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Middle Pleistocene teeth from Arbreda Cave (Serinyà, northeastern Iberian Peninsula)

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Abstract

Objectives: We report the discovery and description of three human teeth from the Middle Paleolithic archaeological levels of Arbreda Cave (Serinyà, Catalonia, NE Iberian Peninsula).

Materials and Methods: The teeth, two molars (one right dm_2 and one right M_2) from Level N (older than 120 kyr) and one P^3 from Level J (dated between 71 and 44 kyr), were morphologically described based on microCT images and compared with Neanderthal and *Homo sapiens* specimens.

Results: The teeth belong to a minimum of three individuals: one adult and one infant from Level N and one juvenile from Level J. The premolar from Mousterian Level J, the best preserved of the three teeth, exhibits characteristics to those from our comparative sample of *Homo neanderthalensis*, such as the crown measurements, EDJ traits, enamel thickness and volume of the pulp cavity.

Discussion: In contrast to the clear Neanderthal characteristics observed in the P^3 from Level J, the high degree of dental wear and poor state of preservation precludes definitive taxonomic designations of the two teeth from Level N. However, the crown dimensions and some tissue proportions are consistent with a probable assignation to *Homo neanderthalensis*. The teeth from Level N come from a context of long and recurrent occupations of the cave, whereas the archaeological context of the tooth from Level J is indicative of short and seasonal occupations of the cave, which may indicate a change in the lifestyle strategies of the last Neanderthals of the Iberian Peninsula.

KEYWORDS
enamel-dentine junction, *homo neanderthalensis*, Mousterian, pulp canal, tissue proportions

1 | INTRODUCTION

The Iberian Peninsula contains many archaeological sites with levels assigned to Mousterian material culture, many of which have yielded human remains assigned to *Homo neanderthalensis*. However, relatively large assemblages of human remains have only been documented at a few of these sites, such as El Sidrón (Piloña, Asturias), Cova Simanya (Sant Llorenç del Munt, Barcelona), Cova Negra (Xàtiva, València) and Boquete de Zafarraya (Alcaucín, Málaga). Far more sites preserve sparse human remains, many of which preserve morphological characters aligning them with Neanderthals. (Garralda, 2005).

Some of the most important discoveries of Neanderthal remains on the Iberian Peninsula have been made along or near the Mediterranean coast, at sites, such as (from north to south) Mollet Cave (Cortada & Maroto, 1990; Maroto, Julià, et al., 2012), Cova del Gegant (Daura et al., 2005; Quam et al., 2015), Cova Simanya (Morales et al., 2023), Tossal de la Font (Olaria et al., 2004-2005), Cova Negra (Arsuaga et al., 2007; Richard et al., 2019), Cova Foradà (Aparicio et al., 2014; Subirà et al., 2003), El Salt (Garralda et al., 2014), Cova Bolomor (Arsuaga et al., 2001, 2012), Sima de las Palomas (Trinkaus & Walker, 2017; Walker et al., 2011, 2012; Walker, Lombardi, et al., 2010), Boquete de Zafarraya (García Sánchez, 1986), and Gibraltar Caves (Bokelmann et al., 2019; Finlayson et al., 2006). The sites of Cova Bolomor dated around 120 kyr BP, and Sima de las Palomas, dated between 128 and 60 kyr BP, have yielded some of the oldest Neanderthal remains of the Iberian Peninsula (Arsuaga et al., 2001, 2012; Walker et al., 2011, 2012; Walker, Lombardi, et al., 2010). The Zafarraya site is one of the most recent Neanderthal sites, currently believed to date from 35 kyr BP (Hublin et al., 1995). These sites that span for an extensive period in which changing environmental conditions would have put pressure on Neanderthals to adapt. However, in recent years, this scenario has become more complex with evidence of the presence of *Homo sapiens* in Europe earlier than expected. From the controversial taxonomic assignment of the Apidima remains (Harvati et al., 2019) to the more recent evidence of the presence of *Homo sapiens* in Grotte Mandrin 56,800 to 51,700 years ago (Slimack et al., 2022) and in Ilsenhöhle cave by 47,500 years ago (Mylopotamitaki et al., 2024; Smith et al., 2024) indicate an earlier than previously established overlap between Neanderthals and modern humans in Europe.

In the present work, we describe, for the first time, three human teeth from the Mousterian levels J and N, of the Arbreda Cave and use a combination of methods to determine their taxonomic affinity. Finally, we interpret these remains within their chronological and regional contexts.

2 | REGIONAL SETTING

The Arbreda Cave site is located in the municipality Serinyà (Girona, Catalonia, NE Spain), in the same area of other relevant Paleolithic sites, such as Reclau Viver (Corominas, 1946), Pau (Soler, 1986), Mollet (Maroto, Julià, et al., 2012) and Mollet III (Soler et al., 2013). All these caves are aligned along a 200-m-long travertine cliff of waterfall origin known as the *Paratge del Reclau* (Figure 1).

The importance of the site was recognized in 1972, when the medical doctor Josep Maria Corominas excavated an 8.80-m-deep test pit, uncovering the longest and most complete record from the Middle to the Upper Paleolithic in Catalonia (Soler et al., 2014). As a result, in 1975 a broader excavation area was defined and excavations resumed, which have continued up to the present (Figure 1).

Arbreda Cave has been referred to as a key site for the study of the nature and chronology of the transition between the Middle and Upper Paleolithic in western Europe (Maroto et al., 1996; Soler et al., 2009; Wood et al., 2014). But below the layers corresponding to that period, the strata also contain a rich Mousterian record that extends at least 4.5 m in depth (Figure 2) (Soler et al., 2014).

The sedimentary filling of Abreda cave is composed of compact clays, tufa sands and rocks, in addition to larger blocks from the collapsed roof of the cave. An upper initial erosive line divides the filling into two main strata. The upper stratum A is composed by *terra rossa*, red clays that accumulated during the postglacial era. Archaeological content is scarce in stratum A, although it has yielded prehistoric human, ceramic, lithic and faunal remains belonging to different Neolithic facies. Stratum B, which lies immediately below A, comprises most of the fill and belongs predominantly to the Upper Pleistocene (Soler et al., 2014). It contains abundant archaeological remains in a succession of archaeological levels (A–N) spanning from the Magdalenian to the Mousterian (Figure 2).

2.1 | The nature and chronology of the middle Paleolithic levels

Stratum B is divided into two major units (B1 and B2) because of the presence of a second erosive surface at a depth of 6.3 m. Unit B1 is made up of a succession of nine levels of Upper and Middle Paleolithic age: Magdalenian (A), Solutrean (B, C), Gravettian (D, E, F), Aurignacian (G, H) and Final Mousterian (I). The B2 sequence contains the Mousterian levels J to N (Soler et al., 2014).

From a technological perspective, the Mousterian levels are homogeneous and do not exhibit any major cultural diachronic change or rupture in the production of lithic artifacts, aside from the presence of 4 Châtelperronian points in the ceiling of level I. Apart from that, all

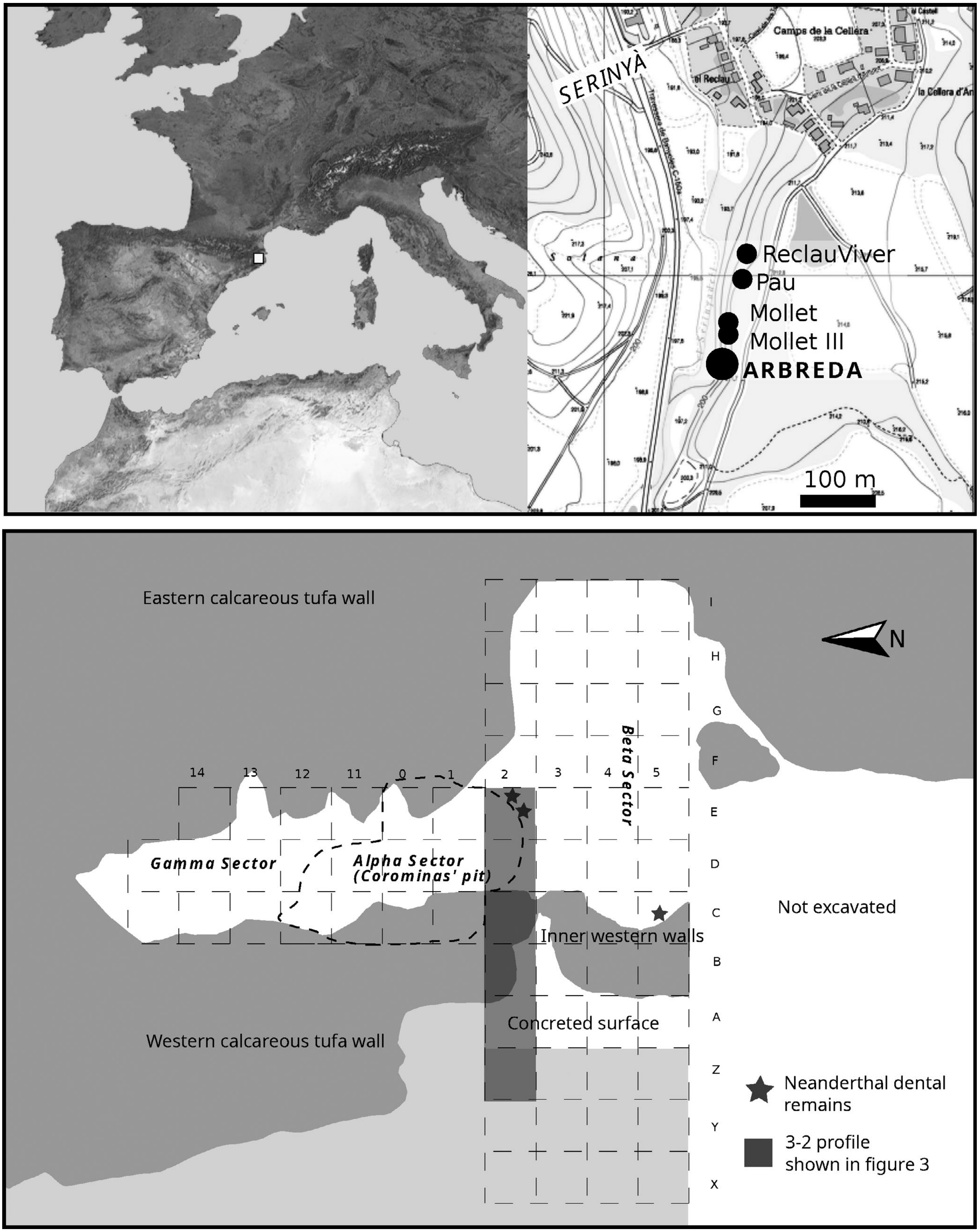

FIGURE 1 Location of the Arbreda Cave among the other sites found in the same travertine cliff (Paratge del Reclau). The diagram below shows the different sectors of the cave and where the three human dentals remains presented in this paper were recovered. The light gray squares are those displayed in the profile (Figure 2).

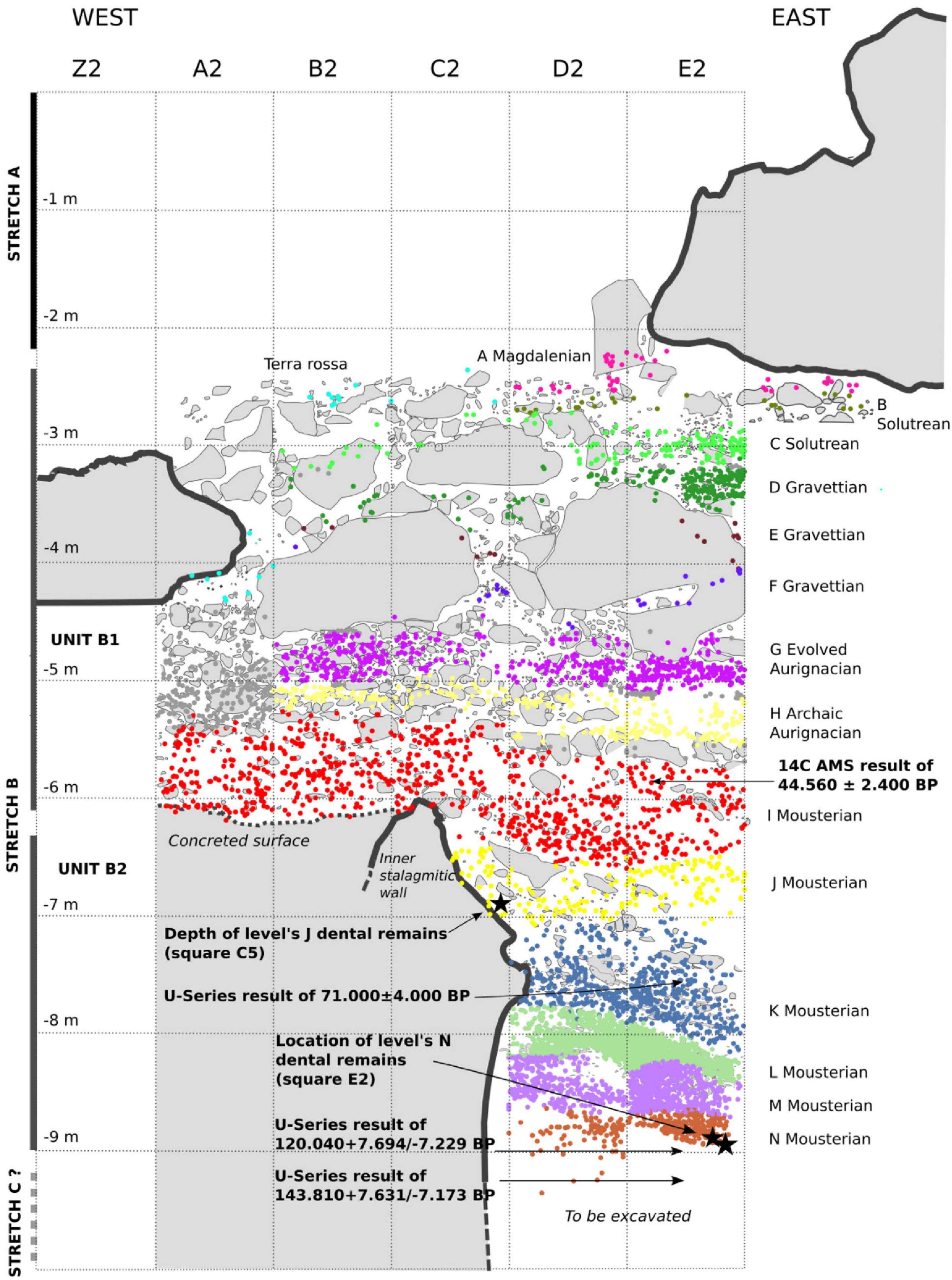

FIGURE 2 West–east profile showing the different archaeological levels from Arbreda Cave. The stars indicate the location of the two human dental remains found in Level N (square E2). The arrows show the location of the stalagmites formed in situ and dated by U-series.

the Mousterian levels have yielded common artifacts, mostly scrappers and denticulates, which were produced primarily on small flakes. These flakes were obtained through the use of Levallois and discoid reduction methods on cobblestones of quartz, quartzite and other local raw materials widely available in the vicinity of the cave (SOM Table S1).

While the Mousterian cultural record from Arbreda Cave (ca. 140.000–40.000 BP) is stable, from the cultural point of view, there is a major contrast in occupation duration between levels K and L, which we interpret as evidence of different Neanderthal settlement strategies. Above the K-L boundary, in levels I, J and K, the evidence of human activities are mixed with abundant remains of *Ursus spelaeus*, which indicate that the cave was regularly used as a hibernation den. The abundance and diversity of cave bear remains, ranging from fetal to senile individuals, indicate that the human occupations from levels I, J and K were probably of short duration and were likely seasonally restricted (Soler et al., 2014).

In contrast, cave bears are nearly absent in levels L through N and the traces of human intervention on the faunal remains (cut marks and breakage impacts) are significantly higher than in the levels above (I–K). (SOM Table S2). The human presence that originated Levels L, M and N was probably more regular or long enough to prevent *Ursus spelaeus* from using Arbreda cave as a hibernation den (Soler et al., 2014).

In 2009, while excavating Level N (the oldest with human remains), two molars were found near one another within the same square meter E2. In 2011, another tooth was discovered while excavating Level J (the youngest level with human remains) in square C5. Apart from these, no other human remains have been identified in the Mousterian sequence either during the current excavation works or after the revision of the archaeological material recovered in the test pit from the initial excavation carried out in 1972.

In order to determine the chronological age of the two specimens from Level N, two stalagmite fragments from square E2 and level N were dated at the Institute of Earth Sciences of the CSIC (Barcelona) (Soler et al., 2014) by means of the uranium-series disequilibrium method (U/Th) using alpha spectrometry (Ivanovich & Harmon, 1992). The first sample is a stalagmite formed in situ where one of the dental remains was found (BE179), which yielded a result of 120.04 + 7694/−7,2 kyr BP. The second sample was obtained from a thin crystalline stalagmite layer formed in situ and discovered below the dental remains and the above-mentioned dated stalagmite at a depth of 9.12 m. This second sample yielded a result of 143.8 + 7.6/−7,2 kyr BP. Therefore, a minimum age of 120 kyr BP and maximum of 143.8 kyr BP is suggested for both molars (Soler et al., 2014), corresponding to the MIS5.

3 | MATERIALS AND METHODS

3.1 | Materials

During the 2009 excavations, square E2 of Level N yielded a deciduous lower right second molar (ARB-E2-BE178) and a permanent lower right second molar (ARB-E2-BE179). Specimens BE178 and BE179 were located one above another at depths of 8.85–8.90 and 8.90–8.95 m respectively (Figure 2). The two human teeth share the same chemical alteration as the other faunal remains from Level N, which gives them a crystalline and brownish appearance that only became visible after removing the adhering matrix. In 2011, the excavation of square C5 from level J yielded another isolated human tooth, ARB-C5-EC139-2434, at a depth of 6.905 m.

The three teeth were associated with both lithic artifacts and faunal remains, but these did not present any particular spatial arrangements different from the other areas of the site. Therefore, the archaeological context does not allow to develop further considerations about how these human remains were incorporated in the deposits.

3.2 | Methods

High resolution μCT images of the specimens were obtained at the Centro Nacional de Investigación sobre Evolución Humana (Burgos, Spain) with a Scanco Medical μCT81 scanner using the following scan parameters: 70 kV, 114 mA, voxel size = 18 μm. A semiautomatic threshold-based segmentation was conducted using Mimics (Materialise, Louvain, Belgium), following the half-maximum height method (Coleman & Colbert, 2007; Fajardo et al., 2002; Spoor et al., 1993) assisted by manual corrections to obtain the inner anatomy of the teeth and the reconstruction of the different tissues.

In order to assess possible postdepositional alterations of the dental surfaces, the teeth were analyzed under a FEI Quanta 600 scanning electron microscope at the Scientific and Technical Services of Universitat Rovira i Virgili (Tarragona, Spain). The original teeth were analyzed under low vacuum mode at high voltage of 15 kv and different magnifications ranging from ×20 to ×500.

The occlusal wear was assessed based on that described in Smith (1984). The age at death was established following Brothwell (1981) and Miles (2001), both based on occlusal dental wear, and AlQahtani et al., 2010; AlQahtani et al., 2014 was used to provide a minimum age for the individuals. Standard measurements of the crown were taken: mesiodistal (MD) and buccolingual (BL) lengths (Hillson, 1996). Due to the high degree of occlusal wear in the lower permanent molar, alternative cervical mesio-distal and bucco-lingual diameters were measured following Hillson et al. (2005). Metric comparisons of the mesiodistal and buccolingual diameters of the premolar crown were made on the basis of published data (Voisin et al., 2012; see SOM Table S3).

The external morphological descriptions of the teeth are based on direct observation of the original specimens and 3D models, using the most common terminology for this type of morphological analysis (Bailey et al., 2009; Benazzi et al., 2011; Martinón-Torres et al., 2012; Martinón-Torres et al., 2013; Zanolli, 2013). The external crown and root morphological traits of the permanent molar and premolar were compared to Neanderthals, Upper Paleolithic modern humans (UPMH), and recent modern humans (RMH) (Kupczik and Hublin, 2010; Martinón-Torres et al., 2012: Zanolli & Mazurier, 2013; Bayle et al., 2017; Becam et al., 2019; Gómez-Olivencia et al., 2020; Zanolli et al., 2019; Garralda et al., 2020). The morphology of the EDJ of the molar was studied following the descriptions by Martínez de Pinillos et al. (2014) and Martinón-Torres et al. (2014), and the traits described by Becam et al. (2019) were scored for the upper premolar. In addition, we classified the morphology of the pulp chamber of the permanent molar and determined the level of bifurcation (Keene, 1966; Kupczik and Hublin, 2010).

We quantified 2D and 3D dental proportions of the upper premolar following standard protocols (Martin, 1985; Olejnzak et al., 2008). We measured in 2D for the premolar: 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 × 2D AET/(cdp area$^{1/2}$), unit free). These measurements were taken in the original anatomical cross-section and on a cross-section corrected to reconstruct the worn enamel following the Pen Tool method (Saunders et al., 2007; O'Hara et al., 2019; O'Hara & Guatelli-Steinberg, 2021). We calculated the 3D coronal pulp volume (Vcp, mm^3) for each tooth, since wear does not affect pulp volume. These proportions and values were compared to previously published data on Middle and Upper Paleolithic fossils and recent modern humans (Bayle et al., 2017; Kupczik and Hublin, 2010; Zanolli & Mazurier, 2013; Zanolli et al., 2019). Finally, we determined the 3D topography of the enamel thickness distribution in each tooth using the segmented enamel and dentine surfaces Avizo software (Termofisher) (Macchiarelli et al., 2008; Bayle et al., 2011; Zanolli et al., 2018, Zanolli, Pan, 2018). These maps provide a rendering by thickness related pseudocolor scale ranging from dark blue (thinner) to red (thicker) and an easy way to synthesize and compare the feature in different samples, which allow the comparison with data from Neanderthal samples available in the NESPOS database (2020) and Qafzeh 10 and 15 (available in ESRF, 2020).

Adjusted z-scores were calculated to compare the quantitative variables measured in the Arbreda fossils to the comparative samples, including dental proportions and 2D dental tissue proportions (Maureille et al., 2001; Scolan et al., 2012). This method makes it possible to compare unbalanced samples with an adjustment to include small data 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.

3.3 | Open data availability

Following the Open Research practices, we share the raw data corresponding to the present study in an open repository. The data that support the findings of this study are openly available in “figshare” http://doi.org/10.6084/m9.figshare.22761365.

4 | RESULTS

4.1 | Description of the teeth from level N

4.1.1 | ARB-E2-BE178

This tooth is a deciduous lower right second molar (dM_2). It preserves the crown and the cervical third of the roots. The small size, the mesiodistal elongation of the occlusal outline, the prominent enamel in the area of cervical line, the bulbous appearance of the crown, the root divergence near the neck and the evidence of root resorption support the identification as a deciduous lower right second molar (Figure 3). The tooth does not exhibit any evidence of pathology, although there is a high degree of occlusal dental wear corresponding with stage 7, which limited our morphological observations. The measured MD and BL diameters are shown in Table 1.

The crown outline is mesiodistally rectangular, with a slight compression in the middle of both the vestibular and lingual aspects. The buccal face is convex, the distobuccal aspect (hypoconid) is more bulging than the protoconid area (mesiobuccal). The lingual face is less convex than the buccal. The mesial face is slightly convex and presents a considerable loss of enamel. The distal surface exhibits an interproximal wear facet with a maximum width of 5 mm.

The dM_2 has two roots, mesial and distal, which are partially reabsorbed. The preserved mesial root is longer than the distal. The μCT images show an elongated pulp chamber and the early bifurcation (in the crown) of the root canals for each – mesial and distal – root. In addition, it can be observed that the lingual pulp horns develop higher from the cervical plane than the buccal horns (Figure 3).

4.1.2 | ARB-E2-BE179

This tooth is a permanent lower right second molar with partially preserved crown and roots (Figure 4). There is a significant loss of enamel due to postmortem chipping on the crown, and only the cervical thirds of the roots are preserved. In addition, it presents a high degree of occlusal wear (stage 6). The enamel loss on the interproximal and buccal surfaces makes it difficult to obtain accurate crown measurements. However, as a thin enamel line is preserved in the cervical area, we took some measurements that represent minimum or cervical diameter of this specimen (Hillson et al., 2005) (Table 2).

The enamel of the buccal surface is almost completely lost *postmortem* with only a thin rim of it remaining around the cervical line, and part of the dentine is also broken. The lingual surface is less convex than the buccal one, and the intercuspal groove divides the metaconid and entoconid. The metaconid is higher than the entoconid. On the mesial surface, enamel is only preserved on the lingual aspect and around the cervical line. The interproximal contact facet is not preserved. On the distal surface, only some enamel around the straight cervical line remains. Although the occlusal surface is affected by occlusal wear and by a significant postdepositional damage, some

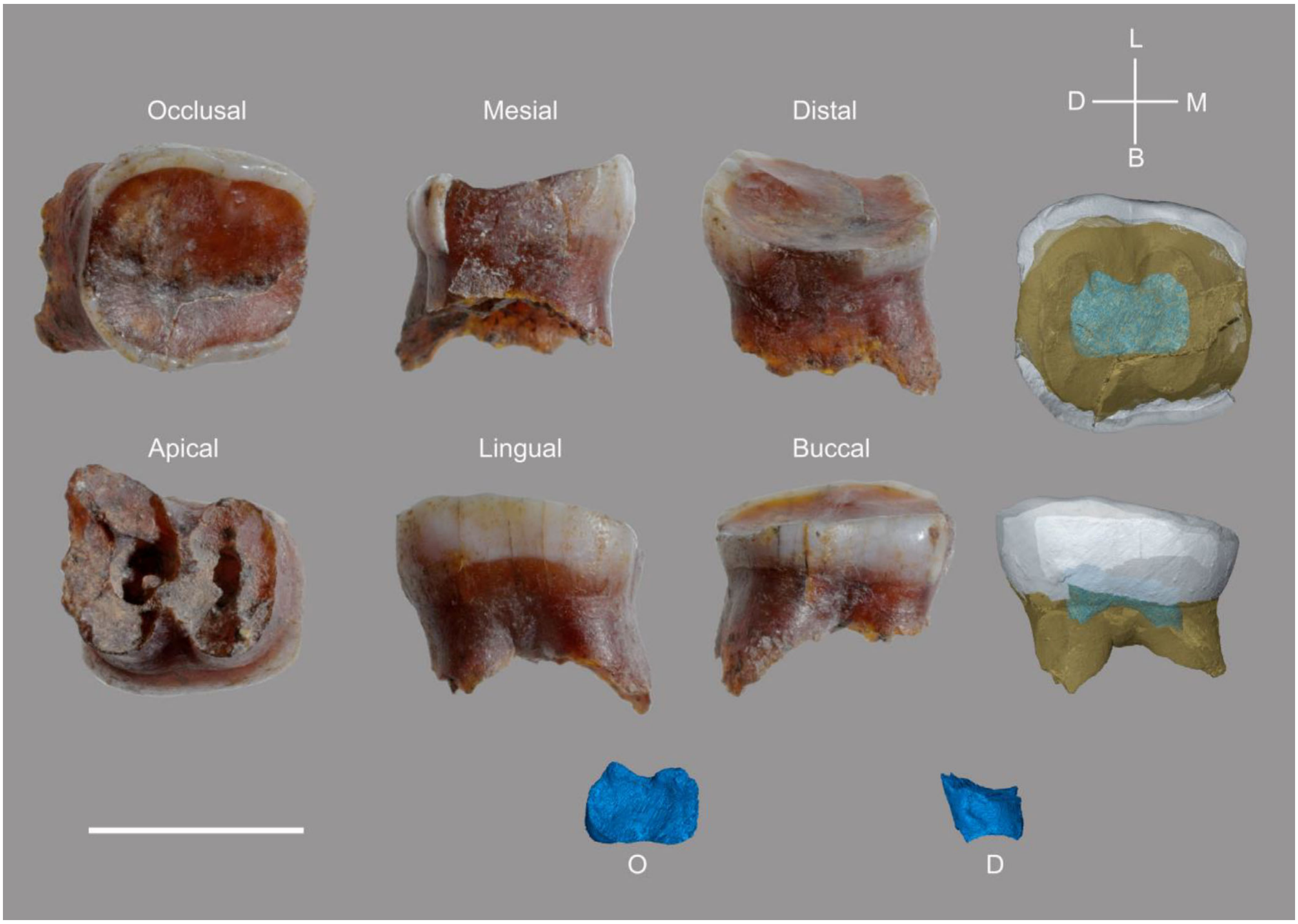

FIGURE 3 Right dm_2 ARB-E2-BE178 in occlusal, mesial, distal, inferior, buccal and lingual views. The virtual reconstruction of the teeth in occlusal and buccal views is also provided. Pulp chamber volumes are shown in occlusal and distal views (in blue). Scale bar = 1 cm.

enamel is preserved on the central fossa and on the metaconid and entoconid, and the four main cusps can be distinguished.

The mesial location of the lingual groove separating metaconid and entoconid suggests that the metaconid was small. At the EDJ, the hypoconulid may be suggested by a small indentation corresponding to a worn fifth cusp. Also, a type 4 trigonid crest (discontinuous DTC with absent MeTC and MdTC) is observable (Martínez de Pinillos et al., 2014; Martinón-Torres et al., 2014) (Table 2, Figure 4).

This molar presents two roots, one mesial and one distal, of which only the cervical third is preserved, before the radicular bifurcation. On the lingual aspect of the tooth, 4.1 mm of root trunk is preserved, whereas 4.8 mm is preserved on the buccal aspect. The μCT images show that the mesial root has two canals (buccal and lingual) and the distal root has a single canal. (Figure 4). The buccal and lingual canals are clearly separated. The distal root is compressed near the cervical line. Based on the description from Kupczik and Hublin (2010), we estimated the bifurcation level of this pulp cavity to be II or III (closer to II) (Table 2). In addition, the coronal pulp volume in this molar is 7.12 mm^3 (Table 3), which is lower than the volumes for all the mean values of the comparative M_1 samples. When comparing this value with the available M2 and M3 data, the Arbreda specimen's volume is higher than both modern human means, and slightly lower than that of both Neanderthal M_2 and M_3. Nonetheless, none of these differences is significant according to the z-score values (SOM Figure S2). All these data confirm the M_2 classification.

4.2 | Description of the tooth from level J

4.2.1 | ARB-E5-EC139-2434

This tooth is a well preserved upper right third permanent premolar. Although the crown is well preserved, it presents a few cracks on mesial, distal and lingual surfaces. Only the cervical third of the broken root is present (Figure 5). The enamel of both cusp tips is slightly smoothed (wear stage 0–1) and there are no interproximal facets, suggesting this tooth had recently erupted. No pathologies are noted. The MD and BL diameters are provided in Table 1. The MD diameter is among the largest in our sample (Table 1 and SOM Table S3). MD and BL dimensions are plotted against the comparative, sample it falls within the Neanderthals and pre-Neanderthal specimens (Figure 6). The MD and Bl adjusted z-scores indicate that the Arbreda premolar

TABLE 1 Comparison of crown metric data between Arbreda teeth and Neanderthals, Upper Paleolithic modern humans (UPMH), and recent modern humans (RMH). For the M_2, only cervical measurements are provided.

		Arbreda		Sima de los Huesos					Neanderthals[a]					UPMH[a]					RMH[a]				
Tooth	Variable	Direct measurement	Estimated	Mean	SD	Min	Max	*n*	Mean	SD	Min	Max	*n*	Mean	SD	Min	Max	*n*	Mean	SD	Min	Max	*n*
dm_2	MD	>9.7	10.12	–					10.3	0.44	9.8	11.1	10	10.65	0.54	9.77	11.1	8	10.03	0.46	8.8	11.7	189
	BL	>9.2	-	–					9.21	0.38	8.7	9.8	10	9.29	0.41	8.50	9.70	10	9.06	0.38	7.8	10.0	240
M_2	MD	9.9	-	–					9.89	0.29	9.5	10.2	4	8.5				1					
	BL	9.1	-	–					9.25	0.83	8.3	10.25	5	8.9				1					
P^3	MD	8.5		7.79	0.50	7.10	8.90	26	7.88	0.73	6.5	9.3	23	7.14	0.62	5.5	8.1	74	6.70	0.38	5.8	7.3	42
	BL	11.2		10.39	0.64	9.20	11.80	27	10.91	0.62	9.9	12.2	28	9.70	0.72	7	11.1	78	8.81	0.49	7.9	9.8	42
P^4	MD		-	7.53	0.54	7.00	8.80	24	7.50	0.78	6.10	8.80	29	6.82	0.51	5.90	7.90	66	6.45	0.46	5.50	7.5	38
	BL		-	10.20	0.67	9.10	11.50	26	10.42	0.68	8.50	11.70	34	9.70	0.68	7.50	11.29	66	9.04	0.49	8.10	9.9	38

Abbreviations: BL, Buccolingual; MD, Mesiodistal.

[a]Origin of the data detailed in SOM Table 3.

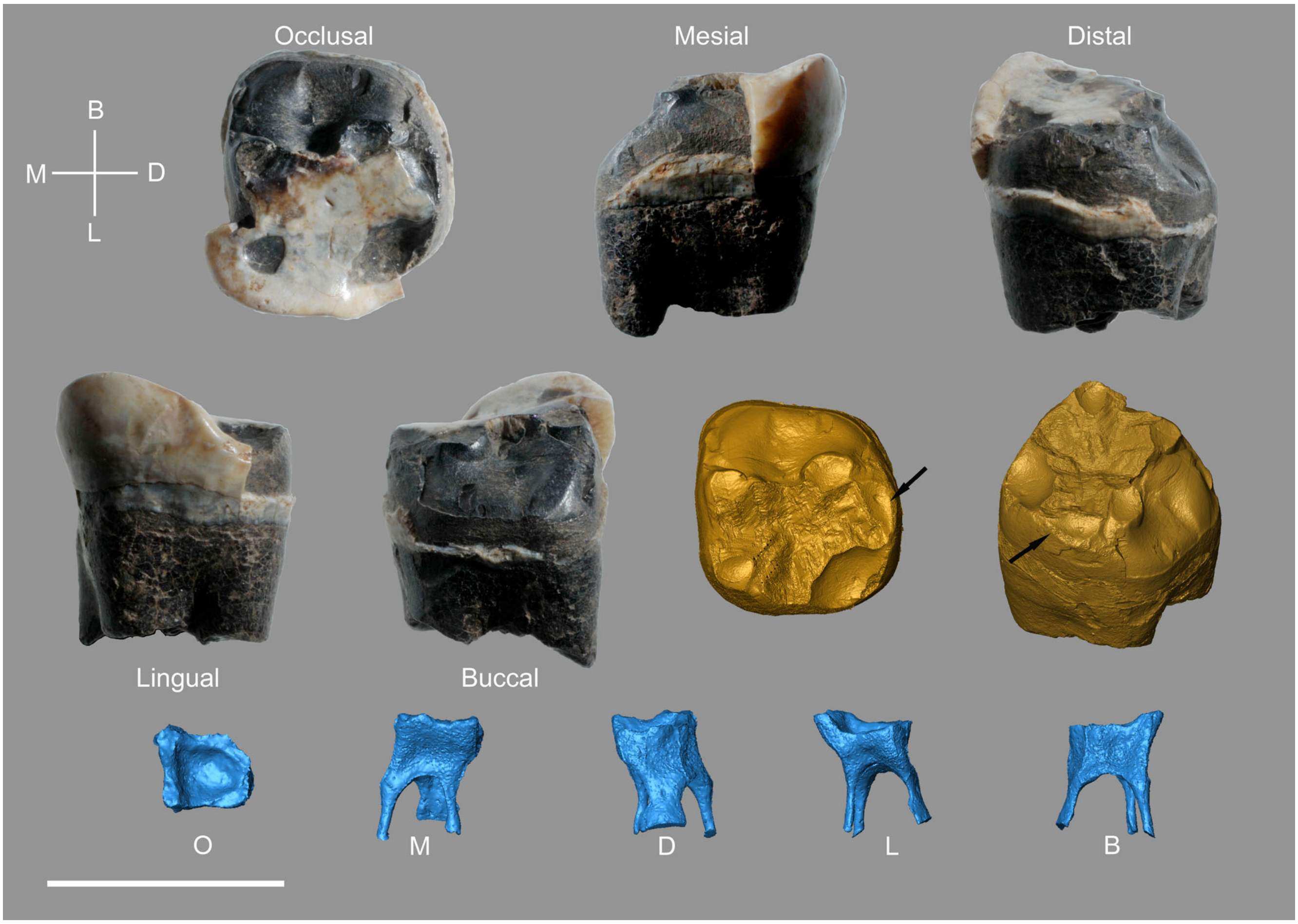

FIGURE 4 Right M_2 ARB-E2-BE179 in occlusal, mesial, distal, lingual and buccal views. The virtual reconstruction of the dentine in occlusal view is also provided. Pulp chamber volumes are shown in occlusal and mesial, lingual, distal and buccal views (in blue). The arrow signals the worn dentine horn corresponding to the fifth cusp. Black dots in the occlusal view of the EDJ indicate the discontinuous DTC. Scale bar = 1 cm.

falls outside the 95% confidence distribution for recent *Homo sapiens* (SOM Figure S3). The buccal face is wider toward the occlusal third with prominent angles exhibiting a slight surface asymmetry, the cusp tip is oriented slightly distally. The mesial marginal ridge is well defined. The distal face is trapezoid in shape, with a less defined marginal ridge, and more cervically located than the mesial face. The occlusal outline is hexagonal in shape, wider in the paracone than in the protocone. The sagittal or developmental groove is straight, finishing in well-marked pit-like mesial and distal fossa. A bifurcated transverse crest runs from the tip of the paracone as far as the tip of the protocone. In the mesial view, the root preserves 4.7 mm below the buccal cusp and 2.1 mm below the lingual cusp. In distal view, the length of the preserved root reaches 8.3 mm below the buccal cusp, and 5.2 mm below the lingual cusp. The EDJ occlusal surface exhibits a continuous transverse crest, non-bifurcated buccal and lingual essential crests, and a paracone distal accessory ridge on buccal aspect (Figure 5; Table 4). The virtual reconstruction of the pulp chamber shows two dentine horns (buccal and lingual) and has a small medial tubercle on the distal marginal ridge (Figure 5). The cusp tips are not especially thick, but both the buccal and lingual aspects near the occlusal surface are slightly worn.

The tissue proportions are shown in Table 5. The proportions fall within the Neanderthal ranges and certain proportions fall outside the ranges of Neanderthals and modern humans (Table 5) (SOM Table 3 and SOM Figure S4). The calculated 2D enamel thickness is 1.10 mm. The crown pulp volume is 6.64 mm^3 (Table 5).

4.3 | Minimum number of individuals and age at death

Besides the proximity of the two teeth from level N, none of the three dental remains show any other evident relationship that would attribute them to the same individual. Despite the loss of some dental parts and the alteration of color of teeth from level N due to chemical factors, analysis of the enamel, dentine and cementum surfaces under scanning electron microscopy ruled out severe taphonomic alterations. The enamel surfaces display features associated with common

TABLE 2 Morphological traits of the Arbreda lower permanent molar and comparison of their frequencies. OES trait frequencies from Martinón-Torres et al. (2012); EDJ data from Martínez de Pinillos et al. (2014) and Martinón-Torres et al. (2014); root morphology data from Kupczik and Hublin (2010).

Tooth region	Trait	Arbreda	Neanderthals						UPMH						RMH					
			M_1		M_2		M_3		M_1		M_2		M_3		M_1		M_2		M_3	
			n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
OES	C5	>2 (estimated)	34/34	100	22/24	83.8	14/16	87.5	27/28	96.4	8/25	32.0	11/18	61.1	108/119	90.7	37/157	23.5	60/126	47.6
	C7	0	9/29	31.0	7/23	30.4	8/15	53.5	15/25	60	19/25	79.2	13/17	76.5	96/116	82.8	139/155	89.7	98/124	79.0
EDJ	C5	3																		
	Trigonid crest	Type 4*	0/16	0	0/9	0	1/10	10	7/15*	46.7	11/14	78.6	2/4	50						
	Talonid crest	Type 0 (absent)	17/19	89.4	10/10	100	8/11	72.7	14/14*	100	14/14	100	4/4	100						
Root	Roots	Separated	13/17	76.5		500	4/15	26.6	4/4	100	4/4	100.0	2/3		20/20	100	10/17	58.8	5/8	62.5
	Bifurcation level	II	7/17	41.2	1/14	7.1	0/14	0	4/4	100	3/4	75.0	0/3	0						
		II-III**	16/17	94.1	9/14	64.3	5/14*	35.7	4/4	100	4/4	100	3/3*	100						
	Mesial canal	Bifurcated			5				4/4	100	2/4	50.0	0/3	0	18/20	90	10/17	58.8		
	Distal canal	Single					15/15	100					3/3	100			10/17	58.8		

*Although it does not correspond completely to Type 4, it is the most similar description.

**Since the root is broken, although the most probable classification is type II; we fused the data of type II and type III in this row for including all possibilities.

TABLE 3 Comparison of the crown-pulp volume value for the Arbreda permanent molar and *Homo heidelbergensis*, *Homo neanderthalensis*, and anatomically modern humans (*Homo sapiens*).

Tooth	Arbreda	*H. heidelbergensis*[a]			*H. neanderthalensis*[b]			AM *H. sapiens*[b]		
		Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
$M_?$	7.12									
M_1		19.33			10.43	5.24	16	10.48	6.36	12
M_2		22.27			10.15	7.83	12	5.17	3.60	16
M_3		6.01	2.76	3	10.07	5.93	13	5.96	2.55	8

[a]Values obtained from Zanolli and Mazurier (2013).
[b]Values obtained from Kupczik and Hublin (2010).

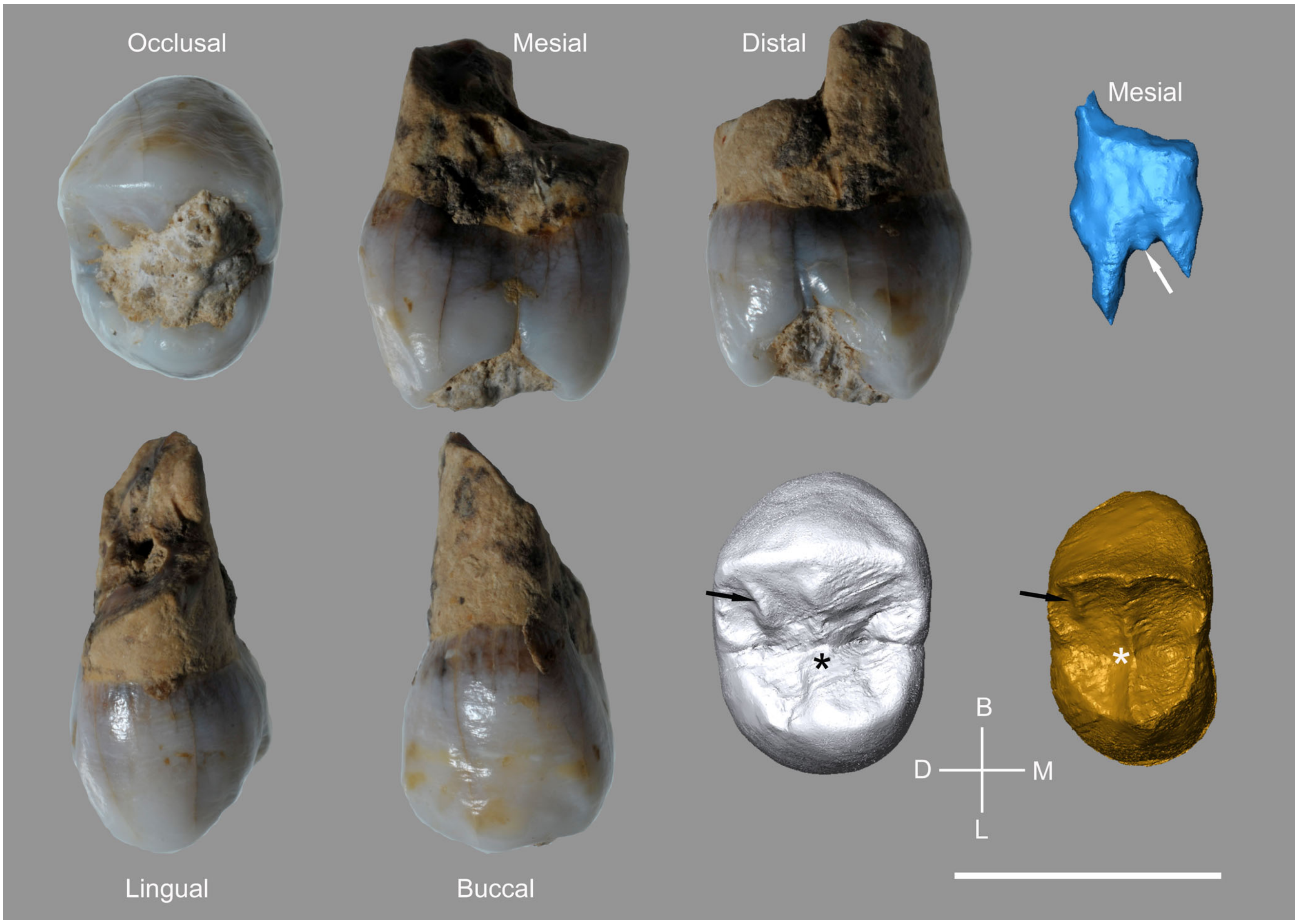

FIGURE 5 Right P[3] ARB-E5-EC139-2434 shown in occlusal, mesial, distal, inferior, lingual and buccal views. Virtual reconstruction of the enamel (white) and dentine (gold) are provided in occlusal view. The pulp chamber volume reconstruction in mesial view is also represented (blue). The white arrow in the pulp chamber signals the medial tubercle; the black arrows in the OES reconstruction and the EDJ reconstruction signal the distal accessory ridge; the black asterisk in the OES reconstruction signals the non-continuous buccal essential crest, and the white asterisk in the EDJ signals the continuous buccal essential crest. Scale bar = 1 cm.

dental use related to diet and masticatory processes. Moreover, the edges of the broken enamel and roots are not eroded, only slightly smoothed. All this evidence is indicative of in situ findings, even though their primary context is difficult to assess.

The two teeth from level N are one deciduous lower molar with evidence of active root resorption (ARB-E2-BE178) and a permanent lower second molar showing heavy occlusal dental wear (ARB-E2-BE179). The stage of root resorption (3/4) of the ARB-E2-BE178 is near the time of replacement (AlQahtani et al., 2010). The high degree of occlusal wear indicates a long period in functional use in the mouth. Accordingly, if this tooth was still in situ, it would belong to an infant ca. 10–12 years of age at death (AlQahtani et al., 2010). The state of the root and the dental wear suggest that it could have been lost as consequence of shedding, which occurs around that age. In this case, this tooth would represent an individual who lost the molar at that time in the cave. Furthermore, the permanent molar ARB-

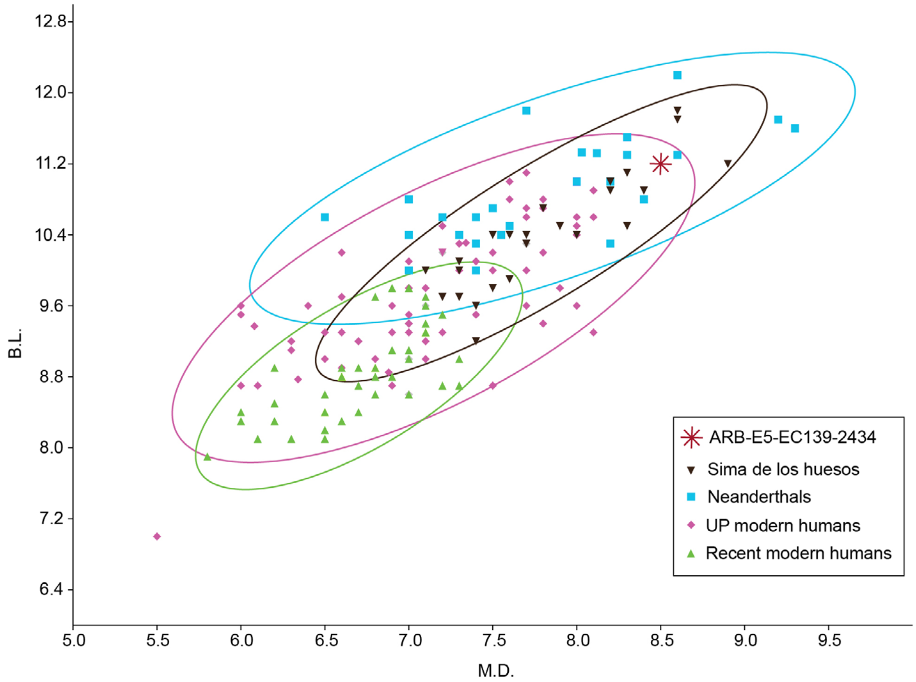

FIGURE 6 Scatter plot with 95% equiprobability ellipses for belonging to the different comparative groups based on P3 measurements. Arbreda (red star), Sima de los Huesos hominins (inverted triangles), Neanderthals (squares), Upper Paleolithic anatomically modern humans (diamonds), modern humans (triangles). BL, buccolingual breadth (mm); MD, mesiodistal length (mm).

E2-BE179 exhibits a high degree of dentine exposure on all the cusps. Based on the severe dental wear the tooth likely belonged to an adult individual.

The premolar ARB-C5-EC139-2434 from the archaeological level J belonged to a young individual, as indicated by the minimal dental wear. Upper P3s emerge in the mouth around 10–13 years (AlQahtani et al., 2010), and the root apex is closed at around 14 years old. The smoothed appearance of the cusp tips indicates that this tooth had emerged but, was not in functional occlusion long before death. Accordingly, the adolescent was like between about 10 and 13 years when died.

Therefore, we proposed a MNI of three: one infantile individual and one adult individual from level N and one juvenile from level J.

5 | DISCUSSION

The three teeth from Arbreda Cave present morphometrical traits that are consistent with a Neanderthal attribution. However, the high degree of occlusal wear and taphonomical damage to the teeth from level N preclude certainty for this attribution. No surface morphology is retained on ARB-E2-BE178 but, the elongated cervical outline, is more similar to that found in Neanderthals (Bennazzi et al., 2012). The permanent second lower molar ARB-E2-BE179 presents some external traits characteristic of Neanderthals, such as the presence of five cusps, which is found in the 83.8% of the Neanderthal comparison sample in contrast to 32.0% in Upper Paleolithic modern humans and 23.5% in European recent modern humans (Martinón-Torres et al., 2013). In addition, the type II-III of root bifurcation and the bifurcation of mesial root canals are common Neanderthal traits (Kupczik and Hublin, 2010). Although the MD and BL measurements are estimates due to the loss of enamel, the minimum measurements both fit well within the range of variation for Neanderthal permanent lower second molars. Finally, the coronal pulp volume is slightly lower than the Neanderthal mean, although there is no significant difference according to the *z*-score values. This low volume of the pulp chamber could be due to a slight deposition of secondary dentine, inferred from the μCT images. However, the presence of a type 4 trigonid crest at EDJ level is more common in *Homo sapiens* than in Neanderthals (Martínez de Pinillos et al., 2014). Although the lack of clear anatomical criteria prevents a conclusive taxonomic designation, the stratigraphic position of these teeth in a well-dated Mousterian level is consistent with their probable assignation to Neanderthals.

In contrast to the heavily worn teeth from level N, the premolar, ARB-C5-EC139-2434, presents a well-preserved crown that exhibits several traits characteristic of Neanderthals. The bulging buccal surface in occlusal view, and the presence of a mesial marginal ridge at OES level are traits associated with Neanderthals (Bailey, 2006; Garralda et al., 2020; Gómez-Robles et al., 2011; Gómez-Robles et al., 2013). Its size is in the high end of Neanderthal range and even in the range of the upper premolars of the pre-neanderthals of Sima de los Huesos (Bermúdez de Castro, 1993; Garralda et al., 2014). At the EDJ, the presence of a continuous transverse crest is a trait shared by 69.2% of the Neanderthal sample, but only is present in the 50% of the Upper Paleolithic and 14.3% of the recent *Homo sapiens* samples. Finally, the tissue proportions are consistent with Neanderthal attribution. The 2D relative enamel thickness (14.74) is close of the Neanderthal comparative data (13.59). The Arbreda value is the same as the Wezmeh 1 specimen (Zanolli et al., 2019) and significantly different from the data of modern human samples (Paleolithic:16.16/ Recent: 16.43). The 3D enamel thickness cartography (SOM

TABLE 4 Comparison of non-metric traits at the occlusal enamel surface (OES), at the enamel-dentine junction (EDJ) and root number between the P^3 and P^4 Neanderthals, Upper Paleolithic modern humans (UPMH), and recent modern humans (RMH). OES trait frequencies from Martinón-Torres et al. (2012); EDJ data from Becam et al. (2019) and Gómez-Olivencia et al. (2020).

			Neanderthals				UPMH				RMH			
			P3		*P4*		*P3*		*P4*		*P3*		*P4*	
Tooth region	**Trait**	**Grade for Arbreda**	***n***	**%**	***n***	**%**	***n***	**%**	***n***	**%**	***n***	**%**	***n***	**%**
OES	Transverse crest	Absent	14/15	93.3	2/16	12.4	4/5	80.0	2/11	18.2	128/128	100.0	113/113	100.0
	Buccal essential crest (BEF)	2	8/15	53.3	10/15	66.6	¼	25.0	4/11	36.4	14/126	11.1	10/106	9.4
	Lingual essential crest (LEF)	1	5/15	33.3	11/14	78.6	¼	25.0	0/11	0.0	5/124	4.0	9/108	8.3
	BMaxPAR	2 (Dist)	4/11	36.4	5/12	41.7	½	50.0	5/9	55.6	11/105	10.5	18/88	20.5
EDJ	Transverse crest	2 (continuous)			9/13	69.2			1/2	50.0			2/14	14.3
	Buccal essential crest	1 (non-bifurcated)			5/13	38.5			1/2	50.0			16/20	80.0
	Lingual essential crest	1 (non-bifurcated)			1/13	7.7			1/2	50.0			20/20	100.0
	Distal accesory ridge	1 (present)			5/13	38.4			1/2	50.0			12/20	60.0
	Mesial accesory ridge	0 (absent)			2/13	15.4			2/2	100.0			8/20	40.0
	Mesial accesory cusp	0 (absent)			13/13	100.0			2/2	100.0			20/20	100.0
	Distal accesory cusp	0 (absent)			10/13	76.9			2/2	100.0			20/20	100.0

Abbreviation: BMaxPAR: Buccal Maxillary Premolar Accessory Ridge.

TABLE 5 Dental tissue proportions and enamel thickness for the premolar and comparative data of P^3 and P^4 from Palomas site, Wezmeh and Neolithic specimens (Modern humans). Comparative data obtained from Bayle et al. (2017) and Zanolli et al. (2019).

	Ve (mm^3)	Vcdp (mm^3)	Vc (mm^3)	Vcdp/ Vc (%)	SEDJ (mm^2)	3D AET (mm)	3D RET	Vcp (mm^3)
Arbreda	201.5	250.93	452.94	55.4	190.29	1.06	18.43	6.64
Neanderthal P^3 ($n = 4$)	141.42 (53.33)	167.68 (44.31)	309.11 (96.78)	54.90 (3.20)	148.05 (30.04)	0.93 (0.17)	16.88 (1.79)	
Neolithic P^3 ($n = 5$)	128.90 (8.38)	110.97 (19.10)		46.04 (3.41)	113.34 (12.48)	1.14 (0.10)	24.01 (3.35)	
Neanderthal P^4 ($n = 2$)	116.76 (46.41)	127.14 (43.81)		52.39 (1.41)	122.53 (28.26)	0.935 (0.16)	18.64 (1.09)	
Neolithic P4 ($n = 3$)	135.40 (17.33)	110.44 (16.46)		44.88 (1.13)	111.7 (9.86)	1.21 (0.10)	25.30 (1.89)	

Figure S1) shows that the pattern of enamel thickness is similar to the one observed in Neanderthal specimens, and that as previously shown in the literature (Zanolli et al., 2019) slightly differs from that of fossil modern humans. In addition, it is worth noting that the enamel thickness on the buccal and lingual sides of the cusps is greater than in the rest of the cusps, a pattern that has previously been documented in other Neanderthal premolars (Zanolli et al., 2019). Overall, the enamel of the Arbreda specimen is thicker in the cusps than other Neanderthal P3, and not as thick in the occlusal surface as Qafzeh 10. On the other hand, the percentage of crown dentine in the Arbreda premolar is higher than that of Sima de las Palomas Neanderthal teeth (Bayle et al., 2017). In summary, most of the dental features, the archaeological context and the chronology of the levels where Arbreda teeth appeared suggest a probable Neanderthal assessment for these remains. This is of special interest as we must place them, especially the premolar from level J, in the current scenario of increasing complexity related to the overlap between Neanderthals and modern humans in Europe earlier than previously thought (Keeling et al., 2023; Mylopotamitaki et al., 2024; Slimak et al., 2022; Smith et al., 2024).

The scarcity of remains found at the Arbreda Cave prevents bioanthropological analyses and raises unresolved questions as to the nature of their deposition in the cave. The archaeological context and the radiocarbon dates (Bischoff et al., 1989; Hedges et al., 1994; Maroto et al., 1996; Maroto, Vaquero, et al., 2012; Wood et al., 2014) are related to Neanderthal occupations all through levels N, M, L, K, J, and I, and the lithic tradition remains very similar all along of the Mousterian sequence (SOM Table S1). However, the faunal remains (SOM Table S2) indicate two very different settlement strategies between the upper (I–K) and the lower (L–N) Mousterian levels. While the lack of ursid remains indicates that the occupations during the formation of N, M and L levels were probably recurrent or of a long-term character, the stratigraphic depth of Levels J and I support the idea that they were formed over an extended timespan and include evidence of much shorter human occupations, which alternated with predominant occupations by *Ursus speleaeus* (Soler et al., 2014).

The oldest remains associated with Neanderthals on the Iberian Mediterranean coast are from the Mollet, Cova Bolomor and Cova Negra sites (Arsuaga et al., 2012; Maroto, Julià, et al., 2012; Richard et al., 2019), all of which were found in levels with Marine Isotopic Stage MIS 7–5 chronologies. In addition, and geographically distant from the Mediterranean coast, Estatuas (Sierra de Atapuerca, Burgos) has yielded a Neanderthal foot phalanx belonging to MIS 5 levels (Demuro et al., 2019; Pablos et al., 2019). In this context, the presence of Neanderthals in level N of Arbreda Cave with a MIS 5 formation time adds new specimens to the existing fossil evidence of older chronology on the Peninsula. It confirms a continuous presence of Neanderthals and occupational strategies of long-term stays in caves from MIS 7 onwards. These changes in the subsistence strategies have also been detected at other sites on the Iberian Peninsula and have been interpreted as evidence of new Neanderthal strategy at the end of the Middle Paleolithic with occupations characterized by small groups for example, Teixoneres Cave, Cova Simanya, El Salt, Lezetxiki, or Prado Vargas (Garralda et al., 2014; López-Onaindia et al., 2023; Morales et al., 2023; Navazo et al., 2021; Zilio et al., 2021). These occupations could also be the result of higher mobility patterns conducted by the small groups of hunter-gatherers. The introduction by the end of the Middle Paleolithic of technical innovations as the Chatelperronian points in wide regions (Catalan and Cantabric areas and southern France) rules out the scenario of isolated communities and points toward the existence of wide relational networks, also supported by a Neanderthal mobility related to the expansion of this technocomplex (Rios-Garaizar et al., 2022).

6 | CONCLUSIONS

The dental remains recovered at Arbreda Cave belonged to three individuals: one infant and one adult from level N, and one juvenile from level J. The severe dental wear and the poor preservation of the two molars from level N complicate specific taxonomic assignation, especially in the case of the deciduous lower molar. However, the permanent lower molar exhibits some features characteristic of Neanderthal specimens, such as the coronal pulp volume. The juvenile premolar from level J exhibits morphologic and metric dental traits attributed to Neanderthals. In all cases, the taxonomic assessment of these teeth as probable Neanderthals is consistent with the stratigraphic context of Arbreda Cave, which is associated with a Mousterian archaeological assemblage and well-dated in situ levels. With chronologies of MIS 5 and MIS 4–3, these teeth should be part of two important periods in the Neanderthal settlements of the Iberian Peninsula. The teeth from Level N are among the oldest remains and the earliest Neanderthal occupations, whereas the premolar from level J belongs to the period close to the species' extinction. These teeth contribute to the growth of the paleoanthropological record of the Iberian Peninsula (Arsuaga et al., 2012; Garralda et al., 2014) and provide new insights into the life of Middle Pleistocene groups.

AUTHOR CONTRIBUTIONS

Marina Lozano: Conceptualization (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Joaquim Soler:** Conceptualization (equal); data curation (equal); funding acquisition (equal); project administration (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Diego López-Onaindia:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); software (equal); writing – original draft (equal); writing – review and editing (equal). **Alba Solés:** Investigation (equal); methodology (equal); writing – original draft (equal). **Ramon Julià:** Investigation (equal); methodology (equal); writing – original draft (equal). **Dolors Ceperuelo:** Formal analysis (equal); investigation (equal); methodology (equal). **Carlos Lorenzo:** Formal analysis (equal); investigation (equal); methodology (equal); software (equal). **Narcís Soler:** Conceptualization (equal); data curation (equal); funding acquisition (equal); investigation (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at http://doi.org/10.6084/m9.figshare.22761365.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from: http://doi.org/10.6084/m9.figshare.22761365.

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