



HAL
open science

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

Diego López-Onaindia, Marina Lozano, Aida Gómez-Robles, Alvaro Arrizabalaga, M. Eulàlia Subirà

► **To cite this version:**

Diego López-Onaindia, Marina Lozano, Aida Gómez-Robles, Alvaro Arrizabalaga, M. Eulàlia Subirà. Neanderthal teeth from Lezetxiki (Arrasate, Iberian Peninsula): New insights and reassessment. American Journal of Biological Anthropology, 2023, 180 (4), pp.745-760. 10.1002/ajpa.24694 . hal-04162689

HAL Id: hal-04162689

<https://hal.science/hal-04162689v1>

Submitted on 16 Jul 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.






L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

BRIEF COMMUNICATION

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

Diego López-Onaindia¹  | Marina Lozano^{2,3}  | Aida Gómez-Robles^{4,5}  |
Alvaro Arrizabalaga⁶  | M. Eulàlia Subirà^{7,8} 

¹Université de Bordeaux, CNRS, Ministère de la Culture, PACEA, UMR 5199, Pessac Cedex, France

²Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain

³Department of History and History of Art, Universitat Rovira i Virgili (URV), Avinguda Catalunya 35, Tarragona, Spain

⁴Department of Anthropology, University College London, London, UK

⁵Department of Genetics, Evolution and Environment, University College London, London, UK

⁶Research Team on Prehistory (IT-1435-22), Facultat de Letras, Universidad del País Vasco (UPV/EHU), Vitoria-Gasteiz, Spain

⁷Unitat d'Antropologia Biològica, Departament de Biologia Animal, Biologia Vegetal i Ecologia, Facultat de Biociències, Universitat Autònoma de Barcelona, Bellaterra, Spain

⁸GREAB, Research Group in Biological Anthropology, Barcelona, Spain

Correspondence

Diego López-Onaindia, UMR 5199 PACEA, Université de Bordeaux. Allée Geoffroy Saint Hilaire, Bâtiment B8. CS 50023. 33615-Pessac Cedex, France.

Email: diego.lopez.onaindia@gmail.com

Funding information

Departament d'Innovació, Universitats i Empresa, Generalitat de Catalunya, Grant/Award Numbers: 2021SGR01239, 2017 SGR 1630; Eusko Jaurlaritz, Grant/Award Number: POS_2019_1_0024; Marie Skłodowska-Curie Actions, Grant/Award Number: N°895713 Neander-TALE; Ministerio de Educación y Cultura, Grant/Award Number: MICINNPID2021-12235NB-C32

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

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. *American Journal of Biological Anthropology* published by Wiley Periodicals LLC.

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-Chiapuso 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 m² (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-Chiapuso 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).

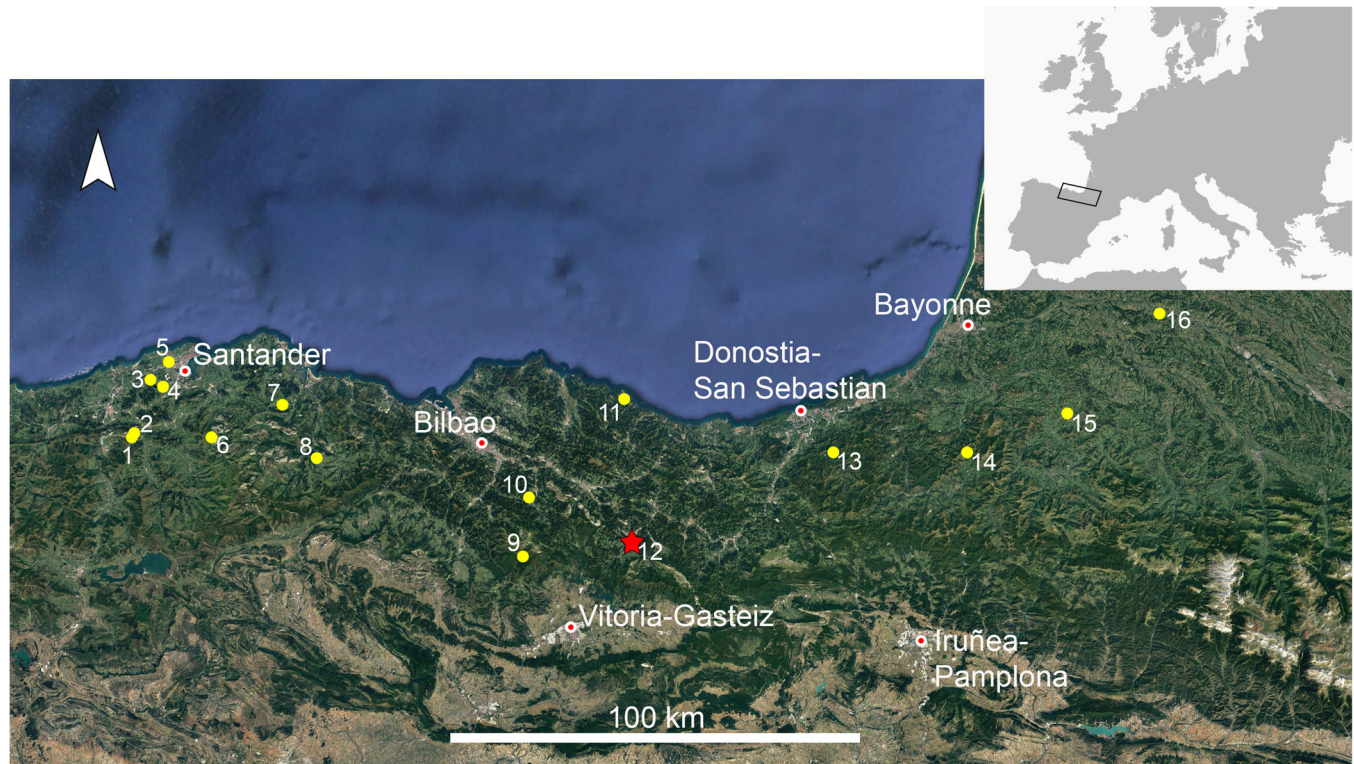


FIGURE 1 Location of Lezetxiki (red star) and other Paleolithic sites with human remains in the east and center of the Cantabrian Region (northern Iberian Peninsula and southwestern France). (1): La Pasiaga (HS; González Echegaray & Ripoll Perelló, 1954); (2): Castillo (N, HS; Garralda, 2005; Garralda 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; Albiu 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).

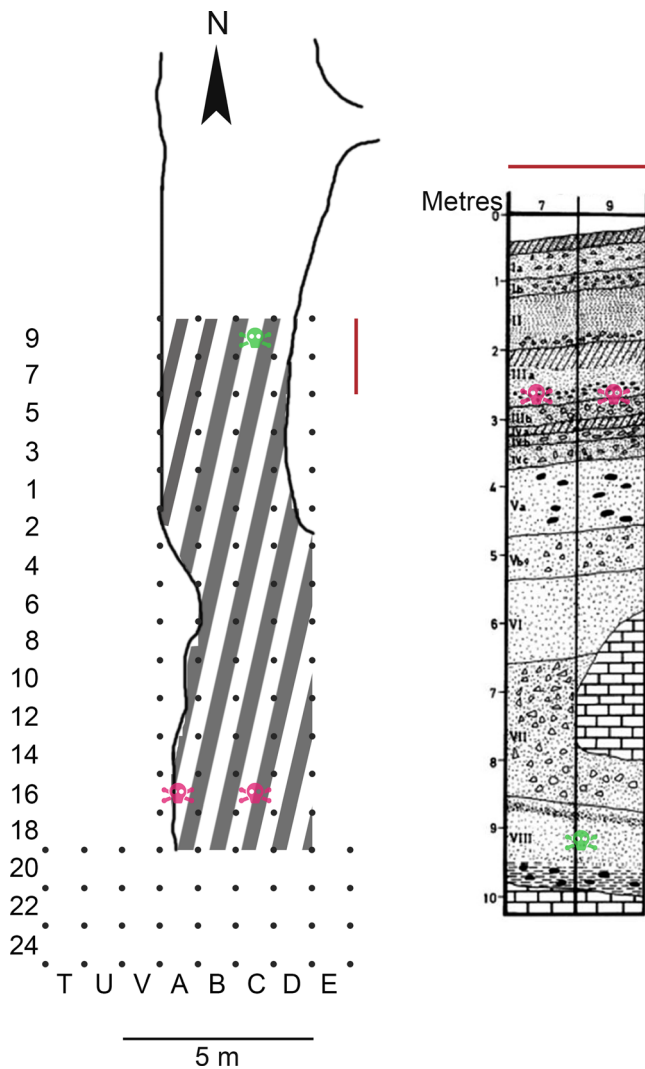


FIGURE 2 Excavation plan (left) and stratigraphic column (right) of Lezetxiki cave (modified from Altuna, 1972; Álvarez-Alonso & Arrizabalaga, 2012). The excavation plan combines the original excavations by Barandiarán (1956–1968) (squares 9–18) with the recent interventions by Arrizabalaga (since 1996). 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 m²), 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 μ A, 0.2 mm copper filter and a voxel size of 18 μ m.

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 M¹ 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 M¹, 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 M¹s and P₃s.

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, mm²), the summed crown dentine and pulp area (cdp area, mm²), the crown area (c area, mm²), 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, mm³), enamel cap volume (Ve, mm³), dentine volume (Vcdp, crown dentine including crown pulp chamber, mm³), and enamel-dentine junction surface area (SEDJ, mm²). 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, Martín-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

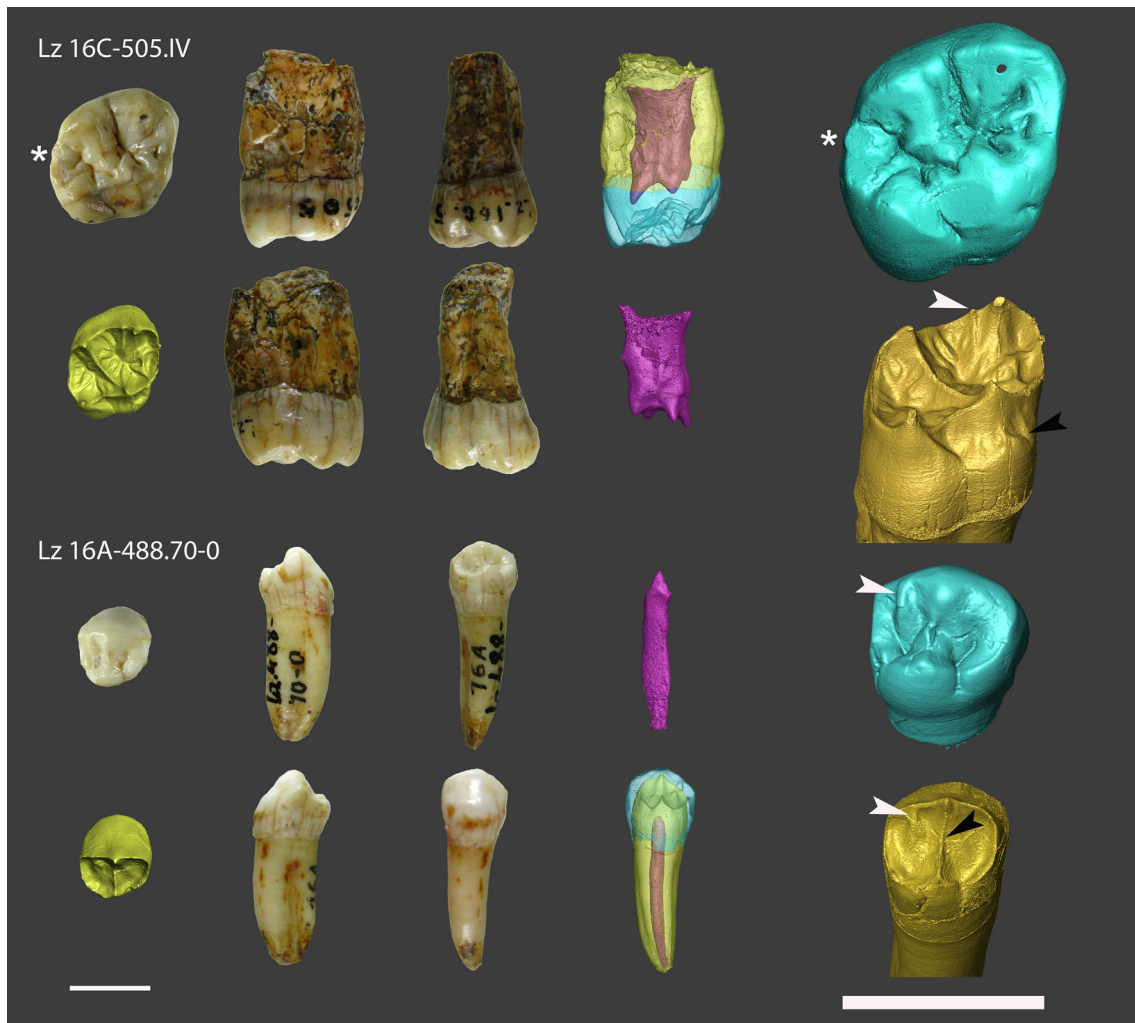


FIGURE 3 Dental remains from Lezetxiki. On the left, the teeth are shown in occlusal, mesial, lingual (top row), distal and buccal views (bottom row). The dentine model is shown in occlusal view, and the rendering of the whole teeth and tissues are in mesial view (M^1) and buccal view (P_3). The pulp 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 Accessory 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)

	Lz.16C.505	SH		Neanderthals		PMH		RMH		
		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 Martín-Torres et al. (2012) and Gómez-Olivencia et al. (2020); EDJ data from Martín 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					
	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	11.00 ± 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	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	7.88 ± 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	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 (RM¹; 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 M¹ pulp chamber provided by Zanolli, Martín-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

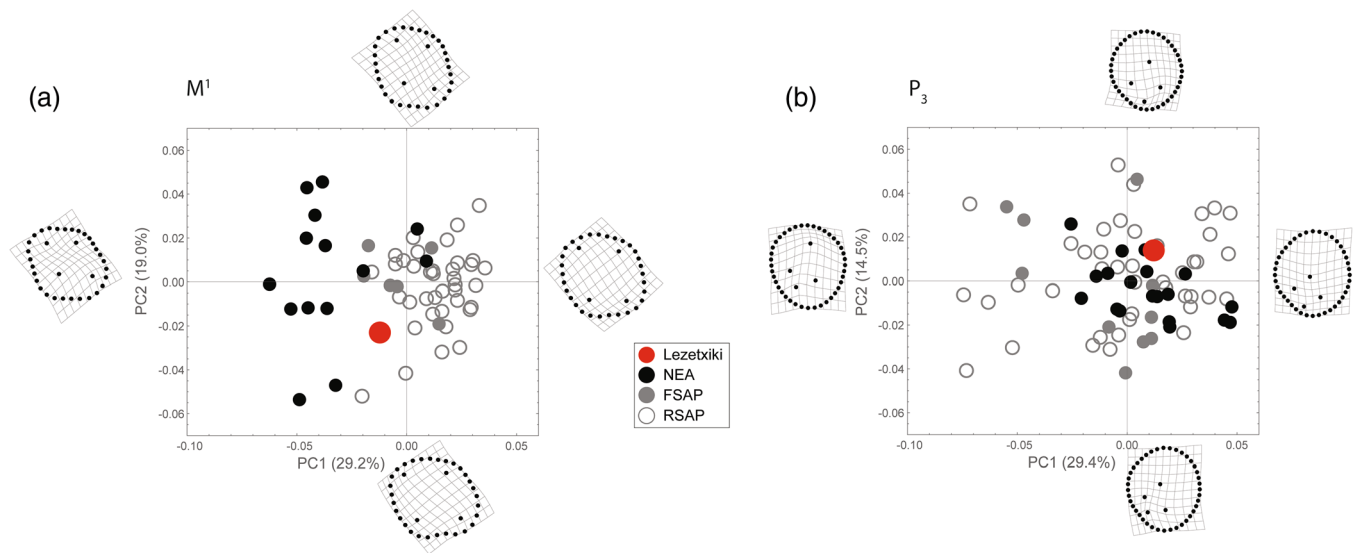


FIGURE 4 Principal components analysis of the occlusal shape of the Lezetxiki teeth. Lz 16C-505. IV (M^1) (a), Lz 16A-488.70-0 (P_3) (b). The Lezetxiki remains (red) have been compared to Neanderthals (NEA), fossil *Homo sapiens* (FSAP), and recent *Homo sapiens* (RSAP). TPS grids show the anatomical 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; Martín-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^1 s 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^1 s, 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-Francis et al., 2018; Martín-Francis 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 M^1 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; Martín-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 (mm ²)	Cdp area (mm ²)	% cdp area	C area (mm ²)	EDJ length (mm)	2D AET (mm)	2D RET
M¹								
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
<i>H. erectus</i> (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
P₃								
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)	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	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)	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	0.46	0.20	0.12	0.06	−4.96
Recent modern humans from Asia (n = 7)		7.13 ± 0.36	35.11 ± 5.07	65.5		18.62 ± 1.41	0.99 ± 0.09	16.16
Adj. z-score		1.21	0.38	-	-	0.13	−0.39	-
Recent modern humans from Northern Europe (n = 13)		7.03 ± 0.4	35.87 ± 2.63	65.46	-	18.63 ± 0.87	1.02 ± 0.13	16.97
Adj. z-score		1.34	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: Biccervical diameter (BCD, mm), Enamel area (e area, mm²), crown dentine and pulp area (cdp area, mm²), percentage of the crown area that is dentine and pulp (% cdp area), total crown area (c area, mm²), 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.

^aData from Smith et al. (2006).

^bData 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 P₃s (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 P₃s (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 P₃ 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 P₃s, 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 M¹ 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)
M¹							
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	-
P₃							
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, mm³), crown dentine and pulp volume (Vcdp, mm³), surface of the enamel dentine junction (SEDJ, mm²), 3D average enamel thickness (3D AET, mm), 3D relative enamel thickness (3D RET), volume of the pulp corresponding to the crown (Vcp, mm³). 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.

^aThese 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 P₃ (Figure 3), Sima de los Huesos hominins (SH), Neanderthals, 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		<i>n</i>	%	<i>N</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
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 cuspid	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 Martín-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).

^aIn Davies et al. (2019) they constitute a single group.

^bThis 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; Martín-Torres et al., 2013). Moreover, the presence of an intermediate/marked post-paracone tubercle is not observed on the M¹s 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 (LP₄) (Basabe, 1970). However, its morphological traits indicate that this is a left lower third premolar (LP₃). Lower P₄s 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 non-metric traits observed in the premolar match those that are most commonly observed in P₃s, particularly in Neanderthals (Bailey, 2002; Davies et al., 2019; Martín-Torres et al., 2012). Indeed, geometric morphometric analyses also suggest a Neanderthal affinity for this

premolar, although the differentiation between Neanderthal and modern human P₃s 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 $57,000 \pm 2000$ 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 (Forte 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 LP₄, has been reclassified as a LP₃. 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).

ACKNOWLEDGMENTS

We would like to thank S. San José (Gordailua – Provincial Government of Gipuzkoa's Heritage Collection Centre), K. Mariezkurrena and J. Altuna for granting access to the Lezetxiki teeth. We are grateful to the José Miguel de Barandiarán foundation for granting us access and permission to consult and reproduce the original fieldnotes of the Lezetxiki excavations. This work was funded by the Dirección General de Investigación de M.E.C, project number CGL2012-38434-C03-03 and MICINN PID202-1-122355N-B-C32; 2017 SGR 1630 Grup de recerca en Antropologia Biològica (GREAB), 2017 SGR 1040 Social, cultural and biological Evolution during the Pleistocene (StEP), and 2021 SGR 01239 of the Generalitat de Catalunya; and 2019 PFR-URV-91 and 22017 Research Groups. This study also received support from the French government in the framework of the University of Bordeaux's IdEx "Investments for the Future" program/GPR Human Past, and the scientific environmental support of the teams EVODIBIO and EURAPAL from PACEA-UMR5199. DLO was supported by the Basque Governments postdoctoral Fellowship (POS_2019_1_0024) and MSC Actions Individual Fellowship (Project No. 895713). We also thank the reviewers and editorial board members for their thorough reading and suggestions to improve this manuscript. Finally, we would especially like to mention and thank J. Altuna and A. Gómez-Olivencia for their conscientious observations, corrections and comments on the manuscript, which have led to improve its quality.

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>.

ORCID

Diego López-Onaindia <https://orcid.org/0000-0002-5266-6416>
Marina Lozano <https://orcid.org/0000-0002-6304-7848>

Aida Gómez-Robles  <https://orcid.org/0000-0002-8719-2660>

Alvaro Arrizabalaga  <https://orcid.org/0000-0001-6127-2972>

M. Eulàlia Subirà  <https://orcid.org/0000-0001-5315-0051>

REFERENCES

- Aguirre Enriquez, E. (2007). Neandertales Ibéricos: Habitat, Subistencia, Extinción. *Revista de la Real Academia de Ciencias Exactas, Físicas y Naturales*, 101, 203–210.
- Albisu Andrade, C., Etxeberria Gabilondo, F., & Herrasti Erlorgorri, L. (2014). Estudio de los restos dentales humanos procedentes de la cueva de Santa Catalina. In: E. Berganza Gochi, J.L. Arribas Pastor (Coords.), *La Cueva de Santa Catalina (Lekeitio, Bizkaia): La intervención arqueológica. Restos vegetales, animales y humanos* (pp. 115–137). Bizkaiko Foru Aldundia, Bilbao.
- Altuna, J. (1963). Primer hallazgo de glotón (*Gulo gulo* L.) en la Península Ibérica. *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 15(3–4), 128.
- Altuna, J. (1972). Fauna de Mamíferos de los yacimientos prehistóricos de Guipúzcoa. Con catálogo de los mamíferos cuaternarios del Cantábrico y del Pirineo Occidental. (Tesis doctoral). *Munibe*, 24(1–4), 1–464.
- Altuna, J. (1990). La caza de herbívoros durante el Paleolítico y Mesolítico del País Vasco. *Munibe (Antropología-Arkeología)*, 42, 229–240.
- Altuna, J., Baldeón, A., & Mariezkurrena, K. (1990). *La cueva de Amalda (Zestoa, País Vasco)* (p. 4). Ocupaciones paleo-líticas y postpaleolíticas.
- Álvarez-Alonso, D., & Arrizabalaga, A. (2012). La secuencia estratigráfica inferior de la cueva de Lezetxiki (Arrasate, País Vasco). Una reflexión necesaria. *Zephyrus*, LXIX, 15–39.
- Arrizabalaga, A. (1995). *La industria lítica del Paleolítico superior inicial en el oriente cantábrico* (Unpublished doctoral dissertation). University of the Basque Country (UPV/EHU), Vitoria-Gasteiz.
- Arrizabalaga, A. (2014). Lezetxiki (Arrasate, Gipúzkoa). In R. Sala, E. Carbonell, J.M. Bermúdez de Castro, J.L. Arsuaga (Coords.), *Los cazadores recolectores del Pleistoceno y del Holoceno en Iberia y el estrecho de Gibraltar* (pp. 105–109). Universidad de Burgos: Fundación Atapuerca.
- Arrizabalaga, A. (2006a). Las primeras ocupaciones humanas en el Pirineo Occidental y Montes Vascos. Un estado de la cuestión en 2005. *Munibe (Antropología-Arkeología)*, 57(II), 53–70.
- Arrizabalaga, A. (2006b). Lezetxiki (Arrasate, País Vasco). Nuevas preguntas acerca de un antiguo yacimiento. In V. Cabrera, F. Bernaldo de Quirós, & J. M. Maillo (Eds.), *En el centenario de la Cueva de El Castillo: el caso de los Neandertales* (pp. 291–310). UNED-Cantabria.
- Arrizabalaga, A., & Iriarte-Chiapuso, M. J. (2018). Cueva de Lezetxiki XXIII Campaña. *Arkeoikuska: Investigación Arqueológica*, 2018, 400.
- Bailey, S. E. (2002). *Neandertal dental morphology: Implications for modern human origins* (unpublished doctoral dissertation). Arizona State University, Tempe.
- Bailey, S. E. (2004). A morphometric analysis of maxillary molar crowns of middle-late Pleistocene hominins. *Journal of Human Evolution*, 47, 183–198. <https://doi.org/10.1016/j.jhevol.2004.07.001>
- Baldeón, A. (1987). *El Paleolítico Medio en el País Vasco* (Unpublished doctoral dissertation). Universidad de Deusto, Bilbao.
- Baldeón, A. (1993). El yacimiento de Lezetxiki (Gipuzkoa, País Vasco). Los niveles musterienses. *Munibe (Antropología - Arkeología)*, 45, 3–97.
- Barandiarán, I., & Cava, A. (2008). Identificaciones del Gravetiense en las estribaciones occidentales del Pirineo: modelos de ocupación y uso. *Trabajos de Prehistoria* 65, 13–28.
- Barandiarán, J. M. (1960). Exploración de la cueva Lezetxiki en Mondragón, (Memorias de los trabajos de 1957, 1959 y 1960, dedicada al M.I. Ayuntamiento de Mondragón). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 12(4), 273–310.
- Barandiarán, J. M. (1963). Exploración de la cueva Lezetxiki (Campaña de 1962). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 15(3–4), 87–102.
- Barandiarán, J. M. (1965). Exploración de la cueva Lezetxiki (Campaña de 1963). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 17, 52–64.
- Barandiarán, J. M., & Altuna, J. (1965). Exploración de la cueva Lezetxiki (Campaña de 1964). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 17, 38–51.
- Barandiarán, J. M., & Altuna, J. (1966). Excavación de la Cueva de Lezetxiki (Campaña de 1965). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 18, 5–11.
- Barandiarán, J. M., & Altuna, J. (1967a). Excavación de la Cueva de Lezetxiki (Campaña de 1966). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 19(1/2), 79–106.
- Barandiarán, J. M., & Altuna, J. (1967b). Excavación de la Cueva de Lezetxiki (Campaña de 1967). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 19(3/4), 231–246.
- Barandiarán, J. M., & Altuna, J. (1970). Excavación de la Cueva de Lezetxiki (Campaña de 1968). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 22(1/2), 51–59.
- Basabe, J. M. (1966). El húmero premusteriense de Lezetxiki (Guipúzcoa). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 18, 13–32.
- Basabe, J. M. (1970). Dientes humanos del paleolítico de Lezetxiki (Mondragón). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 22(3–4), 113–124.
- Basabe, J. M. (1973). Dientes humanos del Musteriense de Axló (Dima, Vizcaya). *Trabajos de Antropología*, XVI(4), 187–202.
- Basabe, J. M. (1982). Restos fósiles humanos de la región Vasco-Cantábrica. *Cuadernos de Sección Antropología-Etnografía*, 1, 68–83.
- Bayle, P., Bondioli, L., Macchiarelli, R., Mazurier, A., Puymerail, L., Volpato, V., & Zanolli, C. (2011). Three-dimensional imaging and quantitative characterization of human fossil remains. Examples from the NESPOS database. In R. Macchiarelli & G.-C. Weniger (Eds.), *Pleistocene Databases. Acquisition, Storing, Sharing* (Vol. 4, pp. 29–46). Wissenschaftliche Schriften des Neanderthal Museums.
- Bayle, P., Le Luyer, M., & Robson Brown, K. A. (2017). The Palomas dental remains: Thickness and tissue proportions. In E. Trinkaus & M. J. Walker (Eds.), *Neandertals from the Sima de las Palomas del Cabezo Gordo, southeastern Spain* (pp. 115–137). Texas A&M University Press.
- Becam, G., Verna, C., Gómez-Robles, A., Gómez-Olivencia, A., Albessard, L., Arnaud, J., Frelat, M. A., Madelaine, S., Schwab, C., Souday, C., Turq, A., & Balzeau, A. (2019). Isolated teeth from La Ferrassie: Reassessment of the old collections, new remains, and their implications. *American Journal of Physical Anthropology*, 169, 132–142. <https://doi.org/10.1002/ajpa.23798>
- Bermúdez de Castro, J. M., & Sáenz de Buruaga, A. (1999). Étude Préliminaire du site Pléistocène Supérieur à hominidé d'Arrillor (Pays Basque, Espagne). *L'Anthropologie*, 103, 633–639.
- Bernaldo de Quirós, F. (1982). Los inicios del Paleolítico Superior Cantábrico. In *Monografías del Museo y Centro de Estudios de Altamira*, 8. Ministerio de Cultura, Dirección General de Bellas Artes y Archivos.
- Bernaldo de Quirós, F., Cabrera, V., Cacho, C., & Vega, L. G. (2006). Proyecto de análisis técnico para las industrias líticas. *Zona arqueológica*, 6, 63–78.
- Bouville, C., Constandse-Westermann, T. S., & Newell, R. R. (1983). Les restes humains mésolithiques de l'Abri Cornille, Istres (Bouches-du-Rhône). *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, 10(s.XIII), 89–110.
- Cabrera, V. (1996). Del musteriense al paleolítico superior. *Gallaecia: Revista de arqueología e antigüedad*, 14–15, 123–130.
- Cabrera, V., Arrizabalaga, A., Bernaldo De Quirós, F., & Maillo, J. M. (2004). La transición al Paleolítico superior y la evolución de los contextos aurinienses (50.000–27.000 BP). In M. Fano, (Coord.) (Ed.), *Las Sociedades del Paleolítico en la Región Cantábrica* (pp. 141–208). Diputación Foral de Bizkaia.
- Carlsen, O. (1987). *Dental morphology*. Munksgaard.

- Carretero, J. M., Quam, R. M., Gómez-Olivencia, A., Castilla, M., Rodríguez, L., & García-González, R. (2015). The Magdalenian human remains from El Mirón cave, Cantabria (Spain). *Journal of Archaeological Science*, 60, 10–27. <https://doi.org/10.1016/j.jas.2015.03.026>
- Castaños, P., Murelaga, X., Arrizabalaga, A., & Iriarte, M. J. (2011). First evidence of *Macaca sylvanus* (primates, Cercopithecidae) from the late Pleistocene of Lezetxiki II cave (Basque Country, Spain). *Journal of Human Evolution*, 60, 816–820. <https://doi.org/10.1016/j.jhevol.2011.01.011>
- Cava, A., Elorrieta, I., & Barandiarán, I. (2009). El Gravetiense de la cueva de Alkerdi (Urdax, Navarra): análisis y contexto de su industria lítica. *Munibe (Antropología-Arkeología)* 60, 51–80.
- Chaline, J. (1970). *Pliomys lenki*, forme relique dans la Microfaune du Würm ancien de la Grotte de Lezetxiki (Guipúzcoa-Espagne). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, 22(1–2), 43–49.
- Coleman, M., & Colbert, M. (2007). Technical note: CT thresholding protocols for taking measurements on three-dimensional models. *American Journal of Physical Anthropology*, 133, 723–725. <https://doi.org/10.1002/ajpa.20583>
- Davies, T. W., Delezene, L., Gunz, P., Hublin, J.-J., & Skinner, M. M. (2019). Endostructural morphology in hominoid mandibular third premolars: Discrete traits at the enamel-dentine junction. *Journal of Human Evolution*, 136, 102670. <https://doi.org/10.1016/j.jhevol.2019.102670>
- Daura, J., Sanz, M., Subirà, M. E., Quam, R., Fullola, J. M., & Arsuaga, J. L. (2005). A Neandertal mandible from the Cova del Gegant (Sitges, Barcelona, Spain). *Journal of Human Evolution*, 49(1), 56–70. <https://doi.org/10.1016/j.jhevol.2005.03.004>
- de la Rúa, C., & Hervella, M. (2011). Estudio Antropológico de los dientes humanos de la cueva de Aitzbitarte III (Rentería, Gipuzkoa) (Paleolítico Superior). In J. Altuna, K. Mariezkurrena, J. Rios J (Eds.), *Aitzbitarte III (Euskal Herria) Giza Aztarnak 33.600–18.400 BP (Sarrerako eremua)/Ocupaciones Humanas en Aitzbitarte III (País Vasco) 33.600–18.400 BP (Zona de entrada a la cueva)* (pp. 385–394). Eusko Jaurlaritzaren Argitalpen Zerbitzu Nagusia, Vitoria-Gasteiz.
- de la Rúa, C. (1990). Los estudios de Paleoantropología en el País Vasco. *Munibe (Antropología-Arkeología)*, 42, 199–219.
- de la Rúa, C., Altuna, J., Hervella, M., Kinsley, L., & Grün, R. (2016). Direct U-series analysis of the Lezetxiki humerus reveals a Middle Pleistocene age for human remains in the Basque Country (northern Iberia). *Journal of Human Evolution*, 93, 109–119. <https://doi.org/10.1016/j.jhevol.2016.02.001>
- Demuro, M., Arnold, L. J., Aranburu, A., Gómez-Olivencia, A., & Arsuaga, J. L. (2019). Single grain OSL dating of the middle Palaeolithic site of Galería de las Estatuas, Atapuerca (Burgos, Spain). *Quaternary Geochronology*, 49, 254–261. <https://doi.org/10.1016/j.quageo.2018.02.006>
- Egocheaga, J. E., Trabazo, R., Rodríguez, L., Cabo, L. L., & Sierra, M. J. (2000). Avance sobre el descubrimiento, características del yacimiento y estudio paleoantropológico de los restos óseos de homínidos mesopleistocénicos de la Cueva de El Sidrón (Piloña, Asturias). *Boletín de Ciencias Naturales RIDEA*, 46, 219–263.
- España, X. (1985). *El Paleolítico superior de la cueva de Lezetxiki (Mondragón, Guipúzcoa) (Unpublished master's thesis)*. Universidad Complutense de Madrid.
- ESRF (European Synchrotron Radiation Facility). (2020). ESRF Paleontological Microtomographic Database. <http://paleo.esrf.eu>
- Fajardo, R. J., Ryan, T. M., & Kappelman, J. (2002). Assessing the accuracy of high-resolution x-ray computed tomography of primate trabecular bone by comparisons with histological sections. *American Journal of Physical Anthropology*, 118, 1–10. <https://doi.org/10.1002/ajpa.10086>
- Falguères, C., Yokoyama, Y., & Arrizabalaga, A. (2006). La Geocronología del yacimiento pleistocénico de Lezetxiki (Arrasate, País Vasco). Crítica de las dataciones existentes y algunas nuevas aportaciones. *Munibe (Antropología-Arkeología)*, 57(II), 93–106.
- Fortea, J., de la Rasilla, M., Martínez, E., Sánchez-Moral, S., Cánaveras, J. C., Cuezva, S., Rosas, A., Soler, V., Julià, R., de Torres, T., Ortiz, J. E., Castro, J., Badal, E., Altuna, J., & Alonso, J. (2003). La cueva de el Sidron (Borines, Piloña, Asturias): primeros resultados. *Estudios Geológicos*, 59, 159–179.
- Garralda, M. D. (2005). Los Neandertales en la Península Ibérica. *Munibe (Antropología Arkeologia)*, 57, 289–314.
- Garralda, M.-D., Maillou-Fernández, J.-M., Higham, T., Neira, A., & Bernaldo de Quirós, F. (2019). The Gravettian child mandible from El Castillo cave (Puente Viesgo, Cantabria, Spain). *American Journal of Physical Anthropology*, 170, 331–350. <https://doi.org/10.1002/ajpa.23906>
- Garralda, M.-D., Maillou-Fernández, J.-M., Maureille, B., Neira, A., & Bernaldo de Quirós, F. (2022). >42 ka human teeth from el Castillo cave (Cantabria, Spain). Mid-upper Paleolithic transition. *Archaeological and Anthropological Sciences*, 14, 126. <https://doi.org/10.1007/s12520-022-01587-2>
- Gómez-Olivencia, A., López-Onaindia, D., Sala, N., Balzeau, A., Pantoja-Pérez, A., Arganda-Carreras, I., Arlegi, M., Rios-Garaizar, J., & Gómez-Robles, A. (2020). The human remains from Axlor (Dima, Biscay, northern Iberian Peninsula). *American Journal of Physical Anthropology*, 172, 475–491. <https://doi.org/10.1002/ajpa.23989>
- Gómez-Robles, A., Bermúdez de Castro, J. M., Martín-Torres, M., & Prado-Simón, L. (2011). Crown size and cusp proportions in *homo antecessor* upper first molars. A comment on Quam et al. 2009. *Journal of Anatomy*, 218, 258–262. <https://doi.org/10.1111/j.1469-7580.2010.01324.x>
- Gómez-Robles, A., Martín-Torres, M., Bermúdez de Castro, J. M., Margvelashvili, A., Bastir, M., Arsuaga, J. L., Pérez-Pérez, A., Esteban, F., & Martínez, L. M. (2007). A geometric morphometric analysis of hominin upper first molar shape. *Journal of Human Evolution*, 53, 272–285. <https://doi.org/10.1016/j.jhevol.2007.02.002>
- Gómez-Robles, A., Martín-Torres, M., Bermúdez de Castro, J. M., Prado, L., Sarmiento, S., & Arsuaga, J. L. (2008). Geometric morphometric analysis of the crown morphology of the lower first premolar of hominins, with special attention to Pleistocene *homo*. *Journal of Human Evolution*, 55, 627–638. <https://doi.org/10.1016/j.jhevol.2008.03.011>
- González Echegaray, J., García Guinea, M. A., Begines Ramírez, A., & Madariaga de la Campa, B. (1963). Cueva de la Chora (Santander). Ministerio de Educación Nacional. Dirección General de Bellas Artes. Servicio Nacional de Excavaciones Arqueológicas, Madrid.
- González Echegaray, J., & Ripoll Perelló E. (1954). *Hallazgos en la cueva de La Pasiega (Puente Viesgo, Santander)*. Ampurias, XV–XVI, 43–65.
- González-Urquijo, J., Ibáñez, J. J., Rios-Garaizar, J., Bourguignon, L., Castaños, P., & Tarrío, A. (2005). Axlor. Excavaciones recientes en Axlor. Movilidad y planificación de actividades en grupos de neandertales. In R. Montes & J. A. Lasheras (Eds.), *Actas de la reunión científica: Neandertales Cantábricos. Estado de la Cuestión* (pp. 527–539). Monografías Del Museo Nacional y Centro de Investigación de Altamira No 20). Ministerio de Cultura.
- Guerrero Sala, L. A., & Lorenzo Lizalde, J. L. (1981). Antropología física en Rascaño. In J. González Echegaray, I. Barandiarán Maestu (Eds.), *El Paleolítico Superior de la Cueva de Rascaño (Santander)* (pp. 279–321). Santander: Ministerio de Cultura. Dirección General de Bellas Artes, Archivos y Bibliotecas.
- Henry-Gambier, D. (2006). Les sépultures de Sorde-l'Abbaye (Landes). In M. Dachary (Ed.), *Les Magdaléniens à Duruthy. Qui étaient-ils, comment vivaient-ils?* (pp. 67–73). Conseil général des Landes, Mont-de-Marsan.
- Henry-Gambier, D., Normand, C., & Pétilion, J.-M. (2013). Datation radiocarbone directe et attribution culturelle des vestiges humains paléolithiques de la grotte d'Isturitz (Pyrénées-Atlantiques). *Bulletins de la Société Préhistorique Française* 110, 645–656.
- Higham, T. F. G., Douka, K., Wood, R., Bronk Ramsey, C., Brock, F., Basell, L., Camps, M., Arrizabalaga, A., Baena, J., Barroso-Ruiz, C., Bergman, C., Boitard, C., Boscato, P., Caparrós, M., Conard, N. J., Draily, C., Froment, A., Galván, B., Gambassini, P., ... Jacobi, R. (2014).

- The timing and spatio-temporal patterning of Neanderthal disappearance. *Nature*, 512, 306–309. <https://doi.org/10.1038/nature13621>
- Iriarte-Chiapuso, M. J. (2013). *Cueva Urkulu (Lastur), III Campaña* (pp. 277–278). *Arkeoikuska*.
- Iriarte-Chiapuso, M. J., Wood, R., & Sáenz de Buruaga, A. (2019). Arrillor cave (Basque Country, northern Iberian Peninsula). Chronological, palaeo-environmental and cultural notes on a long Mousterian sequence. *Quaternary International*, 508, 107–115. <https://doi.org/10.1016/j.quaint.2018.11.007>
- Jarvis, A., Reuter, H. I., Nelson, A., & Guevara, E. (2008). Hole-filled SRTM for the globe Version 4. available from the CGIAR-CSI SRTM 90m Database <http://srtmcsicgiar.org> 15, 25–54.
- Jones, J. R., Richards, M. P., Reade, H., Bernaldo de Quirós, F., & Marín-Arroyo, A. B. (2018). Multi-isotope investigations of ungulate bones and teeth from El Castillo and Covalejos caves (Cantabria, Spain): Implications for paleoenvironment reconstructions across the middle-upper Palaeolithic transition. *Journal of Archaeological Science: Reports*, 23, 1029–1042. <https://doi.org/10.1016/j.jasrep.2018.04.014>
- Keene, H. J. (1966). A morphologic and biometric study of taurodontism in a contemporary population. *American Journal of Physical Anthropology*, 25, 208–209.
- Laluzza-Fox, C., Sampietro, M. L., Caramelli, D., Puder, Y., Lari, M., Calafell, F., Martínez-Maza, C., Bastir, M., Fortea, J., de la Rasilla, M., Bertranpetit, J., & Rosas, A. (2005). Neandertal evolutionary genetics: Mitochondrial DNA data from the Iberian Peninsula. *Molecular Biology and Evolution*, 22, 1077–1081. <https://doi.org/10.1093/molbev/msi094>
- López-Onaindia, D., Lorenzo, C., Etxeberria, F., Herrasti, L., Arribas, J. J., Berganza, E., & Gómez-Olivencia, A. (2021). The Magdalenian human remains from Santa Catalina (Lekeitio, Biscay, northern Iberian Peninsula). *Archaeological and Anthropological Sciences*, 13, 202. <https://doi.org/10.1007/s12520-021-01442-w>
- Macchiarelli, R., Bondioli, L., & Mazurier, A. (2008). Virtual dentitions: Touching the hidden evidence. In J. D. Irish & G. C. Nelson (Eds.), *Technique and application in dental anthropology* (pp. 426–448). Cambridge University Press.
- Maroto, J. (1993). *La mandíbula de Banhyoles en el context dels fòssils humans del pleistocè*. Centre d'Investigacions Arqueològiques.
- Maroto, J., Julià, R., López-García, J. M., & Blain, H. A. (2012). Chronological and environmental context of the middle Pleistocene human tooth from Mollet cave (Serinyà, NE Iberian Peninsula). *Journal of Human Evolution*, 62, 655–665. <https://doi.org/10.1016/j.jhevol.2012.01.009>
- Maroto, J., Vaquero, M., Arrizabalaga, A., Baena, J., Baquedano, E., Jordá, J., Julià, R., Montes, R., Van Der Plicht, J., Rasines, P., & Wood, R. (2012). Current issues in late middle Paleolithic chronology: New assessments from northern Iberia. *Quaternary International*, 247, 15–25. <https://doi.org/10.1016/j.quaint.2011.07.007>
- Martin, L. (1985). Significance of enamel thickness in hominoid evolution. *Nature*, 314, 260–263. <https://doi.org/10.1038/314260a0>
- Martin, R. M. G., Hublin, J. J., Gunz, P., & Skinner, M. M. (2017). The morphology of the enamel-dentine junction in Neanderthal molars: Gross morphology, non-metric traits, and temporal trends. *Journal of Human Evolution*, 103, 20–44. <https://doi.org/10.1016/j.jhevol.2016.12.004>
- Martín-Francés, L., Martínón-Torres, M., Martínez de Pinillos, M., García-Campos, C., Modesto-Mata, M., Zanolli, C., Rodríguez, L., & Bermúdez de Castro, J. M. (2018). Tooth crown tissue proportions and enamel thickness in early Pleistocene *Homo antecessor* molars (Atapuerca, Spain). *PLoS One*, 13, e0203334. <https://doi.org/10.1371/journal.pone.0203334>
- Martín-Francés, L., Martínón-Torres, M., Martínez de Pinillos, M., García-Campos, C., Zanolli, C., Bayle, P., Modesto-Mata, M., Arsuaga, J. L., & Bermúdez de Castro, J. M. (2020). Crown tissue proportions and enamel thickness distribution in the middle Pleistocene hominin molars from Sima de los Huesos (SH) population (Atapuerca, Spain). *PLoS One*, 15, e0233281. <https://doi.org/10.1371/journal.pone.0233281>
- Martinón-Torres, M., Bermúdez de Castro, J. M., Gómez-Robles, A., Prado-Simón, L., & Arsuaga, J. L. (2012). Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *Journal of Human Evolution*, 62, 7–58. <https://doi.org/10.1016/j.jhevol.2011.08.007>
- Martinón-Torres, M., Spěváčková, P., Gracia-Téllez, A., Martínez, I., Bruner, E., Arsuaga, J. L., & Bermúdez de Castro, J. M. (2013). Morphometric analysis of molars in a middle Pleistocene population shows a mosaic of 'modern' and Neanderthal features. *Journal of Anatomy*, 223, 353–363. <https://doi.org/10.1111/joa.12090>
- Maureille, B., Rougier, H., Houët, F., & Vandermeersch, B. (2001). Les dents inférieures du néanderthalien Regourdou 1 (site de Regourdou, commune de Montignac, Dordogne): analyses métriques et comparatives. *Paléo*, 13, 183–200. <https://doi.org/10.4000/paleo.1043>
- Moorrees, C. F. A., Thomsen, S. Ø., Jensen, E., & Yen, P. K. (1957). Mesiodistal crown diameters of the Deciduous and permanent teeth in individuals. *Journal of Dental Research*, 36, 39–47. <https://doi.org/10.1177/00220345570360011501>
- NESPOS Database. (2020). Neanderthal Studies Professional Online Service. <http://www.nespos.org>
- Obermaier, H. (1925). El hombre fósil. Comisión De Investigaciones Paleontológicas y Prehistóricas 9, pp. 1–398.
- O'Hara, M., & Guatelli-Steinberg, D. (2022). Reconstructing tooth crown heights and enamel caps: A comparative test of three existing methods with recommendations for their use. *The Anatomical Record*, 305, 123–143. <https://doi.org/10.1002/ar.24637>
- O'Hara, M., Le Cabec, A., Xing, S., Skinner, M. F., & Guatelli-Steinberg, D. (2019). Safe casting and reliable cusp reconstruction assisted by micro-computed tomographic scans of fossil teeth. *The Anatomical Record*, 302, 1516–1535. <https://doi.org/10.1002/ar.24047>
- Olejniczak, A. J., Smith, T. M., Feeney, R. N. M., Macchiarelli, R., Mazurier, A., Bondioli, L., Rosas, A., Fortea, J., de la Rasilla, M., García-Tabernero, A., Radovic, J., Skinner, M. M., Toussaint, M., & Hublin, J. J. (2008). Dental tissue proportions and enamel thickness in Neandertal and modern human molars. *Journal of Human Evolution*, 55, 12–23. <https://doi.org/10.1016/j.jhevol.2007.11.004>
- Pablos, A., Gómez-Olivencia, A., & Arsuaga, J. L. (2019). A Neandertal foot phalanx from the Galería de las Estatuas site (Sierra de Atapuerca, Spain). *American Journal of Physical Anthropology*, 168, 222–228. <https://doi.org/10.1002/ajpa.23729>
- Pan, L., & Zanolli, C. (2019). Comparative observations on the premolar root and pulp canal configurations of middle Pleistocene *homo* in China. *American Journal of Physical Anthropology*, 168, 637–646. <https://doi.org/10.1002/ajpa.23777>
- Prieto, J., Abenea, J., Montes, R., Sanguino, J., & Muñoz, E. (2001). Hallazgos antropológicos y arqueológicos en el complejo kárstico de El Sidrón (Vallobal, Infiesto, Concejo de Piloña, Asturias). *Munibe (Antropología-Arkeología)*, 53, 19–29.
- Quam, R., Bailey, S., & Wood, B. (2009). Evolution of M¹ crown size and cusp proportions in the genus *homo*. *Journal of Anatomy*, 214, 665–670. <https://doi.org/10.1111/j.1469-7580.2009.01064.x>
- Quam, R., Sanz, M., Daura, J., Robson Brown, K., García-González, R., Rodríguez, L., Dawson, H., Rodríguez, R. F., Gómez, S., Villaescusa, L., Rubio, T., Yagüe, A., Ortega Martínez, M. C., Fullola, J. M., Zilhão, J., & Arsuaga, J. L. (2015). The Neandertals of northeastern Iberia: New remains from the Cova del Gegant (Sitges, Barcelona). *Journal of Human Evolution*, 81, 13–28. <https://doi.org/10.1016/j.jhevol.2015.02.002>
- Quam, R. M., Arsuaga, J. L., Bermúdez de Castro, J. M., Díez, J. C., Lorenzo, C., Carretero, J. M., García, N., & Ortega, A. I. (2001). Human remains from Valdegoba cave (Huérneces, Burgos, Spain). *Journal of Human Evolution*, 41, 385–435. <https://doi.org/10.1006/jhev.2001.0486>
- Rios-Garaizar, J. (2005). Características de la producción lítica al final del Paleolítico Medio en el País Vasco. El caso del nivel B de Axlor (Dima, Bizkaia). In R. Montes & J. A. Lasheras (Eds.), *Actas de la reunión científica: Neandertales cantábricos. Estado de la Cuestión* (pp. 333–348). Monografías Del Museo Nacional y Centro de Investigación de Altamira No 20). Ministerio de Cultura.

- Rios-Garaizar, J. (2010). *Organización económica de las sociedades neanderthales: El caso del nivel VII de Amalda (Zestoa, Gipuzkoa)* (pp. 15–37). Zephyrus.
- Rios-Garaizar, J. (2017). A new chronological and technological synthesis for late middle Paleolithic of the eastern Cantabrian region. *Quaternary International*, 433, 50–63. <https://doi.org/10.1016/j.quaint.2016.02.020>
- Rios-Garaizar, J., Garate, D., Gómez-Olivencia, A., Iriarte, E., Arceredillo-Alonso, D., Iriarte-Chiapusso, M. J., Garcia-Ibaibarriaga, N., García-Moreno, A., Gutierrez-Zugasti, I., Torres, T., Aranburu, A., Arriolabengoa, M., Bailón, S., Murelaga, X., Ordiales, A., Ortiz, J. E., Rofes, J., & San Pedro, Z. (2015). Short-term Neandertal occupations in the late middle Pleistocene of Arlanpe (Lemoa, northern Iberian Peninsula). *Comptes Rendus Palevol*, 14, 233–244. <https://doi.org/10.1016/j.crpv.2014.11.006>
- Rios-Garaizar, J., López-Bultó, O., Iriarte, E., Pérez-Garrido, C., Piqué, R., Aranburu, A., Iriarte-Chiapusso, M. J., Ortega-Cordellat, I., Bourguignon, L., Garate, D., & Libano, I. (2018). A middle Palaeolithic wooden digging stick from Aranbaltza III, Spain. *PLoS One*, 13, e0195044. <https://doi.org/10.1371/journal.pone.0195044>
- Rosas, A., & Aguirre, E. (1999). Restos humanos neandertales de la cueva del Sidron, Piloña, Asturias. Nota preliminar. *Estudios Geológicos*, 55, 181–190. <https://doi.org/10.3989/egool.99553-4174>
- Saenz de Buruaga, A. (2005). *Cueva de Zerratu, en Astigarribia (Mutriku), III Campaña* (pp. 144–153). *Arkeoikuska*.
- Sánchez, M. F. (1991). Analyses palynologiques des remplissages de grotte de Lezetxiki, Labeko et Urtiaga (Pays Basque espagnol) : leur place dans le cadre des séquences polliniques de la côte cantabrique et des Pyrénées occidentales : de la taphonomie pollinique à la reconstitution de l'environnement (Unpublished doctoral dissertation). Muséum national d'histoire naturelle. Paris France.
- Sánchez-Romero, L., Benito-Calvo, A., Marín-Arroyo, A. B., Agudo-Pérez, L., Karampaglidis, T., & Rios-Garaizar, J. (2020). New insights for understanding spatial patterning and formation processes of the Neandertal occupation in the Amalda I cave (Gipuzkoa, Spain). *Scientific Reports*, 10, 8733. <https://doi.org/10.1038/s41598-020-65364-8>
- Sanguino González, J., & Montes Barquín, R. (2005). Nuevos datos para el conocimiento del Paleolítico Medio en el centro de la Región Cantábrica: La Cueva de Covalejos (Pielagos, Cantabria). In R. Montes Barquín & J. A. Lasheras (Eds.), *Actas de La Reunión Científica: Neandertales Cantábricos. Estado de La Cuestión* (pp. 489–504). Monografías Del Museo Nacional y Centro de Investigación de Altamira No 20). Ministerio de Cultura.
- Saunders, S. R., Chan, A. H. W., Kahlon, B., Kluge, H. F., & FitzGerald, C. M. (2007). Sexual dimorphism of the dental tissues in human permanent mandibular canines and third premolars. *American Journal of Physical Anthropology*, 133, 735–740. <https://doi.org/10.1002/ajpa.20553>
- Scolan, H., Santos, F., Tillier, A.-M., Maureille, B., & Quintard, A. (2012). Des nouveaux vestiges néandertaliens à Las Pélénos (Monsempron-Libos, Lot-et-Garonne, France). *Bulletin et Mémoires de la Société d'Anthropologie de Paris*, 24, 69–95. <https://doi.org/10.1007/s13219-011-0047-x>
- Shaw, J. C. M. (1928). Taurodont teeth in south African races. *Journal of Anatomy*, 62, 476–498.
- Slimak, L., Zanolli, C., Higham, T., Frouin, M., Schzenninger, J.-L., Arnold, L. J., Demuro, M., Douka, K., Mercier, N., Guérin, G., Valladas, H., Yvorra, P., Giraud, Y., Seguin-Orlando, A., Orlando, L., Lewis, J. E., Muth, X., Camus, H., Vandevelde, S., ... Metz, L. (2022). Modern human incursion into Neandertal territories 54,000 years ago at Mandrin, France. *Science Advances*, 8, eabj9496. <https://doi.org/10.1126/sciadv.abj9496>
- Smith, T. M., Olejniczak, A. J., Reid, D. J., Ferrell, R. J., & Hublin, J. J. (2006). Modern human molar enamel thickness and enamel-dentine junction shape. *Archives of Oral Biology*, 51, 974–995. <https://doi.org/10.1016/j.archoralbio.2006.04.012>
- Spoor, C., Zonneveld, F., & Macho, G. (1993). Linear measurements of cortical bone and dental enamel by computed tomography: Applications and problems. *American Journal of Physical Anthropology*, 91, 469–484. <https://doi.org/10.1002/ajpa.1330910405>
- Tejero, J. M., Avezuela, B., White, R., Ranlett, S., Quam, R., Tattersall, I., & Bernaldo de Quirós, F. (2010). Un pedazo de la Prehistoria cántabra en Nueva York. Las Colecciones de la Cueva de El Castillo (Puente Viesgo, Cantabria) en el American Museum of Natural History (Nueva York, EEUU). *Munibe (Antropología-Arkeología)* 61, 5–16.
- Toussaint, M., Verna, C., Le Cabec, A., Gómez-Robles, A., Draily, C., Richards, M. P., & Pirson, S. (2018). The late Neandertal permanent lower left third premolar from Walou cave (Trooz, Belgium) and its context. *American Journal of Physical Anthropology*, 164, 193–202. <https://doi.org/10.1002/ajpa.23252>
- Turner, C. G., II, Nichol, C. R., & Scott, G. R. (1991). Scoring procedures for key morphological traits of the permanent dentition: The Arizona State University dental anthropology system. In M. A. Kelley (Ed.), *Advances in dental anthropology* (pp. 13–31). Wiley-Liss.
- Vallois, H., & Delmas, L. (1976). Los frontales de la cueva de El Castillo (España). *Trabajos de Prehistoria* 33, 113–120.
- Wood, R. E., Arrizabalaga, A., Camps, M., Fallon, S., Iriarte-Chiapusso, M. J., Jones, R., Maroto, J., de la Rasilla, M., Santamaría, D., Soler, J., Soler, N., Villaluenga, A., & Higham, T. F. G. (2014). The chronology of the earliest upper Palaeolithic in northern Iberia: New insights from L'Arbreda, Labeko Koba and La Viña. *Journal of Human Evolution*, 69, 91–109. <https://doi.org/10.1016/j.jhevol.2013.12.017>
- Wright, T. (2007). The molecular control of and clinical variations in root formation. *Cell Tissues Organs*, 186, 86–93. <https://doi.org/10.1159/000102684>
- Zanolli, C., Martín-Torres, M., Bernardini, F., Boschian, G., Coppa, A., Dreossi, D., Mancini, L., Martínez de Pinillos, M., Martín-Francés, L., Bermúdez de Castro, J. M., Tozzi, C., Tuniz, C., & Macchiarelli, R. (2018). The middle Pleistocene (MIS 12) human dental remains from Fontana Ranuccio (Latium) and Visogliano (Friuli-Venezia G), Italy. A comparative high resolution endostructural assessment. *PLoS One*, 13, e0189773. <https://doi.org/10.1371/journal.pone.0189773>
- Zanolli, C., Pan, L., Dumoncel, J., Kullmer, O., Kundrát, M., Liu, W., Macchiarelli, R., Mancini, L., Friedemann, S., & Tuniz, C. (2018). Inner tooth morphology of *Homo erectus* from Zhoukoudian. New evidence from an old collection housed at Uppsala University, Sweden. *Journal of Human Evolution*, 116, 1–13. <https://doi.org/10.1016/j.jhevol.2017.11.002>
- Zapata, J., Bayle, P., Vincent Lombardi, A., Pérez-Pérez, A., & Trinkaus, E. (2017). The Palomas Dental Remains: Preservation, Wear, and Morphology. In E. Trinkaus & M. J. Walker (Eds.), *Neandertals from the Sima de las Palomas del Cabezo Gordo, southeastern Spain* (pp. 52–88). Texas A&M University Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: López-Onaindia, D., Lozano, M., Gómez-Robles, A., Arrizabalaga, A., & Subirà, M. E. (2023). Neandertal teeth from Lezetxiki (Arrasate, Iberian Peninsula): New insights and reassessment. *American Journal of Biological Anthropology*, 180(4), 745–760. <https://doi.org/10.1002/ajpa.24694>