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BRIEF COMMUNICATION

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Neanderthal teeth from Lezetxiki (Arrasate, Iberian Peninsula): New insights and reassessment

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Abstract

Objectives: We reassess the taxonomic assignment and stratigraphic context of a permanent upper first molar and a permanent lower third premolar recovered from the archeological site of Lezetxiki in the North of the Iberian Peninsula.

Materials and Methods: We assessed the external and internal morphology of the teeth using qualitative descriptions, crown diameters, dental tissue proportions, and geometric morphometrics. The teeth from Lezetxiki were compared with Middle Pleistocene specimens, Neanderthals, Upper Paleolithic modern humans, and recent modern humans.

Results: Both teeth were consistent with a Neanderthal classification. The upper first molar shows taurodontism, and its cusp proportions and overall morphology match those of Neanderthals. Geometric morphometric analyses of occlusal anatomy classify this molar as a Neanderthal with a posterior probability of 76%. The lower third premolar, which was originally classified as a lower fourth premolar, also shows a Neanderthal morphology. This premolar is classified as a Neanderthal with a posterior probability of 60%.

Discussion: These teeth represent the only adult Neanderthal teeth from the Western Pyrenees region found to date. The teeth were found at a stratigraphic level (designated Level III) that marks the transition level from Mousterian to Aurignacian, and are among the most recent Neanderthal remains from the north of the Iberian Peninsula.

KEYWORDS

dental tissue proportions, geometric morphometrics, microtomography, Paleolithic, stratigraphy

1 | INTRODUCTION

Evidence of Neanderthal presence and activity in the Western Pyrenees and Cantabrian region is well documented since several sites have materials that are dated to the end of the Middle Pleistocene up to Marine Isotopic Stage 4 (MIS4) and MIS3 (71–29 ky). These sites are: Lezetxiki (Álvarez-Alonso & Arrizabalaga, 2012; Baldeón, 1993), Arlanpe (Rios-Garaizar et al., 2015), Axlor (González-Urquijo et al., 2005; Jones et al., 2018; Rios-Garaizar, 2005, 2017), Aranbaltza (Rios-Garaizar et al., 2018), Amalda I (Altuna et al., 1990; Rios-Garaizar, 2010; Sánchez-Romero et al., 2020), Urkulu (Iriarte-Chiapuso, 2013), Zerratu (Sáenz de Buruaga, 2005). However, Neanderthal fossil remains are scarce in this region and come from a few sites in the Basque Country. An upper second deciduous molar was found in Arrillor (Bermúdez de Castro & Sáenz de Buruaga, 1999; Iriarte-Chiapusso et al., 2019). In Axlor, a recent study has reported on a Neanderthal cranial fragment and two deciduous teeth belonging to Neanderthals (Gómez-Olivencia et al., 2020). The site of Lezetxiki has yielded two teeth that were originally attributed to Neanderthals (Basabe, 1970).

Other sites that have yielded Neanderthal remains in the northern Iberian Peninsula include El Castillo (Garralda, 2005; Garralda et al., 2022), Covalejos (Sanguino González & Montes Barquín, 2005), El Sidrón (Egocheaga et al., 2000; Fortea et al., 2003; Prieto et al., 2001; Rosas & Aguirre, 1999), Galería de las Estatuas (Demuro et al., 2019; Pablos et al., 2019), Valdegoba (Quam et al., 2001), Mollet cave (Maroto, Julià, et al., 2012), Banyoles (Maroto, 1993), and Cova del Gegant (Daura et al. 2005; Quam et al., 2015).

The archeological site of Lezetxiki (Arrasate, Gipuzkoa, Iberian Peninsula) (Figure 1) was discovered in 1927, although it was not excavated until a quarter of a century later. The cave of Lezetxiki was excavated in two different periods: between 1956 to 1968, and from 1996 to 2018. In the first period, an interdisciplinary team led by J.M. de Barandiarán excavated an area of over 50 m^2 (Barandiarán, 1960, 1963, 1965; Barandiarán & Altuna, 1965, 1966, 1967a, 1967b, 1970). In the second period, another team led by A. Arrizabalaga and M. J. Iriarte-Chiapusso excavated a new area located to the south of the first excavation in an attempt to complete the sequence recovered during the initial excavations (Álvarez-Alonso & Arrizabalaga, 2012; Arrizabalaga & Iriarte-Chiapuso, 2018).

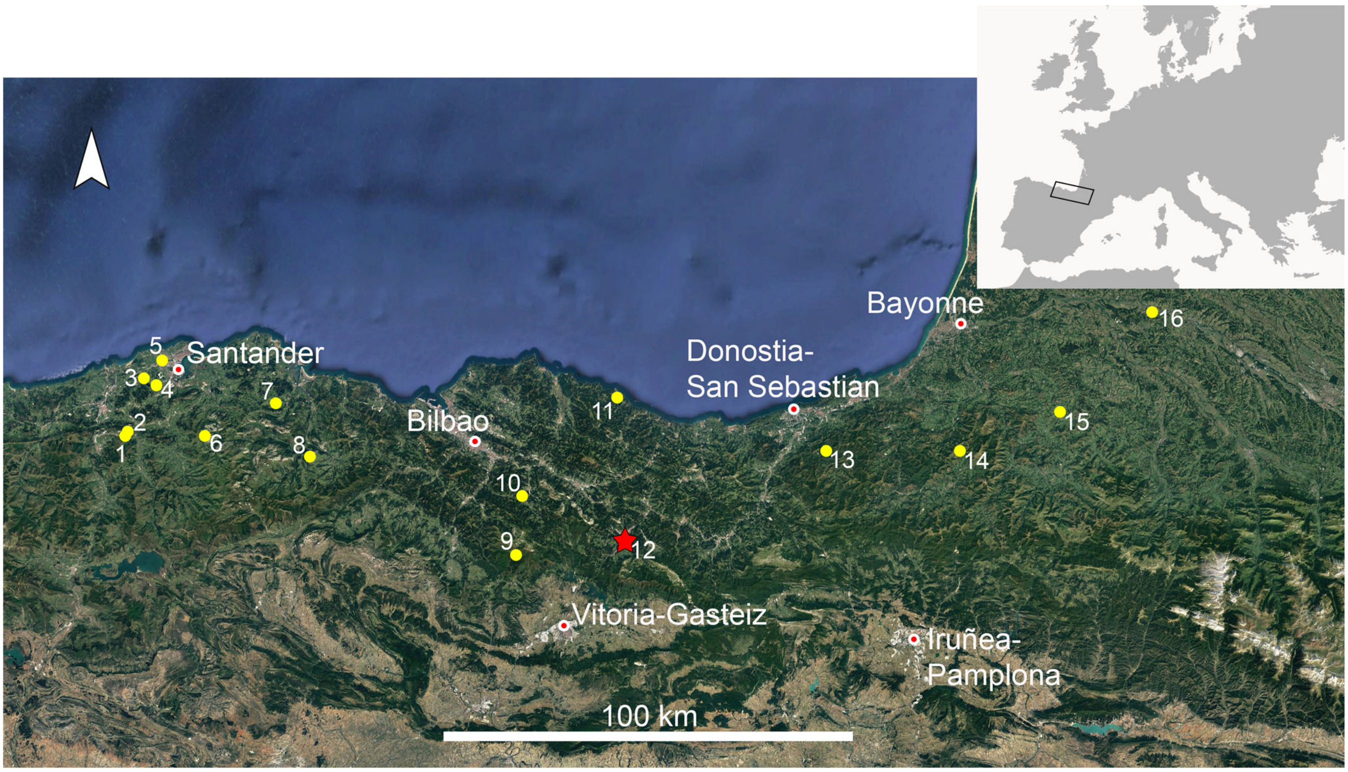

FIGURE 1 Location of Lezetxiki (red star) and other Paleolithic sites with human remains in the east and center of the Cantabrian Region (northern Iberian Peninsula and southwestern France). (1): La Pasiega (HS; González Echegaray & Ripoll Perelló, 1954); (2): Castillo (N, HS; Garralda, 2005; Garralda et al., 2019; Obermaier, 1925; Tejero et al., 2010; Vallois and Delmas, 1976); (3) Covalejos (N, HS; Sanguino González & Montes Barquín, 2005); (4) El Pendo (HS; Basabe, 1982); (5) Morín (HS; González Echegaray & Freeman, 1973; Obermaier, 1925); (6) Rascaño (HS; Guerrero Sala & Lorenzo Lizalde, 1981); (7) La Chora (HS; González Echegaray et al., 1963); (8) Mirón (HS; Carretero et al., 2015); (9) Arrillor (N; Bermúdez de Castro & Sáenz de Buruaga, 1999); (10) Axlor (N, HS; Basabe, 1973; Gómez-Olivencia et al., 2020); (11) Santa Catalina (HS; Albisu Andrade et al., 2014; López-Onaindia et al., 2021); (12) Lezetxiki (N; Basabe, 1970, This study); (13) Aitzbitarte III (HS; de la Rúa & Hervella, 2011); (14) Alkerdi (HS; Barandiarán & Cava, 2008; Cava et al., 2009); (15) Isturitz (HS; Henry-Gambier et al., 2013); (16) Duruthy (HS; Henry-Gambier, 2006). N, Neanderthal; HS, *Homo sapiens*. Source: Data by Jarvis et al. (2008) and Gómez-Olivencia et al. (2020).

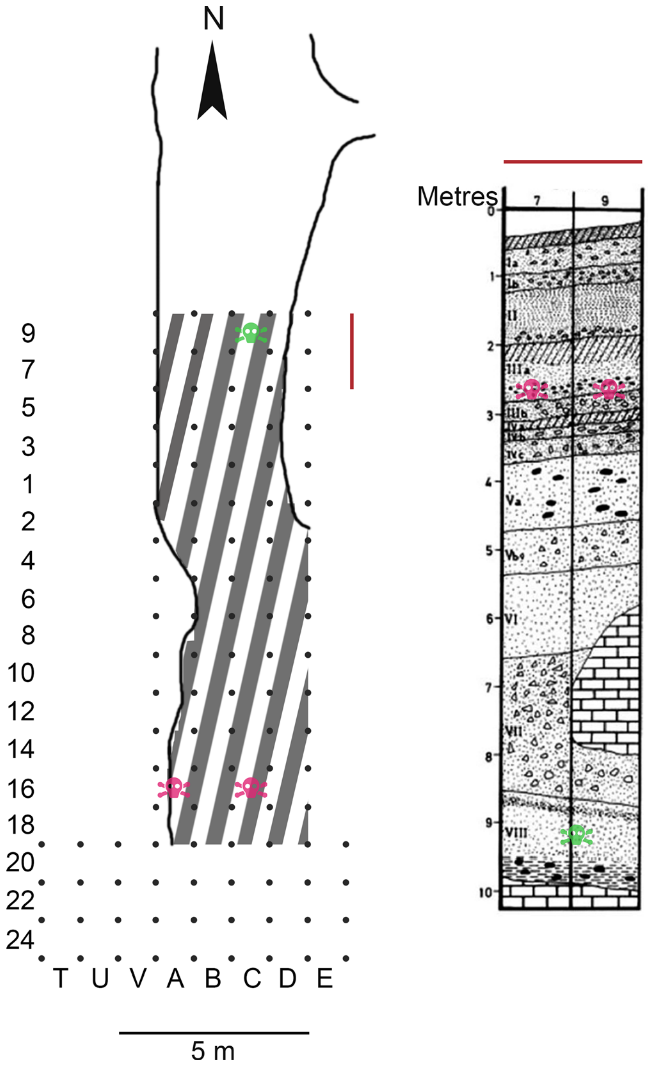

FIGURE 2 Excavation plan (left) and stratigraphic column (right) of Lezetxiki cave (modified from Altuna, 1972; Álvarez-Alonso & Arrizabalaga, 2012). The excavation plan combines the original excavations by Barandiarán (1956–1968) (squares 9–18) with the recent interventions by Arrizabalaga (since 1996). The continuous black line indicates the cave's wall. The shaded area corresponds to the area excavated in the original interventions. The human remains are marked with green and pink skeleton silhouettes for the humerus and teeth, respectively. *The red lines indicate the place where the section belongs to in the plan. **The square numbers in the plan are not in sequential order because Barandiarán (1956–1968) used to give even numbers towards one side from the beginning of the excavation, and odd numbers in the opposite direction from the initial point

The cave consists of a large tunnel (with an estimated surface area of nearly 300 m^2), whose entrance is partially collapsed, and a nine-meter thick stratigraphic sequence. Lezetxiki is often mentioned as a classic site in northern Spain, in connection with its Mousterian occupations and the Middle to Upper Paleolithic transition (observed in Level III—E and F in recent seasons). The authors who have studied the material from Level III (Arrizabalaga, 1995; Baldeón, 1987; Bernaldo de Quirós, 1982; Esparza, 1985), have reached different conclusions regarding the typology of this lithic assemblage, but all of them have highlighted its ambiguous nature. In later extensive studies (Arrizabalaga, 2006a, 2006b, 2014), it was proposed that the lithic assemblage should be attributed, mostly, to the Aurignacian. However, it is possible that certain parts of Level III (probably sub-level IIIb, which had previously been considered sterile) also included Mousterian tools, while the nature of the lithic industry of Level IV is clearly Mousterian (Cabrera et al., 2004). The site is well known for its faunal remains, especially as it reports the first instance of different species (e.g., *Gulo gulo*, *Pliomys lenki*) in the Iberian Peninsula and other outstanding findings (Altuna, 1963; Altuna, 1972; Castaños et al., 2011; Chaline, 1970). In addition, the site has yielded some human remains: two teeth (Basabe, 1970)—analyzed in this paper—and a humerus from MIS 6 (Altuna, 1990; Basabe, 1966; de la Rúa et al., 2016; Falguères et al., 2006).

The teeth, a molar (Lz.15C.505) and a premolar (Lz.16A-488.70-0), were discovered in the 1966 field season (Barandiarán & Altuna, 1967a) (Figure 2). Basabe (1970) suggested that the teeth were probably Neanderthal due to the taurodontism of the molar and published them as belonging to Level IV. Since then, subsequent works have accepted these stratigraphic and taxonomic attributions without further considerations (Aguirre Enriquez, 2007; Basabe, 1982; de la Rúa, 1990). The reassessment of the original field notes indicates that the dental remains were found in level III, which marks the transition from Middle to Upper Paleolithic (Figures S1–S7). The teeth have not been studied since the original description by Basabe (1970) and have rarely been mentioned or included in international or national publications (Basabe, 1982; de la Rúa, 1990; Garralda, 2005). This makes these teeth seldom known to the international scientific community.

Thanks to the new excavations, we have been able to reinterpret the limits of this level and some of the original coordinates in Row 16 (Figure 2). Therefore, it has been possible to reevaluate the differences between sub-levels IIIa and IIIb, where the teeth were recovered. Radiocarbon dates of the level from which the teeth were recovered yielded Aurignacian dates for sub-level IIIa (39.5–32.6 ky cal BP) and Mousterian dates for sub-level IIIb (minimum dates of 46.5 ky BP) (Higham et al., 2014; Maroto, Vaquero, et al., 2012; Wood et al., 2014) (Table S1).

Recent findings reflect the complexity of the Middle to Upper Paleolithic transition in Western Europe. For example, Slimak et al. (2022) have suggested that Neanderthals and modern humans successively replaced each other in Mandrin cave (France) over the last millennia of Neanderthal presence in the region. In addition, a recent study of a maxillary fragment from Axlor cave (Western-Pyrenean region), which was previously classified as a Neanderthal (Basabe, 1973), has indicated a most likely classification as a modern human (Gómez-Olivencia et al., 2020). In this context, considering the new stratigraphic information and the data regarding the origin of the teeth in the Middle to Upper Paleolithic transition, a re-analysis of the dental remains from Lezetxiki cave using modern techniques is warranted. The aim of this study is to determine whether the molar and premolar found at Lezetxiki in 1966 can still be attributed to

Neanderthals when evaluated using modern quantitative and comparative analyses.

2 | MATERIALS AND METHODS

2.1 | Material

The two permanent teeth from the Lezetxiki Cave were analyzed: a permanent upper molar (Lz.16C.505) and a lower premolar (Lz.16A-488.70-0). The field notes by Barandiarán report the original coordinates where the teeth were found, the date when they were recovered, and associated information. The molar was recovered in square 16C (Figures S1 and S2). A denticulated light flint flake was recovered together with the molar and shared the same coordinates (Figure S2). The premolar was recovered in square 16A (Figures S3 and S4). Both the molar and the premolar were found in sediments described as mainly clay, with no disturbances, and above the gravel layer separating sub-levels IIIa and IIIb, attributed to IIIa (Figure 2).

2.2 | Micro-CT scanning and volume segmentation

Both teeth were scanned using the Scanco Medical Micro-CT80 system at the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH) in Burgos (Spain) using the following parameters: 120 kV, 100 μA, 0.2 mm copper filter and a voxel size of 18 μm.

The resulting dataset was segmented by using semiautomatic threshold-based segmentation in Mimics 10.0 (Materialize, Louvain, Belgium), following the half-maximum height method (Coleman & Colbert, 2007; Fajardo et al., 2002; Spoor et al., 1993) assisted by manual corrections. Following segmentation, we obtained the virtual models for the enamel, dentine and pulp cavity. These 3D models for each dental tissue are available at http://doi.org/10.6084/m9.figshare.12075477.

2.3 | Anatomical and metric descriptions

The external morphology and non-metric traits were recorded using standard methods (Bailey, 2002; Carlsen, 1987; Turner II et al., 1991). In addition, we described the morphology and nonmetric traits of the M^1 EDJ following Martin et al. (2017). For the description of the premolar's EDJ morphology, we followed the approach used by Zanolli, Pan, et al. (2018) and Davies et al. (2019).

Mesiodistal (MD) and buccolingual (BL) dimensions of the crown were taken with a digital caliper according to Moorrees' method (Moorrees et al., 1957) and compared to reference groups (Table S3).

The surface area for each of the main cusps of the M^1, as well as the occlusal polygon area, total crown area and the angles between the cusp tips, were calculated from occlusal photographs (Bailey, 2002, 2004).

2.4 | Geometric morphometric analyses

We used 2D geometric morphometric analyses to evaluate the morphological affinities of the Lezetxiki teeth. The configurations of landmarks and semilandmarks described in Gómez-Robles et al. (Gómez-Robles et al., 2007; Gómez-Robles et al., 2008) were digitized on occlusal projections of the 3D models of the Lezetxiki teeth. These teeth were compared with the Neanderthal and modern human samples (including both fossil and recent modern humans) analyzed in these and other later studies (Becam et al., 2019; Gómez-Robles et al., 2007, 2008; Toussaint et al., 2018). Major patterns of variation were summarized through principal components analysis (PCA). In addition, discriminant analysis was used to determine the most likely classification for both teeth. This analysis was based on the first 10 principal components of shape variation, which accounted for more than 90% of the variation for both M^1s and P_3s.

2.5 | Tissue proportions

We quantified 2D and 3D dental proportions following standard protocols (Martin, 1985; Olejniczak et al., 2008). For the 2D enamel thickness and tissue proportions we measured: the bicervical diameter (BCD, mm), the enamel area (e area, mm^2), the summed crown dentine and pulp area (cdp area, mm^2), the crown area (c area, mm^2), and the length of the enamel-dentine junction (EDJ length, mm) on virtual buccolingual cross-sections (mesial in the case of the molar). Based on these measurements, we calculated the 2D Average Enamel Thickness (2D AET $=$ e area/EDJ length, mm) and the 2D Relative Enamel Thickness (2D RET $= 100 \times$ 2D AET/(cdp area$^{1/2}$), unit free). These measurements were taken on the original cross-section and on cross-sections corrected to reconstruct the worn enamel following the Pen Tool method (O'Hara et al., 2019; O'Hara & Guatelli-Steinberg, 2022; Saunders et al., 2007) (Figure S8). For the 3D proportions, we calculated total crown volume (Vc, mm^3), enamel cap volume (Ve, mm^3), dentine volume (Vcdp, crown dentine including crown pulp chamber, mm^3), and enamel-dentine junction surface area (SEDJ, mm^2). These measurements were used to calculate the 3D Average Enamel Thickness (3D AET $=$ Ve/SEDJ, mm) and 3D Relative Enamel Thickness index (3D RET $= 100 \times$ AET/Vcdp$^{1/3}$) (Martin, 1985; Olejniczak et al., 2008).

In addition, we created a 3D topography map of the whole-crown enamel thickness distribution, computing the minimal distance from the outer enamel surface to the EDJ using the segmented enamel and dentine surfaces by applying the 'Surface distance' module on AvizoLite 9.0.1 (Thermo Fisher, France) (Bayle et al., 2011; Macchiarelli et al., 2008; Zanolli, Pan, et al., 2018; Zanolli, Martinón-Torres, et al. 2018).

These proportions were compared to previously published data on Neanderthals and modern humans, including fossil and recent groups (Bayle et al., 2017; Martín-Francés et al., 2018). These samples are available in the NESPOS database (www.nespos.org, 2020) and ESRF database (http://paleo.esrf.eu/, 2020). Adjusted *z*-scores

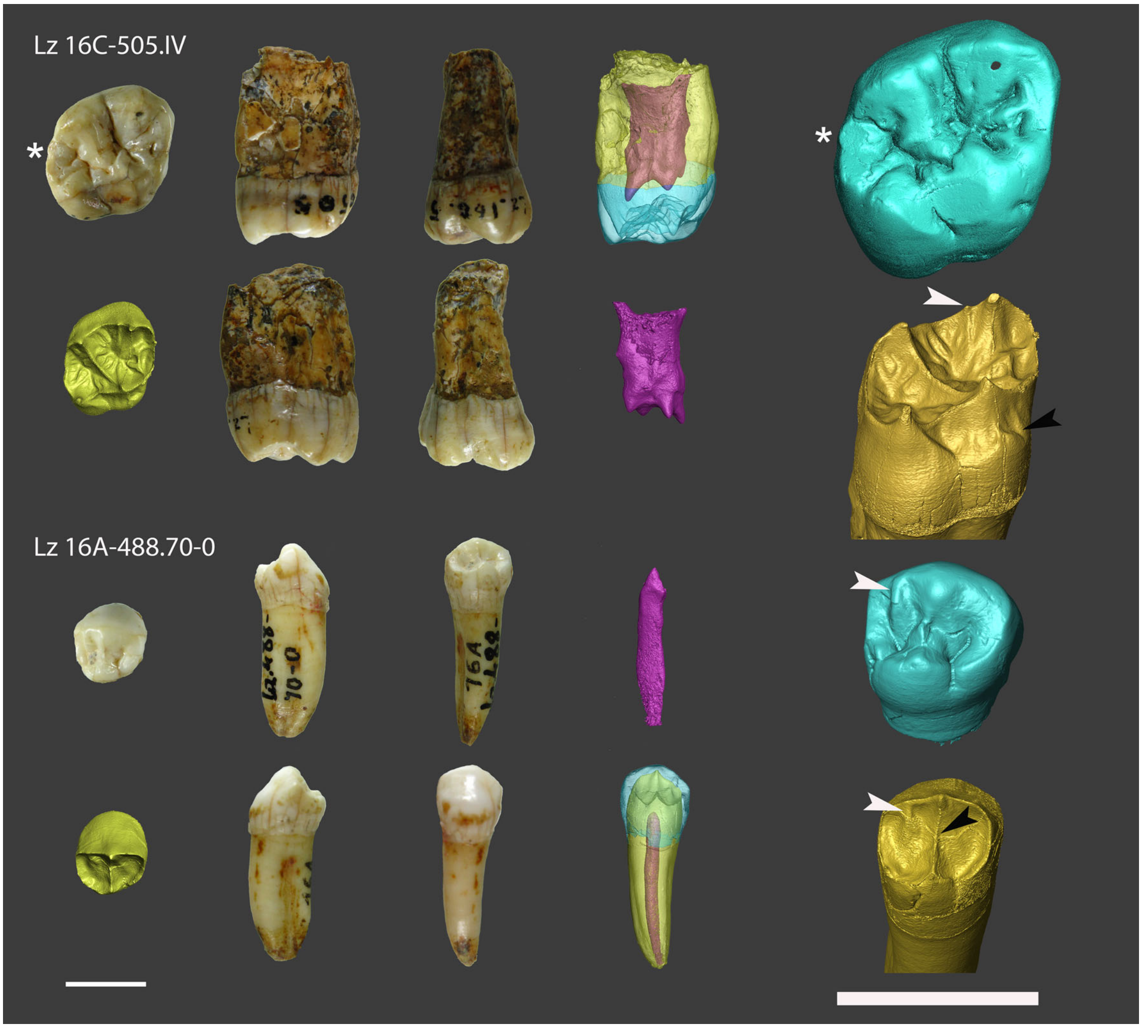

FIGURE 3 Dental remains from Lezetxiki. On the left, the teeth are shown in occlusal, mesial, lingual (top row), distal and buccal views (bottom row). The dentine model is shown in occlusal view, and the rendering of the whole teeth and tissues are in mesial view (M^1) and buccal view (P_3). The pulp chamber is in distal view. On the right side of the figure, the 3D models of enamel and dentine are shown at a larger scale for a detail description. The white arrow on the molar indicates the post-paracone tubercle, and the black arrow indicates the Carabelli's tubercle. On the premolar, the white arrows indicate the Accesory distal crests in enamel and dentine, while the black arrow indicates the complete transverse crest. The scale bars represent 1 cm. *Based on the inspection of the 3D model and the study of the original specimen, we clarify that what appears to be a cusp 5 (metaconule) (white star on photograph and 3D model) in the occlusal photograph on the Lezetxiki UM^1 is an optic effect

TABLE 1 Comparison of nonmetric traits at the occlusal enamel surface (OES) and enamel–dentine junction (EDJ) between the Lezetxiki M^1, Sima de los Huesos hominins (SH), Neanderthals, Paleolithic modern humans (PMH), and recent modern humans (RMH)

		SH		Neanderthals		PMH		RMH	
	Lz.16C.505	*n*	%	*n*	%	*n*	%	*n*	%
OES Score									
Metacone	4	14/17	82.4	13/23	56.5	12/20	60.0	73/127	57.5
Hypocone	5	11/17	64.7	12/23	52.2	6/20	30.0	55/127	43.3
Cusp 5	0	4/16	25	1/22	4.5	2/19	10.5	44/125	35.2
Carabelli	2	0/16	0	2/20	10.0	1/16	6.3	7/124	5.6
Parastyle	0	12/17	70.6	14/20	70.0	16/16	100	121/123	98.4
Mesial accessory tubercle	Pres	4/8	50	5/20	25.0	4/13	30.8	36/79	45.6
EDJ									
Crista obliqua	Type II	-	-	2/19	10.0	1/1	100.0	1/12	8.3
Post-paracone tubercle	Intermediate/marked	-	-	14/19	73.7	1/1	100.0	0/12	0.0

Source: OES trait frequencies from Martinón-Torres et al. (2012) and Gómez-Olivencia et al. (2020); EDJ data from Martin et al. (2017; combining data from early and late Neanderthals together) and Gómez-Olivencia et al. (2020).

TABLE 2 Crown metrics (in mm) from the Lezetxiki teeth and comparison with Middle Pleistocene European groups, Neanderthals, Fossil modern humans (Middle and Upper Paleolithic) and recent modern humans

		Sima de los Huesos					Neanderthals					Fossil modern humans					Recent modern humans				
	Lezetxiki	Mean ± SD	Min	Max	*N*	Adj. *z*-score	Mean ± SD	Min	Max	*N*	Adj. *z*-score	Mean ± SD	Min	Max	*N*	Adj. *z*-score	Mean ± SD	Min	Max	*N*	Adj. *z*-score
M^1																					
MD	11.70	11.00 ± 0.70	9.90	12.30	29	0.49	11.61 ± 1.09	9.10	13.60	28	0.04	10.71 ± 0.71	8.40	12.30	41	0.69	10.03 ± 0.52	8.40	11.40	42	**1.59**
BL	12.00	11.47 ± 0.62	10.30	13.00	29	0.42	12.34 ± 0.70	11.10	14.20	33	−0.24	12.12 ± 0.63	10.00	13.98	42	−0.09	11.27 ± 0.56	10.20	12.50	42	0.65
P_3																					
MD	7.70	7.88 ± 0.42	7.00	9.00	35	−0.22	7.71 ± 0.67	6.10	9.20	33	−0.01	7.12 ± 0.46	6.00	8.00	80	0.63	6.1 ± 0.51	5.50	8.10	43	**1.55**
BL	9.60	8.94 ± 0.55	7.90	10.00	34	0.59	9.05 ± 0.62	7.50	10.20	42	0.44	8.27 ± 0.51	7.00	9.50	81	**1.31**	7.58 ± 0.58	6.60	9.00	42	**1.72**

Note: A detailed list of these samples is in Table S2. Significant Adjusted *z*-score values are shown in bold.
Abbreviations: BL, Bucco-lingual; MD, Mesio-distal; SD, standard deviation; Adj. *z*-score, adjusted *z*-score.

(Maureille et al., 2001; Scolan et al., 2012) were calculated to compare the quantitative variables measured in the Lezetxiki fossils to the comparative samples, including dental dimensions and tissue proportions. This method makes it possible to compare unbalanced samples with an adjustment to include small samples by using the Student's *t* inverse distribution. Values from +1.0 to −1.0 comprise 95% of the variance in the reference sample. Values outside this range are considered statistically significant.

3 | RESULTS: METRIC AND MORPHOLOGICAL DESCRIPTIONS

3.1 | Lezetxiki-16C-505

Lz.16C-505 is a permanent right upper first molar (RM^1; Figure 3), which is fully developed since the root is fully formed, and the apical foramen is closed. The root is affected by taphonomic processes and is consequently cracked, but the crown is well preserved. The tip of the mesiobuccal cusp is worn away, showing a dot of exposed dentine (stage 2+ − 3- of Bouville et al., 1983). The mesial interproximal facet is well defined and long, while the distal facet is absent.

The molar has four cusps and a shallow tubercle of Carabelli (Figure 3, Table 1). The buccal cusps are more mesially located than the lingual cusps. There is a small triangular enamel extension apically towards the cementum of the root on the distal aspect of the CEJ.

At the EDJ, the tooth shows four main dentine horns. Aside from the hypocone, the horn tips of the other cusps are located centrally with respect to the occlusal outline. In addition, the surface shows a type II oblique crest (from protocone to metacone horn tips) that is interrupted just before reaching the protocone dentine horn. Moreover, it shows an intermediate/marked post-paracone tubercle (Table 1).

The 3D model of the pulp chamber shows a single root with a chamber that can be defined as hypertaurodontic (Shaw, 1928), since the 2D Taurodontism Index is 85% (Keene, 1966; Wright, 2007). The coronal part of the pulp chamber shows four large conical horns that diverge and project externally, except for the protocone horn (Figure 3). The hypocone horn is enlarged. This coronal morphology of the pulp chamber matches the description for the Neanderthal M^1 pulp chamber provided by Zanolli, Martinón-Torres, et al. (2018).

The crown of the molar is slightly wider buccolingually (12 mm) than mesiodistally (11.7 mm) (Table 2), with an occlusal surface that has a rhomboidal shape. While the buccolingual diameter is within the range of variation of most of the compared groups the mesiodistal diameter has a relatively high value within the Neanderthal range of variation (Figure S9). According to the adjusted *z*-scores (Table 2), the MD and BL diameters of this M1 fit well within both Neanderthal (Adj. *z*-score = 0.04, Adj. *z*-score = −0.24, respectively) and fossil modern humans (Adj. *z*-score = 0.69, Adj. *z*-score = −0.09, respectively), but the mesiodistal diameter is significantly different from that of recent modern humans (Adj *z*-score = 1.59). The occlusal polygon area is very close to

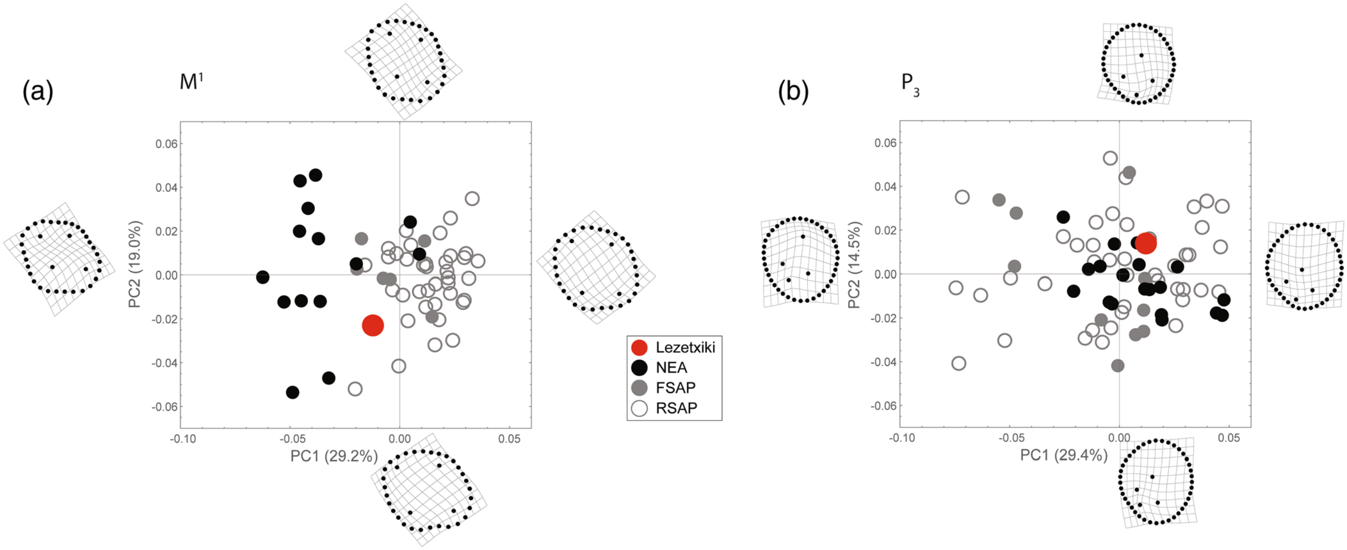

FIGURE 4 Principal components analysis of the occlusal shape of the Lezetxiki teeth. Lz 16C-505. IV (M^1) (a), Lz 16A-488.70-0 (P_3) (b). The Lezetxiki remains (red) have been compared to Neanderthals (NEA), fossil *Homo sapiens* (FSAP), and recent *Homo sapiens* (RSAP). TPS grids show the anatomical variation corresponding to the positive and negative extreme of each PC when all the other PCs are held equal to 0

the Neanderthal mean, and the relative area of the distal cusps is large, as described on other Neanderthal specimens (Gómez-Robles et al., 2011; Martinón-Torres et al., 2013; Quam et al., 2009). In general, the angles between cusp tips fall within the range of variation observed in Neanderthals, although the paracone angle is relatively higher as a result of the relatively increased size of the metacone (Table S3).

Principal components analysis (PCA) of the occlusal morphology places this molar between the area of distribution of Neanderthals and modern humans (Figure 4a). As described previously, Neanderthal M^1s can be easily identified based on their strongly skewed morphology, large and bulging hypocone and reduced occlusal polygon (Bailey, 2004; Gómez-Robles et al., 2007). The Lezetxiki molar shares some of these traits with Neanderthals (e.g., a small occlusal polygon and a large hypocone), but it is considerably less skewed than other Neanderthal M^1s, which drives this intermediate position on the PCA plot. Despite this combination of traits and the 'less Neanderthal' appearance of the crown of this molar in comparison with other classic Neanderthals, the discriminant analysis classifies this specimen as a Neanderthal with a posterior probability of 76%.

2D tissue proportion values differ substantially between corrected and uncorrected measurements when enamel is included (Table 4). However, the variables that involve only dentine and pulp are more consistent, suggesting that the effect of wear is minimal on them. The tissue proportion analyses show that the molar's dentine and pulp values (including the EDJ surface area) and proportions are significantly different when compared to the modern human comparative samples (Bayle et al., 2017; Martín-Francés et al., 2018; Martín-Francés et al., 2020; Olejniczak et al., 2008) (Tables 3 and 4). The value of 3D AET (0.87 mm) shows that the enamel cap in the Lezetxiki molar is significantly thinner (Adj. z-score $= -1.21$) than in the general Neanderthal sample too (Table 4), but this result can be influenced by the worn enamel tip of the paracone. Indeed, the corrected 2D enamel thickness values show that Lezetxiki's M1 falls within the Neanderthal range of variation (2D AET Adj. z-score $= -0.43$; 2D RET Adj. z-score $= -0.62$). However, the enamel thickness values observed in the Lezetxiki molar differ from those observed in Atapuerca-TD6 (*H. antecessor*), Sima de los Huesos (early Neanderthals), *H. erectus* and the recent modern humans studied by Smith et al. (2006) (Table 3). According to the surface distance analysis carried out to create the 3D topography of enamel thickness, this varies from 0.9 to 1.59 mm in the Lezetxiki molar (Figure S10).

3.2 | Lezetxiki-16A-488.70-0

Lz.16A.488.7-0-0 is a left lower third premolar (LP_3). The tooth is fully developed, with the root entirely formed. The crown of this tooth presents several cracks, both in the enamel and the dentine. The tip of the buccal cusp is slightly worn, but there is no dentine exposure (Grade 2, Bouville et al., 1983) (Figure 3). The mesial interproximal wear facet is rounded and well developed, whereas the distal facet is elongated but small.

The occlusal surface of the tooth is slightly asymmetrical due to the bulging of the mesial marginal ridge (Mmr) (Figure 3). The distal marginal ridge (Dmr) slopes slightly from the buccodistal angle of the crown. The Mmr bulges mesially, ending in a well-marked mesiolingual developmental groove that separates the Mmr of the lingual cusp. Moreover, the transverse crest (TRC) is not bifurcated in this premolar. The lingual cusp is well developed and projects lingually. The lingual cusp is rounded and clearly defined by the position of the mesiolingual developmental groove. The general morphology of the tooth also matches previous descriptions for Neanderthal P_3 characteristics (Table 5; Bailey, 2002, Martinón-Torres et al., 2012).

TABLE 3 2D-dental tissue proportions of the teeth from Lezetxiki (before and after wear correction) and comparative samples

	BCD (mm)	e area (mm²)	Cdp area (mm²)	% cdp area	C area (mm²)	EDJ length (mm)	2D AET (mm)	2D RET
M^1								
Lz.16C.505	11.96	20.06	46.04	69.65	66.744	22.64	0.91	13.40
Wear uncorrected	11.96	17.02	45.80	72.91	63.29	22.98	0.77	11.44
TD6 (Atapuerca) (*n* = 4)		23.01 ± 1.84 (20.52–24.56)	42.8 ± 4.23 (37.33–47.66)	64.98 ± 2.4 (61.16–67.72)	65.81 ± 5.22 (60.05–72.22)	20.57 ± 1.23 (19.24–22.14)	1.12 ± 0.06 (1.01–1.21)	17.14 ± 1.15 (16.07–18.38)
Adj. *z*-score		−0.50	0.24	0.61	0.02	0.38	**−1.10**	**−1.02**
Sima de los Huesos (*n* = 3)		22.02 ± 1.19 (20.88–23.25)	38.98 ± 4.28 (36.01–43.88)	63.82 ± 1.36 (62.81–65.37)	61 ± 5.41 (56.89–67.13)	21.08 ± 0.84 (20.22–21.90)	1.04 ± 0.02 (1.03–1.06)	16.76 ± 0.64 (16.03–17.21)
Adj. *z*-score		−0.38	0.38	0.99	0.21	0.27	**−1.52**	**−1.22**
H. erectus (*n* = 2)		30.04 ± 1.61 (28.90–31.17)	49.52 ± 4.12 (46.60–52.43)	62.22 ± 0.7 (61.72–62.72)	79.55 ± 5.73 (75.50–83.60)	22.88 ± 0.95 (22.20–23.55)	1.31 ± 0.02 (1.30–1.32)	18.67 ± 0.56 (18.28–19.07)
Adj. *z*-score		−0.49	−0.07	0.84	−0.18	−0.07	**−1.58**	−0.74
Neanderthals (*n* = 4)		22.98 ± 2.95 (21.03–28.00)	43.94 ± 4.55 (37.19–49.75)	65.68 ± 1.88 (63.88–68.04)	66.92 ± 7.06 (58.22–77.75)	22.36 ± 1.06 (21.08–23.45)	1.03 ± 0.10 (0.93–1.19)	15.50 ± 1.22 (13.80–16.93)
Adj. *z*-score		−0.36	0.17	0.76	−0.04	−0.10	−0.43	−0.62
Recent modern humans[a] (*n* = 37)		25.18 ± 3.16 (20.05–31.82)	42.87 ± 6.25 (32.46–59.44)	62.85 ± 2.67 (57.16–68.98)	68.05	20.64 ± 1.51 (17.66–24.11)	1.22 ± 0.12 (0.98–1.50)	18.75 ± 2.08 (14.46–22.71)
Adj. *z*-score		−0.80	0.25	**1.26**	-	0.46	**−1.28**	**−1.27**
Recent modern humans[b] (*n* = 12)		20.44 ± 3.52 (16.54–28.50)	34.73 ± 2.73 (30.77–41.00)	63.11 ± 3.06 (58.31–67.58)	55.18 ± 5.71 (48.94–69.58)	19.11 ± 0.61 (17.70–19.82)	1.07 ± 0.18 (0.84–1.45)	18.13 ± 2.66 (14.46–22.71)
Adj. *z*-score		−0.05	**1.88**	0.97	0.87	**2.20**	−0.41	−0.81
P_3								
Lz.16A-488.70-O	8.20	17.22	39.81	69.81	57.03	19.06	0.90	14.31
Wear uncorrected	8.20	16.50	39.81	80.70	56.313	19.06	0.87	13.72
Neanderthals (*n* = 3)	7.55 ± 0.29 (7.23–7.77)	15.02 ± 0.34 (14.63–15.27)	34.45 ± 3.56 (30.42–37.16)	69.54 ± 1.81 (67.52–71.02)	49.47 ± 3.88 (45.05–52.32)	18.28 ± 0.89 (17.25–18.84)	0.82 ± 0.02 (0.8–0.85)	14.06 ± 1.16 (13.2–15.38)
Adj. *z*-score	0.52	1.49	0.35	0.03	0.45	0.20	0.73	0.05
Neolithic modern humans (*n* = 2)	6.34 ± 0.11 (6.26–6.41)	14.54 ± 2.09 (13.06–16.01)	29.04 ± 3.32 (26.69–31.38)	66.61 ± 0.55 (66.22–67.00)	43.57 ± 5.40 (39.75–47.39)	16.725 ± 1.48 (15.68–17.77)	0.87 ± 0.5 (0.83–0.90)	16.1
Adj. *z*-score	**1.38**	0.10	0.26	0.46	0.20	0.12	0.06	**−4.96**
Recent moder humans from Asia (*n* = 7)	7.13 ± 0.36	18.49 ± 2.51	35.11 ± 5.07	65.5		18.62 ± 1.41	0.99 ± 0.09	16.16
Adj. *z*-score	**1.21**	−0.21	0.38	-	-	0.13	−0.39	-
Recent modern humans from Northern Europe (*n* = 13)	7.03 ± 0.4	18.93 ± 2.34	35.87 ± 2.63	65.46	-	18.63 ± 0.87	1.02 ± 0.13	16.97
Adj. *z*-score	**1.34**	−0.34	0.69	-	-	0.23	−0.41	-

TABLE 3 (Continued)

	BCD (mm)	e area (mm^2)	Cdp area (mm^2)	% cdp area	C area (mm^2)	EDJ length (mm)	2D AET (mm)	2D RET
Recent modern humans from Southern Africa ($n = 9$)	6.84 ± 0.66	18.30 ± 3.05	30.93 ± 5.73	62.83		17.16 ± 1.53	1.06 ± 0.09	19.06
Adj. *z*-score	0.89	−0.15	0.67	-	-	0.54	−0.75	-

Note: Bicervical diameter (BCD, mm), Enamel area (e area, mm^2), crown dentine and pulp area (cdp area, mm^2), percentage of the crown area that is dentine and pulp (% cdp area), total crown area (c area, mm^2), length of the enamel dentine junction (EDJ length, mm), 2D average enamel thickness (2D AET, mm), and 2D relative enamel thickness (2D RET). Comparative statistical analyses were carried out only with the corrected values. Comparative data for M1 comes from Martín-Francés et al. (2020) and Smith et al. (2006); in the case of the P3 from Bayle et al. (2017). For the comparative data we added the Mean ± Standard Deviation and (Minimum–Maximum values). Numbers in bold indicate significant Adj. *z*-score values.

[a]Data from Smith et al. (2006).

[b]Data from Martín-Francés et al. (2020).

Its EDJ shows two well-defined dentine horn tips on both buccal and lingual cusps and a complete transverse crest from one of the tips to the other; and the lingual marginal ridge is discontinuous on the mesial side (Table 5). Moreover, there is a small accessory cusplet on the distal marginal ridge, and an accessory crest that runs from the distobuccal marginal ridge towards the center of the anterior fovea (Figure 3).

The single root is straight and vertical, with a distal apical bending (Figure 3). In addition, there is a single root canal (Type 1R1), which is the most common observed in both Neanderthal and modern human P_3s (Pan & Zanolli, 2019) (Table 5). The pulp chamber displays a slightly mesiodistally flattened subcircular cross-section along most of its length, starting with a conical shape at the crown level.

Regarding its crown dimensions—7.7 mm mesio-distally and 9.6 mm bucco-lingually—the tooth is medium-sized (Table 2; Figure S9). The crown is short and wide in comparison to modern humans and falls within the range of variation of Neanderthals. Both the mesiodistal and buccolingual diameters show significant differences with the modern human values according to the adjusted *z*-scores (Table 2).

The geometric morphometric analysis of occlusal anatomy shows no clear separation between Neanderthal and modern human P_3s (Figure 4b). Both species overlap substantially, but Neanderthal premolars tend to show a more asymmetric configuration than modern human premolars and a more reduced and lingually placed occlusal polygon (formed by linking the tips of the two cusps and both foveae). The Lezetxiki P_3 plots on the area of the morphospace that includes other Neanderthal premolars, although this distribution overlaps with the modern human distribution. Similarly to other Neanderthal P_3s, the Lezetxiki specimen has a reduced and lingually placed occlusal polygon, but this premolar is generally less asymmetric than other Neanderthals. Based on these traits, the discriminant analysis classifies this specimen as a Neanderthal with a posterior probability of 60%.

The bicervical diameter of the Lezetxiki premolar (8.20 mm) is significantly larger than in the comparative modern human groups (except for the African group) (Table 3). Dental wear interferes with quantifications of premolar tissue proportions to a more limited extent than in the M1. In addition, relative enamel thicknesses (2D and 3D) are within the Neanderthal range of variation (2D: Adj. *z*-score = 0.05, 3D: Adj. *z*-score = −0.24), but they are significantly lower in Neolithic modern humans (Adj *z*-score = −4.96 and Adj *z*-score = −2.35, respectively) (Tables 3 and 4) (Bayle et al., 2017).

4 | DISCUSSION

Lezetxiki-16C-505 was described as a right M^1 by Basabe (1970). In this study, we confirm this classification based on the characteristics of the tooth. Regarding the taxonomic assessment of the molar, Basabe (1970) suggested that this molar was a Neanderthal tooth because it was taurodont. Other traits also indicate a Neanderthal classification, such as the metric values and the angles between cusps

TABLE 4 3D-dental tissue proportions of the teeth from Lezetxiki and comparative samples

	Ve (mm^3)	Vcdp (mm^3)	% Dentine	SEDJ (mm^2)	3D AET (mm)	3D RET	Vcp (mm^3)
M^1							
Lz.16C.505	234.4[a]	428.99	59.68	268.79	0.87[a]	11.54[a]	23.27
Sima de los Huesos (*n* = 3)	268.62 ± 34.64 (240.71–307.38)	291.68 ± 59.12 (251.17–359.52)	51.87 ± 1.78 (50.63–53.91)	207.57 ± 28.95 (180.79–240.14)	1.30 ± 0.01 (1.28–1.30)	19.65 ± 1.44 (18.00–20.65)	-
Adj. *z*-score	−0.23	0.54	**1.02**	0.49	**−9.99**	**−1.31**	
Neanderthals (*n* = 4)	275.14 ± 44.77 (249.44–341.92)	345.56 ± 84.27 (272.93–460.43)	55.36 ± 3.39 (51.25–58.77)	243.96 ± 50.28 (208.03–317.81)	1.14 ± 0.07 (1.07–1.20)	16.39 ± 2.20 (13.93–18.41)	-
Adj. *z*-score	−0.29	0.31	0.40	0.16	**−1.21**	−0.69	
Recent modern humans (*n* = 13)	195.02 ± 25.26 (162.55–229.89)	238.00 ± 51.87 (151.17–304.79)	54.54 ± 4.68 (56.96–61.52)	174.97 ± 33.41 (145.36–255.00)	1.14 ± 0.20 (0.84–1.58)	18.61 ± 3.67 (12.63–23.52)	-
Adj. *z*-score	0.56	**1.33**	0.39	**1.01**	−0.49	−0.69	
P_3							
Lz.16A-488.70-O	120	180.65	52.96	151.91	0.79	13.97	9
MPI (*n* = 1)	101.96	202.75	66.54	165.53	0.62	10.48	-
Neanderthals (*n* = 4)	96.57 ± 8.72 (93.00–105.01)	129.99 ± 23.17 (99.18–155.19)	57.10 ± 4.44 (51.61–61.11)	118.99 ± 17.31 (98.45–140.80)	0.82 ± 0.11 (0.73–0.94)	16.39 ± 3.17 (13.52–20.41)	-
Adj. *z*-score	0.84	0.69	−0.29	0.59	−0.09	−0.24	
Neolithic modern humans (*n* = 2)	96.31 ± 17.66 (83.82–108.80)	97.43 ± 17.12 (85.32–109.53)	50.30 ± 0.19 (50.17–50.44)	100.21 ± 11.43 (92.13–108.29)	0.96 ± 0.06 (0.91–1.00)	20.84 0.23 (20.67–21.00)	-
Adj. *z*-score	0.11	0.38	**1.10**	0.36	−0.22	**−2.35**	
RH	104.63	89.52	46.11	98.11	1.07	23.84	-

Note: Enamel cap volume (Ve, mm^3), crown dentine and pulp volume (Vcdp, mm^3), surface of the enamel dentine junction (SEDJ, mm^2), 3D average enamel thickness (3D AET, mm), 3D relative enamel thickness (3D RET), volume of the pulp corresponding to the crown (Vcp, mm^3). Comparative data for M1 comes from Martín-Francés et al. (2020); in the case of the P3 from Bayle et al. (2017). For the comparative data we added the Mean ± Standard Deviation and (Minimum–Maximum values). Numbers in bold indicate significant Adj. *z*-score values.

[a]These results correspond to minimum values since they are affected by the moderate wear in the crown of the molar.

TABLE 5 Comparison of nonmetric traits at the occlusal enamel surface (OES), enamel–dentine junction (EDJ) and root between the Lezetxiki P_3 (Figure 3), Sima de los Huesos hominins (SH), Neandertals, Paleolithic modern humans (PMH), recent modern humans (RMH), and modern humans (MH, including both Paleolithic and recent)

		SH		Neanderthals		PMH		RMH		MH[a]	
	Lz.16A-488.70-0	*n*	%	*N*	%	*n*	%	*n*	%	*n*	%
OES Score											
Premolar lingual cusps number	1	4/17	23.5	7/33	21.2	7/19	36.8	22/150	14.7		
METPOS (metaconid position)	Med	-	-	-	-	-	-	-	-		
TRC (transverse crest)	Not interrupted	15/18	83.3	17/31	54.8	12/18	66.7	20/157	12.7		
DAR (distal accessory ridge)	Pres	8/15	53.3	21/24	87.5	7/15	46.7	13/134	9.7		
MAR (mesial accessory ridge)	Pres	1/15	6.7	1/22	4.5	1/12	8.3	16/135	11.9		
MLG (mesial lingual groove)	Pres	-	-	14/19	73.7	3/6	50	49/127	38.5		
ASM (crown asymmetry)	Pres	-	-	10/17	58.8	0/3	0	9/120	7.5		
EDJ											
Transverse crest	Complete (Type 1)	-	-	6/10[b]	60.0	-	-	-	-	5/9	56.0
Dentine cuspulid	Mes	-	-	-	-	-	-	-	-		
Marginal ridge type	Mesially discontinuous			4/14[b]	28.6					2/14	14.3
Mesial buccal groove	Absent (Type 0)			6/14	42.8					13/14	92.8
Distal buccal groove	Absent (Type 0)			11/14	78.6					12/14	85.7
Root											
Root canal type	1R1	-	-	5/8	62.5	-	-	13/19	66.7		

Note: OES trait frequencies from Martinón-Torres et al. (2012), Zapata et al. (2017), and Becam et al. (2019); EDJ trait frequencies from Davies et al. (2019); Root trait frequencies from Pan and Zanolli (2019).
[a]In Davies et al. (2019) they constitute a single group.
[b]This value corresponds to the frequencies from Davies et al. (2019) and the estimation done during the current study based on the figure available from Becam et al. (2019).

(Bailey, 2002, 2004; Martinón-Torres et al., 2013). Moreover, the presence of an intermediate/marked post-paracone tubercle is not observed on the M^1s of modern humans (Martin et al., 2017). The results of a discriminant analysis based on a geometric morphometric analysis of the occlusal morphology also suggest that this molar can be classified as a Neanderthal (Gómez-Robles et al., 2007).

Lezetxiki-16A-488.70-0 was previously reported as a left lower fourth premolar (LP_4) (Basabe, 1970). However, its morphological traits indicate that this is a left lower third premolar (LP_3). Lower P_4s show more complex occlusal surfaces with extra fissures and ridges, continuous and prominent transverse crest, and evident marked asymmetrical lingual contours (Bailey, 2002). All these features are absent of Lezetxiki-16A-488.70-0. In addition, the heights of the buccal and lingual cusps are very different, with the former being much taller than the latter, the occlusal surface is less complex, and the lower half of the buccal aspect is swollen, a trait that is more visible in the lateral views (distal and mesial) of the tooth. Finally, the cuspal half of the buccal surface is strongly lingually inclined. These nonmetric traits observed in the premolar match those that are most commonly observed in P_3s, particularly in Neanderthals (Bailey, 2002; Davies et al., 2019; Martinón-Torres et al., 2012). Indeed, geometric morphometric analyses also suggest a Neanderthal affinity for this premolar, although the differentiation between Neanderthal and modern human P_3s is not always unequivocal (Gómez-Robles et al., 2008). Enamel thickness is usually thinner in Neanderthals than in modern humans, and tissue proportions in the Lezetxiki premolar show similarities with published data from Neanderthals (Bayle et al., 2017).

In the case of the molar, the tissue proportion analyses should be considered cautiously, as it is moderately worn. Specifically, as mentioned above, this occlusal wear has probably affected the 3D values for the enamel quantification, and thereby the calculated thickness. This is evident when we observe the differences on the 2D tissue proportions before and after the corrections (Table 3, Figure S8). Nevertheless, the values that make a modern human classification unlikely for the Lezetxiki molar correspond to the dentine and EDJ values. These values are less affected by superficial wear than enamel in this tooth, and are probably reliable in the Lezetxiki molar (Saunders et al., 2007). Moreover, the Lezetxiki molar presents higher absolute and relative values for the dentine than modern humans, showing that it corresponds to a large tooth, but within the Neanderthal range. The presence of wear is inevitable in the comparative samples, but we minimized its confounding effect by selecting only unworn or faintly worn teeth, and applying the necessary corrections (Bayle et al., 2017; Martín-Francés et al., 2020; Olejniczak et al., 2008; Smith et al., 2006).

Based on our study and on the recent taxonomic reassessment of the maxillary fragment and teeth from Axlor (Basabe, 1973), now classified as likely modern humans (Gómez-Olivencia et al., 2020), the two teeth from Lezetxiki (Basabe, 1970) are the only Neanderthal permanent teeth found in the region to date. Moreover, together with the cranial fragment from Axlor (Gómez-Olivencia et al., 2020), they are the only adult Neanderthal remains from the western Pyrenees.

We know now that sub-levels IIIa and IIIb dip significantly in the area where the teeth were found (Figures S5–S7). Moreover, the new excavations also present some examples of both sub-levels being mixed. Therefore, at this moment, it is not possible to determine whether the teeth were originally deposited in sub-level IIIa. Alternatively, their presence at this level could result from the unclear stratigraphy of the site. Additional research efforts in the study of the stratigraphy and direct dating of the Neanderthal remains will be required to shed more light on this question.

The two teeth from Lezetxiki were found in Level III, which includes both Aurignacian and late Mousterian dates, and are younger than 57,000 ± 2000 BP, which corresponds to level V (Sánchez, 1991; Falguères et al., 2006). The other Neanderthal fossil remains found in the north of the Iberian Peninsula (mentioned in the introduction) span from MIS 6 to MIS 3. Thus, together with the remains from El Sidrón (Fortea et al., 2003; Lalueza-Fox et al., 2005) and four teeth from El Castillo, a premolar (Castillo 1466) and three deciduous teeth (Bernaldo de Quirós et al., 2006; Cabrera, 1996; Garralda, 2005; Garralda et al., 2019; Garralda et al., 2022), the remains from Lezetxiki likely represent the latest Neanderthal remains from the region.

5 | CONCLUSIONS

The human teeth recovered from Lezetxiki cave (Arrasate, Basque Country, Iberian Peninsula) have been attributed to Neanderthals since their discovery. These teeth were recovered at a predominantly Aurignacian level of the site that is now known to include a Mousterian sub-level. We have been able to confirm a Neanderthal classification for these teeth, although the premolar Lz.16A-488.70-0, initially diagnosed as a LP_4, has been reclassified as a LP_3. Our analyses add to the evidence confirming a late Neanderthal presence in the north of the Iberian Peninsula. Moreover, the reassessment of their origin in level III increases the scarce fossil record from the periods corresponding to the transition from the Middle to the Upper Paleolithic in the region.

AUTHOR CONTRIBUTIONS

Diego López-Onaindia: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); resources (equal); software (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (lead). **Marina Lozano:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); resources (equal); software (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Aida Gómez-Robles:** Formal analysis (equal); investigation (equal); methodology (equal); software (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Alvaro Arrizabalaga:** Investigation (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **M. Eulàlia Subirà:** Conceptualization (equal); funding acquisition (equal); investigation (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at [http://doi.org/10.6084/m9.figshare.12075477].

DATA AVAILABILITY STATEMENT

The data of this study are available within Tables 2, 3, 4 and 5 of this article, and Table 3 of the Supplementary information file. The micro-CT scans and segmentations of the original materials of this study are available at http://doi.org/10.6084/m9.figshare.12075477.

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