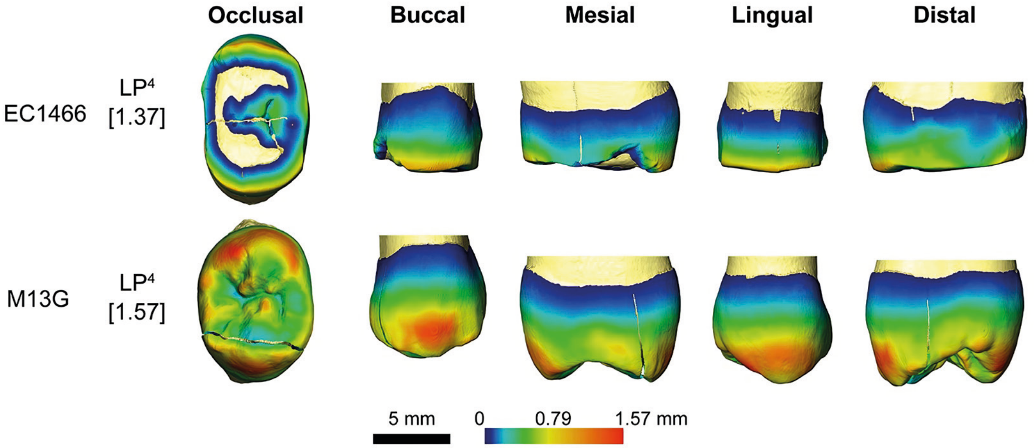

***Fig. 6** - Castillo-1466 ULP4 enamel thickness compared to that of Marillac 13G.*

Tooth metrical comparisons

Crown dimensions. On the bivariate plot of the crown diameters, only the modern group's 95% confidence ellipse is displayed (± 1.96 SD variation range), the sample size for fossils being too small.

In Figure 5, both the mesiodistal and the buccolingual crown diameters of the Castillo-1466 fall in the middle of the cloud of Neanderthal data points. This tooth also plots above the upper limit of the modern human ellipse (especially in the estimated reconstruction of its mesiodistal diameter), as do other Neanderthal teeth. There is, however, a wide variation of ULP4 diameters in Neanderthals, which explains the scatter of the data points, some falling within or outside the modern human ellipse. Note that, in Figure 5, the Neanderthal fossil scattering cannot be considered as highly influenced by interindividual differences of the interproximal attrition and the occlusal wear of the crown (and it is the same for our extant human sample). This may more likely result from the sample constitution with the large teeth of Krapina plotting in the higher part of the Neanderthal variability.

The Upper Paleolithic fossils appeared inside the modern human ellipse, and only a few are outstanding by their dimensions, independently of their chronology (see names and cultures in Supplementary Material Tab. S2).

3D Enamel thickness. Figure 6 shows the 3D enamel thickness map of Castillo-1466 ULP4 compared to that of Marillac 13G (Garralda et al. 2020), the unique available sample. The 3D enamel distribution of both individuals is similar, although the considerable wear of Castillo-1466, contrasts with the Molnar (1971) stage 1 of Marillac 13G.

Tooth root morphometrics. The root of the ULP4 Castillo-1466 is 17.36 mm long (measured on the 3D model from the lingual side to the root apex). Castillo-1466 is very close to, although slightly smaller than the Neanderthal mean reported by Bailey (2005; Azs = -0.11 for N=10 Neanderthals, mean = 17.6 mm and SD = 1.0 mm), and much larger than the two Upper Paleolithic UP4 roots measured in Bailey (2005; 10.5 mm and 13.3mm). Regarding comparisons with recent modern human samples, the root length of Castillo-1466 falls close to the mean and fits within the range of the Australian sample used in Bailey (2005). Yet, it is larger than the reported Bantu, White, Bushman and Japanese means (Bailey 2005). Note that the Castillo-1466 root length falls within the range of variation of the Bantu sample published by Bailey (2005).

The root canal morphology of Castillo-1466 ULP4 (Supplementary Material Fig. S3 and S4) is a variant between the "1R1" and "1R(Bf)$_{1Bf}$" types, described in Pan and Zanolli (2019). It would

Fig. 7 - Castillo-416 hand phalanx compared to the right proximal second hand phalanx of Kebara 2. A: dorsal view; B: palmar view; C and D: proximal and distal views of Castillo-416 (Scale = 50 mm).

correspond to a root with one canal without furcation level except for the apical extremity of the P4 where the canals form two short horns each of them related to the separate root reliefs that can only be observed on the distal view of the premolar.

Infracranial remains

Castillo-416. The fossil was found in 2001 in the middle part of Unit XXI, when cleaning the profile. It consists of the incomplete diaphysis and distal epiphysis of a proximal phalanx, perhaps of the second finger (index) of a robust right hand (Fig. 7). It measures 22.7 mm long by ~ 10.9 mm wide and 8.8 mm high at the most distal part preserved. The proximal epiphysis is broken and incomplete.

The central region shows that the phalanx should have corresponded to an adult's hand, judging by the stage of complete bone development. The external surface has been eroded and the distal epiphysis (*caput phalangis*) is partially destroyed on the anterior and external sides due to taphonomic processes. The medial part of the head preserved is large and robust. The posterior breakage, at approximately half of the diaphysis, is ancient, and the borders are covered by sediments. The diaphyseal section is almost rounded,

***Tab. 2** - Measurements of the incomplete phalanx Castillo-416 and comparative fossils.*

	CASTILLO-416	REGOURDOU (CAST) [A]		COMBE-GRENAL 23[B]	KEBARA 2[C]		SHANIDAR 3	4[D]
	Right?	Right	Left	II/III? Right	Right	Left	Left?	Left
Distal max. breadth	12.6?	11.6?	12.2?	12.5	13.2	13.6	13.0	11.2
Midshaft perimeter	31?	30?	28?	28	33	33	29.5	27.5
Midshaft height	7.8?	5.9?	5.7?	5.8	7.8	7.9	7.5	16.4
Midshaft breadth	10.3?	9.3?	9.2?	10	12	12.3	11	10.0

Measurements of Castillo-416 second proximal phalanx compared to those of several Neanderthals. a: Garralda (present study). b: Garralda and Vandermeersch (2000). c: Vandermeersch (1991). d: Trinkaus (1983).

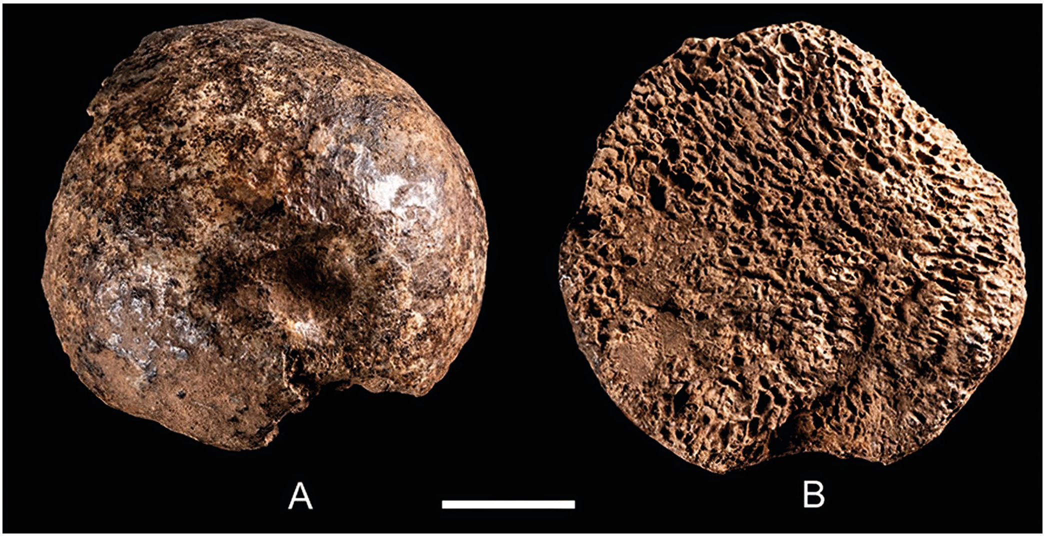

***Fig. 8** - Castillo-228. The femoral head (Scale = 50 mm). A: medial side; B: lateral surface towards the metaphyseal surface on the proximal femoral end.*

similar to what has been described for several other Neanderthals (e.g., La Ferrassie 1 and 2, Heim, 1976; Kebara 2, Vandermeersch 1991).

The phalanx fragment is robust and thick, although the erosion affecting the lateral shaft margins eliminated the traces of muscular attachments. The only available measurements are compared in Table 2 to those of other Neanderthals such as Regourdou 1 (measured on casts), Combe-Grenal 23 (Garralda and Vandermeersch 2000), Kebara 2 (Vandermeersch 1991), and Shanidar 3 and 4 (Trinkaus 1983), because of the chronostratigraphic position of Castillo-416.

Castillo-228. This fossil was found in 2003, in the middle part of Unit XX (grid M18, sector 8). It corresponds to an isolated partially preserved femoral head, rolled, eroded and incomplete, probably of a right femur, showing in the metaphyseal face numerous trabeculae (Fig. 8). The fovea, where the teres ligament inserts, appears deep and ovoid. It can be assigned to an immature individual, considering its small size, hemispherical shape, with the

***Tab. 3** - Castillo-228 femoral head diameters and index compared to those of seven Neanderthals (immatures and adults) and two modern children.*

	VERTICAL DIAMETER (M18)	TRANSVERSAL DIAMETER (M19)	HEAD INDEX (M19/M18X100)
	Right/Left	Right/Left	
Castillo-228	36.6?	36?	98.4?
La Ferrassie 6 [a] (~3-5y.)			87.7
Le Moustier 1 [b]	48	48	100.0/-
La Ferrassie 1 [b]	56/-	-/55	98.2?/-
La Ferrassie 2 [b]	44.5/46	41?/46	92.1?/100
Spy 2 [b]	53/54	53.5/53?	100.9/98.1
Feldhofer 1 [b]	52/52	50.5/52	97.1/100
La Chapelle aux Saints [b]	51?/-	52.5?/-	102.9?/-
Qafzeh 10 [c] (~6y.)	20.7/-	23.4/-	113.0
Lagar Velho [d] (~4.5-5y.)	20.2/-	22.0/-	108.9

Abbreviations: a: Heim, 1982b; b: Heim, 1982a; c: Tillier, 1999; d: Trinkaus et al. 2002. ?: Incomplete measurement

lateral side slightly flattened, and because it has no traces of having started to fuse with the metaphyseal surface on the proximal femoral end. In current populations, the range of age variation for this process is between 11 and 16 years in girls and between 14 and 19 years old in boys (Scheuer et al. 2004). Consequently, we attribute it to a young individual of unknown sex, around 8 years old since the head does not reach the almost circular circumference form and lacks the sharp edges appearing from puberty (Scheuer et al. 2000). Its estimated vertical diameter (Tab. 3) is ~36.6 mm and the transversal one is ~36 mm, with a thickness of ~19.95 mm. The bone is very compact, and the *fovea capitis* is oval (~11.3 mm by ~6.8 mm) and deep. Table 3 shows that the estimated femoral head diameters of Castillo-228 are smaller than those of adult individuals, larger than those of the Mousterian modern child Qafzeh 10 (~ 6 years; Tillier 1999) and the Gravettian immature Lagar Velho (~ 4 years; Duarte et al. 1999), and smaller than those of the Le Moustier 1 adolescent (~13 years, Wolpoff 1999; or ~15.5 years, Thompson and Nelson 2000).

Discussion

The human fossils found in Mousterian contexts are scattered throughout the wide area of the Iberian Peninsula (Garralda 2005) and over a broad chronology. However, in the Cantabrian Mountain range (Fig. 1), where the El Castillo Cave is located, there are three sites with Mousterian human adult remains.

One of them is Lezetxiki Cave (Basabe 1970; Garralda 2005; López-Onaindía et al. 2023), where two isolated teeth were found, the first at the base of level III and the latter in the central part of the sublevel IVa (both assigned to MIS 3; Arrizabalaga 2006). Their morphological and metric characteristics confirm their attribution to Neanderthals.

The second site is Axlor (Basabe 1973; Garralda 2006; Gómez-Olivencia et al. 2020, 2022; González-Urquijo et al. 2021), in which five human teeth belonging to the upper left maxilla of an adult (Basabe 1973) were found in level III and assigned to the recent Mousterian (MIS 3, González et al. 2005, 2021). The only tooth from Axlor that can be compared with Castillo-1466 is the ULP4, which shows a single root (Gómez-Olivencia et al. 2020, Fig. 5) without the complex external root and internal pulp cavity morphology described on Castillo-1466 (see Supplementary Material Fig. S1-11). Note that for Gómez-Olivencia et al. (2020, 2022) this ULP4 could be considered as representing an anatomically modern individual (represented by three upper maxillary teeth: P4, M1 and M3) which would be related to the Upper Paleolithic occupation of the site. In contrast, González-Urquijo et al. (2021) rather classify these teeth as Neanderthals, based on stratigraphic and morphologic evidence, an interpretation mainly based on the comparison of the Axlor ULM1.

Further West is the El Sidrón cave (Asturias), with more than 200 teeth, an estimated MNI of 13 adult and immature individuals (Rosas et al. 2012), and a human bone dating of 48,400 ± 3,200BP (OxA-21 776), confirming other dates that placed this collection in MIS 3 (Wood et al. 2013). These teeth have not yet been published in detail, thus precluding any detailed comparison regarding the morphology of the UP4. However, several studies confirm the assignment of this collection to Neanderthals (Rosas et al. 2006). El Sidrón has also yielded the remains of an immature skeleton (J1) ~7.69 years old (Rosas et al. 2017). This fossil has both femora (the right diaphysis very incomplete and the left one complete) but without the femoral heads, thus precluding the comparison with Castillo-228. Nevertheless, J1 does not present traces of fusion between the metaphyseal surface and the head, and it seems possible that the age-at-death of both children could have been similar.

Although the El Castillo Mousterian fossils are isolated and very incomplete, several features of the morphology and dimensions of the Castillo-1466 tooth secure its attribution to Neanderthals: large size of the buccal cusp, root morphology, or root length. These features are found to various extents in Neanderthals, such as several of Krapina (Patte 1962; Wolpoff 1979), Combe-Grenal (Garralda and Vandermeersch 2000), G. Boccard (Maureille et al. 2008), Rochelot 849 (Couture and Tournepiche 1997), El Salt (Garralda et al. 2014) or Marillac (Garralda et al. 2020).

Pan and Zanolli (2019) investigate a sample of eight Neanderthal UP4, seven of which are from Krapina and one from La Chaise-Abri Bourgeois-Delaunay. They found that the most frequent conformation of the pulp chamber in Neanderthal UP4 is two roots with a buccal and a lingual component (6 out of 7 = 87.5%; Pan and Zanolli 2019). They also report a single (fused) and large root without furcation level in one Neanderthal from Krapina (Gorjanovic-Kramberger 1901), which conformation is more frequent in modern humans (n=13, 30.8%). The pulp morphology of Castillo-1466 does not correspond exactly to the categories described in Pan and Zanolli (2019), which could be explained by the nature of their sample encompassing a variability of Neanderthals restricted to a specific and rather old Neanderthal population from Krapina (end of MIS 6-beginning MIS 5e, Karavanić et al. 2018).

Moreover, the internal morphology of Castillo-1466 ULP4, with an apically positioned root bifurcation of the pulp chamber and associated roots, is peculiar. This may be described as a taurodontism similar to that described on permanent upper premolars from Krapina (Gorjanovic-Kramberger 1907, 1908), and on Neanderthal molars (e.g., Keith 1913; Kupczik and Hublin 2010; Benazzi et al. 2015). Such a taurodontism in Neanderthal upper premolars- seems different from the one published in extant humans' premolars (see Vertucci and Gegauff 1974 for UP3). The Castillo-1466 ULP4 can be considered as a meso to hypertaurodont tooth, after adapting the Middleton Shaw (1928) classification based on the Strandlopers teeth from the Zitzikama rock-shelters and other South African Khoekhoe groups. Moreover, the Castillo-1466 ULP4 pulp chamber morphology seems near to the type 4 described by Vertucci and Gegauff (1979) identified in only 5% of their sample of 400 extant human UP3s. One may hypothesize that the frequent condition observed in the Neanderthals UP3s and UP4s showing two separate roots (buccal and lingual root components) and the occurrence of taurodontism may reflect the retention of a primitive morphology.

Castillo-1466 does not show any toothpick grooves or sub-vertical striations in the interproximal facets. These well-developed facets and the occlusal crown attrition could indicate a somewhat medium to late age-at-death for this individual yet, keeping in mind that they could also be influenced by diet. In addition, the hypercementosis observed on the root apex may be partially due to age, but more significantly to biomechanical stresses (Le Cabec et al. 2013; Massé et al. 2023).

Conclusions

The studied human remains from El Castillo were found in the middle of Unit XX, which are levels with the Mousterian techno-complex of the site and dated towards the early MIS 4 and the beginning of MIS 3.

Considering the chronostratigraphy, one can assume that Castillo-228, a partial right femoral head, can be assigned to an immature Neanderthal, although, there are no described autapomorphies for characterizing this small anatomical region and attributing it reliably to Neanderthals.

Regarding the incomplete hand phalanx, Castillo-416, it should be noted that it does not have distinctive characteristics allowing its assignation to the hand of an adult Neanderthal, smaller than those of the adult males Kebara 2 or Shanidar 3. The finding of Castillo-416 in the Mousterian Unit 20f, its chronology (MIS 4), and the fact that this culture in Western Europe seems to have been developed exclusively by Neanderthals support such an assignation.

The ULP4, Castillo-1466, is for sure a Neanderthal premolar with a medium size crown and root length compatible with Neanderthal traits. Using 3D dental tissues proportions, we describe, for the first time, the expression of a novel trait concerning taurodontism on the Neanderthal upper premolar, which will deserve more thoroughly detailed research in future studies.

Note that among other Neanderthal remains discovered in sites in northern Spain, several deciduous teeth were unearthed in two sites, although these teeth cannot be directly compared to the fossil described in the present study. First, in Arrillor cave (Álava), a maxillary right dm2 was recovered in the AMK formation (MIS 3; Bermúdez de Castro and Sáenz de Buruaga 1999), its crown is very abraded and presents a small Carabelli pit.

The second site is the El Castillo Cave itself, where in Unit XVIII, which is located above the sterile Unit XIX (Cabrera 1984; Cabrera et al. 1993, 1996, 2005; Wood et al. 2018), three deciduous tooth crowns were found. Due to their morphological and metric characteristics, the three fossils have been assigned to Neanderthals (Garralda 2005, 2006; Garralda et al. 2022). What is interesting is that the human group they represented developed a different techno-complex, considered as a transitional industry between the Middle and Upper Paleolithic, which was dated at ~ 42 ka. by multiple analyses (Wood et al. 2018; Garralda et al. 2022).

The description of the Mousterian human fossils from El Castillo's documents the microevolution and biodynamics of those Southwestern Neanderthal groups. For the most recent fossils, this also suggests their possible genetic or cultural contacts with other populations. Unfortunately, such contacts remain at present impossible to discuss because of the lack of concrete physical evidence. Yet, novel analytical approaches, such as the extraction of aDNA from the sediments of different El Castillo Units, are ongoing and will probably help in understanding the human settlement of this northern Spanish Cantabrian region throughout the Mousterian and the transitional period to the early Upper Paleolithic.

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Authors contribution

MDG, ALC and JMM organized the structure of the paper and wrote the different parts, in collaboration with BM. All authors revised, provided feedback, and approved the manuscript.

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